Biodiversity impacts of Chilean needle grass *Nassella neesiana* on Australia's indigenous grasslands

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Abstract

The exotic invasive Chilean needle grass *Nassella. neesiana* (Trin. & Rupr.) Barkworth has been recognised as a major threat to biodiversity in the endangered natural grasslands of south-eastern Australia. Research was undertaken in Canberra and Melbourne grasslands to examine mechanisms by which *N. neesiana* invades native grasslands, the impacts of invasion on vascular plant and invertebrate biodiversity and mechanisms of impact. Time series analysis of historical aerial photographs demonstrated that invasion was absent or very slow when infestations abutted healthy grassland, but grasslands in poor condition experienced linear infestation expansion rates >5 m per year. A field experiment demonstrated that major disturbance (death of the native grasses) was required for *N. neesiana* recruitment from panicle seeds and that intact grassland was not invaded, even with high propagule pressure. Gaps of c. 1 m (as opposed to 10-30 cm) were required for establishment. Pin transect sampling demonstrated that increased senescence of *Themeda triandra* swards correlated with greater invasion. *Nassella neesiana* was found to deplete soil water in spring compared to *T. triandra*, a likely mechanism of biodiversity impact. Areas occupied by *N. neesiana* in three disparate grasslands were found to have significantly reduced native vascular plant diversity (species m^{-2}). Diversity decreased with increasing size of the *N. neesiana* patch. Forbs were the most affected group but one or more dominant grasses were absent at the smallest patch sizes. Exotic plant diversity was similar inside and outside patches. Analysis of sweep net samples determined that invertebrate populations and species richness were significantly reduced in *N. neesiana* grassland, although numerous native insect species consume the plant. Much of the loss of diversity in invaded areas probably precedes invasion and is caused by anthropogenic disturbances including *T. triandra* senescence dieback, mowing and major soil disturbance. Native grasslands in good condition are resistant to invasion.

Declaration

I, Ian Guthrie Faithfull, declare that the PhD thesis entitled *Biodiversity impacts of Chilean needle grass* Nassella neesiana *on Australia's indigenous grasslands* is no more than 100,000 words in length including quotes and exclusive of tables, figures, appendices, bibliography, references and footnotes. This thesis contains no material that has been submitted previously, in whole or in part, for the award of any other academic degree or diploma. Except where otherwise indicated, this thesis is my own work.

[redacted]

Signature

16 April 2012

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Contents

List of abbreviations and foreign words and phrases

ACT	Australian Capital Territory
bp	before present
C	carbon
c.	*circa*, approximately
cf.	*confer*, compare
Ed. Eds.	editor(s)
Edn.	edition
et al.	*et alia* or *et alii*, and others
et. sub.	and subsequently
gen.	genus
ha	hectare
ibid.	*ibidem*, in the same place as above cited reference
in litt.	in correspondence
K	potassium
loc. cit.	*locus citatus*, in the place cited
N	nitrogen
No., no.	number
nov.	new (as in *nov. gen*.)
NSW	New South Wales
op. cit.	in the work previously cited
p., pp.	pages
P	phosphorus
P	probability
pers. comm.	in personal communication
rev.	revised
sed	standard error of differences (between the means of two samples)
sensu	in the sense of, according to
sens..lat..	*sensu lato*, in a broad sense
s.s.	*sensu stricta*, in a strict sense
sp.	species
spp.	more than one species
subsp., ssp.	subspecies
t	tonne
vide	see
vs	versus
ybp	years before present

Convention

Dates recorded in numerical format are in the form dd/mm/yy

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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).

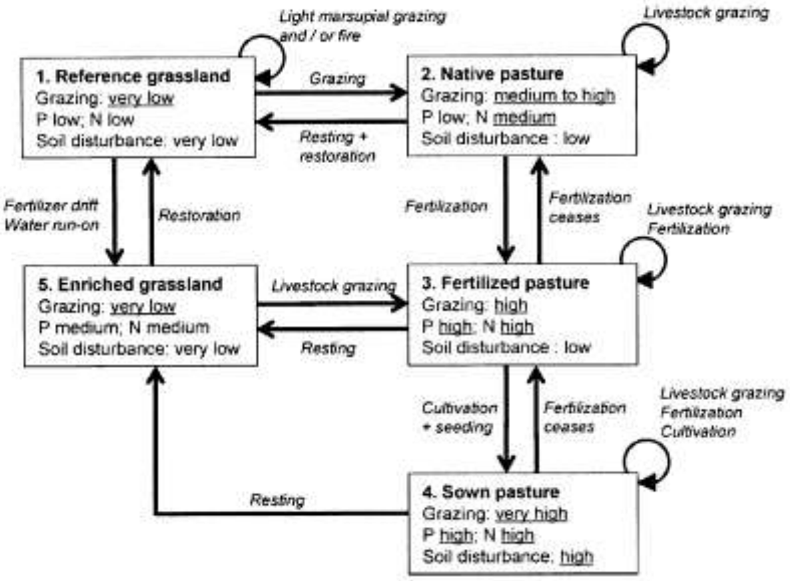

Figure 1.1. The McIntyre and Lavorel (2007 p. 14) ‘state and transition model’ for temperate grassy woodlands of south-eastern Australia.

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.

Chapter 2. Temporal changes in patch and infestation dimensions

“Weeds deal with ecological emergencies. When the emergencies are over, they give way ... and they will usually die out if disturbance ceases ... Weeds thrive on radical change, not stability.”

Alfred W. Crosby, 1986, *Ecological Imperialism. The Biological Expansion of Europe, 900-1900,* Cambridge University Press, Cambridge, UK, pp. 169-171.

Summary

This chapter details rates of change in *N. neesiana* infestation dimensions determined from comparison of historical and modern aerial photography and field measurements over periods of two to six years, and relates these changes to what is known of the contemporaneous disturbance and management regimes. The data indicates that *N. neesiana* patch margins tended to be stable where they abutted healthy, well-managed grasslands, which appear to be resistant to invasion. Patches expanded into disturbed areas and grassland in poor ecological condition at rates that exceeded 1 m per year. The most rapid expansion rates occurred in areas with senescence dieback of *T. triandra*, where patch areas often expanded by more 20% per year, and on roadsides that were frequently mown short, where linear expansion rates >5 m per year were measured. Data from Laverton North Grassland suggests that management by fire may contain or reduce infestations. The dynamics of *N. neesiana* infestations appear to support the theory of an alternative stable state in native grasslands that requires powerful intervention to shift, and indicate that expansion of infestations is driven by inappropriate management regimes.

Introduction

A critical variable determining the overall biodiversity impact of *N. neesiana* is the extent and rates of change of its land cover. However worldwide knowledge about vegetation cover in general is poor and there is a paucity of accurate data, particularly in relation to dynamics (Foody 2002). Vegetation maps rarely depict cover at the scale of interest for most invasive plants and usually at best portray vegetation at the plant community level.

There is a long history of the use of aerial photography and remote sensing in vegetation mapping and weed detection (e.g. Field *et al.* 1993). Several studies have used remote sensing techniques including aerial photography and satellite imagery to determine spread of invasive plants (Byers *et al.* 2002). Chan (1980) was able to map the distribution of grassland types in the Australian Capital Territory using low altitude colour aerial photography. He distinguished eight major grassland types but ignored areas dominated by exotic grasses. Dominant native grass species were determined by colour and texture. *Themeda triandra* and *Bothriochloa macra* were best identified by distinctive colour in autumn, with the latter having a finer, denser texture. Improved pastures and weedy areas were intensely green. Inspection of more recent, small scale, aerial photographs of Canberra demonstrated that *N. neesiana* patches identified on the ground could clearly be distinguished in photographs taken at an appropriate season. It therefore appeared feasible to determine historical changes in infestation dimensions by interpretation of appropriately selected photographs or satellite imagery, in conjunction with ground inspections.

No published data appear to be available on the land cover of *N. neesiana* in Australia at scales other than the local, 'individual grassland' scale, and the maps that exist have limited utility. Rowell (1996), for instance, described the process by which detailed maps of the dominant grass types were prepared for Yarramundi Reach. Ground examination in 10 x 10 m grid cells produced useful maps that included a few cells dominated by *N. neesiana*. Bruce (2001) prepared hand drawn sketch maps of Canberra grasslands showing the extent of *N. neesiana* infestations but these were not part of her actual report. Muyt (2005) estimated the cover/abundance of *N. neesiana* and other major grasses in a grid of 50 x 50 m contiguous cells across the whole of Yarramundi Reach grassland but failed to convert the data to map form. The reported studies are temporally static pictures, difficult to replicate and more or less incommensurable. Yarramundi Reach nevertheless appears exceptional in regard to available studies; if such information exists for other grasslands it is not readily available and would usually be subject to considerable uncertainty due to the absence of contemporary mapping of deliberate control activities targeted at the weed.

The dynamics of *N. neesiana* infestations are poorly understood. The best available data are from New Zealand, where a maximum rate of dispersal on a linear front from known sources was 8 km in 59 years at Marlborough and 3.5 km in 30 years at Waipawa (Connor *et al.* 1993). Slay (2002a 2002c) also provided expansion rate information for New Zealand infestations (Table 2.1).

Similar measurements and estimates are not available for *N. neesiana* in Australia. The ACT Weeds Working Group (2002 p. 4) stated that the "rate of spread and establishment is unknown, but believed to be rapid". *Nassella neesiana* was rated by Platt *et al.* (2005) as having a rapid, rather than a moderate or slow 'rate of dispersal'. The widespread perception that there has been rapid spread in Australia has probably been partly conditioned by recognition failures (Walsh 1998): the date of first establishment at a site has rarely been determined with any accuracy, and infestations may have grown large over many years before the plant was first identified.

Estimates of rates of spread are required at a range of scales. At the regional scale, rare long distance dispersal events are likely to be an important factor. A small number of widely separated new infestations at the regional scale rapidly expand the plant’s range. At the district scale infestations are known to expand first along linear corridors and within properties etc., strongly influenced by human land use, landscape boundaries and other anthropic factors such as mowing. In native grasslands at the local and patch scales, the interaction of the management regime and the integrity of the existing natural vegetation determine the fate of *N. neesiana* propagules and the fate of existing plants.

Table 2.1. Measured and inferred rates of *N. neesiana* spread in New Zealand.

Locality	**Distance (m)**	**Period (y)**	**Rate of spread (m y^{-1})**	**Notes**	**Reference**
Marlborough	8000	59	136	District infestation expansion	Connor *et al.* 1993
Waipawa	3500	30	117	District infestation expansion	Connor *et al.* 1993
New Zealand			120-140	With no active management	Slay 2002c
Hawke’s Bay	3-10	5	0.6-2	Patch expansion	Slay 2002c
	Area (ha)		**(ha y^{-1})**		
Marlborough	1555-3000 (3071)	14-15	101-103	District expansion	Slay 2002a, 2002c
hypothetical	1	5	100	Expansion at 100 m per year	Slay 2002a
hypothetical	1	10	350	Expansion at 100 m per year	Slay 2002a

This chapter examines temporal changes in the dimensions of patches and local infestations at selected sites for which long-term information is available, and their relationship to grassland management regimes. An unsupervised visual classification based on relative spectral and textural similarity of 1 m scale image areas was used to determine historical infestation boundaries. Ground inspections and measurements were used to locate and determine the current dimensions of *N. neesiana* patches and their locations. These data were then used to estimate rates of change in infestation areas and the movement of infestation margins over periods of two to six years. Ground inspections enabled subjective assessment of the qualities of the matrix vegetation and disturbance regimes, and this information was supplemented by records of historical management regimes and interpretation of older aerial photography to identify factors influencing vegetation composition. Judgements were then made of the effects of disturbance and management factors on the ability of the native vegetation to resist invasion and the factors important in determining rates of spread of *N. neesiana*.

Methods

Rates of change in the size of *N. neesiana* infestations and patches were assessed by examination of historical and recent aerial imagery and comparison of current on-ground measurements. Photographs were obtained from government photograph libraries and archives, a commercial supplier of remote sensing imagery, and from Google® Earth (©Digital Globe). Areas of *N. neesiana* patches measured on the ground at Crace, Yarramundi Reach, Dudley Street and Laverton North grassland reserves were compared with areas interpreted from scanned, re-scaled and digitally manipulated historical images. Changes in the areas of dense *N. neesiana* infestations and linear expansion at patch boundaries were calculated over time, and rates of change were estimated. Rates of change at a particular site were estimated by comparison of one image with another, and/or by comparison of data derived from images with measurements taken in the field.

Ground measurements and verification

The positions of prominent and distinct infestations of *N. neesiana* located in on-ground studies were recorded with a GPS device and by measuring their distances from prominent landmarks using a surveyor’s tape and magnetic compass. Some additional patches were initially located from the remote imagery and their positions determined in the same way. The area of each patch inspected on the ground was determined by measuring a series of radii from the nominal patch centre using a surveyor’s tape. The compass direction of each radius was determined with a magnetic compass. A hand drawn sketch of the patch indicated patch boundary features between the outer ends of the measured radii. These data were plotted on graph paper and the approximate area of each patch was calculated manually.

Image analysis

Historical aerial photographs and satellite images obtained on paper were manipulated and re-scaled using a high resolution flatbed scanner, photocopier and image processing software. Images obtained in electronic form were subsampled and manipulated with the same software. Image manipulation mainly involved alteration of colour and contrast using widely available photo editing software products.

Known *N. neesiana* infestations were located on recent photographs by field examination, and additional infestations were identified by their similarity of appearance to the known infestations on the photographs, including spectral and textural characteristics. Late spring and summer photographs were found to provide the best delineation of infestations. Patches were progressively more difficult to delineate in the older, lower resolution images and in old grey-scale photographs. Colour and texture contrasts often enabled ready identification of the dominant native grass *T. triandra* when photos were taken at the appropriate time of year (autumn being best), and uniform swards of other major grasses could also be identified with some certainty after ground-truthing. In general *T. triandra* appears reddish or pinkish and greenish blue, whereas *N. neesiana* often has a pronounced yellowish tinge or is a strong straw yellow colour where mown on roadsides, after the flowering period.

Various difficulties were encountered in interpreting the remotely sensed images. Most important was the low resolution of some images at the scale of interest. Diffuse patch boundaries and intermixtures of *N. neesiana* with other grass species complicated interpretation. Images at the optimum time of year for clear delineation of *N. neesiana* infestations were rarely available. The optimum times of year for identification of other grasses making up the invaded matrix were usually different to that of *N. neesiana*.

Infestations can change their apparent size and shape on remotely sensed images due to parallax errors which are most severe when the area of interest is remote from the centre of the image and when infestations are small. Parallax errors are an inevitable consequence of using photographs from different series. The interaction of slope and variation in camera angles also influences the accuracy of positional and area data obtained from photographs. No attempt was made to account for or quantify such errors. Alterations of apparent size and shape of patches without corresponding change in the number or density of plants also results from varying seasonal growth patterns and responses to rainfall of *N. neesiana* and other dominant grasses, the effects of grazing, fire, etc. A small narrow infestation at the peak of the growth period in a good season might appear much larger than the same infestation during a drought period when foliar cover is much reduced. Errors from such variation were also not accounted for, although they would be minimal at large patch size.

Approximate boundaries of infestations on historical images were determined by comparison of fine scale colour and textural properties of known *N. neesiana* infestations with those of the matrix (usually *T. triandra*) vegetation. An area was considered part of the matrix if it was more similar to the matrix vegetation in that particular area of the image than it was to the *N. neesiana* infestation in that area of the image. Factors affecting image interpretation included variations in image quality due to atmospheric influences (e.g. cloud), in image definition due to shading (by clouds or adjacent trees) and other effects, and fine scale variation in grass cover, density and height, along with other grassland compositional parameters (e.g. admixture of other species). Such variations were subjectively ‘smoothed’, avoiding the complications inherent in algorithmic approaches that accommodate such fine scale variation only with difficulty (Foody 2002). The boundaries of infestations were traced and their areas were manually calculated using graph paper.

The approaches used to measure changes in infestation dimensions at each grassland varied depending on the opportunities presented in the range of aerial images available and the extent of previous on-ground studies. The Dudley Street grassland was small, with an intensively mown roadside verge and very well defined major intrusion of *N. neesiana* bounded by healthy *T. triandra* grassland. Assessments were therefore undertaken of the overall change in the area of *N. neesiana* dominated grassland over a broad, partially infested area (>3 ha), of the linear change in the road verge infestations and the edges of other infestations, and of the change in area and boundary positions of the prominent *N. neesiana* intrusion. Yarramundi Reach exhibited numerous discrete *N. neesiana* patches. The absence or infrequency of biomass reduction management over a long period at this grassland meant that these could be readily identified by their high contrast in historical photographs. At Crace only a single *N. neesiana* ‘patch’ and the wider infestation of which it was a part were assessed. Other patches identified at Crace were generally very small and grazed close to the ground so were difficult to identify in aerial images. At Laverton North many patches identified on the ground were too small and diffuse to be clearly delineated on the aerial images, so some additional discrete patches, prominent in the imagery, were investigated and measured.

Results

Dudley Street grassland, Yarralumla, ACT

Stands of other exotic grasses at the site included *Paspalum dilatatum* and smaller areas of *Festuca arundinacea* Schreb. *Paspalum dilatatum* plants were largely restricted to wetter hollows in 2007 and could generally be readily distinguished from *N. neesiana* and *T. triandra* in aerial photographs, but the *F. arundinacea*, although largely confined to the roadside, was difficult to distinguish from *N. neesiana*. Tall rank grasses, notably *Avena* sp. and *Bromus* sp. occurred at shaded (southern) edges of major exotic tree plantations in 2007. These too were difficult to distinguish from *N. neesiana* in aerial photographs.

Arbitrary boundaries were set on the broad section of grassland in which the area of *N. neesiana* infestation was calculated (Fig. 2.1). These were defined by the edge of Dudley Street and extended approximately 122 m to the north and 260 m east-west, giving a total assessed area of c. 31,720 m^2 (Fig. 2.1). Some of this area (c. 35%) was covered by the exotic tree plantations which are not suitable habitat for *N. neesiana*.

The rate of expansion of the *N. neesiana* infestations in this broad section of the grassland to 2001 (Table 2.2) was calculated over 6 years using an arbitrary date of initial infestation of 31 March 1995. This very approximate estimate was based on Berry and Mulvaney (1995 Vol. 2 Appendices p. 261), who recorded that *N. neesiana* was common at that time along the bicycle path at Yarramundi Reach grassland, c. 2.8 km to the north west of the Dudley Street grassland. A part of the Canberra path network used by cyclists passes across the northern side of the Dudley Street reserve, so *N. neesiana* might have been present at Dudley

Street or dispersed there in that year. If it did, an average rate of expansion of c. 1000 m^2 y^{-1} occurred in the 6 years to 2001 (Table 2.2). The first ACT record of *N. neesiana* dates from 1960 (Gardener 1998) and Vickery *et al.* (1986) listed four ACT localities for the species. If in 2001 *N. neesiana* had been present at this grassland for 41 years the average rate of expansion in this grassland reserve to March 2001 would have been c. 158 m^2 y^{-1}. The average annual rate of expansion from 2001 to 2005, calculated on the basis of 3.81 years between photographs, was c. 9% or c. 550 m^2 yr^{-1} (Table 2.2).

Figure 2.1. Dudley Street grassland, ACT, 21 January 2005, showing the broad area of grassland (pale) and exotic plantation trees (black) assessed for *N. neesiana* areal cover (red line), the *N. neesiana* intrusion (‘patch’, red arrow) upon which estimates of rates of change of area and linear boundary changes were made, and the roadside infestations (green arrows) assessed for linear expansion rates. Pale, yellowish areas are *N. neesiana*; purplish green areas are *T. triandra*.

Table 2.2. Areal extent of *N. neesiana* infestation, proportion of total area infested and calculated rates of expansion of infestations at Dudley Street grassland 1995-2005, based on air photo interpretation.

Date	**Area (m^2)**	**Proportion of total area infested (%)**	**Rate of expansion (m^2 $year^{-1}$)**	**Rate of expansion (% $year^{-1}$)**	**Source (literature or aerial photograph)**
31/3/95	0	0	-	-	Nominal time of first infestation (Berry and Mulvaney 1995)
31/3/01	6220	19.6	1037	-	Canberra 2001 NSW4548(M2261) Run 5 31-3-01 41-62 Land and Property Information
21/1/05	8300	26.2	546	8.8	Canberra 1:25000 NSW4889 (M2460) Run 8 21-1-05 26-50 Department of Lands

A comparison was made of the area of a large *N. neesiana* patch at 35°18.844’ 149°05.490’ (Figs. 2.1, 2.2) that was measured on the ground on 14 October 2007 using a surveyor’s tape and magnetic compass, and the area of this patch assessed from interpretation of the 2001 and 2005 aerial photographs (Table 2.3). In October 2007 the eastern, southern and western edges of the patch had been sprayed with herbicide and the *N. neesiana* in the sprayed band was dead. The core area (“inner zone”) of living *N. neesiana* measured on the ground was substantially less than that estimated from the more recent aerial photograph; however a modest expansion (+2%) was measured if the sprayed band was included. Ground inspections elsewhere at this site in October 2007 revealed that active *N. neesiana* invasion was clearly continuing in some areas where *T. triandra* was senescing.

Table 2.3. Areas of *N. neesiana* patch at 35°18.844’ 149°05.490’ at Dudley Street compared by field measurement on 14 October 2007 and from interpretation of aerial photographs of 31 March 2001 (Canberra 2001 NSW4548(M2261) Run 5 31-3-01 41-62 Land and Property Information) and 21 January 2005 (Canberra 1:25000 NSW4889 (M2460) Run 8 21-1-05 26-50 Department of Lands). Rates of change were calculated based on periods of 6.54 years between the 2001 photograph and the ground measurement, and of 2.73 years between the 2005 photograph and the ground measurement.

Area 2001 photo (m^2)	**Area 2005 photo (m^2)**	**Area 2007 ground measurement (m^2)**	**% change 2001-2007**	**% change 2005-2007**	**Rate of change of patch area 2001-2007 (m^2 $year^{-1}$)**	**Rate of change of patch area 2005-2007 (m^2 $year^{-1}$)**
462	660	540 (inner zone)	+17	-26	+ 12	- 44
462	660	674 (including area sprayed out)	+46	+2	+ 32	+ 5

The area of the patch was also estimated from images available on Google Earth (Table 2.4). Nine images were available over the period from 22 December 2002 to 31 March 2008. The resolution of these images was generally poor, with pronounced pixilation at the scale of interest, but of similar quality to the aerial photography previously assessed, except for the 31 March 2008 image, which has extraordinarily high resolution (Fig. 2.2b). Google Earth provides an onscreen scale that readily enables area calculations.

The earliest of these images (2002) indicates a roughly crescent-shaped infestation with a large central inclusion, apparently of *T. triandra*. Subsequent images show a gradual extension and widening of the arms of the crescent, and the concurrent decrease in the size of the central inclusion until the arms were almost joined in 2005 (Fig. 2.2a). By February 2006 the central inclusion had become isolated and smaller. No inclusion was obvious when the patch was examined in the field in 2007 and by March 2008 no remnant *T. triandra* was evident in the aerial view (Fig. 2.2 b). During the expansion phase, finger-like projections appeared to extend downhill from the south-expanding edge of the patch, following what would appear to be drainage lines.

Figure 2.2. *Nassella neesiana* patch at Dudley Street, ACT. a. 19 April 2005, showing a central inclusion of *T. triandra*; b. 31 March 2008, with the central inclusion of *T. triandra* completely replaced by *N. neesiana*, and relatively stable margins abutting healthy *T. triandra* grassland to the east, south and west, as well as a distinct line around the patch indicating a narrow zone where the outer edge of the *N. neesiana* was chemically controlled.

During the period of 3 years from 22 December 2002 to 12 December 2005 the *N. neesiana* patch is estimated to have expanded by an average of 84 m^2 y^{-1} or 32% y^{-1} (Table 2.4). During the subsequent period of 2.3 years from 12 December 2005 to 31 March 2008 the patch expanded an average 338 m^2 y^{-1} or c 130% y^{-1}. Over this whole period of 6.41 years the patch expanded on average by 195 m^2 y^{-1} or 75% y^{-1}. The area of the patch approximately doubled in the 3 years from 2002 to 2005 and then doubled again in the next 3 years. The central inclusion of *T. triandra* shrunk by an average of c. 20% y^{-1} over this total period.

Table 2.4. Progressive change in area of *N. neesiana* patch at 35°18.844’ 149°05.490’ at Dudley Street 2002-2008 by interpretation of Google Earth images. A central inclusion of native grass within this patch apparently degraded slowly from dense *T. triandra* to sparse *T. triandra* invaded by *N. neesiana* to more or less pure *N. neesiana* over this period. The 31 March 2008 data includes two patch sizes defined by the inner and outer margins of a herbicidal kill zone intended to limit patch expansion. Calculations in square brackets for two images only 18 days apart are clearly unrealistic and indicative of the difficulties of determining patch boundaries from low resolution imagery.

Date	**Patch area without central inclusion (m^2)**	**Area of central *T. triandra* inclusion (m^2)**	**Period between images (years)**	**Rate of change of patch area (m^2 $year^{-1}$)**	**Rate of change of patch area (% $year^{-1}$)**	**Rate of change of central inclusion area (m^2 $year^{-1}$)**	**Rate of change of central inclusion area (% $year^{-1}$)**
Changes from preceding image							
22/12/02	260	220	–	–	–	–	–
11/3/04	353	371	1.22	+76	+29	+124	+56
29/3/04	340	330	0.05	[-260]	[-74]	[-820]	[-221]
19/3/05	400	206	1.06	+57	+17	-117	-36
12/12/05	510	189	0.65	+169	+42	-26	-13
22/2/06	521	113	0.20	+55	+11	[-380]	[-201]
9/10/06	573	124	0.63	+83	+16	+18	+16
2/4/07	797	68	0.48	+467	+81	-117	-94
31/3/08 inner	1044	0	1.00	+247	+31	-68	-100
31/3/08 inner + outer	1288	0	1.00	+491	+62	-68	-100
Changes over longer periods							
22/12/02-12/12/05	–	–	2.97	**+84**	**+32**	**-10**	**-5**
12/12/05-31/3/08 (inner)	–	–	2.30	**+338**	**+66**	**-82**	**-44**
22/12/02-31/3/08 (inner)	–	–	5.27	**+195**	**+75**	**-42**	**-19**

Linear change in infestations was estimated by: a. comparison of one aerial photograph with the other, or by comparison of an aerial photograph with measurements taken in the field from prominent landmarks including the road gutter and a large pine tree (Table 2.5); and b. comparison of distances measured in successive Google Earth images (Table 2.6).

Table 2.5. Linear expansion of *N. neesiana* infestations at Dudley Street grassland 2001-2005 based on aerial photography and field measurements.

Date	**Infested area**	**Linear expansion (m)**	**Period (years)**	**Rate of linear expansion (m year^{-1})**	**Source (aerial photographs, field measurement)**
31/3/01-21/1/05	eastern roadside	19.6-21.8	3.81	5.1-5.7	Canberra 2001 NSW4548(M2261) Run 5, 31-3-01, 41-62 Land and Property Information; Canberra 1:25000 NSW4889 (M2460) Run 8, 21-1-05, 26-50 Department of Lands
31/3/01-21/1/05	western roadside	28.4	3.81	7.5	Canberra 2001 NSW4548(M2261) Run 5, 31-3-01, 41-62 Land and Property Information; Canberra 1:25000 NSW4889 (M2460) Run 8, 21-1-05, 26-50 Department of Lands
31/3/01-21/1/05	core areas	0-33	3.81	0-8.7	Canberra 2001 NSW4548(M2261) Run 5, 31-3-01, 41-62 Land and Property Information; Canberra 1:25000 NSW4889 (M2460) Run 8, 21-1-05, 26-50 Department of Lands
21/1/05-14/10/07	35°18.844' 149°05.490' E-W diameter, inner zone	0.9	2.73	0.3	Canberra 1:25000 NSW4889 (M2460) Run 8 21-1-05 26-50 Department of Lands; field measurement 14/10/07
21/1/05-14/10/07	35°18.844' 149°05.490' E-W diameter, incl. sprayed zone	3.6	2.73	1.3	Canberra 1:25000 NSW4889 (M2460) Run 8 21-1-05 26-50 Department of Lands; field measurement 14/10/07

Table 2.6. East-west diameter and distance north from road of the Dudley Street *N. neesiana* patch from Google Earth imagery 2002-2008. Rates of change for the east-west diameter were calculated as half the change in diameter, assuming patch margin movement occurred on both east and west sides of the patch.

Date	**East-west diameter of *N. neesiana* patch (m)**	**Distance from road edge to south margin of patch (m)**	**Period between images (years)**	**Rate of linear expansion, east-west (m year^{-1})**	**Rate of linear expansion south (m year^{-1})**
22/12/02	27.3	79.1	-	-	-
11/3/04	25.0	78.4	1.22	0.94	0.57
19/4/05	29.6	75.0	1.11	2.07	3.06
12/12/05	30.2	76.2	0.65	0.46	-1.85
22/2/06	34.6	79.5	0.20	11.00	-16.5
9/10/06	35.2	79.1	0.63	0.48	0.64
2/4/07	38.6	79.1	0.48	3.54	0.00
31/3/08	39.1	80.1	1.00	0.25	1.00
22/12/02–31/3/08			5.27	**1.12**	**0.19**

Linear expansion appeared to be most rapid along mown road verges (5-7.5 m y^{-1}), but similar rapid expansions of up to 8.7 m y^{-1} were apparent in some of the core areas of the grassland (Table 2.5). Other infestation margins remained stable over the period. Google Earth images showed a consistent expansion trend in the east-west diameter of the measured patch, but a fluctuating expansion and contraction in the southern margin of the patch (Table

2.6). On average over the period of assessment the patch expanded by c. 1 m on each of the east and west margins and only slightly to the south. Field observations in 2007-2008 indicated that southward expansion was limited by healthy, non-senescent *T. triandra* and westerly expansion occurred into senescent *T. triandr*a.

Expansion of the infestations appears to have been driven by two main management factors, mowing of the *N. neesiana* areas with their remnant tussocks of native grasses, and senescence of *T. triandra* in unmown areas. Mowing close to the ground appears to have accelerated the disappearance of *T. triandra*. When mown, *N. neesiana* is able to produce new tillers that grow near horizontally (City of Whittlesea, no date; direct observations at Yarramundi Reach bicycle path), so is able to prosper in lawns. *T. triandra* lacks such flexibility. Mowing too close to the ground appears to remove the meristematic tissue of *T. triandra* and kills larger tussocks. Mowing also increases the amount and distance of seed dispersal of *N. neesiana*. These factors are discussed in more detail below.

Illustrative of these points, a severe circular scar caused by deep vehicle tyre marks in the core of the healthy *T. triandra* at Dudley Street grassland, that appeared fresh in October 2006, had by 13 October 2007 been occupied by *T. triandra* and *Austrodanthonia* seedlings. Although connected to the roadside, the scarring was apparently sufficiently distant from *N. neesiana* seed sources to preclude invasion.

Yarramundi Reach, ACT

Assessments were made of the change in size of several patches over different periods (Table 2.7). Calculated patch sizes from 2007 or 2008 ground measurements were compared to patch sizes estimated from the 21 January 2005 aerial photograph (Canberra 1:25000 NSW4889 (M2460) Run 8 21-1-05 26-50 Department of Lands). The periods from the time of the aerial photograph to those of the ground measurements were 2.34 years to 25 and 26 May 2007, 2.72 years to 11 and 12 October 2007, 2.74 years to 17-19 October 2007 and 3.75 years to 21-23 October 2008.

Large areas of *Phalaris aquatica* were present at this grassland, but these were relatively easy to distinguish on the images. *Festuca arundinacea* was present in significant stands, sometimes intermixed with *N. neesiana,* and may have been confused with *N. neesiana* in the photo interpretation. Nevertheless it is certain that major rapid expansion of the size of *N. neesiana* patches occurred over the period. All patches were assessed to have increased in size. One doubled in size annually, while several had annual rates of areal increase of 30-70%. There is some indication that larger patches expanded at a proportionally greater rate (Table 2.7).

The main factor driving patch expansion at this grassland over the period appeared to be senescence of *Themeda triandra*. Senescent stands were prevalent throughout the area (Fig.

2.3). There were large areas where *T. triandra* was evidently dying. Where dieback was not occurring, the stands still frequently had extremely high foliar cover (>90%) with a high proportion of dead leaves. Small areas of healthy *T. triandra* occurred in upslope areas in the far south-west of the grassland, and in infrequently mown zones around buildings, along some edges of the grassland and along small sections of the bicycle track. The data indicate that critical levels of *T. triandra* senescence occurred over the period, resulting in very rapid increase in the areal extent and density of *N. neesiana*.

Fig. 2.3. Yarramundi Reach *N. neesiana* Patch R, looking approximately east, with Lake Burley Griffin in the background, 24 October 2008. The patch was bounded to the east and north by highly senescent *T. triandra*. In the foreground *N. neesiana* was invading senesced *T. triandra*. The area of the patch is estimated to have expanded by 13% per year in the period from January 2005 until October 2008.

Table 2.7. Comparison of the size of *N. neesiana* patches at Yarramundi Reach grassland assessed by ground measurement and interpretation of 21 January 2005 aerial photograph (Canberra 1:25000 NSW4889 (M2460) Run 8 21-1-05 26-50 Department of Lands), with calculated proportional change over the periods and annual rates of change.

Patch	**Location**	**Ground assessment**		**Air photograph 21/1/05**		**% change in area**	**Period (years)**	**% change per year**
		Area (m^2)	**Date**	**Area (m^2)**	**Comments**			
		a		**b**		**c**	**d**	
A	35°17.367’ 149°05.047’	369	25/05/07	160	Partially obscured by tree shadows	+131	2.34	+56
D	35°17.443’ 149°04.812’	225	11/10/07	110	Boundaries unclear	+105	2.72	+39
C	35°17.501’ 149°04.897’	156	26/05/07	43		+263	2.34	+112
G	35°17.382’ 149°05.017’	128	24/10/08	73		+75	3.75	+20
P	35°17.426’ 149°04.890’	121	21/10/08	81	Possibly more extensive – S end obscured by mown zone	+49	3.75	+13
B	35°17.453’ 149°04.933’	120	25/05/07	94		+28	2.34	+12
E	35°17.430’ 149°04.955’	103	12/10/07	35	In two sections, 19.0 & 16.5 m^2	+194	2.72	+71
Q	35°17.336’ 149°05.014’	95	23/10/08	31	Patch unclear, ?in two sections 15.0 & 15.9 m^2	+206	3.75	+55
O	35°17.338’ 149°05.008’	94	19/10/07	?	Patch not apparent - in mown zone	-	2.74	-
H	35°17.432’ 149°04.886’	80	17/10/07	?	Patch not apparent - in mown zone	-	2.74	-
F	35°17.439’ 149°04.947’	77	12/10/07	46	In two sections, 18.3 & 27.5 m^2	+67	2.72	+25
R	35°17.326’ 149°05.031’	75	24/10/08	51		+47	3.75	+13
N	35°17.337’ 149°05.064’	60	19/10/07	27		+122	2.74	+45
D ext	35°17.448’ 149°04.812’	54	11/10/07	21	Boundaries unclear	+157	2.72	+58
M	35°17.375’ 149°05.031’	32	19/10/07	14		+129	2.74	+47
K	35°17.451’ 149°04.835’	16	18/10/07	8		+100	2.74	+37
L	35°17.528’ 149°04.842’	15	18/10/07	8	Small patch, location unclear	+88	2.74	+32
I	35°17.512’ 149°04.911’	12	17/10/07	9	Small patch, not certainly identifiable	+33	2.74	+12
J	35°17.509’ 149°04.904’	12	17/10/07	7	Small patch, not clearly discernible	+71	2.74	+26

Crace Grassland Reserve, ACT

Six Google Earth images covering the period from December 2002 to March 2008 were interpreted for an *N. neesiana* infestation at 35°13.693’ 149°07.378’ at Crace (Tables 2.8, 2.9). A number of available images including December 2005 were excluded due to their lack of clarity. The infestation was defined on its northern side by an old fence line and appears to have arisen as a result of overgrazing by rabbits and livestock, probably very similar to the sort of degradation illustrated in Figs. 2.4 and 2.5.

The area of the infestation, which had some very diffuse margins, was roughly measured on the ground on 16 October 2007 and the area of a well-defined section, Patch A, was measured more precisely (Table 2.8). The area of the patch and the wider infestation as interpreted on the ground differed substantially from that interpreted from remote sensing. During the longer period from 2002 to 2008 (Table 2.9) the infestation appears to have fluctuated in size and perhaps increased slightly in area. Overall, the patch and infestation data for this grassland suggest relative stability of *N. neesiana* areas under the regime of intense grazing.

Table 2.8. Area of *N. neesiana* infestation and incorporated Patch A at Crace Grassland, assessed by on ground measurement and interpretation of Google Earth imagery.

	Area (m^2)			**% change**		
	16/10/07 ground	**2/4/07 image**	**31/3/08 image**	**16/10/07-2/4/07**	**16/10/07-31/3/08**	**2/4/07-31/3/08**
Infestation	384	572	599	+49	+56	+5
Patch A	210	148	185	-30	-12	+25

Table 2.9. Progressive change in area of *N. neesiana* infestation around patch A at Crace Grassland Reserve 2002-2008 by interpretation of Google Earth images.

Date	**Infestation area (m^2)**	**Period between images (years)**	**Rate of change of patch area (m^2 y^{-1})**	**Rate of change of patch area (% y^{-1})**
Changes from preceding image				
22/12/02	554	–	–	–
11/3/04	492	1.22	-51	-9
9/4/05	507	1.08	+14	+3
22/2/06	409	0.87	-113	-2
2/4/07	572	1.02	+160	+39
31/3/08	599	1.01	+27	+5
Changes over longer periods				
22/12/02-9/4/05	–	2.30	**-20**	**-4**
9/4/05-31/3/08	–	2.97	**+31**	**+6**
22/12/02-31/3/ 2008	–	5.27	**+9**	**+2**

Figure 2.4. Western side of Crace Grassland Reserve, looking west, 8 May 2007, showing a dense monoculture of *N. neesiana* within the fence of the building compound and a belt of green *N. neesiana* in a drainage line leading downhill from the compound, grazed very short by rabbits.

Figure 2.5. Elevated area in the north-west section of Crace Grassland Reserve, looking south-west towards the Barton Highway with the Black Mountain tower in the background, 8 May 2007. The area in the foreground had been highly disturbed by cattle and kangaroo grazing and was densely infested with *N. neesiana*.

Table 2.10. Comparison of the size of *N. neesiana* patches at Laverton North Grassland assessed by ground measurements and interpretation of 24 January 2006 aerial photograph (2006 City of Wyndham Project, Wyndham_2006Jan24_air_vis_15cm_mg55.ecw), with calculated proportional change over the periods and annual rates of change.

Patch	**Location**	**Ground assessment**		**Air photograph 24/1/06**		**% change in area**	**Period (years)**	**% change per year**
		Area (m^2)	**Date**	**Area (m^2)**	**Comments**			
		a		**b**		**c**	**d**	
A	37°50.709’ 149°47.397’	466	25/11/07	516	Broad, very diffuse boundaries, sparse growth, mixed with and in part bounded by *Austrostipa*	-10	1.836	-5.4
J	37°50.700’ 149°47.405’	139	6/12/07	131		+6	1.865	4
D	37°50.641’ 149°47.415’	129	29/11/07	87	Patch boundaries unclear	+48	1.844	26
S	37°50.701’ 149°47.562’	100	9/5/09	72		+39	3.287	12
N	37°50.733’ 149°47.499’	89	18/12/07	67		+33	1.899	17
O	37°50.760’ 149°47.527’	58	9/5/09	39		+49	3.287	15
F	37°50.658’ 149°47.422’	54	4/12/07	49	Extent unclear	+10	1.860	5
C	37°50.686’ 149°47.400’	44	29/11/07	53	Diffuse patch, boundaries unclear	-17	1.844	-9
T	37°50.753’ 149°47.485’	43	9/5/09	41		+5	3.287	2
K	37°50.722’ 149°47.419’	22	10/12/07	23		-4	1.877	-1
Q	37°50.676’ 149°47.518’	22	9/5/09	24	Patch difficult to discern	-8	3.287	-2
G	37°50.743’ 149°47.415’	21	5/12/07	21		0	1.863	0
I	37°50.673’ 149°47.409’	17	6/12/07	-	Unclear	-	1.865	-
H	37°50.743’ 149°47.403’	11	5/12/07	7		+60	1.863	31
M	37°50.697’ 149°47.477’	9	18/12/07	8		+13	1.899	7
L	37°50.694’ 149°47.470’	7	18/12/07	10		-30	1.899	-16
B	37°50.744’ 149°47.390’	5	25/11/07	12	Very small patch, boundaries unclear	-58	1.836	-32
E	37°50.660’ 149°47.466’	5	4/12/07	5	Very small patch, boundaries unclear	0	1.860	0
P	37°50.746’ 149°47.553’	3	9/5/09	2		+50	3.287	15
R	37°50.690’ 149°47.538’	1	9/5/09	1	Tiny patch, not identifiable	0	3.287	0

Laverton North Grassland, Victoria

Similar problems were encountered in interpretation of aerial photography of Laverton North Grassland as at the other grasslands. A further difficulty was the more frequent presence of more or less uniform stands of *Austrostipa bigeniculata* (Hughes) S.W.L. Jacobs & J. Everett which appeared very similar to those of *N. neesiana* in remote sensed images and, as evident on the ground, frequently co-occurred with *N. neesiana*. Indeed some *N. neesiana* patches had pronounced bands of this native grass on their edges. In general the patches at Laverton North carried much lower grass cover, with a higher content of native grasses, and a much higher proportion of bare ground, and were more diffuse than at Yarramundi Reach and Dudley Street grasslands. Several of the measured patches contained only sparse *N. neesiana*, or were highly irregular in shape, and a number contained zones where other grasses were possibly more dominant. Probably all but the smallest patches included tussocks of native grasses. These difficulties indicate that wide error margins for the areas calculated by ground measurements and air photo interpretation.

Nevertheless, the data (Table 2.10) show a very strong contrast to the situation at Yarramundi Reach and Dudley Street grasslands. Five of 18 patches at Laverton North apparently decreased in area over the periods assessed, and no change in size was recorded for three additional patches. The assessed rates of change in the areas of *N. neesiana* patches was markedly less than in the senescent grasslands, with a maximum increase of c. 30% per annum.

Major expansions of the *N. neesiana* populations at this site occurred in an earlier period and were clearly associated with degradative historical management regimes. Severe overgrazing occurred in the 1970s, soil disturbance from earth moving equipment associated with construction activity led to small-scale elimination of native vegetation in the 1980s and early 1990s, and *T. triandra* senescence probably occurred in the period when burning was not undertaken. Grader scrapes that removed all of the standing vegetation and 50-80 mm of soil were one method used in attempts to re-establish rare native plants at this site (Morgan 1999b). Some *N. neesiana* patches delineated on the ground could clearly be correlated with major disturbances shown in older photographs, including soil disturbance, the installation of an oxygen pipeline, regular mowing, and livestock tracks, although other patches could not be correlated with such damage.

Deliberate burning is believed to be the only management practice undertaken since 2002 in the area of the grassland where the assessed patches occurred. The size of some patches was estimated to have reduced under the regime of regular burning. Overall the fire-based management appears to have resulted in stabilisation of infestations and may have favoured partial recolonisation by native grasses. In terms of *N. neesiana* populations, reduction of *T.*

triandra biomass and consequent prevention of *T. triandra* senescence is probably the most important benefit of regular burning. But burning has also resulted in a very open sward structure with large inter-tussocks spaces suitable for high populations of seed-harvesting ants. These destroy a large proportion of *N. neesiana* panicle seeds, thus contributing greatly to restricting its dispersal. Fire destroys grass seed on the ground (Morgan 1999a), and a fire regime that was timed to coincide with *N. neesiana* seed production (late spring-early summer) may enable the later flowering *T. triandra* to flower and seed post-fire, if at a much reduced level, a regime that could possibly improve *N. neesiana* control and advantage the dominant grass.

The total area occupied by *N. neesiana* at this grassland has been limited by the near absence of seed-dispersing mammals (few rabbits and hares) and the flat terrain, but seed movement over a few metres by ants has been observed. *Nassella neesiana* is nevertheless present across the whole Reserve.

Discussion

Errors and accuracy

Difficulties in interpretation of remotely sensed imagery and reconciliation of image interpretations with patch areas measured on the ground mean that only general trends can be firmly established from the foregoing data. Measurement and expression of accuracy of maps derived from remotely sensed data are difficult because of the many types of potential errors, lack of agreement on appropriate error measurements and their derivation, and basic flaws in widely used approaches (Foody 2002). The probability of correct classification of an image area or pixel decreases with decreasing patch size and increasing heterogeneity in the landscape or of land cover types (Smith *et al.* 2003, Boschetti *et al.* 2004). But the probabilities of correct/incorrect classification for each individual class of land cover within a classification are not consistently affected by these variables (Smith *et al.* 2003). When remotely sensed imagery is used to assess land cover dynamics, the assessment of accuracy is even more difficult, and there is “no standard approach” (Foody 2002 p. 195). Errors of omission, in which an area that belongs to a particular class is overlooked or not registered, and errors of commission, in which an area is misclassified, are two major error sources in interpretation of remotely sensed images. Error estimation is also dependent on the often untested assumption that one data set (e.g. the ground assessment) represents truth, to which the other (the image interpretation) is compared (Foody 2002, Boschetti *et al.* 2004). At its simplest, an accuracy assessment can be made by comparing areas simultaneously measured on the ground and from the remote image, however both data sets may contain such classification errors (i.e. misidentification of the dominant grass) as well as locational errors (e.g. patch positions incorrectly located). Error measurements that have been widely used typically ignore boundary complexities, which introduce the likelihood of further difficult-to-quantify error components, such as ‘mixed pixels’ which cannot be allocated into discontinuous classes (Foody 2002). Whatever the resolution of an image there are always ‘mixed pixels’ (Foody 2002). However the identification of bands of mixed pixels was the key element in this study because the aim was to determine changes in locations of boundaries and edges. The main error issues in this study therefore appear to be misclassification (incorrect identification of *N. neesiana* or not-*N. neesiana* areas), and smoothing or interpolation across bands of ‘mixed pixels’ in zones of heterogeneous vegetation.

No attempt has been made to quantify error in this study because of these difficulties and complexities and the highly variable range of remote image products assessed. Errors are suggested by the failure to detect in the imagery some patches recognised on the ground, and by a number of cases where there appear to be marked differences in areas of patches measured on the ground and in near-contemporaneous images. Failures to detect patches assessed on the ground in images, as at Laverton North, may be related to positional accuracy mismatches between the images and the ground and GPS measurements. But more likely this was due to the very open nature of this grassland during particular times, the diffuse nature of many *N. neesiana* patches and boundaries, and the poor quality of available images. In practical terms, contemporaneous dichotomous (*N. neesiana*/not-*N. neesiana*) interpretations of aerial imagery and ground vegetation were undertaken and found to be well correlated, but accuracy measures could not be obtained for historical images because of their widely variable quality and the impossibility of contemporaneous ground truthing.

General trends

Despite these caveats, the interpretations of aerial photos and associated studies on the ground indicate clearly that historical changes in infestation areas have been strongly influenced by the health of surrounding grassland and the differing management and disturbance regimes at the sites. *Nassella neesian*a invasions tended to be slow, except where the native grassland was in poor ecological condition (Table 2.11). The results also give broad order of magnitude estimates of *N. neesiana* expansion rates under these different regimes. The most rapid rates of expansion in patch areas occurred in the unmanaged grassland at Yarramundi Reach, where large scale senescence dieback of *T. triandra* was recently occurring, accompanied by alarmingly rapid expansion of *N. neesiana*. The Dudley Street study confirms that the boundaries of *N. neesiana* infestations moved rapidly where senescence was high and remained stable where there was no senescence. The highest linear expansion rates were measured on the roadside at Dudley Street, in a frequently mown zone (Fig. 2.6). The

Laverton North studies suggest that the ‘abundance trajectory’ (Byers *et al.* 2002) of *N. neesiana* need not necessarily always trend upwards. A patch at Crace was relatively stable under the regime of moderate to intense grazing.

Table 2.11. Selected estimates of changes in the area of *N. neesiana* infestations at four grasslands, derived from ground measurement (usually the “final date” and “final area”) and interpretation of aerial photographs (“initial date” and “initial area” and sometimes final area and date).

Site	**Area**	**Comparison**	**Initial date**	**Final date**	**Initial area**	**Final area**	**Rate of change (% year)**
Dudley St	central area	photos	31/3/01	21/1/05	19.6 ha	26.2 ha	+7
Dudley St	patch	photo/ground	31/3/01	14/10/07	462 m^2	674 m^2	+7
Yarramundi	patches	photo/ground	21/1/05	5/07 or 10/08	8-160 m^2	12-369 m^2	+12 to +112
Crace	patch	photos	22/12/02	31/3/08	554 m^2	599 m^2	+2
Laverton North	patches	photo/ground	24/1/06	9/5/09	24-72 m2	22-100 m2	-2 to +15

Figure 2.6. Mowing the road verge along the south-west edge of the Dudley Street grassland, where very rapid linear expansion rates of *N. neesiana* were measured. Mowing enhances spread by increasing native grass mortality and by dispersal of *N. neesiana* seed.

Rates of change

Rates of areal expansion measured at the Australian sites (Table 2.11) are broadly in agreement with those recorded and estimated in New Zealand (Table 2.1). Under suitable conditions, infestations can rapidly expand. Patch expansion rates of c. 1 m per year appear to be common, and increases in area of c. 10% per year at the patch and site scale occur in the absence of appropriate management.

Habitat heterogeneity has a strong influence on the rate of change of infestation dimensions. Areas of intact, healthy grassland appear to be resistant to invasion, but areas within a few metres may have much reduced resistance. The most rapid expansion rates were observed at the unmanaged, unburnt, grassland at Yarramundi Reach, where senescence of *T. triandra* was widespread and severe. However some *N. neesiana* patches in areas of that site where the *T. triandra* was healthier remained relatively stable. The trajectory from 2005-2008 was towards massive, irreparable ‘collapse’ of much the *T. triandra* matrix, accompanied by expansion and coalescence of discrete patches of *N. neesiana*.

Over the period from 2002 to 2008 infestations expanded rapidly in mown zones along the north verge of Dudley Street and on the north side of the Dudley Street grassland and into areas of senescent *T. triandra*. Where *N. neesiana* patches abutted healthy *T. triandra* grassland the infestation boundaries remained relatively stable over a period of several years. Mowing probably accelerated the elimination of competing *T. triandra* and resulted in more rapid transition to almost pure *N. neesiana* stands, particularly along the frequently mown road verge, due to both increased dispersal of *N. neesiana* seed by the mowing equipment and differential negative effects of repeated close cutting on the native grasses.

Effects of grazing

Livestock grazing is a degrading pressure in *T. triandra* grasslands and facilitates weed dispersal and invasion, but is preferable to the complete absence of biomass reduction management (Wong and Morgan 2007). Lunt and Morgan (2000) found that *N. neesiana* presence and density was strongly negatively correlated with that of the dominant grass (*T. triandra*) and was probably a long-term result of destruction of *T. triandra* by previous heavy grazing and ploughing at Derrimut grassland.

At Crace, a grassland managed by grazing of kangaroos and strategic grazing of cattle, the infestations remained more or less stable over the period of study. Although the presence of these grazers would presumably enhance *N. neesiana* seed dispersal, it also greatly limited *N. neesiana* seed production. *Nassella neesiana* and the dominant native grass *T. triandra* were kept very short in the studied areas over the period 2006-2008 by this grazing (see Figs. 2.4 and 2.5). The density of *N. neesiana* seed production at Crace appeared to be only a small fraction of that in the ungrazed Yarramundi Reach grassland. Perhaps the most important outcome from biomass reduction under the grazing regime at Crace was the prevention of *T. triandra* senescence. A large proportion of this grassland was examined on the ground and no senescent stands were found. However numerous small patches and isolated plants of *N. neesiana* clearly occurred in situations resulting from high intensity grazing, including around gates and along animal tracks (Fig. 2.7). The most heavily infested areas on the western side of the Reserve appeared to have long histories of high rabbit densities or intensive human impact associated with previous military uses of the sites.

Although Laverton North Grassland Reserve has not been grazed since it was reserved in 1983, its long history of intensive utilisation by livestock appears to have predisposed much of the area to invasion. The positions of various infestations corresponded with areas denuded by grazing, in particular along stock trails.

Figure 2.7. *Nassella neesiana* patch G, Crace Grassland, ACT (outlined approximately in yellow), 21 October 2008, was crossed by a heavily trafficked Grey Kangaroo track and may have originated as a result of such devegetation.

Effects of mowing

Rapid spread and persistence of *N. neesiana* in mown zones is probably attributable to two main factors: decreased survivorship and biomass production of native grasses when frequently cut short (Chan 1980, Nie *et al.* 2009), and much enhanced *N. neesiana* seed dispersal on slashing and mowing machinery (Liebert 1996, Trengrove 1997, Erakovic *et al.* 2003, Erakovic 2005, Moerkerk 2005a 2005b 2006a 2006b). Bruce (2001) found that *N. neesiana* was generally more abundant at sites in the ACT that were mown to some extent, that it was never absent from areas that were entirely mown, and at infested sites where mowing occurred it was generally spreading from mown into unmown areas. In fact, the overall distribution of *N. neesiana* in the ACT has been viewed as extremely well correlated with mown areas (Bedggood and Moerkerk 2002).

Chan (1980) demonstrated that repeated close (2 cm above ground) mowing at intervals of ≤3 months of dominant native grasses *T. triandra*, *Austrostipa bigeniculata* and *Austrodanthonia* spp. resulted in reduced yields and reproductive fitness. The least affected of the native grasses examined was *Bothriochloa macra* because of its low habit and the prevalence of prostrate tillers. Similar results were obtained by Nie *et al.* (2009) on a range of native grasses cut at 3-5 week intervals to a height of 2, 5 or 10 cm. All species tested had reduced survivorship when cut to 2 cm height, but plant survival was least with the two C_4 grasses, *T. triandra* (c. 51%) and *B. macra* (c. 57%). Cutting to 5cm increased survivorship to c. 85% with *T. triandra* and >95% with *B. macra*. Cutting at 5 and 10 cm enabled *T. triandra* to increase its shoot biomass compared to the 2 cm cut far more than the other species. These data indicate that close mowing of native grass swards will preferentially eliminate *T. triandra*. Chan (1980) also found that the timing of mowing in respect of the seasonal phenology was important. *Themeda triandra* appears to have another feature that prejudices its survival when repeatedly mown. Tussocks gradually accumulate litter and soil, so that the base of older tussocks tends to be markedly higher than the surrounding ground surface. The tendency to form mounds results in further elevation of the axillary buds, making them more susceptible to mowing. However Groves (1975) found that the seedlings of a *T. triandra* provenance from Kosciuszko National Park had wider and shorter leaves and a more prostrate form than a Canberra provenance, with new tillers arising nearly horizontally. Such a form may be better adapted to mowing and grazing.

Nassella neesiana appears to have a more prostrate tillering habit than *T. triandra* and most of the subdominant native grasses. Grech (2007 p. 4) for example considered its habit to more closely resemble that of *Lolium* spp. and *Dactylis glomerata* L. than the “very pronounced tussock growth” of *Nassella trichotoma* and *Poa labillardierei* Steud. Erakovic *et al.* (2007) observed that slashing of roadside *N. neesiana* infestations is known to “encourage the formation of dense flat ... swards as upright plants are eliminated”. The ability of *N. neesiana* to produce near-horizontal tillers when frequently mown, as noted by City of Whittlesea (no date), appears to be a trait expressed in much of the Australian *N. neesiana* population. However under regimes of frequent mowing, the possession of tillers that produce seeds (basal cleistogenes) may be as important a factor in the displacement of native grasses by *N. neesiana* as differential survivability when cut to low heights. These qualities have enabled the proliferation of *N. neesiana* in nature strips in Canberra (Jenny Cameron and Sarah Sharp pers. comms.) and have helped propel its replacement of native grasses in mown strips along pathways, such as the Yarramundi Reach bicycle path (Fig. 2.8). It is therefore worth reiterating that the whole of Yarramundi Reach was managed by mowing several times a year until 1995, when the regime was changed to mowing one third of the area each year (Frawley *et al.* 1995), and that *N. neesiana* has been present at the grassland at least since 1995 (Berry and Mulvaney 1995).

Figure 2.8. Yarramundi Reach grassland, ACT, 7 May 2007, showing the bicycle path and Black Mountain in the background. The wide mown zone along the path is almost entirely dominated by *N. neesiana*. A sharp boundary with areas dominated by *T. triandra* occurs at the edge of the mown zone in many places (e.g. far left) but some unmown areas have been partially invaded (e.g. right foreground).

Effects of fire

No general expansion of infestations occurred at Laverton North, indeed some patches appeared to have contracted under a management regime of regular (3-4 year) burning. A lack of vertebrate vectors of *N. neesiana* seeds at this grassland (few rabbits and hares and little human activity) has probably played a role in restricting further spread. Most of the studied patches at Laverton North clearly occurred on areas that were previously denuded of the dominant native grasses by earthmoving equipment, road construction or grazing. However some areas similarly damaged were reoccupied by native grasses. In contrast the absence of frequent fire at Yarramundi Reach resulted in rapid extensive invasion of *N. neesiana*, evidently due to *T. triandra* senescence dieback.

Hocking (2005b) investigated the effects of fire on *N. neesiana* under low rainfall conditions. Late spring burning was found to reduce the population densities of mature *N. neesiana* tussocks by over 90% but increase the densities of small and very immature tussocks, due to fragmentation of some large plants. Early spring burning also reduced the density of large tussocks, and burning reduced tussock area by more than 75%. Fire in late spring removed all the viable seed and approximately halved the production of new seed. Britt (2001) found that burning of *N. neesiana* swards, after application of 1 litre of methylated spirits to square metre areas surrounded by a metal frame, eradicated adult plants in an infested pasture. The effect of burning on the size of plants is one reason why infestations were much harder to identify at Laverton North than at the ACT grasslands. Fire also results in some 'subdivision' and mortality of *T. triandra* tussocks. McDougall (1989 p. 42) found that *T. triandra* tussocks at Laverton North fragmented after burning "forming colonies rather than discrete plants", with four times more plants in burnt areas than in unburnt, but that burnt areas carried more seedlings. Henderson (1999) found that there appeared to be some death of *T. triandra* tussocks at Laverton North Grassland when burnt once or twice in two years under drought conditions, but death of tussocks was neither widespread nor uniform in the areas burnt. Differential negative effects of fire on *N. neesiana* compared to the possibly better adapted native species may partly explain the much higher diffuseness of *N. neesiana* patches at Laverton North.

It can be inferred from the work of Peart (1979 1984) that *N. neesiana* panicle seed is adapted for surface germination and has little capability of self burial. *Nassella neesiana* has a persistent, very robust, twice-bent awn (Barkworth 1990, Edgar *et al.* 1991) which probably impairs more than very shallow seed burial. Bourdôt and Hurrell (1992) found that 99% of the soil seed bank in a New Zealand pasture was in the top 25 mm of the soil. The soil seed bank of panicle seed is primarily in surface litter, or at the soil surface, where it is subject to destruction by fire. Seeds of *T. triandra* by contrast appear to be able to achieve shallow burial (Peart 1979), possibly assisted by the readiness with which the awns are shed (Groves and Whalley 2002). African studies by Lock and Milburn (1970) indicate that the seeds bury themselves at a mean depth of 11 mm, where they are protected from fire, or amongst the base of the plant, and more seedlings occur within established plants than in intertussock spaces.

The *T. triandra* seed bank thus appears to have pronounced fire survivability and fire enables improved establishment. But the production of basal cleistogenes, as possessed by *N. neesiana*, is reportedly important in maintaining a species under conditions of frequent fire (Dyksterhuis 1945) and in *N. neesiana* the basal cleistogenes in particular are likely to survive fire in situ (Bourdôt 1989). Under a regime of regular burning it may be that neither species has a pronounced advantage in regards to seedling recruitment, although this may be dependent on the precise timing of the fires. Fire evidently causes occasional mortality of both *T. triandra* and *N. neesiana* and a regime of frequent fire may explain the diffuse nature of the infestations at Laverton North. *Nassella neesiana* may be more likely to maintain occupancy via cleistogenes where fire kills one of its tussocks, but may be less likely to occupy the site of a killed *T. triandra* tussock because of reduced production of panicle seed and a soil seed bank that is more concentrated close to the surface. Reliance solely on panicle seed with better burial capabilities may advantage *T. triandra* in colonising areas where *N. neesiana* tussocks have been killed. Theory predicts that high perimeter to area ratios increase vulnerability to invasion (Byers *et al.* 2002). Further data analysis is required to determine whether an apparent greater admixture of *T. triandra* in high perimeter: area *N. neesiana* patches at Laverton North is in fact evident and thus suggestive of *T. triandra* reinvasion of areas it formerly occupied.

Management and restoration

A number of the grasslands heavily invaded by *N. neesiana* may be characterised as ‘enriched grassland’ as defined in the state-and-transition model of McIntyre and Lavorel (2007). Such areas have been cultivated or managed for grazing, remain nutrient enriched as a result of such disturbance, and tend to be dominated by robust exotic perennial grasses and exotic rosette-forming herbs such as *Plantago lanceolata* L. and *Hypochoeris radicata* L. Many former pastures on the edges of urban areas are in this state (McIntyre and Lavorel 2007) and some disused pastures dominated by *Nassella* spp. can be included in this category. In the presence of intense propagule pressure from exotic grasses, major *T. triandra* senescence dieback enables direct transition from the ‘reference grassland’ state to the ‘enriched’ state (Wijesuriya 1999, Wijesuriya and Hocking 1999). Enriched grassland areas have various similarities with the “old fields” or “ex-arable fields” targeted for grassland restoration in Europe and North America, including residual soil fertility and dispersal limitations on native species recolonisation, that provide severe constraints on natural regeneration of the community (Öster *et al.* 2009). Times scales well in excess of 50 years can be expected for natural reassembly to a state approximating a semi-natural grassland in these northern hemisphere areas (Öster *et al.* 2009). Changes to a degraded state may be thought of as irreversible or very hard to reverse transitions across ecological thresholds “triggered by events that are typically unprecedented” and which result in a plant community “constrained by a different set of biological and soil processes” (Sadler *et al.* 2010 p. 434). More readily reversible transitions can be used to define ‘phases’ within a state (Sadler *et al.* 2010): the gradual densification of a *T. triandra* sward could be so classified, with fire the process that reverts the system to the initial phase, and an ultimate phase of high density which is perhaps twice as long as the minimum fire return interval and is determined by local edaphic and climatic conditions.

Conclusions

Possibly the most important finding from this component of the study is an obvious one: *N. neesiana* infestations are not transient phenomena but occupy the ground more or less indefinitely in the absence of powerful intervention, and constitute an alternative stable state. The second major conclusion is that the expansion rate of *N. neesiana* infestations is rapid when management activity is inappropriate. When *T. triandra* is allowed to senesce through lack of biomass reduction, resistance to invasion collapses and linear expansion rates of >5 m per year can be expected. Mowing/slashing regimes that involve frequent short cutting result in rapid expansion along roadsides, in some instances that were measured rates of spread were even faster than in some areas of severe senescence dieback. Differential mortality of native grasses and *N. neesiana* when closely and frequently cut may be a more important driver of invasion in such mown areas than dispersal of propagules by mowing machinery alone. Where infestations abut areas of native grassland in good condition their boundaries are stable over periods of several years. Grazing regimes may result in the stabilisation of infestation boundaries, at best, but at worst appear to promote invasion by killing *T. triandra* and through the creation of bare ground in intensively trafficked areas. A management regime consisting solely of regular fire appears to result in lower expansion rates or the containment of infestations, and may gradually reduce population density and areal coverage of patches. In the longer term native grasslands kept healthy by biomass reduction are resistant to *N. neesiana* invasion, and associated losses of plant biodiversity are kept low.

Although the findings of this study appear robust, the measured trends reported should be characterised as preliminary ‘rough and ready’ approximations: a very limited set of suitable images were qualitatively assessed, with little constraint on the possibility of observer bias. Infestation boundaries are not smooth, and invasions fronts must always first consist of small, sometimes scattered individuals that cannot be identified from the types of images used and may be difficult to detect on the ground. Further studies should employ established GIS systems, geodetic techniques that correct for projection errors and a range of defined image metrics including textural, pixel-based measurements and structural (patch area/perimeter) measures to assess time series images, to better quantify system trajectories (Sadler *et al.* 2010). Meaningful error estimates should be incorporated (see Foody 2002, Smith *et al.* 2003, Boschetti *et al.* 2004). The increasing quality and availability of remotely-sensed imagery with much shorter periods between images, due to better satellite coverage, should make the task considerably easier in the future. Assessment of the biodiversity impact of *N. neesiana*, at least by determination of rates of displacement of *T. triandra* grassland, appears to be eminently feasible on an ongoing basis, and such a system could be deployed to trigger management intervention before ‘irreversible’ transition of *T. triandra* grassland to a degraded state.

Chapter 3. Historically quantified infestations revisited

"*Stipa neesiana* is a serious threat to remnant stands of native grassland, including the Laverton North Grassland Reserve ... invasion has now occurred over a wide area ... several large patches are extremely dense and spreading ... It is a particular concern ... that the spread ... will destroy research plots containing threatened plants. Expansion of the presently invaded areas will significantly degrade the conservation value of the Reserve ..."

M.J. Bartley, R.F. Parsons and N.H. Scarlett of the Botany Department, La Trobe University, in a letter to the Victorian Department of Conservation and Environment, 7 May 1990.

Summary

This chapter compares contemporary data on the cover of *N. neesiana* and the vegetation of small invaded areas at Yarramundi Reach and Laverton North grasslands with data recorded in historical botanical surveys. Contrary to published predictions, the infested areas assessed were found to have not greatly expanded over periods approaching two decades. *Nassella neesiana* cover values were found to have fluctuated markedly over time. Disturbances that destroy native grassland vegetation demonstrably enable *N. neesiana* invasion, but may also destroy *N. neesiana* populations without subsequent reinvasion. *Nassella neesiana* can disappear from areas where it has not achieved high cover, but once it has achieved high cover it can maintain its presence. Major soil disturbance can permanently decimate the native grassland flora and disturbances that kill the native flora appear to be a more important cause of vascular plant diversity loss than active invasion by *N. neesiana* itself.

Introduction

Under the theory of competitive exclusion a more competitive invader can occupy the niche previously occupied by a native species (Woods 1997, Seabloom *et al.* 2003, Cox 2004). *Nassella neesiana* has been characterised as an "aggressive" (McDougall and Morgan 2005 p. 35), very competitive (Cook 1999), highly invasive (Morfe *et al.* 2003) weed and a strong resource competitor (Iaconis 2003) that is rapidly expanding its range (Lunt and Morgan 2000), has the ability to actively invade native grasslands (Hocking 1998, 2007) and potentially outcompete *Themeda triandra* (Ens 2002a). Some weeds can invade in the absence of major prior disturbance, by virtue of their superior competitive abilities (Carr 1993) and *N. neesiana* appears to have sometimes been classed amongst them. However Bourdôt and Hurrell (1989a p. 415) considered its invasiveness in sheep pastures to be due to "adaptations that enable the plant to survive the hazards of semi-arid, low-fertility environments, rather than to high competitive ability". Fears about its high invasiveness in native grassland may be exaggerated and its success in these systems may have more to do with their mismanagement and the level of anthropogenic disturbance to which they are subject, rather than to superior competitive abilities. Intact grasslands on the Victorian basalt plains are highly resistant to weed invasion (Patton 1935) and when not overgrazed, species-rich, high quality grassland is in general less weed-invasible (Beames *et al.* 2005). Morgan (1998d) for example found that exotic plant richness was negatively correlated with native plant richness. Minimisation of disturbance to maintain an intact stratum of native ground vegetation is one of the prime measures needed to prevent exotic weed invasion (Davies 1997). Exotic stipoid grasses in Australia have generally invaded areas with a history of disturbance, in which the native plant communities are already highly degraded (Gardener and Sindel 1998). If superior competitive abilities are driving invasion it could be expected that infestations that are not deliberately controlled should generally expand over time. If invasions are largely disturbance-driven, it could be expected that *N. neesiana* infestations would expand more in areas subject to more intense or frequent anthropogenic disturbance and to have had less success in better managed grasslands.

The aims of this component of the study were to determine whether infestations that were historically quantified by botanical workers have expanded, remained stable or contracted, and the circumstances under which these changes have occurred. Changes that have occurred in the extent of infested areas, their species composition and other characteristics should provide further insight into, and better quantification of, the biodiversity impact of *N. neesiana,* and help to illuminate factors that have influenced its invasion.

Two sets of historical data were found that appeared suitable for reassessment: (1) square metre floristic quadrats assessed for the purposes of long term monitoring of grassland condition and floristic change along permanently marked transects in a number of Australian Capital Territory grasslands (Environment ACT database), and (2) detailed studies of the vegetation at Laverton North Grassland before and after the installation of a below-ground oxygen pipeline, which were intended to guide restoration activities (McMahon *et al*. 1990, Todd 1991, Muir and Carr 1994).

Data on *N. neesiana* and other vegetation from the earlier baseline studies was compared with current data by reassessment of the same areas, using, where possible, the same methods, and the findings are interpreted in terms of effects on vascular plant diversity and the influence of particular management regimes at the grasslands in question.

ACT sites

Permanently marked transects in the ACT were set up by Sarah Sharp of Environment ACT in the early 1990s and were monitored annually by Environment ACT staff from 1993 to

2002. The cover class of all species was recorded in square metre quadrats at set distances along the transects (S. Sharp pers. comm. 8 May 2007). The transects had initially been located in high quality areas, which often had no *N. neesiana* present, so the historical records of *N. neesiana* cover were few. Transects were inspected in grasslands at Crace, Dudley Street and Yarramundi Reach grasslands, but only those in the latter grassland warranted study, there being 25 database records of *N. neesiana* in transect quadrats at the site over the nine years of observations. Reference to original data sheets revealed one further record at this grassland. Cover values for each species present in a quadrat had been recorded in this database to the nearest 5%.

Nassella neesiana appears to have been first recorded in published literature at Yarramundi Reach by Berry and Mulvaney (1995) who noted that it was not one of the major weeds, but was "common along the bicycle path" (Berry and Mulvaney 1995 Vol. 2 Appendices p. 261). However the Environment ACT database records it with high cover along one transect in 1993, when the monitoring first commenced.

Laverton North oxygen pipeline

The Laverton North records were made by Ecological Horticulture Pty Ltd (later renamed Ecology Australia Ltd), a consulting company engaged by the pipeline proponent, Air Liquide Australia Ltd. Permission to construct the below ground pipeline across Crown land at the western end of the Reserve was granted by the Department of Conservation and Environment in October 1990 (Muir and Carr 1994). The pipeline was built to deliver gaseous oxygen from the Air Liquide gas treatment plant on Kororoit Creek Road, immediately to the south of the Reserve, to the Smorgon steel mill to the north of the Reserve and the north of the Princes Highway, and the company was licensed to operate it for 20 years (Craigie 1993). The pipeline was allowed to be laid along the southern edge of the grassland for 125 m then north through the grassland for 280 m, then for 290 m along the Highway within the Reserve (Craigie 1993). The permit required that land affected by construction works be rehabilitated and that areas rehabilitated be maintained for a period of five years. Rehabilitation works were required to include vegetation re-establishment and weed control (Muir and Carr 1994). The location of the pipeline is currently indicated by signage and steel posts set in the ground (Fig. 3.1).

The vegetation of the pipeline zone was surveyed prior to construction (McMahon *et al.* 1990) and twice after construction (Todd 1991, Muir and Carr 1994). McMahon *et al.* (1990) prescribed methods to re-establish *Themeda triandra* in areas denuded by construction, by application of *T. triandra* hay, but the restoration undertaken was largely unsuccessful (Todd 1991, Muir and Carr 1994, personal observations). All three studies estimated cover of vascular plant species, using the Braun-Blanquet scale, in 5 m x 20 m quadrats with their long axes over the pipeline (G. Carr pers. comm. April 2007). The latter two studies reportedly resurveyed the same quadrats as those in the initial study, which were marked with wooden pegs.

Figure 3.1. Location of the north-south section of the oxygen pipeline across the Laverton North Grassland, looking north, 13 April 2007. Recently burnt grassland can be seen in the Reserve to the right.

McDougall (1987 p. 36) recommended that the spread of *N. neesiana* in the reserve "should be monitored", and the plant had a major presence before pipeline construction (McMahon *et al.* 1990). Construction activities reputedly resulted in further invasion (Frances Overmars pers. comm.). Humphries and Webster (1992 p. 2) wrote that "aggressive invasion" at the reserve needed "immediate attention" if the grassland values were to be preserved. Kirkpatrick *et al.* (1995 p. 35) stated that the "rate of spread in the two grassland reserves [Derrimut and Laverton North] ... [had] shocked botanists".

Pipeline construction activity resulted in major disturbance including burial of the surface soil, replacement of surface soil with subsoil, widespread elimination of vegetation leaving only exposed soil, and severe soil compaction where vehicle traffic was heavy (Todd 1991). Lack of soil settling and water logging were also notable along the pipeline trench immediately post-construction (Todd 1991). Cover of weed species doubled, 18 spp. disappeared, 25 previously unrecorded species appeared, and native *Austrodanthonia* and *Austrostipa* grasses were largely eliminated (Todd 1991).

For the purposes of the current study it was hypothesised that destruction of the native plant cover, particularly the dominant native grasses, by pipeline works, the failure of the attempt to revegetate the disturbed zone with *T. triandra*, and the proximity of actively seeding *N.*

neesiana in the immediate vicinity of the disturbed zone should have enabled *N. neesiana* to become dominant in the disturbed areas.

Methods

Australian Capital Territory

Cover data for all quadrats on permanent transects in which *N. neesiana* occurred in any year from 1993 to 2002 at Yarramundi Reach grassland was extracted from the Environment ACT database or paper records. The permanent transects (Table 3.1), marked with steel star pickets with white plastic caps, were located using the hand drawn maps on Environment ACT files and during field inspections with Sarah Sharp. Transects were closely inspected, and if no *N. neesiana* was detected along the whole transect, cover values of zero for *N. neesiana* were recorded for the full length. Inspection on 9 May 2007 found no *N. neesiana* along transects A and C.

If *N. neesiana* was detected in a transect, the vegetation of the whole transect was quantified in detail. The presence and cover along the whole of these transects was assessed on 23 May 2007. A GPS device was used to record the location of each end of the transects (Table 3.1). Projective foliar cover values (the proportion of ground covered by foliage) were estimated using a 1m x 1m steel frame quadrat with 2 crossbars dividing the square metre into quarters, and attached strings at 10 cm intervals further subdividing the area and forming 100 subquadrats each of 0.01 m^2. Cover was estimated to the nearest percent for each vascular species and for bare ground and litter. All species detected were recorded; those with less than 1% cover were recorded as present. Square metre quadrats were assessed progressively along each transect, and numbered successively from 1 to 30 from the start to the end of the transect. Time series data was graphed.

Table 3.1. Locations of permanent transects at Yarramundi Reach re-assessed for *N. neesiana* cover on 23 May 2007.

Transect	**Location**	
	start	**finish**
A	35°17.269’ 149°05.110’	35°17.284’ 149°05.096’
B	35°17.535’ 149°04.956’	35°17.540’ 149°04.974’
C	35°17.416’ 149°04.947’	35°17.421’ 149°04.958’
D	35°17.441’ 149°04.933’	35°17.454’ 149°04.918’

Reassessment of Laverton North 1990s 10 m x 5 m quadrats, April 2007

An attempt was made to re-examine the quadrats surveyed in the previous studies. However identification of their locations using the latitude/longitude data provided by McMahon *et al.* (1990) proved to be impossible. The most likely explanation appears to be the poor quality of GPS position data available at that time (Geoff Carr pers. comm. 2007). Fortunately

McMahon *et al.* (1990) also mapped the locations of their quadrats in relation to the pipeline, enabling them to be approximately relocated using scaling techniques, although with some uncertainty due to the loss of ground marker pegs over the years (Figure 3.2).

The positions of the re-located quadrats was recorded with a GPS device and by ground measurements and the quadrats, each of 100 m^2, were botanically assessed from 22 to 30 April 2007 using a 1 m x 1m steel frame subdivided at 0.5 m into four equal areas (Table 3.2).

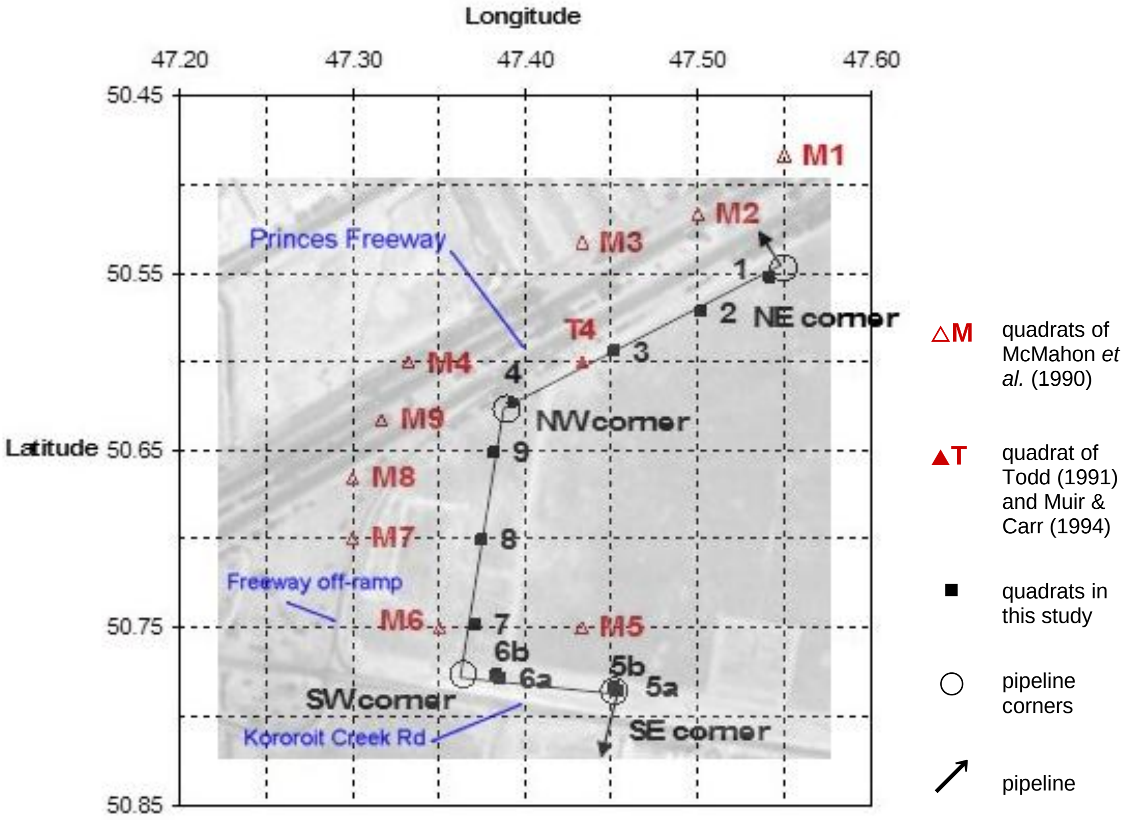

Figure 3.2. Location of the oxygen pipeline at Laverton North in relation to the quadrats applied in this study, the nine quadrats of McMahon *et al.* (1990) and the supposedly co-located quadrat 4 of Todd (1991) and Muir and Carr (1994) (M4 supposedly collocated with T4), based on their cited latitudes and longitudes.

Table 3.2. Location and date of assessment of quadrats at Laverton North Grassland in the April 2007 study.

Quadrat	Pipeline	Lat Long (of point or quadrat centre)	Quadrat location (centre of quadrat)	Assessment date
-	NE corner	37° 50.548’S 144° 47.550’E	-	-
1	N	37° 50.553’S 144° 47.542’E	12.1 m SW of NE corner	27April 2007
2	N	37° 50.572’S 144° 47.502’E	82.4 m SW of NE corner 192.8 m NE of NW corner	27 April 2007
3	N	37° 50.595’S 144° 47.452’E	107.2 m NE of NW corner	27 April 2007
-	NW corner	37° 50.627’S 144° 47.390’E	-	-
4	NW corner	37° 50.624’S 144° 47.394’E	8.9 m NE of NW corner	26 April 2007
-	SE corner	37° 50.786’S 144° 47.452’E	-	-
5a	S	37° 50.786’S 144° 47.454’E	4.9 m W of SE corner, 0- 5 m N of fenceline	22 April 2007
5b	S	37° 50.784’S 144° 47.452’E	4.9 m W of SE corner, 5-10 m N of fenceline	30 April 2007
6a	S	37° 50.779’S 144° 47.386’E	28.1 m E of SW corner, 0-5 m N of fenceline	22 April 2007
6b	S	37° 50.777’S 144° 47.384’E	28.1 m E of SW corner, 5-10 m N of fenceline	30 April 2007
-	SW corner	37° 50.777’S 144° 47.365’E	-	-
7	W	37° 50.748’S 144° 47.372’E	55.1 m N of SW corner	24 April 2007
8	W	37° 50.701’S 144° 47.376’E	146.6 m N of SW corner	26 April 2007
9	W	37° 50.652’S 144° 47.383’E	225.5 m N of SW corner 58.6 m S of NW corner	26 April 2007

Laverton North zone study, January 2008.

Doubts about whether the quadrats assessed corresponded closely enough with the quadrats that had earlier been studied by McMahon et al. (1990), Todd (1991) and Muir and Carr (1994) led to a new examination in January 2008. Five quadrats of 5 m x 2 m were surveyed in each of three parallel zones, running north-south across the site (Table 3.3):

1. grassland within the Reserve, managed by fire and burnt on 6 April 2007 (Fig. 3.3);

2. the pipeline zone (Fig. 3.4); and

3. rank, unmanaged grassland to the west of the pipeline (Figure 3.5).

The ‘reserve’ zone was c. 19 m east of the pipeline, and the ‘unmanaged’ zone was c. 10 m west of the pipeline. A strip of mown grassland to the west of a low fence occupied some of the area between the pipeline and reserve zones. A wide buffer was allowed at the end of each zone to minimise edge effects and ensure that the reserve zone did not include areas of disturbance associated with the pipeline and that the other zones did not include areas that appeared to be subject to regular mowing. Quadrats were randomly located along north-south transects through each zone, with their long axes aligned along the transect.

The position of the north-west corner of each quadrat was recorded with a GPS device, along with its measured distance from the southern boundary fence (Table 3.3). The projective foliar cover of *N. neesiana* and other species was estimated in each quadrat using a 1 m x 1 m steel frame subdivided at 0.5 m into four equal areas. The number of tussocks of *N. neesiana* in each quadrat was counted and the size of each tussock was determined within categories of small (<5 cm diameter tussock), medium (5-10 cm diameter) and large (>10 cm diameter), but this data is not reported here. Quadrats in the 'Reserve' zone were assessed on 26 January, in the 'Unmanaged' zone on 27 January and in the 'Pipeline' zone on 30 January.

Cover values for the species detected were grouped into categories for analysis based on Walsh and Stajsic (2007): native perennial grasses, exotic perennial grasses, annual grasses, native forbs and exotic forbs.

Table 3.3. Location and date of assessment of quadrats in the January 2008 zone survey at Laverton North. A GPS reading was taken for the north-west corner of each quadrat, which was a measured distance north of the south fenceline (along Kororoit Creek Road).

Zone	**Quadrat**	**Latitude**	**Longitude**	**m N of S fence**
Reserve	1	37° 50.746'	144° 47.383'	65
Reserve	2	37° 50.706'	144° 47.393'	140
Reserve	3	37° 50.664'	144° 47.403'	220
Reserve	4	37° 50.644'	144° 47.406'	255
Reserve	5	37° 50.631'	144° 47.409'	280
Unmanaged	1	37° 50.721'	144° 47.362'	106
Unmanaged	2	37° 50.677'	144° 47.372'	191
Unmanaged	3	37° 50.662'	144° 47.375'	216
Unmanaged	4	37° 50.652'	144° 47.378'	236
Unmanaged	5	37° 50.642'	144° 47.379'	256
Pipeline	1	37° 50.725'	144° 47.371'	89
Pipeline	2	37°50.720'	144° 47.372'	104
Pipeline	3	37° 50.695'	144°47.377'	154
Pipeline	4	37° 50.689'	144° 47.378'	164
Pipeline	5	37° 50.681'	144° 47.379'	179

Figure 3.3. The ‘reserve’ zone at the western end of Laverton North Grassland Reserve, 28 January 2008, looking north.

Figure 3.4. The ‘unmanaged’ zone on private land immediately west of the Laverton North Grassland Reserve, 28 January 2008, looking north.

Figure 3.5. The ‘pipeline’ zone, immediately west of Laverton North Grassland Reserve, 28 January 2008, looking north.

Statistical analysis

Statistical analysis was not applied to the small Yarramundi Reach data set or to the replicate quadrat study at Laverton North. The mean cover of different species or groups of species from the January 2008 Laverton North zone survey was analysed as a five replicate one way analysis of variance, after angular transformation, with a single quadrat as the unit of analysis. Preliminary analysis indicated that the largest differences were between the pipeline zone and the other two zones; thus the treatment effects were divided into two orthogonal contrasts, namely: (i) the pipeline area *vs* the other two areas and (ii) the reserve *vs* the unmanaged area. The mean numbers of native, exotic and all species were analysed similarly, except using a square root transformation. Due to the low cover of native forbs and consequent discreteness of the data, a permutation variance ratio test was used to test the difference between zones for native forbs. In this test the P value for the F value is compared to the permutation distribution of the data values, rather than to F tables based on the normal distribution.

Results

ACT transect quadrats

Cover of *N. neesiana* consistently maintained high values in only a single quadrat, on transect D (Table 3.4, Fig. 3.6). In every other quadrat cover was not observed to exceed 30% over the period. The grass appeared, achieved minor cover, and then more or less disappeared in five of eight quadrats in which it was recorded. *Nassella neesiana* cover fluctuated markedly over the period but there was no evidence that it achieved and maintained overwhelming dominance apart from this one quadrat.

The assessment of the whole of transect B in 2007 showed that cover of *N. neesiana* did not exceed 20% in any quadrat along the entire length of the transect (Fig. 3.7), although the grass had first been recorded in the transect in December 2000 (Table 3.4). It occurred in two quadrats in 2003 from which it was absent in 2007, although this section of the transect was found to be occupied in 2007 by *Austrostipa bigeniculata*, for which it might have previously been mistaken.

In 2007 transect D was dominated by *N. neesiana* at one end but by *T. triandra* and some *Poa labillardierei* at the other (Fig. 3.8). The historical ACT data (Table 3.4) indicate that there had been reasonably high cover of *N. neesiana* in 1993 in quadrat 8 (Environment ACT quadrat D2), but that the grass then disappeared for 9 years. It was detected again at high cover at this point in 2007. The profile of cover along this transect (Fig. 3.8) indicates that quadrat 8 was at that time about 3-4 m from the high-cover fringe of an expanding *N. neesiana* infestation and approximately 6-7 m from its outer edge, so the earlier data suggest that from zero cover in 2002 the infestation had expanded at the rate of approximately 1.3 m y^{-1}.

Table 3.4. Percent foliar cover of *N. neesiana* in quadrats along permanent transects at Yarramundi Reach. Columns 1 and 2 give the quadrat code numbers used by Environment ACT and columns 3 and 4 the corresponding numbers used in this study. Environment ACT cover values are to the nearest 5%.

Envt ACT		**This study**		**Environment ACT data**										**This study**
				1993	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2007**
Transect	**Quadrat**	**Transect**	**Quadrat**	**6/12/93**	**15/12/94**	**28/12/95**	**9/12/96**	**3/12/97**	**1/12/98**	**30/12/19**	**13/12/00**	**13/12/01**	**18/12/02**	**23/05/07**
A	**3**	**A**	**13**	0	0	0	0	0	5	0	5	5	0	0
B	**2**	**B**	**8**	0	0	0	0	0	0	0	0	0	5	0
B	**3**	**B**	**13**	0	0	0	0	0	0	0	5	0	5	0
C	**1**	**C**	**3**	0	0	0	0	15	0	0	0	0	0	0
C	**3**	**C**	**13**	0	5	5	5	5	0	0	0	0	0	0
C	**5**	**C**	**23**	0	25	15	5	0	0	0	0	5	0	0
D	**1**	**D**	**3**	85	55	75	85	95	65	65	45	35	55	55
D	**2**	**D**	**8**	30	0	0	0	0	0	0	0	0	0	63

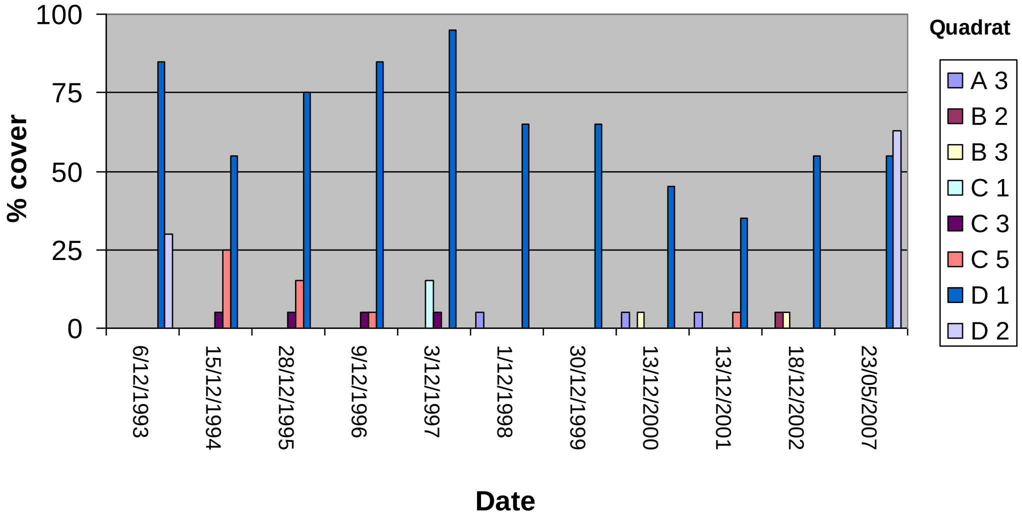

Figure 3.6. Variation in the cover of *N. neesiana* in quadrats along permanent transects at Yarramundi Reach grassland, 1993-2007. Note that cover values were not recorded during the years 2003-2006.

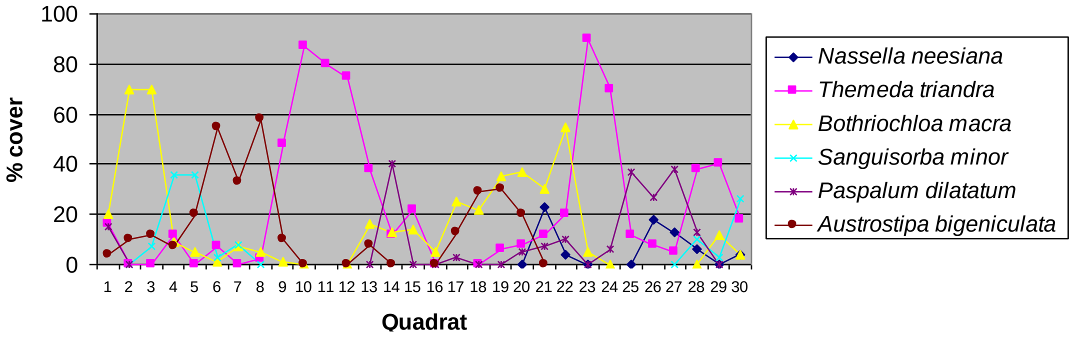

Figure 3.7. Percent foliar cover of major species contributing to ground cover along transect B, Yarramundi Reach grassland, 23 May 2007.

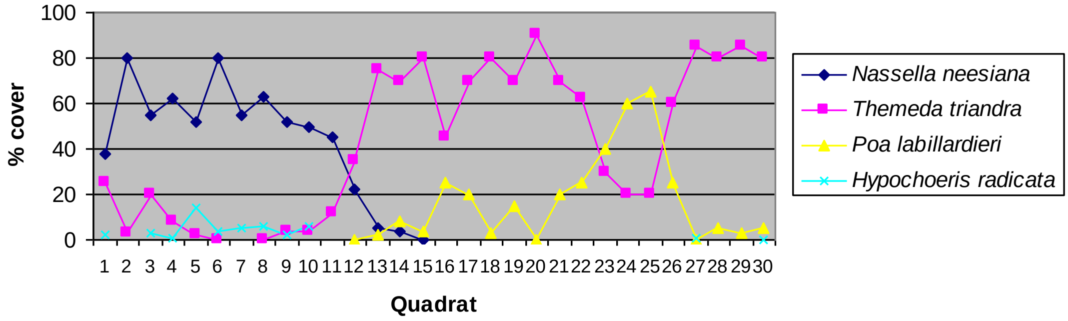

Figure 3.8. Percent foliar cover of major species contributing to ground cover along transect D, Yarramundi Reach grassland, 23 May 2007.

Figure 3.9 (Next page). Sequential cover/abundance ratings of major species and bare ground in quadrats along the oxygen pipeline at Laverton North grassland, 1990 (McMahon *et al.* 1990), 1991 (Todd 1991), 1994 (Muir and Carr 1994) and 2007 (this study).

Cover classes: 0.1 = <5% cover, few individuals; 1 = cover <5%, any number of individuals; 2 = cover 5-20%, any number of individuals; 3 = cover 20-50%, any number of individuals; 4 = cover 50-75%, any number of individuals; 5 = cover 75-100%, any number of individuals.

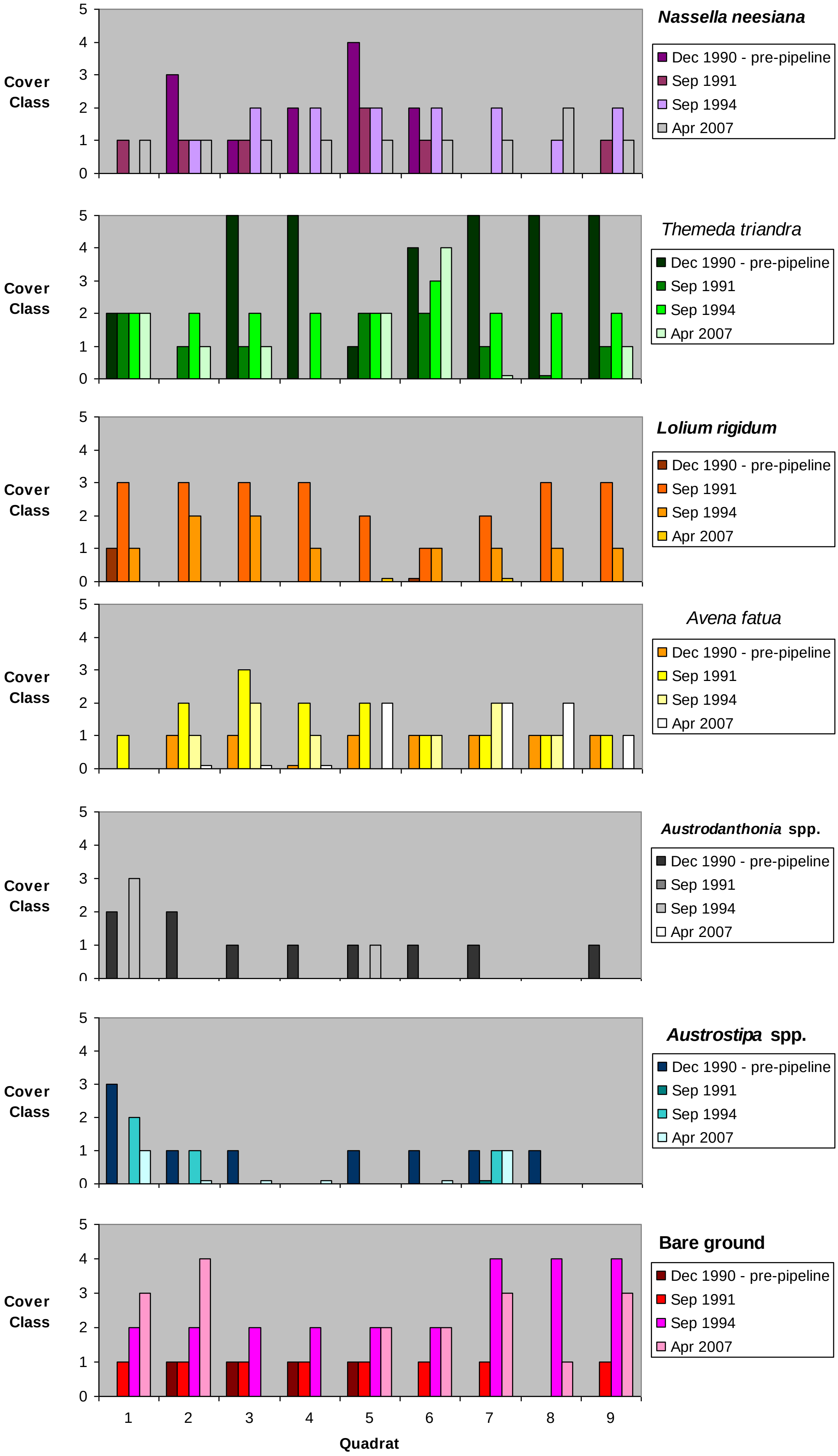

Figure 3.9 (caption on previous page).

Laverton North pipeline quadrats

In 1990, prior to construction of the pipeline, the cover of *T. triandra* exceeded 75% in five of nine 5 x 20 m quadrats assessed by McMahon *et al.* (1990), and one additional quadrat had cover of 50-75% (Fig. 3.9). Three of the quadrats with >75% *T. triandra* cover in 1990 contained no *N. neesiana* at that time (quadrats 7, 8 and 9, Fig. 3.9). Cover of *T. triandra* in these three quadrats plummeted after pipeline construction but substantial bare ground did not result in the following year. In quadrat 9, *N. neesiana* achieved measurable cover (<5%) in 1991, although the main response was from *Lolium rigidum*. In 1994 *N. neesiana* increased its cover in this quadrat to 5-20%, *L. rigidum* cover fell and 50-75% of the area was bare ground. Plant cover in quadrats 7 and 8 showed a similar response, with an initial increase of *L. rigidum*, followed by substantial bare ground and increased cover of *N. neesiana* in 1994 from undetectable levels in 1991.

Before pipeline construction the other two quadrats with >75% *T. triandra* cover (quadrats 3 and 4) had *N. neesiana* cover of <20% (Fig. 3.9). After pipeline construction there was a marked response from the disturbance-driven annual grasses *Lolium rigidum* and *Avena fatua*, which both increased their cover, while *N. neesiana* cover remained more or less stable in quadrat 3 and dropped to an undetectable level in quadrat 4. By 1994 *N. neesiana* had increased in both these quadrats while some *T. triandra* cover (5-20%) had been maintained. By 2007 *N. neesiana* had maintained its presence in these quadrats, but had not achieved high cover, and *T. triandra* had disappeared from one quadrat and retained cover only in a small area in the other.

Quadrat 6 had *T. triandra* cover of 50-75% before the pipeline work and maintained it a relatively stable level (5-75%) over the whole period (Fig. 3.9), despite the initial presence of *N. neesiana* in 1990. *N. neesiana* had maintained its presence in this quadrat by 2007.

N. neesiana cover actually fell after pipeline construction in the two quadrats (quadrats 2 and 5) in which its cover was greatest (>20%) prior to construction, and remained lower than initial values for the whole period.

Quadrat 1 had mixed native cover of *T. triandra* and *Austrodanthonia* and *Austrostipa* spp. before the pipeline works, and no *N. neesiana*. Minor *N. neesiana* invasion occurred in the following year, but the grass never achieved high cover.

Deliberate *T. triandra* revegetation efforts were largely a failure. *T. triandra* did not regain high cover in any quadrat. There was also little or no recovery of the subdominant *Austrodanthonia* and *Austrostipa* species.

Laverton North zone study

In January 2008, native perennial grasses covered approximately one third of the ground in quadrats located in the reserve and unmanaged zones, but constituted a very minor proportion of total vascular plant cover in the pipeline zone, with the difference being highly significant (Table 3.5). The almost complete absence of *Themeda triandra* in the pipeline zone was the main contributing factor. That zone had significantly greater mean coverage of exotic annual grasses (23%), mainly consisting of *Avena* spp., significantly greater mean cover of litter (mainly derived from the exotic grasses), and significantly less mean cover of native forbs (Table 3.5). It also had close to a significantly higher proportion of bare ground ($p = 0.053$).

Mean *N. neesiana* cover in the pipeline zone was double that in the unmanaged zone, which in turn was more than three times that in the reserve zone, however due to very high variance between quadrats there was no significant difference in its cover between any of the zones. And although the reserve zone appeared to have reduced cover of exotic perennial grasses as a category, this too was not significant.

The mean number of native species per quadrat and the mean total number of species per quadrat in the pipeline zone was significantly less than in the other two zones (Table 3.6).

Discussion

Yarramundi Reach

The limited data from Yarramundi Reach suggest that *N. neesiana* does not necessarily come to dominate small areas where it occurs (that is, it may not be an aggressive invader), that its cover at the square metre scale can shift markedly from year to year and that it can disappear from areas in which it may initially establish and form low cover, possibly due to competition from and the development of very high cover by *T. triandra*. Evidence from one quadrat indicates that an *N. neesiana* invasion front can expand at a rate of 1.3 m y^{-1}.

However variation in the overall density of grass growth from year to year may greatly affect cover values at this scale (square metre quadrats), and significant cover of grasses of the size of *N. neesiana* may be recorded without any *N. neesiana* plants having a rooted presence in a quadrat, but instead may be over-hanging from an adjacent quadrat in some years. Climatic variations in the productivity of *N. neesiana* and other species present in the area may explain much of the variation. It is likely that the apparent coming and going of the grass is not real and is due in part to the difficulty of accurately relocating unmarked square metre areas from year to year along extended transects on uneven ground. Mistakes in the data collection may have led to different areas being assessed from year to year.

Table 3.5. Mean projective foliar cover of plant species and categories, litter cover and proportion of bare ground (%) in five 10 m^2 quadrats in each of three management zones (Reserve, Unmanaged, Pipeline) at Laverton North, January 2008. Significant P values in bold.

Cover (%)	**sed**	**Back transformed**			**P-Values**	
		Reserve	**Unmanaged**	**Pipeline**	**Pipeline vs Other**	**Reserve vs Unmanaged**
Native perennial grasses	4.8	31	33	4	**0.00011**	0.77
Themeda triandra	3.9	29	25	0	**8.1 x 10^{-7}**	0.47
Exotic perennial grasses	4.1	15	25	25	0.38	0.10
Nassella neesiana	8.2	2	7	14	0.17	0.32
Phalaris aquatica	6.7	7	19	8	0.51	0.15
Exotic annual grasses	4.5	4	6	23	**0.0025**	0.58
Avena spp.	4.5	0	6	23	**0.00030**	**0.034**
Native forbs	3.6	1	4	0	**0.042***	0.15*
Exotic forbs	5.0	10	10	15	0.36	0.93
Litter	1.8	9	13	30	**1.3 x 10^{-6}**	**0.049**
Bare ground	2.8	45	37	32	0.053	0.12

* using permutation variance ratio test

Table 3.6. Mean numbers of native, exotic and total vascular plant species per 10 m^2 in three management zones at Laverton North, January 2008.

Number of species	**sed**	**Back transformed**			**P-Values**	
		Reserve	**Unmanaged**	**Pipeline**	**Pipeline vs Other**	**Reserve vs Unmanaged**
Native	0.22	4.9	6.1	2.5	**0.0019**	0.24
Exotic	0.23	9.6	8.5	6.9	0.087	0.43
Total	0.26	14.6	14.7	9.5	**0.0073**	0.96

Identification failures or misidentifications may have contributed. One conclusion that can be reached is that the sampling of a few small quadrats along a 30 metre transect does not provide much insight into the interannual variation in *N. neesiana* dominance or changes in the area of an infestation.

Laverton North

Nassella neesiana invasion along the oxygen pipeline at Laverton North has been anecdotally attributed to the destruction of native plants resulting from pipeline construction. The data demonstrates that invasion did occur in some disturbed areas along the pipeline, even over a long time frame. Areas along the north-south section of the pipeline (quadrats 7-9) that had previously lacked *N. neesiana* were subject to major destruction of *T. triandra* and developed increased cover of annual grasses the following year, with *N. neesiana* invasion in one quadrat. By 1994 all three of these quadrats had high levels of bare ground and all had been occupied to some extent by *N. neesiana*. By 2007 *N. neesiana* had maintained its presence in these quadrats but had not achieved high cover and there were still substantial areas of bare ground.

Some areas lost *N. neesiana* cover as a result of pipeline works and did not recover it. Exotic annual grasses increased their cover in these areas, or the ground remained bare (at least at the time of assessment). In other areas (quadrats 3 and 4 along the Princes Highway) *N. neesiana* was already present in areas of very high *T. triandra* cover prior to pipeline construction. Invasion accompanying high *T. triandra* cover is indicative of probable senescence dieback of *T. triandra* as the cause of invasion. Failure to find any significant difference in the cover of *N. neesiana* between the pipeline zone and the other zones adds some weight to this impression.

The zone study demonstrates that pipeline construction resulted in devastation of native species, including *T. triandra*, subdominant native grasses and native forbs, and that no recovery had occurred by 2008, 18 years later, despite active attempts to re-establish *T. triandra* and other natives. Areas of bared ground created by disturbances such as pipeline construction would be expected to be colonised by other species. Chan (1980 p. 10) noted that *T. triandra* “can and does invade and dominate almost any ground that is cleared and protected from grazing”. However the studies of Morgan (2001 p. 908) in basalt plain grasslands found that recruitment of most native species was always very rare or completely absent, “despite their abundance in the standing flora”. A near-complete failure of native species to re-establish is clearly apparent in the pipeline zone, which by 2008 was still dominated by exotic annual grasses, mainly *Avena* spp., had zero recolonisation by the dominant native grass *T. triandra* and an almost complete absence of native forbs. Despite attempted amelioration, pipeline construction transformed the affected land into a new metastable vegetation state, which natural processes seem powerless to shift.

Role of *Themeda triandra* senescence in the invasion

Senescence dieback of *T. triandra* is preceded by high foliar cover of *T. triandra* (Morgan and Lunt 1999) and values of 75-100% of *T. triandra* cover were recorded by McMahon *et al.* (1990) prior to pipeline construction in some areas where *N. neesiana* had already invaded. Similar high cover of *T. triandra* persisted at the grassland for some years – for example, Craigie (1993 p. 7) noted that most of the reserve was dominated by very dense *T. triandra*, with cover generally exceeding 90%. High cover of *T. triandra* can be achieved rapidly at this site: Lunt and Morgan (1999a) recorded mean cover in a frequently burnt zone of 63%, 20 months after the most recent fire. They also noted that substantial mortality of *T. triandra*, preceded by senescence, occurred in the Reserve after 1986. Occurrence of senescence dieback in the reserve and unmanaged zones, allowing *N. neesiana* invasion, may account for the lack of any significant difference in *N. neesiana* cover in the three zones, and for the lack of a significant difference in the mean number of native species between the reserve and the unmanaged zones.

Effects of revegetation and herbicidal control works

The impacts of deliberate revegetation and weed control works are confounding factors in the interpretation of the cover and species richness values. Efforts to revegetate with *T. triandra* were clearly a failure as observed by Todd (1991) and Muir and Carr (1994), and confirmed by both the repeated quadrat study and the zone study.

Deliberate herbicidal weed control was undertaken through some of this period. Todd (1991) recommended spot spraying or hand weeding of a set of exotic species including *N. neesiana*. Muir and Carr (1994) recommended spraying of the whole easement with a selective broadleaf herbicide and control of *N. neesiana* and other exotic perennial grasses with spot spraying. These activities were required for a period of five years (i.e. to 1995) and may have led to changes in the dominant vegetation. In particular the reduced total vascular plant species richness in the pipeline zone (Table 3.6), partly due to reduced exotic richness, may be attributable in part to herbicidal control works. However records of the actual spraying undertaken and the species controlled are not available.

Conclusions

Concerns that the initial quadrat areas at both Yarramundi Reach and Laverton North were not relocated with great precision require that the findings for the repeat studies be treated with considerable caution.

However repeated monitoring of *N. neesiana* presence in a few small quadrats at Yarramundi Reach indicate that its cover can fluctuate markedly from year to year, that it may disappear from areas in which its establishes with low cover, that it can maintain its presence with relatively high cover for periods exceeding 13 years and that infestations can expand at rates of >1 m y^{-1}.

The Laverton North studies demonstrate that severe soil disturbance involving major destruction of the native flora does not necessarily lead to *N. neesiana* invasion in areas where it is widely present. The ground can be captured and held for a long period by exotic annual grasses as well as exotic perennials. Fears about massive occupation by the grass as a near-monoculture at Laverton North have proved to be poorly founded. The zone study data indicate that the native floristic diversity was significantly greater in the unmanaged zone and in the regularly burnt Reserve than along the pipeline, suggesting that construction permanently destroyed most of the native flora. There is some indication that the management regime in the Reserve has resulted in lower cover of *N. neesiana* and other exotic perennial grasses, but the differences are not statistically significant.

At Laverton North the *N. neesiana* invasion that had already occurred before construction of the oxygen pipeline, possibly due to senescence dieback of *T. triandra*, was not exacerbated by pipeline works in some areas. In other areas the disturbances associated with construction resulted in a high proportion of bare ground that was not occupied by *N. neesiana*. Substantial invasion did occur in some parts of the disturbed area, but high cover only occurred on a relatively small part of the overall area disturbed. Revegetation works and herbicidal control activities were confounding factors that contribute considerable uncertainty to the interpretation of the findings, and determination of the mechanisms involved in each area are difficult.

Overall the results concur with the findings of Morgan (2001) that conservation of the native vascular flora requires maintenance of the existing bud and tuber bank, i.e. ongoing survival of living individuals in the standing vegetation. The findings indicate that *N. neesiana* invades as a consequence of soil disturbance that kills the native vegetation, that this capacity for invasion is highly variable depending on site specific characteristics, including what other species are available for invasion, and that, under some circumstances, similar disturbance that kills *N. neesiana* can result in its displacement by annual grasses.

Chapter 4. Disturbance and seed inundation field experiment

"Invasion ... [is] … simply a subset of the possible recolonization responses to disturbance"

R.J. Hobbs and L.F. Huenneke (1992 p. 332).

"... any disturbance that removes intact vegetation tends to promote the seedling establishment of grasses"

G. P. Cheplick (1998 p. 98).

Summary

The mechanisms that enable *N. neesiana* invasions are poorly understood, but well-managed grasslands with relatively intact cover of native grasses appear to be resistant to invasion. This chapter describes a field experiment in a *T. triandra* grassland to test the hypothesis that invasion is disturbance-driven, and to investigate the effects of a range of disturbances on *N. neesiana* recruitment. Replicated square metre experimental plots were treated by either killing all the existing dominant native tussock grasses with herbicide, half the dominant tussock grasses in a mosaic pattern or no tussock grasses, and applying either nutrients (N, P, N+P) or sugar (to immobilise nutrients), along with appropriate controls. Viable panicle seeds of *N. neesiana* were then applied at 500/m^2 to half the plots. Killing all the native tussocks enabled by far the greatest *N. neesiana* establishment, and produced much higher biomass and growth of *N. neesiana* plants to maturity in <1 year. Areas in which smaller gaps were created ('half kill' plots) had greatly reduced recruitment and much lesser biomass of new *N. neesiana* plants. Intact grassland control plots were highly resistant to invasion. Addition of fertilisers had no significant effect on *N. neesiana* recruitment or biomass production, but application of sugar significantly reduced establishment. Establishment and productivity of juvenile plants was probably facilitated by a nutrient pulse resulting from the decay of the killed vegetation. Once established, *N. neesiana* had a minor (but statistically detectable) suppressive impact on the biomass of native grasses and of other plant species as a group, despite achieving only low cover. The primary juvenile period of growth of *N. neesiana* was found to be less than one year for the most advanced 50% of plants in the cohort some *N. neesiana* plants were able to establish, grow and produce viable seed within this one year time frame.

Introduction

There is no general theory that explains the susceptibility of plant communities to invasion by exotic weeds, but propagule pressure and disturbance are generally recognised as key mechanisms (Eschtruth and Battles 2009). In Australia there is little quantitative information on the mechanisms that enable environmental weed invasions, and few studies have incorporated deliberate experimental manipulations to investigate the effects, but the same key factors appear centrally important (Adair and Groves 1998, Grice 2004a, Grice *et al.* 2004, Coutts-Smith and Downey 2006).

Propagule pressure is a complex function, based on age at reproductive maturity and fecundity, dependent on propagule dispersal mechanisms and the availability and incidence of dispersal agents, and ultimately determined by the ability of the propagules to find suitable habitat and establish new populations (Williamson and Fitter 1996). In situations where an invasive species is already present and reproducing, use of the term "propagule rain" may be preferable (Lockwood *et al.* 2009). Production and dispersal of *N. neesiana* seed is relatively well understood because of the significance of the weed in agriculture, and research that has investigated this (Gardener 1998, Grech 2007). Seeds appear to be dispersed mainly by human activities, primarily on mowing and slashing machinery and vehicles, and by livestock via external attachment, but also within the digestive tract of domestic animals, particularly sheep (Bedggood and Moerkerk 2002, Gardener *et al.* 2003a, Snell *et al.* 2007). No definitive published information appears to be available on the period required before young *N. neesiana* plants enter the reproductive phase for the first time. Benson and McDougall (2005) listed the primary juvenile periods of many grasses but failed to provide one for *N. neesiana*. According to Sethu Ramasamy (RMIT University, pers. comm. 13 June 2007) plants in their first year of growth do not flower. Large soil seed banks (>2500 seeds m^{-2}) have been measured in infested agricultural grasslands (Bourdôt and Hurrell 1992, Hurrell *et al.* 1994, Gardener 1998, Gardener *et al.* 2003b) and substantially smaller ones (often <1000 viable seeds m^{-2}) in conservation areas (Beames *et al.* 2005, Hocking 2005b). An abundance of uncontrolled infestations along carriageways around many temperate grassland remnants and within the remnants themselves ensures that a new flux of seed rain is produced each year.

The other processes that enable, or contribute to the capacity of, *N. neesiana* to actively invade have not been clearly determined. In general, areas with higher susceptibility to weed invasion either have strong, temporally-varying change (i.e. high levels of natural or artificial disturbance) that creates periods of abundant under-utilised resources (e.g. high nutrient levels, high soil water availability), or are subject to anthropogenic application of resources (Hobbs 1989, Davis *et al.* 2000, Cox 2004). Disturbance has generally been found to favour exotic plant invasions over native vegetation re-establishment (Hobbs 1991, D'Antonio *et al.* 1999, Prieur-Richard and Lavorel 2000) although some authors (e.g. Carr 1993) argue that major invasions of some plants occur without such disturbance. The tenet that disturbance is a prerequisite for invasion is implicitly based on the notion that in undisturbed, successionally mature vegetation, surplus resources are absent (Carr 1993), minimised or unobtainable by the existing flora. The fluctuating resources theory posits that a "plant community becomes more susceptible to invasion whenever there is an increase in the amount of unused resources" (Davis *et al.* 2000). The community becomes more susceptible to invasion by a particular exotic plant if the particular resource that becomes available was previously limiting the growth or survival of that plant (Hobbs 1991). Continuity of the invasion requires that gains the invader makes are not lost when the supply of the resource contracts.

Conversely, resistance to invasion is provided by undisturbed vegetation that is utilising all of the available resources. A majority of plant diversity studies and experiments at small spatial scales (patch, plant association) indicate that greater resistance is provided when the vegetation is more species diverse (Prieur-Richard and Lavorel 2000, Symstad 2000, Dunstan and Johnson 2006). However even at the small scale (1 m^2) contradictory results have been found, suggesting that environmental factors other than plant diversity may frequently be important in determining invasibility (Stohlgren 2007). For instance cover and abundance data from surveys at Derrimut Grassland Reserve, Victoria, suggest that *N. neesiana* seedling establishment is uncommon in areas of dense, low diversity stands of the dominant grass *T. triandra* (Lunt and Morgan 2000). A native-based community or one of its members may repel even a superior competitor simply by the priority effect that established residents have over invaders (Symstad 2000, Körner *et al.* 2008). In temperate native grasslands of south-eastern Australia, the biomass of the non-dominant inter-tussock species is generally exceeded by that of the dominant native grasses by at least one to two orders of magnitude, and in areas that remain unburnt and ungrazed, the dominant native grass may account for >90% of plant biomass (Lunt and Morgan 2002). *Themeda triandra*, the dominant native grass in temperate native grasslands of south-eastern Australia, is probably the main provider of biotic resistance to invasion, and appears to function as a keystone species (Prober and Lunt 2009).

Conditions suitable for grass seedling recruitment in perennial grasslands are generally rare or infrequent (Lauenroth and Aguilera 1998). Habitat disturbance is an important factor in the creation of suitable sites for the germination of grass seeds, and any disturbance that damages or kills the existing vegetation favours the establishment and survival of juvenile grass plants, whether native or exotic (Cheplick 1998). Numerous experimental studies have demonstrated negative effects on grass recruitment due to the presence of established grasses (Lauenroth and Aguilera 1998), including effects from the roots and litter. An invader is favoured by disturbance if its competitors are recruitment-limited, or the invader is better able to exploit the resources made available by the disturbance (Seabloom *et al.* 2003). Recruitment limitation of native species has long been recognised as a problem in Australian temperate grasslands, mainly due to their small, ephemeral seed banks (Lunt 1990b 1995a, McIntyre 1993, Stuwe 1994, Morgan 1998a 1998b 1998c 2001). Because of this, disturbances are likely to favour exotic species that have larger seed banks if other resources for recruitment are available. The post-disturbance vegetation may have multiple stable states determined by which species arrives first (the ‘priority effect’) and the ability of that species to reduce the availability of limiting resources to potential competitors (Seabloom *et al.* 2003, Körner *et al.* 2008). Water may be the key resource in Australian temperate grasslands but nutrients are demonstrably important (Wijesuriya and Hocking 1999).

Nutrient enrichment is a major cause of alien grass invasion worldwide (Milton 2004) and can, in the long term, substantially alter the floristic composition of temperate grasslands (Morgan 2007). Nutrient increases and/or soil disturbances appear to be a critical cause of invasions by high biomass perennial exotic Poaceae in the *T. triandra* dominated grasslands of south-eastern Australia (Morgan 1998d). Exotic plants proliferate in these systems when there is soil disturbance that creates bare ground and releases nutrients normally locked up in the crown and roots of the dominant native grasses (Wijesuriya 1999, Wijesuriya and Hocking 1999). Invasion of high-biomass perennial exotic grasses appears to require intense pulses of N and possibly P in these grasslands (Morgan 1998d, Wedin 1999, Groves and Whalley 2002, Groves *et al.* 2003).

In unmanaged *Themeda triandra* Forssk. grasslands, senescence and partial or complete *T. triandra* death, leading to a similar process of nutrient enrichment, may permit or contribute to *N. neesiana* invasion (Lunt and Morgan 2000). Evidence and field observations indicate that a site occupied by a dominant native grass, that suffers no significant soil disturbance, remains resistant to invasion (Hocking 1998, Phillips 2000). This is probably largely the result of the very high levels of sequestration of system nutrients in the tissues of the dominant grass, and may be due in part to the ability of C_4 grasses such as *T. triandra* to use available soil N more efficiently than C_3 grasses such as *N. neesiana* (Wijesuriya 1999, Murphy and Bowman 2009). *Themeda triandra* swards produce low quality litter with a C: N ratio >30:1, which decays slowly because microbial decomposers are N-limited, resulting in little or no release of nitrate and ammonium into soil solution. Thus *T. triandra* appears able to perpetuate its competitive advantage by a variety of mechanisms that enable it to monopolise key nutrient resources (Wedin 1999, Groves and Whalley 2002).

Reduction of available soil nutrients to restore degraded grasslands can include biomass reduction such as burning, and application of labile C, which is believed to feed, or provide substrates for rapid growth of soil microbes that can temporarily ‘mop-up’ available soil N and other nutrients and decrease rates of N mineralisation and nitrification (Reever Morghan and Seastedt 1999, Wijesuriya and Hocking 1999, Eschen *et al.* 2007, Morgan 2007, Chigineva *et al.* 2009, Prober and Lunt 2009). Addition of sucrose to soil can rapidly stimulate microbial activity, probably mostly of Gram negative bacteria (Nottingham *et al.* 2009). Sugar application has frequently been used effectively to decrease above-ground biomass and reduce the competitive ability of invasive plants, which tend to proliferate in soils with high nutrient levels (Reever Morghan and Seastedt 1999, Prober *et al.* 2005, Eschen *et al.* 2007, Smallbone *et al.* 2008, Prober and Lunt 2009). The technique has sometimes been called ‘reverse fertilisation’. In Australia it has been demonstrated to be an effective technique for the restoration of *T. triandra* and some native forbs in degraded woodlands dominated by exotic annuals (Prober *et al.* 2005, Smallbone *et al.* 2007, Prober and Lunt 2009).

For the research reported here, an experiment was established to test an ‘invasion requires disturbance’ hypothesis for *N. neesiana* and assess whether intact grassland would provide resistance to invasion. The aim was to examine the types of disturbance required to enable invasion of a *T. triandra* grassland, and determine which of a range of disturbances result in higher rates of *N. neesiana* seedling establishment and survival. The experimental design is similar to pioneer work described by Hobbs (1989) in Australia. A range of disturbances involving killing of the existing dominant native grasses (‘pre-treatments’) followed by the application of N or P fertiliser or sugar (‘nutrient treatments’) was applied in replicated 1 m^2 plots in relatively intact native grassland. Propagule pressure (‘seed treatment’) was applied by spreading *N. neesiana* seeds on a subset of plots. A range of control plots was also integrated into the trial.

Methods

A distinction between seedlings and juvenile plants was not made in this study, due to the rapid growth of *N. neesiana* seedlings and difficulty in clearly distinguishing the stages of development in the field. *Nassella neesiana* plants that resulted from seeding are referred to as juvenile plants unless reproductive structures were present.

Study area

The experimental site was a native grassland at Iramoo Wildlife Reserve, Cairnlea, Victoria, 15 km west of Melbourne. The experimental area was located on the southern side of management zone M2, with the centre of the experimental area at 37°45.231’ 144°47.405’

(Figs. 4.1, 4.2). Choice of site was limited by the nature of the experiment. Managers of grasslands of high conservation value were unwilling to allow the deliberate spreading of seeds of a declared noxious weed, which is illegal under the Victorian *Catchment and Land Protection Act 1994*, in high quality remnants under their control. The compromise involved acceptance of a lower quality, more weed infested grassland already carrying severe infestations of *N. neesiana* in some areas, and with significant populations of the exotic *Nassella trichotoma* (Nees) Hack. ex Arechav.

W1 Wildflower 1
W2 Wildflower 2
T1 Themeda 1
T2 Themeda 2
M1 Mixed vegetation 1
M2 Mixed Vegetation 2
M3 Mixed Vegetation 3
E1 Exotic 1
E2 Exotic 2
S1 Stony rise 1
TL1 Tree line 1
TL2 Tree line 2
► Gate

Figure 4.1. Iramoo Wildlife Reserve, Cairnlea, Victoria, showing the land management units and the location of the field experiment (small rectangle) on the southern side of M2.

Figure 4.2. Site of the disturbance experiment at Iramoo Grassland Reserve, Cairnlea, Victoria, 25 June 2007, looking SE before the commencement of treatment on 10 July. ‘Tree line 2’ in the distance at left and unburnt grassland of M3 in the midground at right.

A relatively uniform experimental area lacking obvious soil disturbance was selected, with a relatively uniform density of the dominant native grass *Themeda triandra* (Fig. 4.2). The site had been burnt for management purposes on 2 April 2007 and several times prior to this on a 3-4 year ecological burning cycle. Soil was a cracking clay. Small patches of *N. neesiana* existed within 2 m of the chosen areas and dense patches within 60 m. A few existing *N. neesiana* plants within and close to the edges of the buffer zone were killed with herbicide or removed by hand prior to initiation of the experiment. The possibility of recruitment resulting from long-distance dispersal was thus reduced. Other than occasional human visits the possible long distance seed vectors were restricted to foxes and birds. No rabbits were present within the reserve.

A permit was obtained from the Victorian Department of Primary Industries that allowed dispersal of *N. neesiana* seeds.

Plot layout

Ninety 1 m x 1 m plots were established in a rectangular block (5 x 18 plots) defined at each corner by short wooden stakes, with 1 m buffer zones between plots (Fig. 4.3).

Pre-existing vegetation

Initial condition of the vegetation was determined by counting the number of individual plants and estimating canopy cover of existing vegetation in all 90 one square metre plots over the period 26 June to 9 July in the following categories: *N. neesiana*, *T. triandra*, other native grasses, *N. trichotoma*, the exotic *Romulea rosea* (L.) Eckl. (Iridaceae), native forbs and other exotic forbs. Species were classed as native or exotic using Walsh and Stajsic (2007). The cover of plant litter, cryptogram crust, bare ground and rocks was similarly assessed. The identity of the other grasses and forbs present in each plot was determined.

The experimental area was dominated by native perennial grasses but *N. trichotoma* had a major presence. There was an average of 26.9 *T. triandra* tussocks m^{-2}, 9.6 *N. trichotoma* tussocks and 2.7 tussocks of other native grasses (mainly *Austrostipa bigeniculata* with some *Austrodanthonia* spp.). Due to recent burning, mean total projected foliar cover (aerial or canopy cover) of vascular species at commencement was only 12% (i.e. 88% bare ground including 0.1% rocks) with cryptogam crust cover of 0.2%. Proportions of the foliar cover represented by the major species were *T. triandra* 72.0%, *N. trichotoma* 17.1%, other native grasses 3.0% and *Romulea rosea* 5.0%. (Total = 97.1%). Proportions of above-ground biomass in untreated plots at the conclusion of the experiment in November 2008 represented by the main species were: *N. trichotoma* 33.5%, *T. triandra* 33.0%, *Austrostipa bigeniculata* 20.9%, *Romulea rosea* 11.2% and exotic annual grasses (mainly *Bromus hordeaceus* L.) 0.6% (= 98.6%).

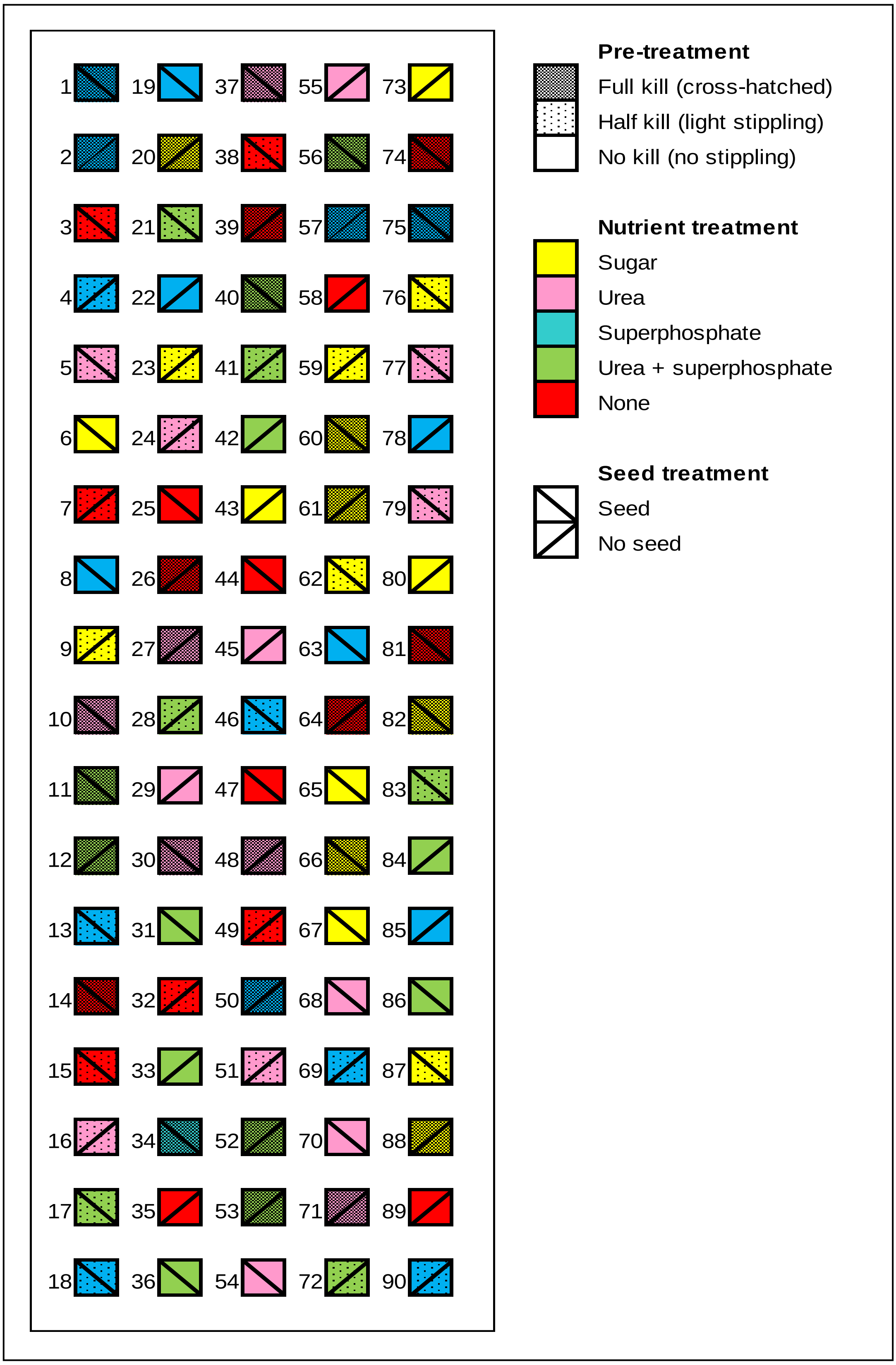

Figure 4.3. Plot layout and treatment regime in the disturbance experiment.

Nassella neesiana soil seed bank

To assess any pre-existing *N. neesiana* seed bank, two soil cores of 3.5 m diameter (9.6 cm^2) and 5 cm depth were taken in the buffer zone close to the north and west edges of each plot on 6-10 July (a total of 180 cores). Preliminary tests, undertaken by mixing awned and de-awned *N. neesiana* panicle seeds with soil from the site, established that a 3.35 mm sieve would trap most *N. neesiana* seeds in a soil slurry and that the remaining seeds would by trapped in a 1.2 mm sieve. Cores were soaked in water for a few hours or overnight, then broken up in water with a spatula and agitated until the soil was reduced to fine particles. The soil slurry was washed through a 3.35 mm sieve on top of a 1.2 mm sieve. Larger debris including roots and stones were removed from the coarse sieve with forceps before picking out seeds. Seeds were similarly removed from the fine sieve. Fines that passed through both sieves were inspected for seeds after drainage.

The viability of seeds detected was determined by squeezing the seed with fine forceps under magnification to determine whether the seed was filled (i.e. containing an embryo and endosperm) or unfilled.

Previous studies at the site demonstrated that late spring burning removed all viable *N. neesiana* seeds on the soil surface and that neither early or late spring burning resulted in major recruitment (Hocking 2005b). The autumn burning before this experiment was expected to have a similar impact and to destroy most seed on or near the soil surface.

Soil nutrient status

The soil at the site was sampled on 11 July 2007 and analysed by the Nutrient Advantage laboratory of Incitec Pivot Ltd. (Werribee, Victoria). Thirty soil cores of 3.5 cm diameter and 10 cm depth were taken. Core samples were evenly spaced along the 6 rows in the plot layout, with 5 samples per row. Sampled soil was thoroughly mixed in a bucket and stored in a cool box with freezer blocks. A subsample of 500 g was delivered for analysis within 2 hours of sampling. Analyses were performed on soil dried at 40°C and ground to 2 mm particle size or less.

Pre-treatments

Three pre-treatments were applied on 10 July 2007: 1. spraying of all existing grass tussocks with glyphosate (glyphosate isopropylamine salt, 360 g/litre, “Glyphosate 360”) at 10 ml/L, the label rate for perennial grasses (= ‘full kill’); 2. spraying half the tussocks (= ‘half kill’) at the same application rate; 3. no artificial kill of existing vegetation. In ‘half kill’ plots every second tussock was sprayed in a mosaic pattern, rather than every tussock in half the plot. ‘Full kill’ pre-treatments are considered to have created large gaps (1 m2) in the native vegetation while ‘half kill’ pre-treatments created small gaps (10-30 cm).

Follow Up Treatments

Five treatments were applied on 13 July 2007 (week 0):

1. Nitrogen fertiliser at 10 kg N ha^{-1} (2.17 g m^{-2} of Incitec Pivot Granular Urea, 46.0% N by weight);

2. Phosphorus fertiliser at 10 kg P ha^{-1} (4.83 g m^{-2} of Incitec Pivot Triple Super, a granular preparation, 20.7% P by weight: 16.1% water soluble P, 4.0% citrate soluble P, 0.6% citrate insoluble P; 1.0% S as sulfate, 15.0% Ca as superphosphate).

3. Both nitrogen and phosphorus fertiliser – at the same rates as in 1 and 2;

4. Carbon (sucrose) at 0.22 kg C m^{-2} (white cane sugar, 42% C by weight);

5. control - no fertiliser or sugar.

A second treatment at the same rates was applied on 19 September (week 9) in anticipation of a substantial rainfall event, however only 7 mm was recorded during the remainder of the month. A third and final treatment at the same rates was made on 22 November (week 17). Substantial rainfall was recorded on 21 November (17 mm) and 14 mm on 22 November. Fertilisers and sugar were applied by hand broadcasting, and were not deliberately washed into the soil. Total additions of N and P were thus 30 kg ha^{-1}, and the total addition of C was 6600 kg ha^{-1}.

Fertilisation treatments were similar to those used in previous studies. Wijesuriya (1999) applied 0.832 g m^{-2} of both N and P per month for 3 months; that is c. 25 kg ha^{-1} of each nutrient over 3 months. In south-east Australian temperate perennial pastures, superphosphate has generally been applied at the rate of 28 kg P ha^{-1}at the time of sowing, followed by annual applications of 15 to 18.5 kg P ha^{-1} (Moore 1993). Eschen *et al.* (2007) used 0.22 kg $m^{-2}$of C as a mixture of sucrose and sawdust, with 3 applications over 3 months.

Sugar was applied at a high rate and the plots appeared as if dusted by a light fall of snow. Sugar was gradually washed into the soil by precipitation and did not appear to be removed by ants or other macroscopic organisms. At the time of application of the second and third treatments no sugar from the previous treatments was apparent on treated plots. Sugar was expected to have only short term effects (Prober *et al.* 2005) on nutrient uptake by soil microbes and its impact was expected to dissipate rapidly due to decay of microbial biomass and release of plant-captured nutrients back into the soil. Short-term ‘immobilisation’ of nutrients via sugar application was expected to reduce establishment and survival of juvenile plants of *N. neesiana* and of all other vascular plants.

Seed treatment

Nassella neesiana panicle seed was collected on private grazing land at Greenvale, Victoria (north of Somerton Road, c. 1.4 km WNW of the intersection of Mickleham and Somerton Roads), on 24 December 2003 by Charles Grech and stored in paper bags in the laboratory. Petri dish germination tests (February-March 2007) demonstrated 84% seed viability. Seeds were counted in lots of 500 in the laboratory. 'Unfilled' seeds (lacking an embryo) were readily detected by their lighter weight and hollow lemma and were rejected. Seed was applied by broadcasting at a density of 500 seeds m^{-2} on 13 July 2007 to three replicates of each of the disturbance-treatments. No seed was applied in the other set of replicates.

Seed, fertiliser and sugar were applied evenly by hand in still conditions. The 3 pre-treatments, 5 nutrient treatments and 2 seeding treatments gave a total of 30 treatments which were replicated 3 times (= 90 plots). Treatments were assigned randomly to plots (Fig. 4.3).

Rainfall and watering regime

Rainfall over the period of the experiment was recorded at the Iramoo Sustainable Community Centre, approximately 300 m to the north-east of the experimental area (Fig. 4.4). Data is approximate, particularly for the number of rain days, since the rain gauge was monitored only on week days. Because of ongoing dry conditions, deliberate watering was undertaken with watering cans in December 2007 in an attempt to facilitate *N. neesiana* establishment, using water from a lake on nearby Jones Creek. A ten litre aliquot was applied to each plot on 10 December 2007 and a further five litre aliquot on 19 December, equivalent to 10 mm and 5 mm of rainfall respectively. Water applied in December was 15 mm and rainfall 42 mm, giving a total of 57 mm of which 26% was supplemental water. Streamwatch data from the lake over several years had detected no significant N or P levels.

Assessment

The fate of seed applied was examined ten days after seed application. A search was made in the buffer zones around seeded plots and any seeds detected were counted. The 'burial status' of the first 20 seeds observed on each seeded plot was determined. Seeds were considered 'buried' if >50% of the lemma was concealed by soil.

All plots were photographed prior to disturbance treatment and photography was repeated on several occasions during the course of the experiment when other assessments were undertaken.

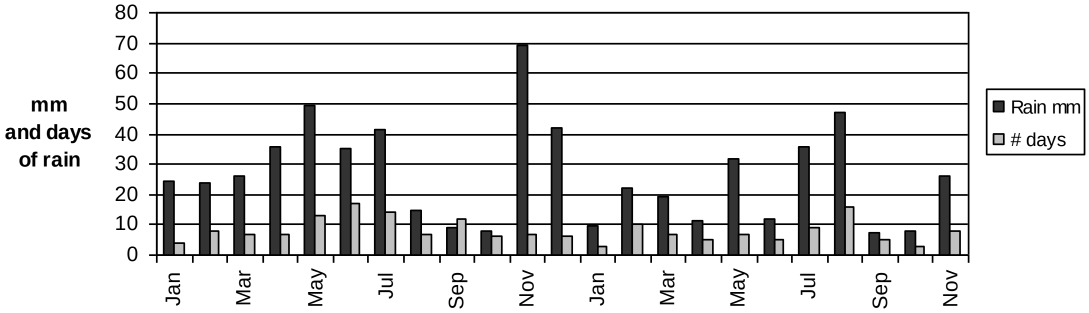

Figure 4.4. Monthly rainfall and number of rain days from January 2007 to November 2008, over the period of the experiment (July 2007 seed application to November 2008 biomass harvest) and the preceding six months. Supplemental watering totaling 15 mm was applied in December 2007.

N. neesiana plant counts

Establishment of *N. neesiana* was assessed by counting the number of plants in each plot at intervals over a period of 69 weeks.

Cover

The canopy cover of *N. neesiana* and major pre-existing species and species groups was assessed at intervals using a 1 m^2 quadrat subdivided by a 10 x 10 cm grid. The most critical cover estimates were undertaken prior to disturbance treatments and at 69 weeks (end of trial). Counts were also taken of *T. triandra* tussocks and other native and exotic tussock grasses. The percentage canopy cover of *N. neesiana*, *T. triandra*, other native grasses, other exotic grasses, native and exotic forbs, cryptogram crust and bare ground was determined on each occasion.

Biomass

At the end of the experiment the standing phytomass of each species in each plot was harvested by clipping all plants at close to ground level (<0.5 cm). Material of each species in each plot was harvested directly into separate paper bags. The biomass harvest was conducted over an 18 day period from 6 to 25 November 2008. *Nassella neesiana* plants were all harvested on 6-7 November before seed fall.

Harvested biomass was initially allowed to dry indoors under ambient conditions before being dried to constant weight in ovens at c. 90°C. Each sample was weighed immediately after removal from the oven to minimise subsequent atmospheric moisture uptake. Soil and other debris were removed before weighing.

N. neesiana plant production characters

Harvested *N. neesiana* plants were individually bagged at the time of harvest, and individually weighed. After drying and weighing the number of 'living' and dead leaves was counted or estimated for each plant. The reproductive characters of each plant were also determined, namely the number of panicles, emerged glume pairs, emerged awns and loose (released after harvest) seeds, in order to examine treatment effects on fecundity and assess the primary juvenile period of the grass. A range of reproductive characters was assessed because panicles may have few or many flowers, glumes are often sterile and seeds may be rapidly shed.

Post experiment

All detectable *N. neesiana* plants still surviving in the experimental area were removed, including their roots, after biomass harvest. The area was inspected 6 and 9 months later and any *N. neesiana* or other noxious weeds detected were killed with herbicide. This was one of the conditions of the permit allowing distribution of *N. neesiana* seeds on the site in the first instance.

Statistical analyses

Data on the number of *N. neesiana* plants that established under various treatments and on the biomass of *N. neesiana* and categories of other plants was analysed using general analysis of variance (ANOVA, F tests). Mean values per plot are reported, equivalent to means per square metre. Analysis was undertaken on the basis of a fully randomised treatment design and the following treatment structure:

Seed* Kill*(Sugar/(Nitrogen*Phosphorus))

The analyses undertaken are listed in Table 4.1.

Transformations were undertaken to achieve the best normalisations of the means. Transformations performed are reported in the results tables.

There were negligible numbers of *N. neesiana* plants in unseeded control plots, and at harvest there was negligible biomass of *N. neesiana* in unseeded plots, 'no kill' plots and 'half kill' plots, so analysis of treatment impacts was in many cases restricted to seeded plots or 'full kill' seeded plots. When there was a significant response to nitrogen or phosphorus, the sugar treated plots were compared to control plots, not with fertilised plots. When there was no significant response to fertilisers, sugar-treated plots were compared with both control (no nutrient treatment) and fertilised plots to improve precision of the analysis.

Data on *N. neesiana* production characters is reported as median values per square metre. Transformations were undertaken to achieve the best normalisation, as reported in the results tables. Analysis of the effects of sugar, nitrogen and phosphorus treatments was undertaken using general ANOVA and the following treatment structure:

Sugar/(Nitrogen*Phosphorus)

Table 4.1. Analysis of variance used for all treatment effects. Many analyses were restricted to seeded plots or 'full kill' seeded plots, and therefore only used part of this analysis of variance (see the Statistical analyses section).

Effect	**Degrees of freedom**
Seed (none v seeded)	1
Kill (none v half v full)	2
Sugar (none v applied)	1
Seed by Kill interaction	2
Kill by Sugar interaction	2
Seed by Sugar interaction	1
Seed by Kill by Sugar interaction	2
Nitrogen within no sugar (none v applied)	1
Phosphorus within no sugar (none vs applied)	1
Nitrogen within no sugar by Phosphorus within no sugar interaction	1
Seed by Nitrogen within no sugar interaction	1
Seed by Phosphorus within no sugar interaction	1
Seed by Nitrogen within no sugar by Phosphorus within no sugar interaction	1
Kill by Nitrogen within no sugar interaction	2
Kill by Phosphorus within no sugar interaction	2
Kill by Nitrogen within no sugar by Phosphorus within no sugar interaction	2
Seed by Kill by Nitrogen within no sugar interaction	2
Seed by Kill by Phosphorus within no sugar interaction	2
Seed by Kill by Nitrogen within no sugar by Phosphorus within no sugar interaction	2
Residual	60

Results

Soil nutrient status

The soil at the site was brown (Munsell) medium clay with nutrient levels and other characteristics as shown in Table 4.2.

Table 4.2. Soil analysis for the experimental site, sampled on 12 July 2007. CEC = cation exchange capacity. Analysis by Incitec Pivot Limited.

	mg/kg		**%**		**Meq/100g**
Available Potassium	390	Potassium (CEC)	7.7	Potassium (Amm-acet.)	1.0
Nitrate Nitrogen	1.1	Calcium (CEC)	29	Calcium (Amm-acet.)	3.8
Ammonium Nitrogen (KCl)	5.1	Magnesium (CEC)	45	Magnesium (Amm-acet.)	5.9
Phosphorus (Colwell)	8.5	Organic Carbon	2.1	Sodium (Amm-acet.)	2.2
Phosphorus (Olsen)	3.84			Aluminium (KCl)	0.10
Sulfate Sulfur (KCL40)	5.8				
Chloride	30			K/Mg ratio	0.17
Copper (DTPA)	1.4			Ca/Mg ratio	0.64
Zinc (DTPA)	1.8			pH (1:5 water)	6.7
Manganese (DTPA)	31			pH(1:5 $CaCl_2$)	5.3
Iron (DTPA)	140			Electrical conductivity (dS/m)	0.12
Boron (Hot $CaCl_2$)	1.8			Cation exchange capacity (Meq/100 g)	13.0

Soil seed bank

No *N. neesiana* seeds were found in the soil cores sampled prior to application of *N. neesiana* seeds. *Themeda triandra* seeds, similar in size and shape to those of *N. neesiana*, comprised 89% of seeds detected, with a mean of 1.38 seeds per core (c. = 1400 seed m^{-2}), of which 92% were deemed non-viable after visual inspection, and a high proportion were substantially decayed. Seeds of *Austrostipa bigeniculata*, *Austrodanthonia* spp., *Vulpia* sp., *Walwhalleya proluta* and unidentified grasses were also detected, but all with a mean abundance of <0.05 seeds per core. Many cores contained corms of *Romulea rosea*.

Seed burial and dispersal

Ten days after seed application (23 July 2007), 49% of the seeds examined had ‘buried’ themselves in the soil (>50% of the lemma concealed by soil). Overall, a high proportion of the seed had attached to the soil or burrowed into tussock bases, often only to a depth that concealed the lower half of the callus. Over 95% of seeds retained their awns. Inspections in the buffer zones revealed that very little seed had moved out of plots: 29 seeds were found off-plot, 0.13% of the seeds applied. No seeds were found beyond 11 cm from a plot edge.

A few awnless seeds were still apparent in plots 39 weeks after seed application (15-16 April 2008) but a high proportion of these appeared to have decayed and to be no longer viable.

Recruitment and growth

No seed germination was detected on 23 July 2007, 10 days after seed application and none by 2 November. Rainfall during this period was well below average (Fig. 4.4). The first juvenile plants were detected on 22 November, c. 18 weeks after seed application, when 16 were counted (Fig. 4.5).

Germination and establishment apparently occurred as a single prolonged event from late spring through to mid-summer, c. 17-27 weeks after seed was applied, but mostly between 18 and 22 weeks after seed application (Fig. 4.5). The first major rainfall event after seed application occurred on 5 November when 28 mm was recorded, preceded by 5.5 mm on 2 November (Fig. 4.4). Mass germination occurred in the subsequent four weeks to 19 December 2007 (Fig. 4.5). Recruitment was clearly associated with substantial rainfall in November and December (Fig. 4.4) assisted by supplementary watering. Peak plant counts occurred at 27 weeks, in mid-late December. A few plots continued to show net increases in the number of plants through to 17-21 January 2008 (week 27), but in most plots the number of plants declined, and thereafter there was continued net decline in most treatments (Fig. 4.5). Ungerminated seed, evidently from its distribution originating from the deliberate seed dispersal treatment, was still evident in most seeded plots during detailed assessment on 17-21 January 2008.

Plant numbers declined over late summer and autumn (weeks 35-39) corresponding with a very dry period. Losses were the result of two major factors: predation by grasshoppers, probably mostly the Yellow-winged Locust, *Gastrimargus musicus* (Fabricius), and soil moisture stress. Drought stress appeared to be more severe close to plot edges where competition for water and nutrients with pre-existing grasses in the buffer zones would have been more severe (Fig. 4.6).

By 26 September 2008 strong lateral shooting had commenced on larger plants, but no panicles had emerged. Elsewhere in the grassland only a single bolting plant was observed. By the time of biomass harvest (69 weeks) many plants had produced panicles, and numerous plants had set seed (Table 4.3), but there were also many small plants that showed no signs of entering the reproductive phase.

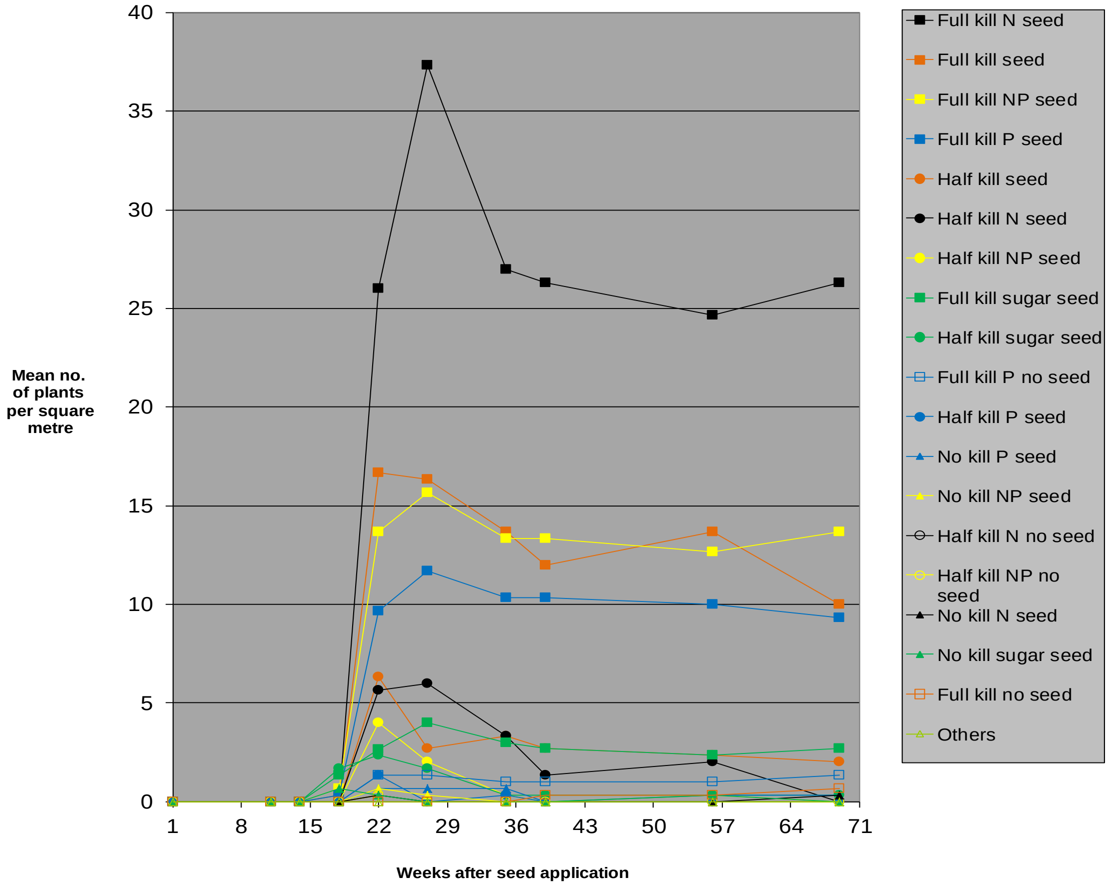

Figure 4.5. Time trend of the mean number of *N. neesiana* plants per plot (plants m^{-2}) for each treatment over the course of the experiment. Seed was applied on 13 July 2007 (= week 0). The first major rainfall occurred at week 16. Plants were harvested at week 69. ‘Full kill’ treatments are indicated by squares, ‘half kill’ treatments by circles and ‘no kill’ treatments by triangles. Seeded treatments are indicated by solid symbols and unseeded treatments by outline symbols. Nitrogen treatments are indicated in black, phosphorus treatments in blue, N + P treatments in yellow and sugar treatments in green. Treatments without nutrient or sugar addition are in orange. “Other” treatments include almost all the no-seed treatments. A number of treatments that resulted in minimal establishment have coincident means and therefore overlap in the chart.

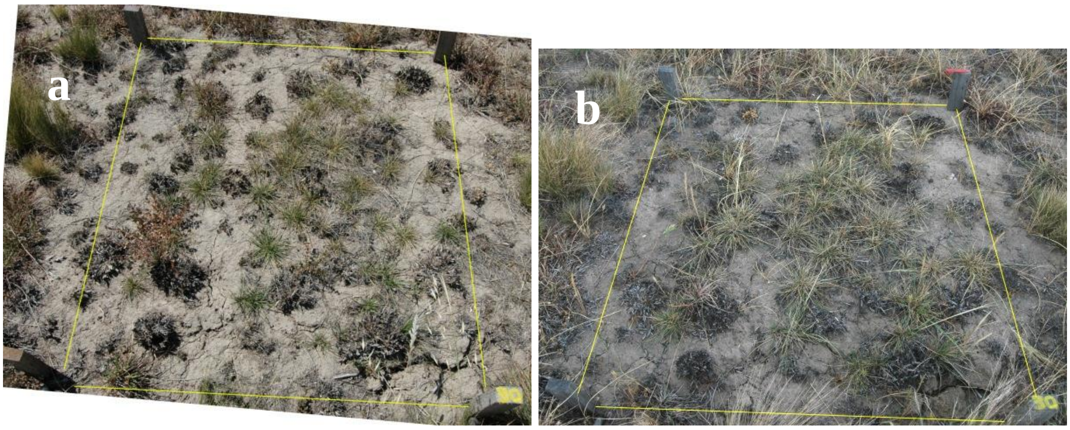

Figure 4.6. Recruitment pattern of *N. neesiana* in a 'full kill' plot with substantial establishment (Plot 30). a. 17 January 2008, 27 weeks after seed application; b. 3 November 2008, 69 weeks after seed application. New *N. neesiana* plants established away from the plot edges, suggesting that below-ground competition, probably mainly for water, had a strong influence on establishment. Establishment around the bases of killed tussocks is also evident.

Table 4.3. Median number of *N. neesiana* panicles m^{-2}, glume pairs m^{-2}, emerged awns m^{-2}, detached seeds m^{-2} and leaves m^{-2} for those plots with *N. neesiana* present.

	Seed	**Kill**		
		Full	Half	None
Median number of panicles m^{-2}	**No**	9.5	-	-
	Yes	16	0	0
Median number of glume pairs m^{-2}	**No**	204	-	-
	Yes	277	0	0
Median number of emerged awns m^{-2}	**No**	136.5	-	-
	Yes	80	0	0
Median number of detached seeds m^{-2}	**No**	84	-	-
	Yes	116.5	0	0
Median number of leaves m^{-2}	**No**	188.5	-	-
	Yes	842.5	63	34

Effectiveness of kill treatments

Visual inspection 15 weeks after herbicide treatment indicated that the 'full kill' and 'half kill' treatments were highly effective (Fig. 4.7). All the grass tussocks and almost all the standing vegetation was killed in 'full kill' plots and approximately half the pre-existing vegetation was killed in 'half kill' plots.

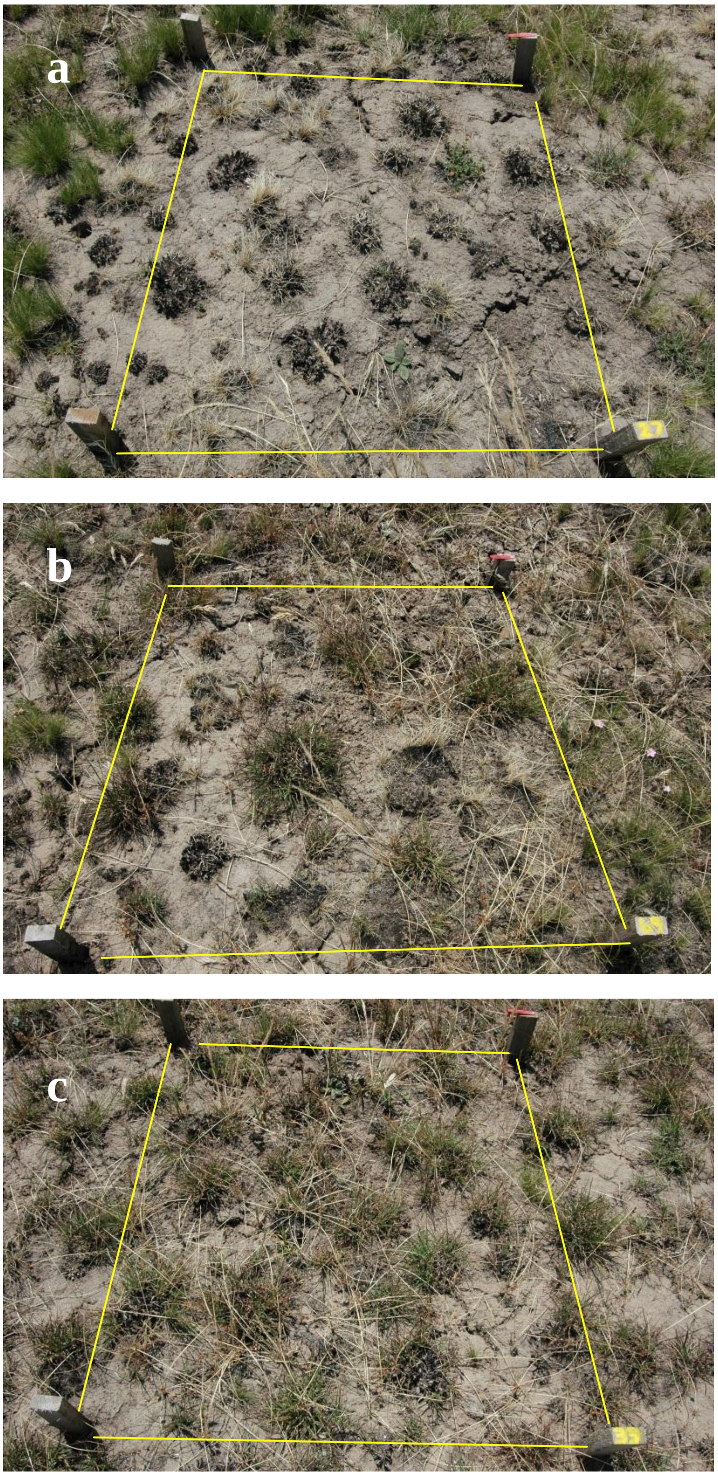

Figure 4.7. Effects of (a) ‘full kill’ (plot 27), (b) ‘half kill’ (plot 33) and (c) ‘no kill’ (plot 69) treatments in the disturbance experiment as at 8 November 2007, 15 weeks after herbicide treatment, indicating the effectiveness of the herbicide kill on the pre-existing vegetation.

The efficacy of the kill treatments was confirmed at the time of biomass harvest, c. 70 weeks after the kill treatments were applied. The kill and ‘half kill’ treatments had significant impacts on above-ground biomass of the dominant grasses (Table 4.4). ‘Full kill’ treatments carried mean dry phytomass of 58.5 g m^{-2}, 'half kill' plots mean phytomass of 133.5 g m^{-2} and 'no kill' plots 171.5 g m^{-2}. The 'full kill' treatments carried an average 34% of the biomass of 'no kill' treatments, while 'half kill' treatments carried on average 78% of the biomass of 'no kill' treatments. 'Half kill' plots had recovered a major portion of their cover, mainly from regrowth from tussocks that were not killed, but they still contained considerably sparser cover and much less biomass than plots that were not defoliated (Table 4.4, Fig. 4.8). A weaker impact on native grass biomass as compared to other exotic perennial grasses (mainly *Nassella trichotoma*) in 'half kill' plots reflects preferential targeting of exotic species with herbicide at the time of treatment (Table 4.4). The kill treatments also significantly boosted annual grass biomass.

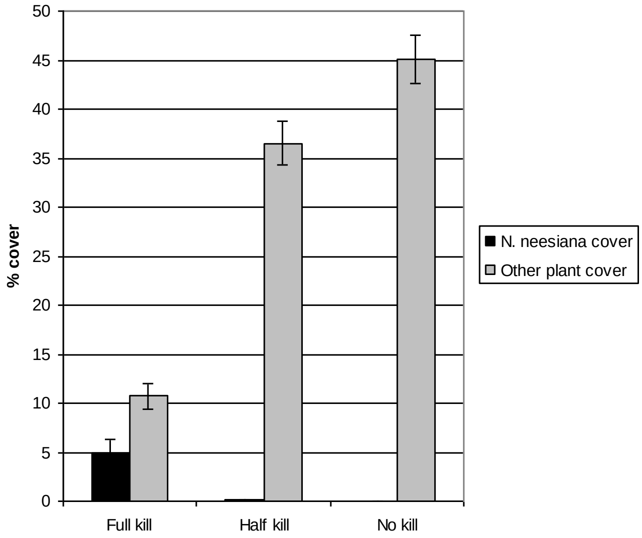

Figure 4.8. Mean projective foliar cover (%) of *N. neesiana* and all other plants combined, by kill treatment in seeded plots at the time of biomass harvest, c. 69 weeks after seed application. Error bars show standard errors.

Of equal significance was the result that 'no kill' plots to which *N. neesiana* seed had been added produced very few *N. neesiana* seedlings, and of those that did establish, even fewer survived beyond the juvenile stage (Fig. 4.5). This was the outcome, regardless of the nutrient treatment. 'No kill' plots to which seed was added had low overall percentage cover of vegetation at both the time of seed addition, and over the experimental period so suppression of *N. neesiana* plant establishment by above-ground competition for light is unlikely to have been a significant factor, especially given the extent to which *N. neesiana* plant establishment did not occur. This is strong evidence that native grasslands with intact vegetation are resistant to invasion by *N. neesiana*, even under high seed rain, and that the basis of this resistance is linked to below-ground competition for resources.

Table 4.4. Effects of kill treatments and *N. neesiana* seed application on biomass of vascular plant species and groups 69 weeks after *N. neesiana* seed application. 'Exotic perennial grasses excluding *N. neesiana*' = *Nassella trichotoma* + *Nassella hyalina*. Significant P values in bold. Back transformed values g m^{-2}. P values for *N. neesiana* were calculated using permutation tests of the analysis of variance.

Kill treatment	***Nassella neesiana* seed**	***Nassella neesiana***	**Exotic perennial grasses excluding *N. neesiana***	**Native grasses**				**Exotic annual grasses**	**Native forbs**	**Exotic forbs**	**Total excl. *N. neesiana***	**Total**
				Total	***Themeda triandra***	***Austrostipa bigeniculata***	***Austrodanthonia* spp.**					
Transformation		$\log_{10}(y+10)$	$\log_{10}(y+0.5)$	$\log_{10}(y+10)$	$\log_{10}(y+10)$	$\log_{10}(y+1)$	$\log_{10}(y+0.1)$	$\log_{10}(y+1)$	$-1/(y+0.1)$	$\log_{10}(y)$	$\sqrt{(y)}$	$\sqrt{(y)}$
sed		0.057	0.171	0.048	0.060	0.159	0.247	0.119	1.319	0.108	0.562	0.608
P values												
Kill main effect		**<0.001**	**7.1×10^{-19}**	**7.7×10^{-30}**	**1.7×10^{-21}**	**7.9×10^{-11}**	0.13	**0.0087**	0.169	0.089	**6.4×10^{-24}**	**2.8×10^{-18}**
Seed main effect		**<0.001**	0.62	0.072	0.67	0.11	0.24	0.716	0.235	0.227	0.085	0.74
Kill by seed interaction		**<0.001**	0.57	**0.013**	0.18	**0.039**	**0.045**	0.476	0.498	0.495	0.551	0.25
Back transformed means (g m^{-2})												
Full kill	No	1	0	16	10	1.8	0.7	6.8	0.1	14.1	50	51
	Yes	23	1	8	6	0.5	0.3	7.7	0.0	12.6	36	66
Half kill	No	0	12	81	50	15.0	0.6	5.8	0.1	19.5	137	137
	Yes	1	9	77	58	5.7	1.1	4.5	0.1	19.5	129	130
No kill	No	0	42	88	59	12.2	0.6	2.9	0.1	20.9	175	175
	Yes	0	30	95	61	19.0	2.5	4.0	0.1	14.1	168	168

Two other grasses on site related to *N. neesiana*, the exotic perennials *Nassella trichotoma* and *N. hyalina* (= 'exotic perennial grasses excluding *N. neesiana*') did not regrow in any 'full kill' plots and their biomass remained strongly depressed at the time of biomass harvest (Table 4.4). Biomass of other plant categories in 'full kill' plots recovered to a greater extent. Exotic annual grasses returned with greater biomass than in untreated areas (Table 4.4).

Impact of disturbance treatments on *N. neesiana* recruitment and biomass

Strong establishment of *N. neesiana* had occurred by 19 December 2007, 22 weeks after seed application. The effect of kill treatments on recruitment at this time was highly significant, with nearly four times as many juvenile plants established on 'full kill' plots (large gaps) as on 'half kill' plots (small gaps), and ten times as many on 'half kill' plots as on 'no kill' plots ('no' gaps) (Table 4.5). After 27 weeks, a very similar pattern was apparent (Fig. 4.9). Sugar had a strongly suppressive effect on establishment, reducing it by 87% in 'full kill' plots, and by 53% in 'half kill' plots after 22 weeks (Table 4.5). These patterns in the number of plants recruited remained very similar after 69 weeks, when the experiment was terminated.

Although a small number of plants did establish on unseeded plots and 'half kill' seeded plots, the only plots with major *N. neesiana* presence were 'full kill' seeded plots (Table 4.6).

Table 4.5. Effects of kill and sugar treatments on the mean number of *N. neesiana* plants on 19 December 2007, 22 weeks after seed application. Transformed $\log_{10}(y+1)$ where y = mean number of *N. neesiana* plants m^{-2}.

	Back transformed		
Sugar	**Full kill**	**Half kill**	**No kill**
No	11.6	3.0	0.3
Yes	1.5	1.4	0.3

SED within column 0.222 SED within first row 0.141
SED within second row 0.281
P value kill main effect $\mathbf{8.2\times10^{-7}}$ (highly significant)
P value sugar main effect **0.022**
P value sugar x kill interaction 0.096

Effects of kill and sugar treatments on biomass at time of harvest were also significant (Table 4.7). 'No kill' plots to which seed had been added had zero *N. neesiana* biomass and 'half kill' plots had minor amounts. 'Full kill' plots had approximately 75 times as much *N. neesiana* biomass as 'half kill' plots. Sugar treatment resulted in an approximately 10 fold decrease in biomass in 'full kill' plots and a roughly 3 fold decrease in 'half kill' plots.

Table 4.6. Proportion of plots (out of 15) in which *N. neesiana* was present, 69 weeks after seed application, by seed and kill treatments. There were 90 plots in the experiment, of which 45 were seeded and 45 not seeded. ‘Full kill’, ‘half kill’ and ‘no kill’ treatments were each applied to one third (15) of the plots in each seed treatment. Exact 95% binomial confidence intervals in parentheses. This analysis is a test of the hypothesis that the proportion in comparable replicates = 0.5. The only plots with major *N. neesiana* presence were ‘full kill’ seeded plots.

Seed	**Full kill**	**Half kill**	**No kill**
No	0.13 (0.02, 0.40)	0 (0, 0.22)	0 (0, 0.22)
Yes	0.8 (0.52, 0.96)	0.2 (0.04, 0.48)	0.13 (0.02, 0.40)

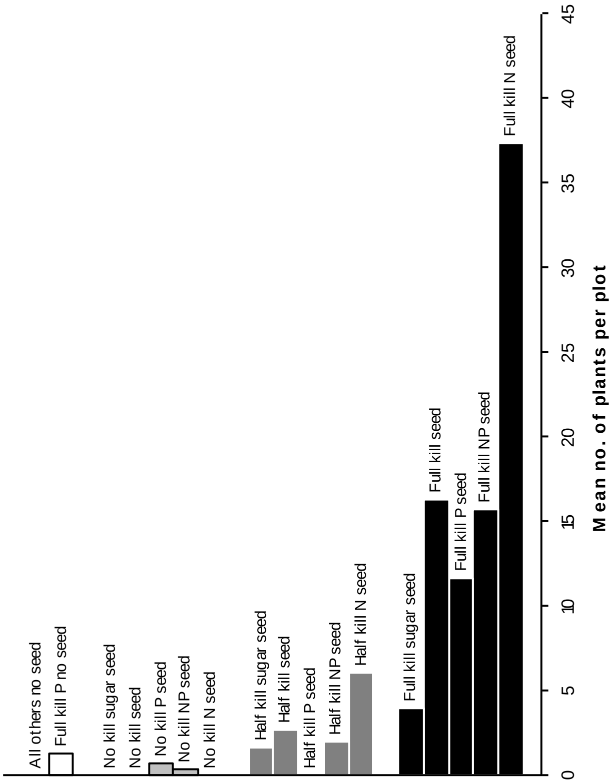

Figure 4.9. Mean number of juvenile *N. neesiana* per plot (= plants m^{-2}) by treatment, 27 weeks after seed application. Treatments consisted of combinations of full, half or no kill of existing vegetation; nitrogen fertilisation (N), phosphorus fertilisation (P), both nitrogen and phosphorus (NP), no fertiliser, or sugar; and seed or no seed.

After 69 weeks the biomass of *N. neesiana* on the plot with the highest establishment (Plot 11, ‘full kill’, N+P, seed) was 127 g, 62% of the mean total plant biomass in untreated plots, and the total biomass for that plot was 169 g, 82% of the mean total biomass in untreated plots. The mean biomass of *N. neesiana* on ‘full kill’ seeded plots was 32 g m^{-2} (Table 4.8).

Nutrient treatments had no significant impact on the mean biomass of *N. neesiana* plants that established (Table 4.9). Too few plants established in ‘half kill’ and ‘no kill’ plots to evaluate the effect of kill treatments on biomass per plant, except to note that addition of nutrients did not relieve suppression of *N. neesiana* plant establishment on ‘no kill’ plots. The nutrient treatments also had no significant effect on the biomass of *N. neesiana* within ‘full kill’ seeded plots at the time of harvest (Table 4.10). Nutrient addition (N and P) treatments also had no detectable impact on the numbers of *N. neesiana* that established (Table 4.11) or on the biomass per unit area (Table 4.12).

Table 4.7. Effect of kill and sugar treatment on *N. neesiana* mean above-ground biomass m^{-2} within seeded plots, 69 weeks after seed application. Transformed $\log_{10}(y+1)$, where y = *N. neesiana* biomass. Back transformed means (g m^{-2}).

	Sugar	Full kill	Half kill	No kill
Transformed	**No**	1.37	0.12	0.02
	Yes	0.5	0.06	0.00
Back transformed	**No**	22.7	0.3	0.0
	Yes	2.2	0.1	0.0

seds	Full Kill No Sugar	Full kill Sugar	Half Kill No Sugar	Half Kill Sugar	No Kill No Sugar	No Kill Sugar
Full Kill No Sugar	-					
Full kill Sugar	0.411	-				
Half Kill No Sugar	0.202	0.377	-			
Half Kill Sugar	0.247	0.404	0.185	-		
No Kill No Sugar	0.185	0.368	0.084	0.166	-	
No Kill Sugar	0.186	0.369	0.087	0.167	0.031	-

P value kill main effect **8.5×10^{-9}** (highly significant)

P value sugar main effect **0.050**

P value sugar x kill interaction 0.058

Table 4.8. Median *N. neesiana* biomass (g m^{-2}), for those plots with *N. neesiana* present, 69 weeks after seed application.

Seed	Full kill	Half kill	No kill
No	12	-	-
Yes	32	5	0

Table 4.9. Effects of nutrient treatments on the mean biomass per *N. neesiana* plant, 69 weeks after seed application. Transformed $\log_{10}(y)$, where y = biomass. Back transformed means (g).

	Back transformed			
	No	**Yes**	**sed**	**P value**
Sugar	2.7	3.9	0.206	0.49
Nitrogen	2.7	2.7	0.225	0.97
Phosphorus	2.3	3.3	0.225	0.39

Table 4.10. Effects of sugar, and nitrogen and phosphorus fertilisation on *N. neesiana* biomass 69 weeks after seed application, within 'full kill' and seeded plots. Transformed $\log_{10}(y+10)$. Total back transformed mean (g m^{-2}). *N. neesiana* biomass showed no significant response to sugar, N or P treatments.

	Back transformed			
	No	**Yes**	**sed**	**P value**
Sugar	29	6	0.230	0.13
Nitrogen	21	48	0.206	0.35
Phosphorus	36	41	0.206	0.82

Table 4.11. Effects of nitrogen and phosphorus treatments on the mean number of *N. neesiana* plants m^{-2} on 19 December 2007, 22 weeks after seed application. Transformed $\log_{10}(y+1)$ where y = mean number of *N. neesiana* plants m^{-2}.

	Back transformed			
	No	**Yes**	**SED**	**P value**
Nitrogen	2.6	3.5	0.115	0.42
Phosphorus	3.5	2.6	0.115	0.38

Table 4.12. Effects of nitrogen and phosphorus fertilisation on mean biomass m^{-2} of *N. neesiana* within 'full kill' plots 69 weeks after seed application. Transformed $\log_{10}(y+1)$. Total back transformed mean (g m^{-2}). There was no interaction between N and P.

	Back transformed			
	No	**Yes**	**sed**	**P value**
Nitrogen	2.0	2.4	0.171	0.72
Phosphorus	2.5	1.9	0.171	0.55

Treatment effects on *N. neesiana* characteristics at harvest

At the time of biomass harvest almost all *N. neesiana* plants were <1 year old. The mean number of leaves per plant was 80 and the range 9-394. Ninety five of 204 plants (47%) had produced panicles within this first year of growth, of which 4 had only unemerged panicles (covered by the leaf sheath). The average number of panicles on reproductive plants was 3, the maximum was 16, and the maximum number of glume pairs on a single plant was 337. Nearly half the plants at the time of biomass harvest had produced panicles, mostly with set seed, none were older than 53 weeks and a high proportion were <1 year old. The primary juvenile period can evidently be less than 1 year.

Few *N. neesiana* plants established on seeded 'no kill' and 'half kill' plots and the median number of leaves m^{-2} on those 'no kill' plots where they did establish was only 34 and for 'half kill' plots 63, while on 'full kill' seeded plots it was 843 (Table 4.3). Even in plots where there was good establishment, little cover had developed by the time of harvest (Fig. 4.10, *N. neesiana* with total across all plants of c. 800 leaves m^{-2}). Mean *N. neesiana* cover on 'full kill' seeded plots was approximately 5% at the time of biomass harvest, less than half that of other species combined (Fig. 4.8). The maximum *N. neesiana* cover in a single plot was 17%.

Reproductive outputs per square metre were relatively small compared with long established swards, but the populations of young plants produced in excess of 200 seeds m^{-2} from around 10 or more panicles m^{-2} (Table 4.3). 'No kill' plots had zero reproductive output, and in 'half kill' plots the recorded reproductive attributes were close to zero, with only five plants producing a total of six panicles. Similarly only 5 plants reached the reproductive stage on unseeded plots, producing a total of 19 panicles.

No significant differences (P = 0.05) were found in the effects of treatment with sugar or fertilisation with N or P on the mean number of *N. neesiana* panicles m^{-2}, glume pairs m^{-2}, emerged awns m^{-2}, detached seeds m^{-2} and leaves m^{-2} within 'full kill' and seeded plots (Tables 4.13-4.15). However a significant negative effect of sugar (P = 0.075) on the number of leaves at the 10% level was apparent and all the reproductive outputs were lower where sugar treatment had been applied (Table 4.15). Similarly all the plant production attributes were higher where urea had been applied than where it had not, suggesting that a larger experiment with more replicates would have detected significant positive effect of N fertilisation on *N. neesiana* (Table 4.13, back transformed values). Superphosphate treatment produced no similar consistent trend (Table 4.14).

Figure 4.10. One of the largest plants, fruiting for the first time, just prior to biomass harvest, 69 weeks after seed application (plot 11). This plant germinated sometime between 22 November and 19 December 2007 so was between 47 and 50 weeks old.

Table 4.13. Effect of nitrogen on the median number of *N. neesiana* panicles m^{-2}, glume pairs m^{-2}, emerged awns m^{-2}, detached seeds m^{-2} and leaves m^{-2} for those plots with *N. neesiana* present within 'full kill' and seeded plots.

	Nitrogen	**SED**	**P value**	**Back transformed**
Median number of panicles m^{-2} (transformed log (y+1))	**No**	0.350	0.48	9
	Yes			16
Median number of glume pairs m^{-2} (transformed log (y+10))	**No**	0.402	0.64	125
	Yes			204
Median number of emerged awns m^{-2} (transformed log (y+10))	**No**	0.348	0.59	58
	Yes			95
Median number of detached seeds m^{-2} (transformed log (y+10))	**No**	0.332	0.90	69
	Yes			77
Median number of leaves m^{-2} (transformed log (y+100))	**No**	0.274	0.43	550
	Yes			970

Table 4.14. Effect of phosphorus on the median number of *N. neesiana* panicles m^{-2}, glume pairs m^{-2}, emerged awns m^{-2}, detached seeds m^{-2} and leaves m^{-2} for those plots with *N. neesiana* present within 'full kill' and seeded plots.

	Phosphorus	**SED**	**P value**	**Back transformed**
Median number of panicles m^{-2} (transformed log (y+1))	**No**	0.350	0.62	9
	Yes			15
Median number of glume pairs m^{-2} (transformed log (y+10))	**No**	0.402	0.71	131
	Yes			190
Median number of emerged awns m^{-2} (transformed log (y+10))	**No**	0.348	0.73	88
	Yes			62
Median number of detached seeds m^{-2} (transformed log (y+10))	**No**	0.332	0.34	46
	Yes			110
Median number of leaves m^{-2} (transformed log (y+100))	**No**	0.274	0.79	810
	Yes			660

Table 4.15. Effect of sugar on the median number of *N. neesiana* panicles m^{-2}, glume pairs m^{-2}, emerged awns m^{-2}, detached seeds m^{-2} and leaves m^{-2} for those plots with *N. neesiana* present within 'full kill' and seeded plots.

	Sugar	**SED**	**P value**	**Back transformed**
Median number of panicles m^{-2} (transformed log (y+1))	**No**	0.392	0.11	12
	Yes			2
Median number of glume pairs m^{-2} (transformed log (y+10))	**No**	0.450	0.16	160
	Yes			25
Median number of emerged awns m^{-2} (transformed log (y+10))	**No**	0.389	0.24	73
	Yes			18
Median number of detached seeds m^{-2} (transformed log (y+10))	**No**	0.371	0.25	73
	Yes			20
Median number of leaves m^{-2} (transformed log (y+100))	**No**	0.307	0.075	730
	Yes			100

Impact of *N. neesiana* on other plants

While virtually all of the native *T. triandra* was killed on 'full kill' plots, there was minor regrowth and subsequent growth of a number of other plant species including the native grasses *Austrostipa bigeniculata* and *Austrodanthonia* spp. At the conclusion of the experiment, after the growth of *N. neesiana* plants and regrowth of other species, it was possible to test whether the *N. neesiana* that grew had impacted on the biomass of these other species. Substantial impact on other plant categories resulting from seeding with *N. neesiana* occurred only with native grass biomass in 'full kill' plots, the mean native grass biomass being reduced by half, but the overall impact across treatments was only significant at the 10% level (P = 0.072, Table 4.4). Suppression of native grasses by *N. neesiana* in the 'full kill' seeded plots contributed to a near-significant (P = 0.085) negative impact of seed treatment on total biomass excluding *N. neesiana*.

A significant kill x seed interaction in the statistical analysis (Table 4.4) indicates that where *N. neesiana* was present, it strongly displaced and out-competed native grasses. The effect was not apparent in 'half kill' plots, where the number of *N. neesiana* plants was very limited. *Austrostipa bigeniculata* and *Austrodanthonia* spp. were significantly affected. Regrowth of *T. triandra* was probably affected to a similar extent, there being a marked suppression of biomass recovery in seeded plots, but the kill x seed interaction was not significant under these experimental conditions. There was no significant kill x seed interaction effect with any other category of plants. Other exotic perennial grasses (mainly *Nassella trichotoma*) were not affected, nor were exotic annual grasses.

It is clear that *N. neesiana* needs an ecological opening of sufficient size to establish, so only prospered in the 'full kill' plots. There is some evidence from these trials that native grasses come back if the space is not occupied by *N. neesiana*. However native species had established poorly on kill plots at the time of biomass harvest, indicating that even the dominant native grasses had either negligible soil seed banks, or conditions for recruitment were unsuitable, or both.

In summary, once established, *N. neesiana* had a suppressive effect on the growth of native grasses, exotic annual grasses, and the other *Nassella* species present. It had a small suppressive effect on native grasses and was able to hold its place in competition with other species.

Effect of sugar treatments on other plants

Although the experiment was not designed to investigate the effects of sugar treatment on plant species other than *N. neesiana*, analysis revealed some significant effects on their biomass (Table 4.16). At the time of biomass harvest (c. 69 weeks after the first and 52 weeks after the last sugar treatments), the average above-ground biomass of *N. neesiana* within sugar-treated, seeded and 'full kill' plots was greatly reduced (-79%) but the effect was not significant (Table 4.16). Sugar addition reduced *N. neesiana* establishment, but after the dissipation of the sugar effect there was compensatory growth of the plants which did establish. Sugar addition significantly reduced above-ground biomass of all plant species combined (-32%), all species excluding *N. neesiana* (-29%), exotic forbs (-53%), exotic annual grasses (-56%), exotic perennial grasses excluding *N. neesiana* (-50%), and native perennial grasses (-18%) with all the main native grass species present contributing to the effect. Native forbs were the only plant group for which no response was measured, but these were present with very low biomass throughout the trial.

Effect of fertiliser treatments on other plants

The experiment was also not designed to investigate impacts of fertilisation on the biomass of species other than *N. neesiana*, but again analysis revealed some significant effects (Tables 4.17, 4.18). Nitrogen was applied by surface broadcasting of pelletised urea. Pellets slowly reduced in size over the experimental period, and some small pellet remnants were still apparent on the soil surface at the time of biomass harvest. In contrast to sugar, the effects of nitrogen addition thus extended over the whole experimental period. Addition of urea more than doubled the resulting average above-ground biomass of *N. neesiana* within seeded and 'full kill' plots, but the effect was not significant (Table 4.17). Nitrogen fertilisation had no effect on above-ground biomass of all species combined, but significantly reduced biomass of *Themeda triandra* (33% reduction) and significantly increased biomass of exotic annual grasses (48% increase) and *Austrodanthonia* spp. (171%).

Superphosphate was applied as pellets, which broke down more rapidly than those of urea but took many months to disappear. The impact of phosphorus addition thus probably extended over the whole of the experiment. Addition of superphosphate had no significant effect on the resulting above-ground biomass of *N. neesiana*. However average above-ground biomass of all plant species combined was increased by approximately one third, mainly due to a highly significant increase in biomass of exotic annual grasses (379%) (Table 4.18). Phosphorus fertilisation also significantly increased the biomass of *Austrodanthonia* spp. (158%). Biomass of exotic perennial grasses excluding *N. neesiana* was increased by c. 50% but the effect was not significant. Except for native forbs and *Themeda triandra*, application of P increased the biomass of the other plant groups by 12-16%.

Off-plot seed movement

At the time of biomass harvest a total of 204 *N. neesiana* individuals were found within plots, and 2 plants within the buffer zones outside plots. A total of six plants established in two of the 45 unseeded plots, indicating that a small amount of seed movement occurred after broadcasting. Plots in the experiment had either 3, 5 or 8 neighbour plots depending on whether they were located at corners, sides or centrally within the experimental area (Fig. 4.3). The random arrangement of the treatments resulted in unseeded plots having a range of 0-87.5% of their neighbour plots that were seeded. The average proportion of neighbour plots that were seeded was 51.2% for the 43 unseeded plots in which *N. neesiana* did not establish. The two unseeded plots in which establishment did occur had respectively 80% and 50% of their neighbour plots seeded; thus one was more likely to be contaminated with seed from neighbours than the unseeded plots in which no establishment occurred, and one had approximately the average likelihood of contamination. .

Table 4.16. Effect of sugar treatments on above-ground biomass of vascular plant species and groups 69 weeks after *N. neesiana* seed application. When there was a significant response to nitrogen or phosphorus (see Tables 4.17 and 4.18) the sugar treated plots were compared to control plots, not with fertilised plots. When there was no significant response to fertilisers, sugar-treated plots were compared with both control (no nutrient treatment) and fertilised plots (N, P and N+P) to improve precision of the analysis. Thus the data for '*Austrodanthonia* spp.' and 'exotic annual grasses' are only for 0 nitrogen and 0 phosphorus treatments; for '*Themeda triandra*' only for the 0 nitrogen treatments, and for 'total biomass excluding *N. neesiana*' and 'total biomass' only for 0 phosphorus. Data for *N. neesiana* was analysed only for 'full kill' seeded plots. 'Exotic perennial grasses excluding *N. neesiana*' = *Nassella trichotoma* + *Nassella hyalina*. Significant P values in bold. Back transformed means g m^{-2}.

Treatment	***Nassella neesiana***	**Exotic perennial grasses excluding *N. neesiana***	**Native grasses**				**Exotic annual grasses**	**Native forbs**	**Exotic forbs**	**Total excluding *N. neesiana***	**Total**
			Total	***Themeda triandra***	***Austrostipa bigeniculata***	***Austrodanthonia* spp.**					
Transformation	$\log_{10}(y+10)$	$\log_{10}(y+0.5)$	$\log_{10}(y+10)$	$\log_{10}(y+10)$	$\log_{10}(y+1)$	$\log_{10}(y+0.1)$	$\log_{10}(y+1)$	$-1/(y+0.1)$	$\log_{10}(y)$	$\surd(y)$	$\surd(y)$
sed	0.230	0.136	0.034	0.048	0.115	0.225	0.109	0.95	0.078	0.45	0.48
P value	0.13	**0.045**	**0.043**	0.35	0.088	0.12	**0.045**	0.11	**0.00018**	**0.00075**	**0.00036**
Back transformed means (g m^{-2})											
No sugar	29	6.1	50	40	6.8	0.4	2.7	0.1	19	102	110
Sugar	6	4.0	41	35	3.9	0.1	1.2	0.1	9	72	76

Table 4.17. Effect of nitrogen fertilisation on above-ground biomass of vascular plant species and groups 69 weeks after *N. neesiana* seed application. Data for *N. neesiana* was analysed only for 'full kill' seeded plots. Significant figures in bold. 'Exotic perennial grasses excluding *N. neesiana*' = *Nassella trichotoma* + *Nassella hyalina*. Significant P values in bold. Back transformed values g m^{-2}.

Treatment	***Nassella neesiana***	**Exotic perennial grasses excluding *N. neesiana***	**Native grasses**				**Exotic annual grasses**	**Native forbs**	**Exotic forbs**	**Total excluding *N. neesiana***	**Total**
			Total	***Themeda triandra***	***Austrostipa bigeniculata***	***Austrodanthonia* spp.**					
Transformation	$\log_{10}(y+10)$	$\log_{10}(y+0.5)$	$\log_{10}(y+10)$	$\log_{10}(y+10)$	$\log_{10}(y+1)$	$\log_{10}(y+0.1)$	$\log_{10}(y+1)$	$-1/(y+0.1)$	$\log_{10}(y)$	$\sqrt{}(y)$	$\sqrt{}(y)$
sed	0.206	0.111	0.031	0.039	0.103	0.159	0.077	0.85	0.070	0.35	0.39
P value	0.35	0.41	0.29	**0.0021**	0.12	**0.011**	**0.036**	0.57	0.42	0.60	0.43
Back transformed means (g m^{-2})											
No nitrogen	21	6.7	52	40	5.3	0.7	5.4	0.1	18	117	123
Nitrogen	48	8.4	48	27	8.3	1.9	8.3	0.1	20	121	130

Table 4.18. Effect of phosphorus fertilisation on above-ground biomass of vascular plant species and groups 69 weeks after *N. neesiana* seed application**.** Data for *N. neesiana* was analysed only for ‘full kill’ seeded plots. Significant figures in bold. ‘Exotic perennial grasses excluding *N. neesiana*’ = *Nassella trichotoma* + *Nassella hyalina*. Significant P values in bold. Back transformed values g m^{-2}.

Treatment	***Nassella neesiana***	**Exotic perennial grasses excluding *N. neesiana***	**Native grasses**				**Exotic annual grasses**	**Native forbs**	**Exotic forbs**	**Total excluding *N. neesiana***	**Total**
			Total	***Themeda triandra***	***Austrostipa bigeniculata***	***Austrodanthonia* spp.**					
Transformation	$\log_{10}(y+10)$	$\log_{10}(y+0.5)$	$\log_{10}(y+10)$	$\log_{10}(y+10)$	$\log_{10}(y+1)$	$\log_{10}(y+0.1)$	$\log_{10}(y+1)$	$-1/(y+0.1)$	$\log_{10}(y)$	$\sqrt{(y)}$	$\sqrt{(y)}$
No phosphorus	1.56	0.82	1.75	1.64	0.83	-0.10	0.62	-5.2	1.24	10.1	10.5
Phosphorus	1.61	1.00	1.80	1.63	0.94	0.28	1.16	-4.2	1.32	11.6	12.1
sed	0.206	0.111	0.031	0.039	0.103	0.159	0.077	0.85	0.070	0.36	0.39
P value	0.82	0.10	0.13	0.66	0.28	**0.022**	**2.4×10^{-9}**	0.25	0.23	**0.00010**	**0.00015**
Back transformed means (g m^{-2})											
No phosphorus	36	6.1	46	34	5.8	0.7	3.2	0.1	17	102	110
Phosphorus	41	9.5	53	33	7.7	1.8	13.5	0.1	21	135	146

The proportion of unseeded plots in which *N. neesiana* established was zero in ‘half kill’ and ‘no kill’ treatments and 0.13 for ‘full kill’ plots (Table 4.6). Major *N. neesiana* presence occurred only in ‘full kill’ seeded plots, so any off-plot seed movement had no effect on the experimental findings.

Discussion

The hypotheses that invasion by *N. neesiana* requires disturbance and that intact native grassland is resistant to invasion were tested and substantially confirmed by application of panicle seed to native grassland plots that were either left intact, partially killed, or fully killed, and to which fertiliser treatments or ‘inverse fertilisation’ using sugar were applied . Significant *N. neesiana* establishment, as measured by the number of plants that recruited and their biomass, occurred only where the native vegetation was killed, and much greater establishment occurred in ‘full kill’ plots, where the ecological ‘gaps’ created were large. Intact native grassland was found to be resistant to invasion. Fertiliser additions had no significant effect on recruitment or resulting biomass, but sugar application significantly reduced establishment in ‘full kill’ plots, and probably ‘half kill plots’ (although differences in the latter were not significant under the experimental conditions used) indicating that minimisation of the levels of plant-available soil nutrients at the time of *N. neesiana* germination and recruitment will reduce establishment, and that disturbances that result in increased soil nutrient availability are likely to assist *N. neesiana* invasion. The analysis compared sugar effects against pooled fertilised plots and control plots. Positive fertiliser effects on *N. neesiana* may nevertheless have occurred, being non-significant due to the low number of replicates in the experiment, so the approach has potential to exaggerate the real effects of sugar treatments.

Germination and establishment

Unnatural starting conditions are a general problem in experiments with plant communities (Körner *et al.* 2008). The timing of seed application created similar conditions to those that would normally occur, but may have enabled a higher proportion of the seed to remain on site (rather than decay or be removed by predators) until conditions became suitable for germination. *Nassella neesiana* panicle seed germinates mostly in spring (Snell *et al.* 2007). Panicle seed is generally shed in December and January, and according to Gardener *et al.* (2003b) has an after-ripening requirement of 3-12 months, so the earliest germination from the most recent seed crop could occur in autumn, but is more likely in spring. The seed used here was fully after-ripened, being over 3 years old, and was applied in mid-winter and germinated in spring. The rainfall and supplementary watering during the experiment provided conditions suitable for plant recruitment. Natural recruitment events in perennial grasslands are generally rare to infrequent, and require a particular set of microenvironmental conditions, the most important of which is adequate rainfall at a suitable time (Lauenroth and Aguilera 1998). Rainfall that soaks the soil and keeps it moist for several days is required for germination of many grasses (Baskin and Baskin 1998). Most seedlings in this experiment appeared in the first wet month after seed was applied, and the recruitment that occurred appeared to result almost entirely from this one event. Once established, young grass plants are able to resist desiccation for relatively long periods (Lauenroth and Aguilera 1998), and this occurred with *N. neesiana* juvenile plants over a dry summer, in which drought stress caused relatively minor attrition of the population.

The extent to which the experiment approximated the range of real disturbances that occur in temperate native grasslands is debatable. Previous work at the Iramoo site (Mason 2005) demonstrated that *N. neesiana* established from the soil seed bank at mean densities of 7.4 (± 2.1) m^{-2}, ten months after herbicidal spraying of mixed, dense *N. neesiana*/*N. trichotoma* infestations (total mean tussock density of c. 18 plants (±4) m^{-2}), followed by tilling to 5 cm depth and application of *T. triandra* thatch, whereas seedling density in unsprayed plots where the existing *Nassella* cover was left intact was only 0.75 plants (±0.31) m^{-2}. The similarities between the Mason (2005) data set and the experimental results reported here are plain: recruitment occurs in disturbed ground, but in low numbers, and there is no or negligible recruitment where existing dominant tussock plant cover is not killed.

Peart (1979) tested a range of awned grass diaspores and generally found the highest germination rates when seeds were buried horizontally at a depth of 5 mm. However the native grass seed most similar to *N. neesiana,* that of *Austrostipa verticillata* (Nees ex Spreng.) S.W.L. Jacobs & J. Everett germinated at a high rate (c. 45%) when the seed was lodged vertically (callus down) and half buried, and at much lower rates when lying flat on the soil surface or with just the callus buried. This corresponds with the observations of *N. neesiana* germinations reported here. ‘Safe sites’ for germination (Baskin and Baskin 1998) appeared to include areas where increased levels of soil water may have been expected, e.g. soil hollows and cracks, but these were also areas where penetration of the callus into the soil was more likely.

Large numbers of seedlings may have emerged and died between monitoring events, and may have been unrecorded. Most plant mortality occurs before seedling emergence, and in general it is not known what proportion occurs before germination, nor is the proportion of seeds that germinate, but fail to emerge or survive, easy to determine (Fenner 1987).

The rate of seed application in the experiment was limited by the availability of *N. neesiana* seed and the practicality of counting out large seed lots. Five hundred seeds m^{-2} may be considered to be towards the lower end of what might be expected under natural conditions.

This seeding density was approximately one third of the estimated maximum panicle seed production m^{-2} found by Gardener (1998) in an agricultural grassland on the New England Tablelands in the least productive of the three years he investigated, and a potential annual seed yield of c. 30,000 m^{-2} has been estimated (Slay 2001). However seed bank studies in southern Victoria native grasslands (Hocking 2005b) indicate that 500 seeds m^{-2} is a more realistic representation of actual seed banks than 1000 seeds m^{-2}. In addition, it is likely that a significant proportion of panicle seeds in the seedbank are not germinable.

Only *N. neesiana* seed was deliberately added, so other grasses present either had to have an existing seed bank, or to set and disperse seed to the defoliated plots within the timeframe of the experiment – most likely in mid to late spring. The results obtained (dominance of *N. neesiana* in some seeded plots) can thus be interpreted as a priority effect, resulting from earlier arrival of *N. neesiana*. Differences in arrival time of propagules of as little as 3 weeks can have profound effects on the composition of the subsequent vegetation, with first arriving species dominating the resulting biomass, and first arriving species of one functional group (e.g. grasses) greatly suppressing the growth of later arriving functional groups (Körner, *et al.* 2008). Pre-existing soil seed banks appeared to be low, so significant recolonisation of the bared areas by natives required a new season of seed production, 6 months into the experiment and after the main *N. neesiana* recruitment event.

Fluctuation in mean plant numbers in each treatment over the latter half of the experiment (Fig. 4.5) appeared to be the net result of limited additional germination, coalescence of plants growing very close together, division of some plants, possible regrowth of defoliated or apparently dead seedlings from concealed plant parts, and possible miscounting due to confusion with young *Austrostipa bigeniculata*. Continued presence of small juvenile plants (<10 leaves) 39-56 weeks after seed application suggests that seed germination continued at a low rate over a long period, but that plant mortality after the main germination outnumbered new recruitment.

Increased plant numbers at harvest (week 69), compared with the previous assessment (week 67) were in part due to the greater ease in distinguishing individual plants when they were removed from the ground, but may have been partly the result of inadvertent subdivision of tiller assemblages.

Effects of vegetation kill treatments

The experiment confirms existing understanding that *N. neesiana*, at least in part, recruits from panicle seeds and prospers in situations where competition from other plants is greatly reduced. Established grasses in general have strong negative effects on the recruitment of new grass seedlings and the growth and survival of juvenile plants (Lauenroth and Aguilera 1998). Competitive effects are mediated more through underground structures than above-ground parts; the intensive adventitious root systems enable very high capabilities for resource absorption in the soil occupied (Lauenroth and Aguilera 1998), so areas that appear unoccupied above ground ('intertussock gaps') in a long established grassland are nevertheless probably more or less fully occupied in ecological terms below-ground. Lesser establishment in 'half kill' plots than 'full kill' plots reflects this fact. *Nassella neesiana* panicle seeds reportedly germinate only in gaps and bare areas (Gardener *et al.* 1996a, Gardener *et al.* 1999) and various studies have likewise shown that seedlings readily establish when there is reduced or no competition from existing grasses. Where there is a seed bank of *N. neesiana*, areas bared with herbicide "generally produce a large germination ... within 12 months" (Duncan 1993) and are 'quickly reinvaded' (Bourdôt and Ryde 1986). Cover and abundance data from surveys at Derrimut Grassland Reserve, Victoria, suggested that seedling establishment of *N. neesiana* was uncommon in areas of dense *T. triandra* (Lunt and Morgan 2000), a relationship confirmed by experiment in the Iramoo manipulations reported here. In experimentally bared ground (by glyphosate application) seedling emergence ceased after the regrowth of surrounding vegetation (Gardener *et al.* 2003b), suggesting, according to Gardener *et al.* (1996a) that sunlight and disturbance that creates bare ground are 'germination triggers'. Mason (2005) attributed the ability of *N. neesiana* seedlings to establish well on areas cleared by herbicide application and tilled, to increased levels of available resources both above and below ground.

In the trial reported here, kill treatments created bare ground, and such open areas encourage the activities of some ants species - conversely ant diversity and activity is reduced when a dense grass sward shades the soil surface (Greenslade 1979). Ants were observed harvesting experimentally deposited *N. neesiana* seeds during the course of the experiment. It is possible that increased ant activity including seed harvesting may have occurred in 'full kill' plots because of their greater openness. However 'no kill' plots did not carry dense vegetation (e.g. Fig. 4.7c). The maximum standing phytomass in a 'no kill' plot was 250 g m^{-2} (2500 kg ha^{-1}) and the average for such plots was 175g m^{-2}, with maximum cover of 70% and average cover 46%. This compares for example to 6900-8700 kg ha^{-1} in *T. triandra* grassland unburned for several years in southern Victoria measured by Stoner *et al.* (2004) and 3000 and 6000 kg ha^{-1} in *T. triandra*/*Poa labillardierei* grassland with 50% *T. triandra* cover found by Dunin and Reyenga (1978) in New South Wales. 'No kill' areas seemed to be similarly inhabited by seed-harvesting species and provided other resources (nectar, plant exudates, invertebrate prey, seeds of other plant species) for ants that may well have made them considerably more attractive for ant foragers than the more open 'full kill' plots.

Effects of fertilisation

The soil P levels determined as part of soil nutrient analysis were very low (<5 mg/kg Olsen) compared to disturbed agricultural soils (Garden *et al.* 2003, Johnston *et al.* 2003, Charles Grech pers. comm.), but within the ranges determined for similar grasslands at Derrimut and Laverton North by Wijesuriya (1999). Available P levels below 25 mg/kg Colwell are considered “marginal” for pasture production in native pastures (Roberts *et al.* 2006), although ‘whole system’ nutrient assessments that includes the amount of P locked up in native vegetation and not ‘available’ in the soil is a more pertinent measure of nutrient status. O’Dwyer (1999) found that concentrations of available soil P above 14µg/g in *Austrodanthonia* grasslands were associated with weedy sites. Combined nitrate and ammonium N was slightly higher than the maxima of extractable N determined at Derrimut and Laverton North by Wijesuriya (1999). Potassium levels were markedly higher than, and organic carbon levels were about half those measured at Derrimut and Laverton North by Wijesuriya (1999).

Low available soil nutrient levels are typical in *T. triandra* grasslands: most of the nutrients are incorporated within the biomass of the dominant grass, and these are released when the tussock grasses are killed (Wijesuriya 1999, Wijesuriya and Hocking 1999, Hocking and Mason 2001).

The fertiliser pellets applied were not deliberately incorporated into the soil, took many months to disappear, and in the case of urea had not entirely disappeared by the time of biomass harvest. Soil nutrient measurements were not undertaken during the course of the experiment so it is unclear to what extent the applied nutrients were available for plant growth during particular phases of *N. neesiana* establishment. The estimation of available nutrients is an involved process (e.g. see Wijesuriya 1999) and was beyond the scope of this thesis.

Establishment of *N. neesiana* at the experimental site was not limited by available nutrients when the pre-existing vegetation had been killed: fertilisation with N, P, or both nutrients had no significant effect on the number of plants that established, the total biomass of *N. neesiana* per plot, or the mean biomass of plants that established. *Nassella neesiana* is common in the Southern Pampa and Flooding Pampa of Argentina (Soriano *et al.* 1992, Perelman *et al.* 2001, Honaine *et al.* 2006) where soils are notably deficient in P (Soriano *et al.* 1992), so *N. neesiana* may be somewhat ‘pre-adapted’ to Australian conditions where P is often deficient. However Grech (2007) found that *N. neesiana* juvenile plants responded strongly to P addition in pot trials in soils with an Olsen P of 6 mg kg^{-1} (P “deficient”) by increasing leaf area, shoot weight, root length and weight, and root to shoot ratio, and mature plants also displayed a growth response. The responses in the Iramoo experiment suggest that P was not limiting under the prevailing conditions.

Lack of response of *N. neesiana* establishment or biomass to added N and P may not be particularly surprising. The great majority of plants established in 'full kill' plots which would have been enriched by the high levels of nutrients resulting from the breakdown of the vegetation that was killed (Wijesuriya and Hocking 1999). At the time of biomass harvest all *N. neesiana* plants were small, with a small absolute nutrient requirement that was evidently readily met from the soils enriched by plant decay, in the absence of substantial competition. Plants recruited almost entirely in 'full kill' plots where the deliberately applied fertilisers probably merely represented surplus nutrient resources. However the lack of an establishment response in 'half kill' and 'no kill' plots indicates that competition for resources other than soil nutrients was the controlling factor. Plenty of unshaded ground was available (77% bare ground before treatment) so competition for light was likely to be of no importance. Establishment patterns – concentrated away from plot boundaries (e.g. Fig.4.7) – and loss of juvenile plants due to drought suggest that competition for water may have been a dominant limiting factor for establishment and growth. This would explain why 'half kill' plots did not show and increase in *N. neesiana* plant establishment when N + P were added.

The negative impact of N fertilisation on *T. triandra* biomass would advantage *N. neesiana* when the two species co-occur under conditions of N enrichment. *Themeda triandra* is supposedly adapted to a low N environment and so would be disadvantaged when growing in competition with species that respond to N enrichment (Garden *et al.* 2003). Smallbone *et al.* (2008) found in pot experiments that *T. triandra* exhibited no growth response to increasing N enrichment of the soil, while the exotic annual grass they tested responded strongly. Wedin (1999) found that increased N levels favoured C_3 species over C_4 species. Prober *et al.* (2005) demonstrated that sugar applications that reduced soil nitrate levels enhanced the establishment and abundance of *T. triandra*. Badgery *et al.* (2005) found that of four Australian native grass species tested (*T. triandra, Bothriochloa macra* (Steud.) S.T. Blake, *Austrodanthonia racemosa* (R.Br.) H.P. Linder and *Microlaena stipoides* (Labill.) R.Br.), only the C_3 *M. stipoides* was competitive with the C_3 *Nassella trichotoma* (Nees) Hack ex Arechav. at high N levels, while all of the native grass species were more competitive than *N. trichotoma* at low soil fertility. Morgan (2007) found that responses to added N in *T. triandra* grasslands in western Victoria that lacked any substantial exotic flora were dependent on fire history, with annually burnt grasslands showing major increases in living biomass in response to N addition, and infrequently burnt (>4 years) areas showing declines of c. 20%. N appeared to be a limiting resource under conditions of frequent fire, and added N may have been immobilised in litter in the unburnt grasslands. It is also possible that native grasses growing vigorously under frequent fire regimes may deplete soil nutrients to a greater extent than plants growing more slowly when fire is less frequent. The grass and forb components reacted similarly to N addition, in contrast to the results of the Iramoo experiment where only grasses exhibited significant biomass changes. However forbs at Iramoo were a very minor component of the biomass and a measurable response probably could not have been expected.

Nutrient addition is believed to increase the fecundity of exotic grasses in annually burned *T. triandra* grassland (Morgan 2007) but there was no evidence in the Iramoo experiment that *N. neesiana* reproductive outputs were increased by the application of N and P fertilisers.

Lack of a strong growth response of native grasses to phosphorus in the experiment (except for *Austrodanthonia* spp.) despite the very low prior Olsen P values, may reflect that they are adapted to low P soils, so do not respond when superphosphate is applied. It is also possible, that under these particular experimental conditions, water was a greater limiting factor than soil nutrients, for the native grasses. Increased growth from *Austrodanthonia* spp. under P fertilisation would improve its competitiveness with *N. neesiana*. However Garden *et al.* (2003) reported progressive declines in biomass of *Austrodanthonia* spp. (mainly *A. duttoniana* (Cashmore) H.P. Linder) in “low” P pasture soils at Yass, NSW under increasing levels of P fertilisation (5.5, 11, 22 kg P ha^{-1}) that were not explained by responses in other pasture species, and at Harrogate, SA, slight increases in unidentified *Austrodanthonia* spp. from very low levels. Effects of added P on *Austrodanthonia* spp. may be species specific or dependent on small variations in P levels. These authors also reported slightly increased biomass of *T. triandra* in pasture at Bendigo, Victoria, with increasing P levels.

In pot experiments Groves *et al.* (1973) recorded a significant positive response of *T. triandra* to N and P when applied together but not to either nutrient when applied alone. However no such positive interaction was found in this experiment. Groves *et al.* (2003) found that *T. triandra* and *Austrodanthonia carphoides* became less competitive than four common introduced annual and perennial grasses as complete nutrient levels were increased. Grown alone *T. triandra* and *A. carphoides* produced maximum biomass per unit area at nutrient levels double the normal, and decreased biomass production at higher nutrient levels. Some seedlings of these native species died at high nutrient levels, which were “presumably” toxic. The exotic C_3 pasture grasses reached biomass production maxima at quadruple nutrient levels. *Themeda triandra* was the most productive species at the lowest nutrient level and its productivity declined steadily with increasing nutrient levels relative to the most productive species.

Effects of sugar

Wijesuriya (1999) demonstrated that addition of sucrose to deliberately dug and homogenised *T. triandra* grassland soil resulted in rapid, near complete exhaustion of soil nitrates, presumably due to increased microbial activity. In these soil-disturbed plots, a high biomass of exotic annual grasses and exotic Asteraceae weeds developed, but when sucrose was added the biomass produced was much lower. Prober *et al.* (2005) demonstrated that sucrose addition in woodlands reduced soil nitrate to low levels and resulted in major reduction in the growth of exotic annuals and enhanced establishment and abundance of *T. triandra*. Reduction of plant-available nutrients via this mechanism presumably explains the strong effect of sugar on *N. neesiana* establishment in the experiment reported in this chapter. However this is mainly inference, since no evidence was gathered that sugar altered the levels of available nutrients, or that increased microbial nutrient uptake was responsible for the decreased plant growth. Perhaps the strongest circumstantial evidence that nutrient immobilisation occurred is from the findings of Wijesuriya (1999), who measured major reductions in N and P levels in the same types of soils, and in the immediate region in which the Iramoo experiments were carried out, at two separate sites. Although numerous previous studies have demonstrated that such nutrient reducing effects of sugar are usual, much remains unknown about the exact mechanism of how sugar applied to soils reduces nutrients.

Addition of simple carbohydrates to the soil often increases rates of decomposition of ‘recalcitrant’ C compounds in the litter and humus and increases the non-microbial pool of mineralised soil C (termed the ‘priming effect’), but may cause decreases, and this appears to be dependent on the particular composition and structure of the saprotrophic soil community, the nature of the C inputs and other abiotic factors (Chigineva *et al.* 2009, Nottingham *et al.* 2009). R-strategists (primary decomposers) are usually increased, while secondary decomposers (k strategists) that decompose recalcitrant materials may be suppressed when populations of primary decomposers are stimulated (Chigineva *et al.* 2009). Thus sugar application may either increase the supply of plant-available nutrients by increasing rates of organic decay, or decrease the supply by providing a substrate for rapid population growth of a fraction of the soil microbe community, or both effects at the same time. The priming effect can increase C losses to the atmosphere as CO_2 that exceeds the amount of added C (Nottingham *et al.* 2009), or may decrease C losses (Hoyle *et al.* 2008). Carbon responses of soil microbial communities to added labile C are not consistent across soil types and ecosystems (Hoyle *et al.* 2008); therefore it appears likely that current consensus understanding about nutrient fluxes resulting from C addition (i.e. ‘add C to mop up nutrients’) may also be simplistic.

Application of sucrose to soil might have reduced *N. neesiana* establishment by affecting the macrobiota. Addition of labile carbon has been found to greatly alter populations of soil animals. Chigineva *et al.* (2009) recorded the near doubling of Collembola populations and a five-fold increase in earthworm biomass resulting from sucrose additions at the rate of 100 g C m^{-2} $month^{-1}$. These animals may attack seeds or seedlings. Sugar might attract ants, which, if they are seed-harvesting species, might then have removed more seeds from the sugar-treated plots. The brief assessments of the amount of seed apparent on the surface during the experiment provide no support for this proposition. Ants were observed removing *N. neesiana* seeds, but they were never observed removing sugar; neither was increased ant activity observed on sugar-treated plots.

Alpert and Maron (2000) found that use of carbon-based soil additives to decrease plant-available N had a differential negative impact upon exotic plants in a California coastal grassland, and suggested the use of such techniques to counter invasion. Prober *et al.* (2005) also found that C addition (sugar treatment) strongly reduced the growth of exotics, but the exotics did not include perennial grasses. However Reever Morghan and Seastedt (1999) found that C addition similarly suppressed biomass production of both native and invasive plants. In the experiment reported here, the C treatment significantly reduced the biomass of all groups of exotic species and had no significant effect on any of the native species groups, supporting existing findings (Prober *et al.* 2005, Smallbone *et al.* 2007, Prober and Lunt 2009) that the technique has great potential for use in rehabilitation of Australian temperate grassy ecosystems.

Sugar and water stress

Sucrose may have had effects on soil chemistry and the plant-soil-microbe system that affected the outcome of the experiment by mechanisms other than the reduction of plant-available nutrients. Application of sugar may have disrupted water uptake by roots. Normally a water potential gradient exists from the soil through the plant to the atmosphere. Increasing the concentration of the soil solution via dissolved sugar results in decreased solute potential (osmotic potential). If soil water potential is less than that inside the roots, water may diffuse out by osmosis. Both plants and soil microbes incur energetic costs of osmoregulation, so dissolved sucrose in the soil water may result in water stress and increased costs to plants in maintaining turgor. However other studies have generally not voiced concerns that the reverse fertilisation effects of sugar application may be outweighed by effects on water relations in the soil.

Off-plot seed movement

The panicle seeds of *N. neesiana* are classed as creeping diaspores (Davidse 1986, Connor *et al.* 1993) that are able to move along the ground and position themselves in microsites favourable for germination (Gardener and Sindel 1998, Sinclair 2002). Creeping diaspores of grasses generally result in little actual dispersal via ‘creeping’, this adaptation being more important in enabling microsite lodgement (Peart 1979, Davidse 1986). Their movement capabilities on rough, dry ground appear to be very limited and insufficient to cross the 1 m buffer zones between plots in the experiment. Either a pre-existing soil seed bank or other dispersal factors must be invoked to explain establishment in unseeded plots.

Seed may have been moved on to unseeded plots by extreme wind events or by the activity of animals. Seed-harvesting ants (*Pheidole* sp.) were observed carrying *N. neesiana* seeds from plots to their nests and excavating some seeds that were firmly anchored in the ground by their calluses, and may have been responsible for some seed dispersal. These ants are seed predators, but may occasionally abandon seeds before they are delivered to the nest, or discard viable seeds outside their nests.

Although a total of 22,500 seeds were applied in the seed treatment, only 204 plants had established on the experimental plots at the time of biomass harvest (0.9 % of the individuals applied). Some of the same factors that may have resulted in movement of seed to unseeded plots may have been responsible for disappearance of seed from the treated areas. Ants are the most likely cause of major losses. None of the bird species frequently observed foraging on the ground in the Iramoo grassland are specialised granivores, although all are known to consume grass seeds (Barker and Vestjens 1989 1990).

Natural resistance to invasion

It has been recognised for many years that natural temperate grasslands in good condition are strongly resistant to invasion by exotic plants. Patton (1935 p. 175) noted in respect of the grasslands of the Victorian basalt plains that “So long as the natural vegetation covering, open though it be, is maintained, entrance to new-comers is denied.” The dominant tussock grasses not only command most of the space and light but may also starve the intertussock species of moisture and nutrients (Keith 2004). Prober and Lunt (2009) argued convincingly that *T. triandra* provides much of this biotic resistance in these grassy ecosystems: it is a keystone species that regulates N cycling and so controls invasion by exotic species. The experiment at Iramoo confirms this established understanding: removal of *T. triandra* enabled *N. neesiana* invasion.

The claim of Muyt (2001 p. 73) that fire “generates bare ground and reduces immediate competition, conditions that are ideal for seed germination” of *N. neesiana* has been proven false. There was little evidence in the experiment that more than minor *N. neesiana* establishment occurred in untreated plots, despite the very recent fire, open vegetation structure and low cover by native grasses. Bare ground is probably occupied beneath the soil surface, mainly by roots of the dominant grasses, which presumably would in part at least survive the fire or recover rapidly post-fire and pre-empt resources for potential invaders; the native grasses may even be stimulated to take up additional nutrients, as the dead material in their crowns is removed, stimulating faster rates of growth. Pot studies have demonstrated that below-ground competition for water and nutrients in grasslands is generally of much greater importance than aboveground competition (Schmidt *et al.* 2008). The native flora is adapted for frequent fire and is not significantly impacted when fire intervals are <5 years

(Wong and Morgan 2007). However very long fire intervals may allow the development of very high standing plant biomass, enabling hotter, longer-lasting, more destructive fires, that may kill the dominant native grasses, or reduce their capacity to take up and hold nutrients and water, and thus allow *N. neesiana* invasions. Fires at intervals of >5 years in *T. triandra* grasslands are too infrequent to maintain native plant diversity (Wong and Morgan 2007).

Sharp (1997) created 1 m^2 areas of bare ground experimentally using glyphosate herbicide in Dry *T. triandra* and *Austrodanthonia* grasslands in the ACT and studied colonisation of the gaps for 18 months. As found in the Iramoo experiment after 16 months, native grass cover did not recover to pre-treatment levels after 18 months. She found that exotic grass cover and richness initially increased, but after 18 months decreased to levels similar to those prior to treatment. Native and exotic forb richness and cover was increased. Evidently the continuity of occupation by invading species may not be assured. However there was no indication in the Iramoo experiment that the gains made by *N. neesiana* might later be lost.

Burke and Grime (1996) demonstrated that the creation of bare ground in limestone grassland by removal of indigenous plant cover, particularly the dominant grass, directly controlled the subsequent cover of sown introduced species, and that fertilisation (with NPK) greatly magnified the establishment success of the invading species. Resistance to invasion was hypothesised to result from “the combined effects of biomass and litter production by the residents” (Prieur-Richard and Lavorel 2000 p. 3). In contrast, Tilman (1997) demonstrated that addition of seeds of new native or exotic species to 1 m^2 plots of intact native grassland resulted in increased plant diversity, indicating that the assembled community was not saturated and could readily accommodate additional species with little effect on the existing components. However this was in a sod-grass rather than a tussock grass grassland, so different mechanisms might be operating.

Nassella neesiana was able to occupy the disturbed areas at Iramoo because there was little competition from native species. Native seed banks in Australian temperate grasslands are generally small and ephemeral (Lunt 1990b 1995a 1996, Morgan 1995a 1998c, Lunt and Morgan 2002). None of the native perennial inter-tussock species in existing native temperate grasslands are obligate seed regenerators, almost all being obligate resprouters, or resprouting and with limited seedling production, and mostly able to set, and actually setting seed within 12 months of regeneration (Lunt 1990c, Morgan 1996 1998c, Lunt and Morgan 2002). Thus disturbance that kills the existing native plant population effectively leaves clear ground for invasion by an invader such as *N. neesiana* that produces high propagule pressure. Restoration of these grasslands, as in native grasslands elsewhere in the world (Callaway and Maron 2006), is arguably constrained by lack of native seeds, rather than the presence of a dominant exotic competitor.

Only a small proportion of *N. neesiana* seeds applied in this experiment resulted in established plants. The number of established plants within plots after 16 months was accounted for by only 0.9% of the seeds applied. In individual plots, the maximum recruitment was in plot 30 where 63 plants resulted from 500 viable seeds (12.6%), 69 weeks after seed application. Prior testing indicated >80% viability of the *N.neesiana* seeds that were applied, and inspections indicated that there was very minor amount of seed lodgement outside plot edges. High levels of seed or seedling mortality or removal are therefore indicated.

Harvester ants (*Pheidole* sp.) are known to harvest large numbers and high proportions of broadcast grass seeds in some circumstances in Australia (Campbell 1966), and observations during this experiment indicated that they probably destroyed or removed a large proportion of the seed applied. Indeed, *Pheidole* sp. devoted extraordinary efforts to excavating and removing some of the *N. neesiana* seeds applied to plots that were firmly embedded upright in the soil. Campbell (1966) found that pasture grass seeds become unattractive to *Pheidole* spp. when they have swelled prior to germination. He demonstrated that the proportion of seed harvested depends directly on the foraging time available between seed application and the occurrence of rainfall sufficient to stimulate germination. In the Iramoo experiment c. 16 weeks elapsed from the time of *N. neesiana* seed application to the time of major germination, during the winter and early spring period when seed production by the existing vegetation would have been at a minimum. Reduced availability of other food sources might therefore have resulted in more thorough ant harvesting of *N. neesiana* seeds than under other circumstances. Nevertheless it is clear that biotic resistance to invasion arises not just from the flora.

Competitive effects of *N. neesiana*

The *N. neesiana* plants that established had a marked suppressive effect on the growth of native grasses. This is probably best characterised in part as a priority effect due to the establishment of plants in the absence of other competition. Space and resources pre-empted by *N. neesiana* were unavailable for use by other species. Simultaneous application of native seed would be required to properly examine competitive effects.

Primary juvenile period and first seed production

The demonstration that the primary juvenile period, leading to viable seed production, can be less than one year reinforces the need to control new outbreaks as an urgent priority to minimise propagule pressure at the expanding edges of infestations.

Contrasting ecology of cleistogenes

The experiment described above examined establishment from panicle seeds, which have a very different biology to that of stem and basal cleistogenes (Gardener 1998). Dyksterhuis

(1945) found that cleistogenes of the closely related *N. leucotricha* commonly failed to germinate within a year of their production and germinated especially within old, closely grazed, dead tussocks, while panicle seeds, in contrast, germinated in areas cleared of litter, outside of tussocks. Observations reported by Slay (2001) indicate that *N. neesiana* cleistogenes, particularly the basal cleistogenes, behave similarly to those of *N. leucotricha*. Panicle seeds of *N. neesiana* have previously been reported to germinate only in bare areas (Gardener *et al.* 1996a) or when gaps are created in pastures (Gardener *et al.* 1999). The limited evidence suggests *N. neesiana* stem and basal cleistogenes probably have higher rates of germination in closed swards or in unkilled areas of vegetation than panicle seeds, and juvenile plants of cleistogene origin might have higher survival rates than panicle seeds in areas with existing plant cover.

Conclusions

Nassella neesiana was able to establish or colonise at the experimental site only where there was propagule pressure accompanied by disturbance involving the death of the dominant grasses. Establishment in the absence of competition from established dominant grasses is arguably a trivial result that conforms with general understanding of the conditions required for recruitment of perennial grasses. Removal of competition by other plants generally results in increased seedling survivorship (Fenner 1987). That disturbance of ground previously unoccupied by *N. neesiana* enables *N. neesiana* invasion is also unsurprising, although the concept appears notably absent from the agriculturally-oriented Australian *N. neesiana* literature (e.g. Snell *et al.* 2007). Probably of more significance is the incapacity of *N. neesiana* to establish in areas occupied by native grass tussocks, even though there was little competition above-ground for light. Also significant is that some of this resistance to invasion was maintained even in ‘half kill’ of native tussocks – so that the there was significantly less than a directly proportional outcome for *N. neesiana* establishment on the ‘half kill’ plots – that is, removal of half the native tussocks resulted in much less than half the replacement by *N. neesiana* plants than occurred in ‘full kill’ plots. The results do however greatly clarify the issue of whether *N. neesiana* is an ‘active’ invader, i.e. that it possesses superior competitive abilities, or instead is a ‘passive’ invader that follows disturbance. The low levels of *N. neesiana* establishment in half kill plots also suggests that native grasslands are significantly resistant to invasion, and that large ecological gaps are required before *N. neesiana* can establish in any numbers.

The important question of “which disturbances are most likely to lead to invasions” (Hobbs 1991 p. 100) is also clearly answered by the Iramoo experiment: disturbances that kill the dominant existing grasses. The finding that sugar application results in a major reduction in *N. neesiana* establishment further elaborates this understanding. It is presumed that sugar functioned as a ‘reverse fertilisation’ treatment by stimulating soil microbe populations. Major increases in available soil nutrients would have occurred in the ‘full kill’ plots due to rapid decay of the killed vegetation, and temporary immobilisation of these nutrients using sugar presumably severely reduced *N. neesiana* recruitment. Deliberately added nutrients were presumably immobilised in the same way, or in vegetated plots were preferentially sequestered by the existing vegetation. This again is in general conformity with existing knowledge: disturbance is important for weed establishment when it increases the availability of a limiting resource (Hobbs 1989 1991, Davis *et al.* 2000). Recruitment may be expected to be first limited by whatever is the most limiting resource for seedling establishment and growth. Rainfall driven *N. neesiana* seedling establishment, along with the observed patterns of juvenile plant consolidation away from plot edges, and mortality due to drought, plus the reported results of nutrient addition suggest that the most critical resource for recruitment in this experiment may have been water, not N or P.

Within 18 months of the application of 500 *N. neesiana* seeds m^{-2} to cleared ground, a population of *N. neesiana* plants was established that was able to produce >200 panicle seeds m^{-2}. Under conditions of continuing strong disturbance *N. neesiana* appears precocious and fecund enough to provide the propagule pressure necessary to continue to invade new areas from sites it has only recently occupied.

Maintenance of native plant diversity (mainly inter-tussock forbs) in the natural temperate grasslands of south-eastern Australia requires *inter alia* the reduction of cover of dominant grasses, prevention of senescence dieback of *T. triandra*, the retention of intertussock spaces and the creation of recruitment opportunities for native plants (Reynolds 2006, Wong and Morgan 2007). The conundrum for these grasslands is that such activities at the same time may create more open areas and relief from competition above and below ground that may increase susceptibility to invasion by *N. neesiana* and other exotic weeds. Regular opening of gaps (at least the maintenance of intertussock space) is required for forb seedling recruitment in *T. triandra* grasslands (Morgan 1995b, Sharp 1997) and recruitment of many forb species may require more severe small scale soil disturbances formerly achieved by native vertebrates (Robinson 2003 2005, Reynolds 2006). In the experiment reported in this chapter, it was found that the creation of large gaps (1 m^2) by killing the native vegetation (in ‘full kill plots’) had the strongest influence on *N. neesiana* establishment, and that small gaps (10-30 cm) enabled very little survival of juvenile *N. neesiana* to maturity (in ‘half kill’ plots). Gaps are colonised by the species present in the seed bank and by dispersed seeds. If soil seed banks are absent, the timing of gap creation determines which dispersed seeds arrive first and can gain an advantage. The timing of the disturbance in relation to the availability of seed of potential colonising species is of critical importance (Körner *et al.* 2008). Where a soil seed bank is present, its species composition is likely to have an influential role in determining the vegetation that subsequently develops. Where the soil seed banks of native species is generally low, as commonly occurs in these grasslands (Lunt 1990b, Morgan 1998c) and was evidently the case in the experimental area, gaps are likely to be filled by the exotics in the seed bank and whatever more highly dispersible species exist in the immediate area. If native grasses are dispersed onto the disturbed ground before the arrival of *N. neesiana* and prior to conditions suitable for germination, then native species may well occupy the disturbed ground. Evidence that this happens when *T. triandra* seeds are deliberately applied after strong disturbance in these temperate native grasslands has been provided by Phillips (2000) and Mason (1998 2004).

Apart from the above considerations there is little reason to suspect that the results obtained at this one site cannot be generalised to other similar grasslands. *Nassella neesiana* may also invade in the absence of major disturbance, but the experiment indicates that if it does, invasion would be at a much slower rate and in greatly reduced numbers. Testing of such a proposition is difficult given that anthropogenic alteration of the native grassland environment is nearly universal, and ‘natural’ disturbance is widespread and appears also to be a requirement for establishment of native grassland species.

Chapter 5. Relationship between senescence of *Themeda triandra* and invasion by *N. neesiana*

"... Kangaroo Grass plays an active role in slowing (but not necessarily stopping) invasion by Chilean Needle-grass ... the most cost-effective method of slowing invasion ... is likely to be by maintaining a healthy sward ..."

Ian Lunt and John Morgan, 1998a.

Summary

This chapter reports the results of a correlative study of the relationship between the amount of senescence of *T. triandra* and invasion by *N. neesiana*. Characteristics of senescence in grasses are first discussed. The widespread occurrence in temperate and tropical grasslands of fire-adapted dominant C_4 grasses that accumulate large quantities of dead biomass is then described in relation to the current study. The phenomenon of senescence dieback, where lack of fire or other biomass reduction results in death of such dominant grasses is discussed, with particular focus on *T. triandra*. The impact of *T. triandra* sward densification on grassland plant diversity is outlined, along with the negative consequences for plant diversity in the absence of biomass reduction. A pin transect sampling technique with samples at 10 cm intervals on six transects (total length of 27.7 m) was used to quantify the amount of *N. neesiana* present in relation to the proportion of dead to living *T. triandra* in areas where *T. triandra* swards were highly senescent. The results of sampling in three grasslands are presented, along with qualitative observations of senescence processes in the grasslands studied. Higher *N. neesiana* presence was found to be significantly correlated with increased *T. triandra* senescence, and evidence was gathered to support previous studies suggesting that major invasion of *N. neesiana* is, at least in part, a consequence of allowing senescence to continue into the dieback phase. It is proposed that a significant proportion of plant diversity loss correlated with *N. neesiana* presence can be explained by the separate process of senescence dieback of the dominant native grass, and that this dieback subsequently also enables *N. neesiana* invasion. In summary, it is likely that substantial reduction in native plant diversity that has been attributed to *N. neesiana* commonly results from this prior disturbance process of *T. triandra* senescence, rather than from active invasion of *N. neesiana* into biodiverse grassland areas.

Introduction

Grass senescence

Senescence of foliage and cessation of leaf growth occurs in all grasses in response to drought and is a mechanism to reduce plant mortality from water stress, by the gradual 'abandonment' of foliage (Norton *et al.* 2008). Leaf abscission layers are commonly absent in Poaceae, so senesced foliage is often retained on the plant and may reduce the plant's productivity and fecundity (Mingo and Oesterheld 2009). The limited development of above-ground structural material limits the height to which the canopy of grass species can reach before self-shading becomes detrimental (Lauenroth and Aguilera 1998). In general, self-shading results in reduction in potential photosynthetic gains by an individual plant, but it also has the potential to limit the growth of competitors (Lauenroth and Aguilera 1998). Grasses that exhibit periods of true dormancy are characterised by total cessation of growth, near complete herbage senescence and dehydration of young leaf bases, while species with partial dormancy exhibit only partial growth cessation that may be a dehydration avoidance strategy, expressed in any season when there is soil moisture stress (Norton *et al.* 2008), a response to climatic extremes or a phenological reaction to normal seasonal climatic variation. Rates of accumulation and disappearance of senesced material are dependent on a range of variables including the prevalence of fire, grazing and other disturbances, microbial decomposition and climatic factors.

Senesced grass may be consumed by herbivores and a proportion is broken down by detritivores. Rates of consumption and decay are in part dependent on the C: N ratio of the live foliage and the litter (Groves and Whalley 2002). The foliage of C_4 grasses has a higher C:N ratio (>30:1) than that of C_3 species, so has lower nutritional quality and lower palatability to herbivores, and a higher proportion of leaves die without being eaten (Moore 1993, Moretto and Distel 2002). Their litter is more resistant to microbial breakdown than that of non-C_4 plants (Wedin 1999, Groves and Whalley 2002) so proportionately more of it can accumulate. Evidence indicates however that C_4-derived soil organic carbon compounds decompose much faster than C_3 derived material once they enter the soil organic carbon pool in mixed C_3/C_4 soils (Wynn and Bird 2007). Higher C: N and lignin: N ratios in the foliage and litter of C_4 grasses may reduce nitrogen mineralisation rates (Levine *et al.* 2003) and this tendency to monopolise the nutrient pool acts to inhibit potential competitors. Commonly the large standing dead biomass accumulated by C_4 species makes the tropical and temperate ecosystems in which they dominate more prone to fire, and the grasses involved are often viewed as fire facilitators (Mingo and Oesterheld 2009).

The native grasses present in the temperate natural grasslands of south-eastern Australia are a mixture of C_3 and C_4 species, but the major dominant is one such species, the post-fire resprouting, C_4 *T. triandra* (Andropogoneae: Anthistriinae). *Themeda triandra* rapidly accumulates large amounts of biomass as standing litter (attached to the plant), and this biomass accumulation is apparently an adaptation that enables it to perpetuate its dominance by providing appropriate conditions for frequent burning (Hocking and Mason 2001). Litter of *T. triandra* decomposes less rapidly than the litter of the subdominant C_3 *Austrostipa* and *Austrodanthonia* spp. due to its high C: N ratio. *Themeda triandra* and the grasslands in which it dominates are tolerant of frequent fire, and regular burning or other biomass reduction is necessary to reduce *T. triandra* dominance and maintain plant diversity (Lunt and Morgan 2002). Burning should occur “as a general rule, more often than ... deemed necessary” (Wong and Morgan 2007, p. II). In the absence of fire and grazing, *T. triandra* tussocks can accumulate biomass rapidly, ground cover often approaches 100% within a few years, and the proportion of senescent foliage rapidly reaches very high levels, providing a continuous fuel bed. In ungrazed grassland Lunt and Morgan (1998a) recorded biomass doubling in the first year post-fire, doubling again in the second year to c. 5 tonnes ha^{-1} with c. 50% of the biomass dead, and doubling again >6 years post-fire, by which time biomass levels of 8 t ha^{-1} had been reached, of which over 5 t ha^{-1} consisted of dead material. There was little loss by decay by 3 y after the fire.

Senescence dieback of C_4 tussock grasses

The phenomenon of fire-facilitating biomass-accumulation has been widely reported worldwide for other dominant temperate and subtropical C_4 caespitose grasses (Mueller Dombois 1973, Knapp and Seastedt 1986, Everson *et al*. 1988, Uys *et al*. 2004, Overbeck and Pfadenhauer 2007, Bond *et al.* 2008). In the absence of biomass reduction by fire or grazing, tussocks of these species, typically members of the Andropogoneae (Bond *et al.* 2008), gradually accumulate masses of standing dead litter which shades out and kills shade-intolerant new tillers (Knapp and Seastedt, 1986, Everson *et al*. 1988). In the context of temperate grasslands in Australia this has often been referred to simply as *T. triandra* “senescence”. However in other parts of the world the process of biomass accumulation and its effect on plant productivity and survival have often been described under different rubrics e.g. ‘continuous densification of cover’ (Mueller Dombois 1973), “detritus accumulation” (Knapp and Seastedt 1986) and “hollow crown phenomenon”(Wan and Sosebee 2000). Two main hypotheses have been invoked to explain biomass accumulation - fire facilitation and grazing defence (Mingo and Oesterheld 2009). The fire facilitation hypothesis proposes that accumulator species are favoured by fire, and so have evolved characteristics that facilitate frequent burning to perpetuate their dominance. The grazing defence hypothesis proposes that retention of dead biomass deters vertebrate grazers, dilutes the foliage quality of the plant and thereby reduces consumption of living material (Mingo and Oesterheld 2009).

These hypotheses are not mutually exclusive, and elements of both need to be invoked to explain the origins and functioning of grasslands that have developed under a range of fire and grazing regimes from ancient to historical times.

There is clear evidence from a range of grasslands that lack of biomass reduction results in poor health and eventual dieback of fire-dependent dominant grasses. Overbeck and Pfadenhauer (2007) observed that periodic removal of accumulated biomass was required in C_4 dominated southern Brazilian grasslands to remove shade, reinvigorate tillering and increase tussock survival. Higher humidity under the litter cover over a period of a few years, causing decay of below ground plant parts, was suggested as a cause of mortality. Mueller Dombois (1973) found that *Andropogon virginicus* L. (Andropogoneae) rapidly accumulates masses of standing dead shoots after fire in Hawaii, and during its partial dormancy period in the wet season most of the current year's growth senesces. Little litter is produced in the first year post-fire, but subsequently the "successive increase in litter fraction ... may ... have an effect on reducing the green-blade fraction" (*op. cit.* p. 7). Tussocks of the southern African C_4 *Eragrostis curvula* (Schrad.) Nees (Eragrostideae) that are not defoliated for >10 years develop a dead centre ("decadent crown") believed to be caused by accumulation of dead biomass that suppresses the development of new tillers (Wan and Sosebee 2000). Development of a central litter load increased the number of senesced tillers in the tussock interior, and removal of the dead material significantly increased tiller recruitment by making more light available to basal buds. However plants that were clipped to 15 cm height produced significantly more tillers when their litter was retained, possibility because of the mulching effect of litter retention. Depletion of soil water under the centre of tussocks without litter build-up was greater than at tussock edges throughout the growing season and this may have caused increased tiller senescence in the tussock centre. Shading was considered to be the main factor regulating tiller recruitment, by decreasing bud viability, but dieback of tussock centres may also be caused by drought effects (Wan and Sosebee 2000). Other factors considered important in the decline in plant health due to increasing senescence include slower soil warming at the commencement of the growing period, and changes in nutrient cycling (Knapp and Seastedt 1986, Mingo and Oesterheld 2009).

Actual dieback of plants resulting from biomass accumulation may not always occur with the various species, and is usually prevented by disturbance events. As long as the senescence process has not proceeded too far, fire re-invigorates the sward. Post-fire effects include increased photosynthetic activity, growth rates and sexual reproduction (Overbeck and Pfadenhauer 2007).

Senescence dieback of *T. triandra*

Senescence dieback of *T. triandra* was described in the late 1990s by Ian Lunt and John Morgan after studies of the outcomes of management on Victoria's first major grassland reserves, the Derrimut and Laverton North Grassland Reserves on the western side of Melbourne (Lunt and Morgan 1998a *et. sub.*). Previous consensus had been that the standing biomass of *T. triandra* stands could vary markedly over time, or reached a steady state in which new biomass accumulation was matched by decomposition (Morgan and Lunt 1999, Lunt and Morgan 2002). The influential study by Groves (1965) for example found that much of the dead *T. triandra* biomass in narrow railway grasslands in Melbourne eventually moved off-site or otherwise disappeared.

Major *T. triandra* mortality "over many hectares" (Lunt and Morgan 1998b p.8) occurred at the ungrazed Melbourne grasslands when fire frequency exceeded 5 y, and when fire was finally used, plant and tiller densities were much lower than in frequently burnt grassland (Morgan and Lunt 1999, Lunt and Morgan 1999a). This mass dieback has been described as "grassland collapse" (C. Hocking pers. comm.). *Themeda triandra* stands that are not burnt, or otherwise biomass-reduced, gradually develop massive quantities of dead leaves and litter, which if not removed cause tiller and plant senescence (Lunt and Morgan 2000). The rate of biomass accumulation post- fire is highly variable and dependent on site productivity and particularly soil water availability (Kirkpatrick *et al.* 1995, Lunt and Morgan 2002). Senescence is more likely to occur on more productive grassland sites, where *T. triandra* can produce large biomass crowns in a short period, and in situations where the processes that remove dead material, by wind, animal grazing etc., are more constrained. Senescence is particularly prevalent at sites where biomass reduction by grazing or fire is removed – in the 1990s this often occurred when biodiverse grasslands were first protected in reserves and management regimes were radically changed (Craigie and Hocking 1999).

The *T. triandra* senescence dieback effect has been attributed to "self-shading" (Lunt and Morgan 1998b 2000), with "insufficient light penetrating through the canopy of old foliage to the young tillers to enable them to photosynthesise sufficient energy" (Lunt *et al.* 1998). Accumulated dead material "smother[s] the tussocks and prevent[s] new growth from reaching sunlight" (Lunt and Morgan 1998b). The few live tillers that survive in senescent tussocks tend to have "long, twiggy stems that enable the new growth to reach up above the dead leaves into the sunlight", and these are "extremely weak and sensitive" and are "easily pulled out by hand" (Lunt and Morgan 1998b p. 8). Eventually the weak tillers die; the tussock consists of a mound of dead grass (Lunt and Morgan 1998b) and the dead canopy collapses, forming a dense, thick layer on the soil surface (Morgan and Lunt 1999) which slowly decomposes to form a 'mulch mat' over the ground (Lunt and Morgan 1998b p. 8).

According to Muyt (2005 p. 3), the dense *T. triandra* thatch "undermines the growth of [the grass] itself; plants become increasingly brittle and subject to collapse".

Above ground decline is reflected by declines in live root biomass (Morgan and Lunt 1999). In the period before mass dieback at Laverton North Grassland, McDougall (1989 p. 43) reported that tussocks in unburnt areas "had a very small basal area" and "were generally poorly rooted" with the roots of new tillers "failing to produce functional roots", so the plants were "easily killed by trampling". Such senescent plants also commonly produced aerial tillers from flowering culms, probably to increase their amount of elevated photosynthetic tissue. [Incidentally Groves (1975 p. 956) identified the production of aerial tillers as a characteristic of one form of *T. triandra*, which he collected at Tomerong near Nowra on the south coast of NSW and considered to probably represent form A of Vickery 1961. It had "enhanced capacity to form many leaves up the flowering stem, in the axils of which new tillers may develop towards the end of summer".] These changes indicate that senescence is associated with a general lack of vigour.

Themeda triandra perpetuates its own dominance by controlling the cycling of major nutrients (N, P), the major proportion of the nutrient pools of these grasslands being held in its crowns and roots, so little is mobilised by fire. The proportion of biomass represented by roots in grasslands may well have been underestimated, since the root hairs of grasses are frequently very long and may not be as short-lived as in other plants (Clark and Fisher 1986). High levels of senescence increase the levels of available nutrients in the soil, probably as a result of increased rates of decay of both above and below ground vegetation due to increased moisture and temperature under the thatch of dead leaves, and by reduced nutrient uptake by living biomass (Hocking and Mason 2001). Senescence dieback of the dominant grass results in a major nutrient pulse in the soil, primarily from decay of *T. triandra* crowns and roots (Wijesuriya 1999, Wijesuriya and Hocking 1999). Individual grass plants also concentrate C and soil nutrients in the soil beneath them (Lauenroth and Aguilera 1998), and these resources become available to other plants when the grass dies. Such nutrient pulses may commonly be of short duration, but are known to influence the establishment of other species (Lauenroth and Aguilera 1998).

The period required for *T. triandra* senescence dieback is variable and in part dependent on the productivity of the site and climatic conditions. Most ungrazed grasslands not burnt for greater than 5-6 years will be well advanced in the biomass accumulation process (Morgan and Lunt 1999, Lunt and Morgan 2002, Wong and Morgan 2007) and full senescence may frequently occur after 10 years (Lunt and Morgan 1998b). Lunt and Morgan (1999b) reported dense closed *T triandra* swards at Derrimut Grassland after just two years in the absence of grazing and fire. McDougall (1989) reported rank growth with *T. triandra* tussocks and litter filling most of the former intertussock spaces at Laverton North after ten years without fire or grazing. But at sites with low soil fertility and moisture levels the process may require considerably longer periods or never occur (Kirkpatrick *et al.* 1995). Lower site productivity and drought were suggested as contributory factors to the lack of *T. triandra* dieback in box woodlands on the Central Western Slopes of New South Wales after 14 years without fire, despite high litter accumulation (Prober *et al.* 2007). Any conditions that prevent vigorous *T. triandra* growth leading to the formation of a closed canopy should preclude the development of senescence (Lunt and Morgan 1998b).

Nevertheless, the underlying mechanisms of *T. triandra* senescence dieback appear to be incompletely understood and further investigation is required. Death of swards after extended periods of biomass accumulation might be due in part to altered water relations, rather than the postulated ‘self-shading’, with lowered transpiration resulting in higher humidity and soil water content beneath tussocks, that facilitates root and crown decay, as suggested by Overbeck and Pfadenhauer (2007) for Brazilian grasslands. The effect of pathogenic fungi on plant death has not been investigated although ‘root-rots’ may be important in dense senescent swards.

After burning, if the senescence process has not preceded too far, *T. triandra* usually regains high cover quickly, returning to pre-fire biomass levels in 2-4 years (Morgan 1994, McDougall and Morgan 2005). A complete dense canopy with 100% cover can be formed after 3-4 years (McDougall 1989) and this appears to be the minimum period required before significant senescence can develop. A maximum fire interval of five years has been recommended to prevent senescence dieback in systems where it is likely to occur (Lunt and Morgan 1998b, Craigie and Hocking 1999, Wong and Morgan 2007).

Impact of biomass accumulation and senescence dieback on plant diversity

The relationship between fire frequency and plant diversity in fire adapted grasslands is complicated by many factors, but in general too low or too high a frequency results in decline of the dominant grass and the interstitial species. The effects on the dominant grasses are a prime consideration. Fire-dependent C_4 dominants decrease or disappear from grasslands when burning is too infrequent, so grass species composition of a sward is largely determined by fire frequency (Bond *et al.* 2008). *Themeda triandra* decreased from >70% cover in frequently burnt South African grasslands to <10% when fires were excluded for 4 years or more (Uys *et al*. 2004).

In respect of the other plants, reduction of excessive biomass of dominant perennial grasses in productive grasslands is frequently a critical factor in maintaining native diversity and limiting weed invasion (Prober *et al.* 2007). Commonly, in the absence of regular biomass reduction by fire, grazing or mowing, litter accumulation and shading by standing dead biomass results in the suppression of the smaller intertussock native vascular plant species (McIntyre 1993, Kirkpatrick *et al.* 1995, Morgan 1998e). Entire populations of perennial forbs can disappear within a short period in *T. triandra* grasslands in the absence of fire, as a result of shading combined with the short-lived seedbank of many species that contribute to plant diversity (Morgan 1998e). Where such grassland is unburnt for >5 years the cryptogam crust also degenerates due to litter accumulation, shading and increased earthworm activity (Scarlett 1994). In temperate natural grasslands of south-eastern Australia periodic biomass reduction is required to maintain the vascular flora, mainly because a large proportion of it consists of species whose soil seed banks more or less disappear after 1 year and often within a much shorter period (Lunt 1990c 1995a, McIntyre 1993, Stuwe 1994, Morgan 1998c). Morgan (1995b) for example found that 90% of *Rutidosis leptorhynchoides* seed germinated within a few weeks of autumn rains, and Morgan (1998c) found that a high proportion of native species had extremely transient seed banks.

Canopy gaps are critical for recruitment of much of the native flora (Morgan 1998b), but unburnt *T. triandra* grasslands typically consist of closed cover of *T. triandra*, which prevents growth and seed production by most of the other vascular species. Sharp (1997) experimentally confirmed that litter removal is required to facilitate establishment and relieve suppression of the smaller native grasses and the low-growing and small forb components in ACT grasslands. Thus, few plants other than dominant grasses are able to survive in long unburnt *T. triandra* swards, soil seed banks are greatly reduced, and burning will not bring back the lost diversity. For these reasons low fire frequency is recognised as a threat to several endangered grassland plant species including *Senecio macrocarpus* (Hills and Boekel 1996) and *Rutidosis leptorhynchoides* (Morgan 1995a, Humphries and Webster 2003). Lack of fire or some other management regime with similar effects is therefore a threat to the continued existence of the more mesic species-rich, *T. triandra* dominated grasslands. Suppression of other native species by the dominant grasses is not generally a problem in grasslands on shallow rocky soils and on the inland plains, where fire is not necessary to maintain indigenous vascular plant diversity (Kirkpatrick *et al.* 1995).

However all native species are not necessarily negatively affected. Lunt and Morgan (1999b) found that a set of adaptable, ruderal ‘weedy’ natives such as *Lachnagrostis filiformis* (G.Forst.) Trin. and *Senecio quadridentatus* Labill. did not decline in the absence of biomass removal. These were able to recolonise, or survive in the soil seed bank under dense cover and regenerate after its removal. Similarly, Morgan (1998c) found that a small proportion of the native flora had large soil seed banks, mostly monocots (*Isolepis* spp., some Juncaceae) but including a few dicots, which might be advantaged by *T. triandra* dieback.

Senescence dieback represents a form of secondary succession. In a community lacking exotic species, affected areas would have been re-occupied by a community of native species that may have had substantially different composition to the flora replaced. However as pointed out by Ramakrishnan and Vitousek (1989) the effects of an invading species on such successional processes are difficult or impossible to assess when the features of secondary succession in the absence of exotics are more or less unknown. Exotic weeds are now generally pervasive in these systems (Kirkpatrick *et al.* 1995) and tend to have large, long-term soil seed banks (Morgan 1998c, Lunt and Morgan 1999b) that are more likely than a large proportion of the native flora to survive the period of *T. triandra* senescence and regenerate, or be regularly replenished in large numbers by wind from nearby sites. Senescence dieback therefore often enables invasion by exotics, facilitated by the major nutrient pulse that accompanies and follows the death of the dominant grass (Hocking 1998, Wijesuriya 1999, Wijesuriya and Hocking 1999). In the absence of exotic seed sources, dead swards might be colonised by more opportunistic and more highly dispersive native grasses and forbs, along with the few native species that have long-lived soil seed banks, but in more degraded grasslands with higher exotic cover, areas that have died back appear to be highly prone to exotic colonisation and dominance.

On the other hand, too frequent fire can harm the dominant grass matrix and may negatively affect the native biodiversity. Prober *et al.* (2007) found that fires at 2 year intervals in grassy *Eucalyptus* woodlands caused high mortality of *T. triandra* tussocks and resulted in poor sward resilience. Bryophyte diversity in areas of *T. triandra* grassland burnt at 1-2 year intervals was found by Morgan (2004) to decline compared to areas burnt less frequently, but O’Bryan *et al.* (2009) found an opposite effect.

In summary, absence of fire in the temperate natural grasslands of south-eastern Australia can result in widespread death of *T. triandra* through senescence, and progressive, long-lasting loss of native vascular plant diversity. Death of the dominant grass opens the sward to invasion by weeds, which are promoted by a strong nutrient pulse resulting from decay of *T. triandra* roots and crowns. This can result in replacement of diverse grassland areas by perennial exotic grasses and forbs. To determine if *N. neesiana* is one such weed that is promoted in its capacity to invade by senescence of native grass, areas of senescent *T. triandra* were sampled to determine if there was any correlation between the presence of *N. neesiana* and the degree of *T. triandra* senescence. The study was designed to test whether senescence of *T. triandra* was likely to be one contributing factor in *N. neesiana* establishment, not whether it was the only mechanism promoting *N. neesiana* invasion.

Methods

Study sites

Investigations were undertaken at Yarramundi Reach, Dudley Street and Laverton North grasslands. Details of these sites are provided in Chapter 1. During the period of study Yarramundi Reach was widely and severely affected by *T. triandra* senescence dieback, while at Dudley Street dieback was restricted to small irregular areas in the western end, and along parts of the expanding boundary between dense *N. neesiana* and relatively healthy *T. triandra* grassland. Laverton North has been severely affected by senescence in the past, but during the study period active dieback was restricted to small areas in unburnt privately owned land, to the west of the Reserve, an unmanaged, degraded area with tall, rank grasses in which widespread *T. triandra* dieback was occurring in a sparse mosaic pattern.

Sampling

Areas of highly senescent *T. triandra* with co-occurring *N. neesiana* were visually identified at the three sites. Straight line transects were laid out with a measuring tape, usually from *N. neesiana* dominated areas into areas dominated by *T. triandra*. A “pin” consisting of a 5mm diameter wooden dowel with a sharpened end, colour-banded at 5 cm intervals, was used to make each assessment (Fig. 5.1). The pin was placed vertically in the ground and the number of pin intercepts (vegetation touches) to the pin of each species, live or dead, were counted in each of the 5 cm height categories. Intercepts with detached litter were not counted. The live or dead status of the plant material intercepted was assessed at the point of interception. Grass leaves mature and senesce progressively from the tip to the base (Wheeler *et al.* 1990), so a major but undetermined proportion of the ‘dead’ intercepts were probably leaves with live bases. The method nevertheless provided an overall assessment of the proportion of dead or dying vegetation. Pin samples were repeated at 10 cm intervals along each transect. Six transects with a total length of 27.7 m were assessed at three grasslands (Table 5.1).

Figure 5.1. Sampling ‘pin’ used in the study: a thin wooden dowel, sharpened at one end, marked in 5 cm bands. Pin lying horizontally on an *N. neesiana* sward, sharp end at left.

Table 5.1. Locations, designations, dates and lengths of pin transect samples in areas of senescent *Themeda triandra*. Yarramundi Reach Patch G north transect was also used to assess patch boundary characteristics.

Site	**Location**	**Designation**	**Date**	**Transect length (cm)**
Yarramundi Reach	35°17.384’ 149°05.008’	Patch G, north transect, Peg 0391	13/10/07	450
Yarramundi Reach	35°17.332’ 149°05.087’	Peg 0884	25/4/08	430
Yarramundi Reach	35°17.326’ 149°05.083’	Peg 0085	25/4/08	310
Dudley Street	35°18.841’ 149°05.444’	Peg 0886	26-7/4/08	450
Dudley Street	35°18.842’ 149°05.451’	Peg 0887	27-8/4/08	450
Laverton North	37°50.718’ 144°47.365’	Peg 0220	11/3/08	680

Analysis

The numbers of pin intersects with *N. neesiana*, dead and total *T. triandra* and other species at all heights at each point were graphed for all sample points along each transect. Points where both *T. triandra* and *N. neesiana* occurred were identified at Yarramundi Reach and Dudley Street but there was no overlap at Laverton North, which was excluded from further analysis.

The relationship between the degree of *T. triandra* senescence and *N. neesiana* presence and was analysed by the following method. Each transect was treated as a replicate (5 replicates).

1. An arbitrary choice was made that >9 pin intercepts with *T. triandra* per point represented a reasonably large amount of *T. triandra*.

2. The number of *N. neesiana* pin intersects versus the ratio of dead/total *T. triandra* pin intersects at all points with such reasonably large presence of *T. triandra* was graphed for each transect. At many pin points no *N. neesiana* was present or the amount of *T. triandra* was small.

3. A trend line for each replicate was fitted using Microsoft Excel and the slope of the line was calculated. A line with a positive slope would indicate increased *T. triandra* senescence corresponding to increased *N. neesiana* presence, a line with a slope of zero would indicate no relationship and a line with a negative slope would indicate a reduction in *N. neesiana* presence.

4. A two sided sign test was used to determine whether there were more values on one side of 0, i.e. more negative than positive slopes.

Results

Pin transects

The distribution of *N. neesiana*, dead *T. triandra*, total *T. triandra* and other plant species along pin transects indicated that *N. neesiana* occurred at numerous points where the proportion of dead *T. triandra* approached 100% (Figs. 5.2, 5.4, 5.6, 5.8, and 5.10). However *N. neesiana* was absent at other points with similarly high *T. triandra* senescence. At points where both *N. neesiana* and *T. triandra* were detected and there were >9 *T. triandra* pin intersects, there was a consistent trend to higher presence of *N. neesiana* as the proportion of dead to living *T. triandra* increased (Figs. 5.3, 5.5, 5.7, 5.9, 5.11).

At Yarramundi Reach patch G (Fig. 5.2), *T. triandra* was not detected within the main body of the *N. neesiana* infestation (0-230 cm). Within the areas dominated by *T. triandra*, *N. neesiana* occurred at points with *T. triandra* senescence levels close to 100% (300, 310, 380, 430 cm), at points with lesser *T. triandra* senescence (440 cm) and at points with no co-occurring *T. triandra* (320-350 cm). *Nassella neesiana* was absent at some points with *T. triandra* senescence at or close to 100% (260 cm, 390 cm). The annual exotic grass *Vulpia* sp. by far predominated amongst other species. At points where the presence of *T. triandra* was reasonably high (>9 pin intercepts), increased presence of *N. neesiana* correlated with increased *T. triandra* senescence (Fig. 5.3).

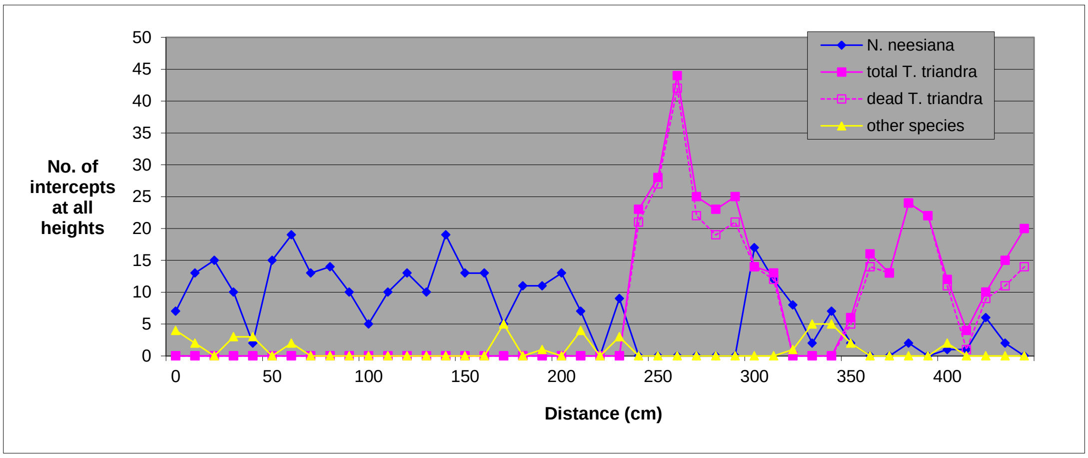

Figure 5.2. Distribution of *N. neesiana*, dead *T. triandra*, total *T. triandra* and other plant species along a pin transect at Yarramundi Reach, Patch G, 13 October 2007. The transect ran from dense, uniform *N. neesiana* into senescing *Themeda* (280 cm) to senescent *Themeda* (360-390 cm +) with small *N. neesiana* plants establishing underneath it.

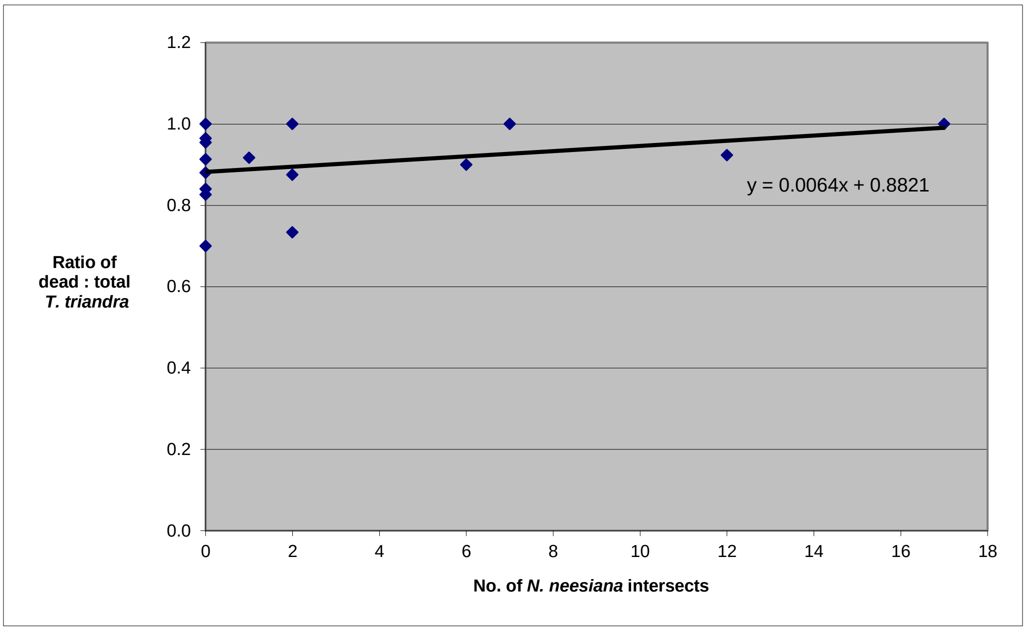

Figure 5.3. Relationship between the number of *N. neesiana* pin intersects at a transect point and the ratio of dead to living *T. triandra* pin intersects at that point, where the number of *T. triandra* pin intersects at the point was >9, at Yarramundi Reach patch G, 13 October 2007.

In the transect from Yarramundi Reach peg 0884 (Fig. 5.4) *N. neesiana* was strongly associated with totally senescent *T. triandra* (360-510 cm) and was almost totally absent at points where *T. triandra* had some living leaves (300-360 cm, 510 cm +). Other species, a mixture of native and exotic forbs and grasses, had little cover. On this transect there were only a few points at which *N. neesiana* was detected where the presence of *T. triandra* was reasonably high (>9 pin intercepts), and at all of them only dead *T. triandra* foliage was detected (Fig. 5.5).

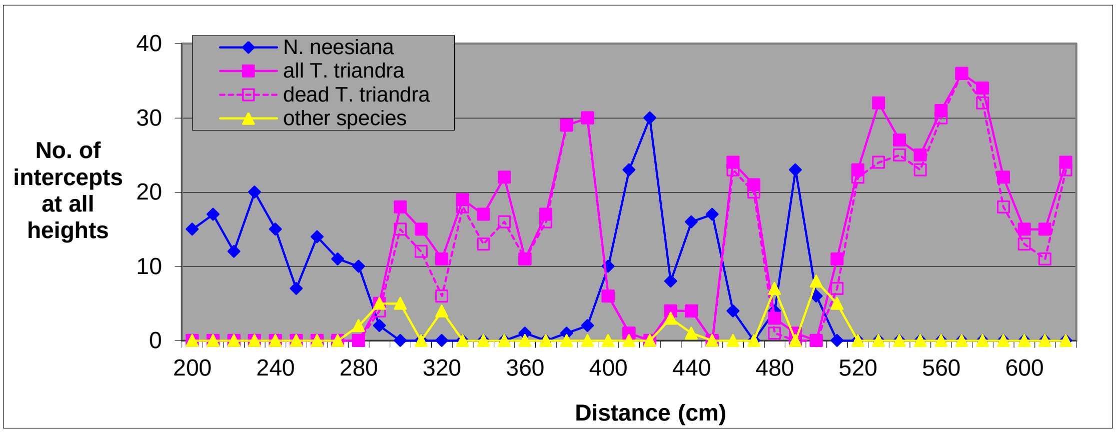

Figure 5.4. Distribution of *N. neesiana*, dead *T. triandra*, total *T. triandra* and other plant species along a pin transect at Yarramundi Reach peg 0884, 25 April 2008: transect from dense *N. neesiana* through a zone in which the two dominant grasses were intermixed (280-510 cm) into a dense *T. triandra* sward.

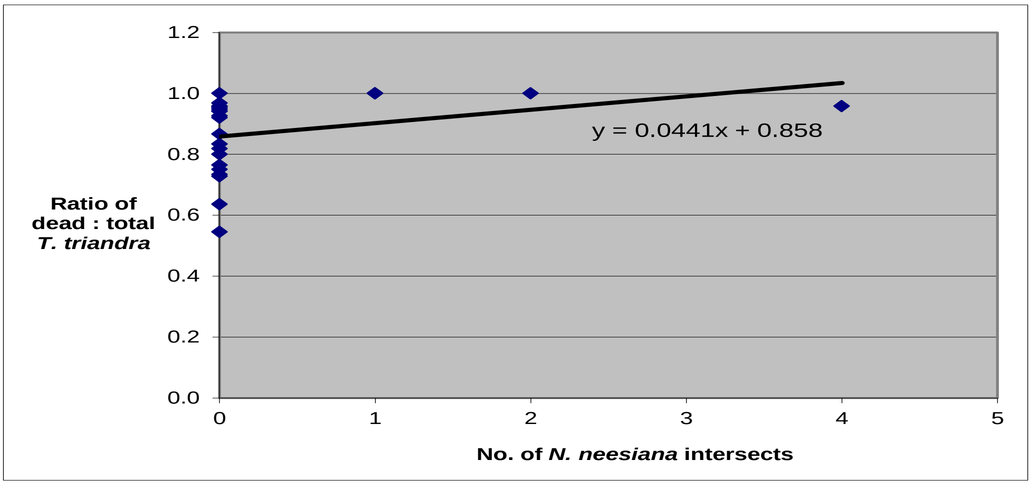

Figure 5.5. Relationship between the number of *N. neesiana* pin intersects at a transect point and the ratio of dead to living *T. triandra* pin intersects at that point, where the number of *T. triandra* pin intersects at the point was >9, at Yarramundi Reach peg 0084, 25 April 2008.

At Yarramundi Reach peg 0885 (Fig. 5.6) *N. neesiana* presence in the invasion zone at the edge of an *N. neesiana* patch was again strongly associated with extremely senescent *T. triandra* (c. 180-330 cm from the start of the transect). *Nassella neesiana* was absent from areas where *T. triandra* had higher proportions of living leaves (340 cm +). The other species, mainly the annual grasses *Bromus hordeaceus* L. and *Avena* sp. had little presence but were mainly concentrated in the highly senescent zone. There were a substantial number of points at which *N. neesiana* was detected where the presence of *T. triandra* was reasonably high (>9 pin intercepts), and the relationship reveals strongly increased presence of *N. neesiana* with increasing *T. triandra* senescence (Fig. 5.7).

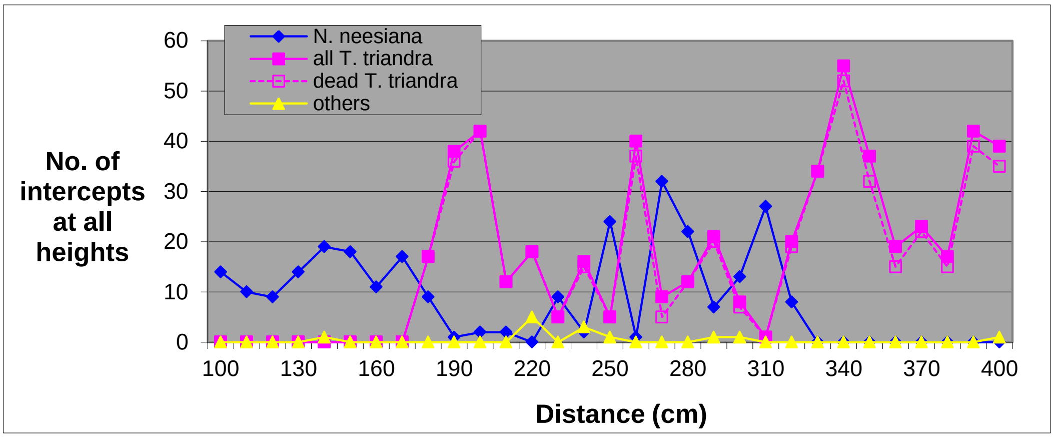

Figure 5.6. Distribution of *N. neesiana*, dead *T. triandra*, total *T. triandra* and other plant species along a pin transect at Yarramundi Reach peg 0885, 25 April 2008: transect from *N. neesiana* infestation through a complex zone of *N. neesiana* invasion (180-330 cm) into dense senescent *T. triandra*.

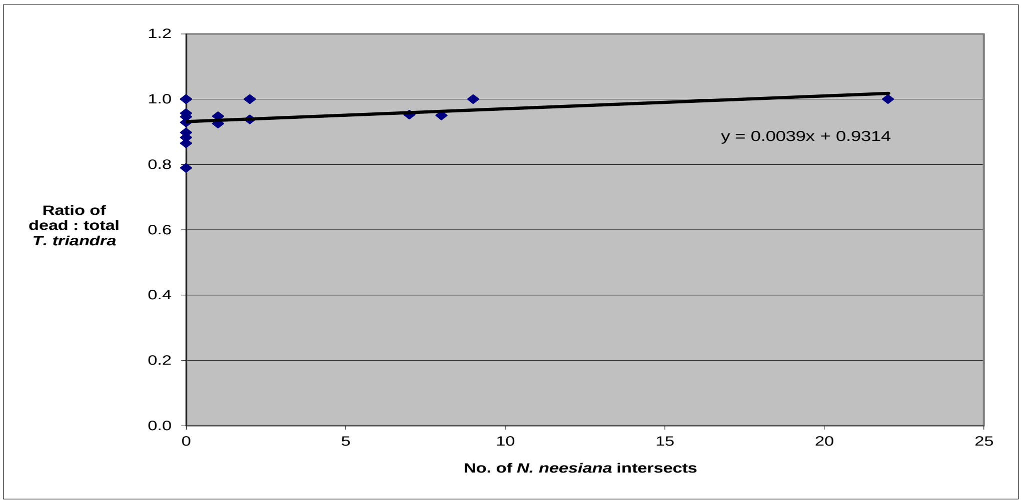

Figure 5.7. Relationship between the number of *N. neesiana* pin intersects at a transect point and the ratio of dead to living *T. triandra* pin intersects at that point, where the number of *T. triandra* pin intersects at the point was >9, at Yarramundi Reach peg 0085, 25 April 2008.

At Dudley Street grassland peg 0886 (Fig. 5.8) high *N. neesiana* presence occurred only at points with extremely senescent *T. triandra* (330-370 cm), but low presence was detected at some points with moderate amounts of living *T. triandra* (e.g. at 390 cm), and some points with fully senescent *T. triandra* had not been invaded (e.g. 120-140 cm). The peak of "other species" at 240-250 cm is a tussock of *Austrodanthonia* sp. Lower proportions of dead: living *T. triandra* were recorded at this grassland than at Yarramundi Reach. There were a substantial number of points at which *N. neesiana* was detected where the presence of *T. triandra* was reasonably high (>9 pin intercepts), and the relationship reveals a slight increase in the presence of *N. neesiana* with increasing *T. triandra* senescence (Fig. 5.9).

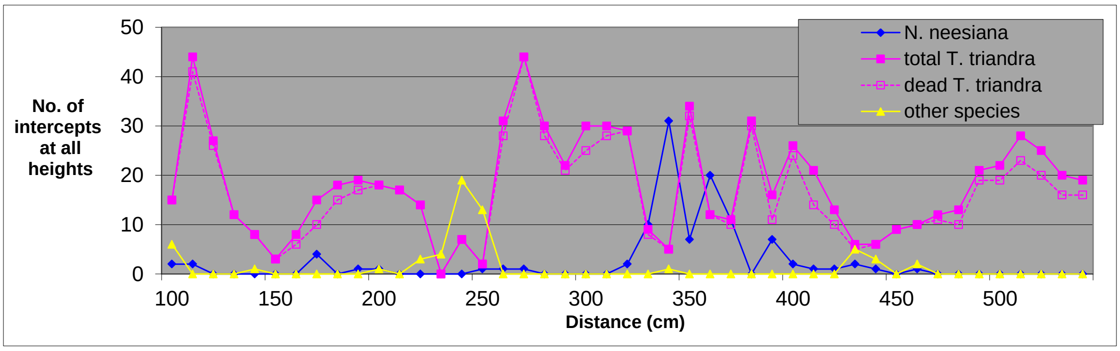

Figure 5.8. Distribution of *N. neesiana*, dead *T. triandra*, total *T. triandra* and other plant species along a pin transect at Dudley Street grassland peg 0886, 26-27 April 2008. Transect entirely in *T. triandra* grassland with variable incursions of *N. neesiana*.

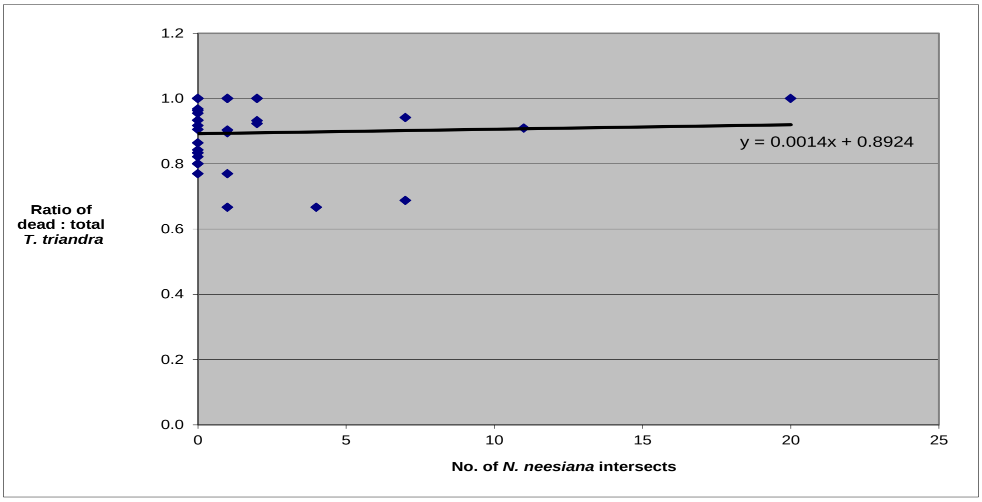

Figure 5.9. Relationship between the number of *N. neesiana* pin intersects at a transect point and the ratio of dead to living *T. triandra* pin intersects at that point, where the number of *T. triandra* pin intersects at the point was >9, at Dudley Street peg 0086, 26-27 April 2008.

The transect at Dudley Street peg 0887 ran approximately parallel with and 1-1.5 m away from that at peg 0086. Again, higher *N. neesiana* presence largely corresponded with highly senescent *T. triandra* (e.g. 260-289 cm), and at points with higher proportions of living *T. triandra* the exotic grass was more or less absent (Fig. 5.10). Pin intersects on the exotic forb *Plantago lanceolata* L. accounted for a very high proportion of “other species” and its presence was also associated with higher levels of *T. triandra* senescence. There were numerous points at which *N. neesiana* was detected where the presence of *T. triandra* was reasonably high (>9 pin intercepts). The relationship again reveals a marked increase in the presence of *N. neesiana* with increasing *T. triandra* senescence (Fig. 5.11).

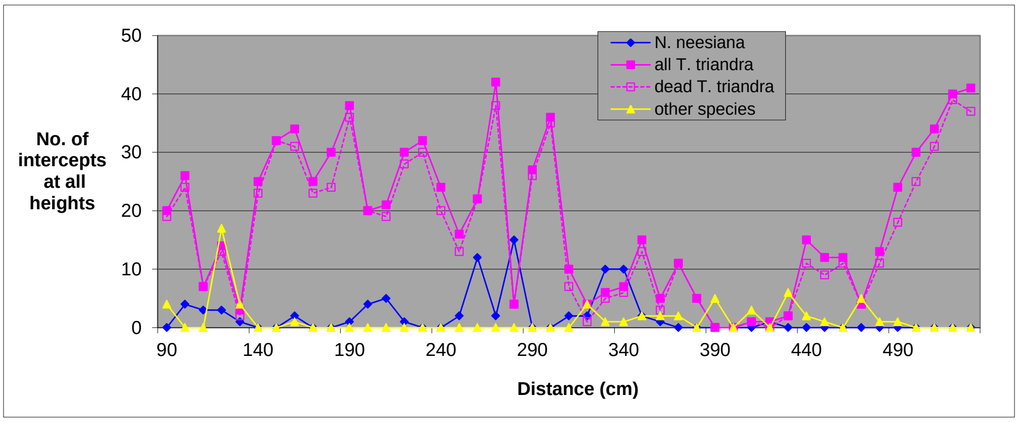

Figure 5.10. Distribution of *N. neesiana*, dead *T. triandra*, total *T. triandra* and other plant species along a pin transect at Dudley Street grassland peg 0887, 27-28 April 2008. The transect was entirely within a *T. triandra* sward of variable densities. Small *N. neesiana* were scattered amongst the *T. triandra*, particularly around highly senescent *T. triandra* tussocks.

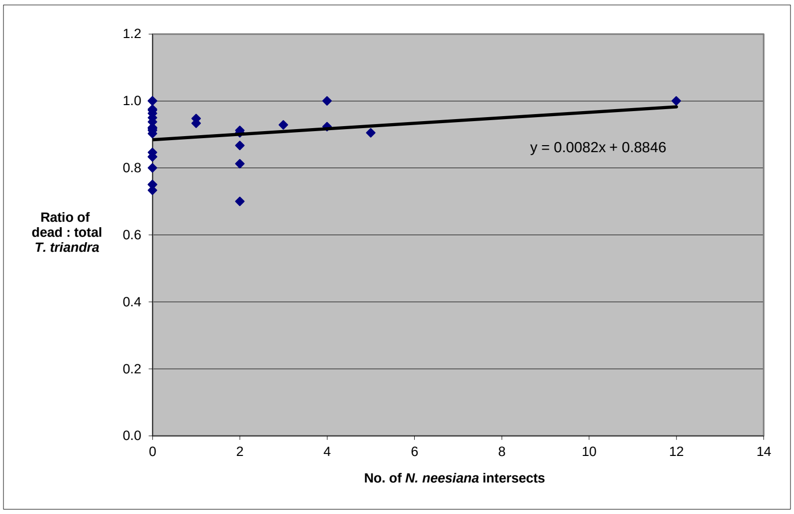

Figure 5.11. Relationship between the number of *N. neesiana* pin intersects at a transect point and the ratio of dead to living *T. triandra* pin intersects at that point, where the number of *T. triandra* pin intersects at the point was >9, at Dudley Street peg 0887, 27-28 April 2008.

The single short transect at Laverton North revealed only 100% senescent *T. triandra* and no co-occurrence of the two species (Fig. 5.12). Due to the sparse distribution and low cover of plants in areas where *T. triandra* was senescent at this grassland and the nearly uniformly high proportion of senescent *T. triandra* it proved impossible to position a straight line transect with points at 10 cm intervals to enable effects to be evaluated in the same way as the Canberra grasslands.

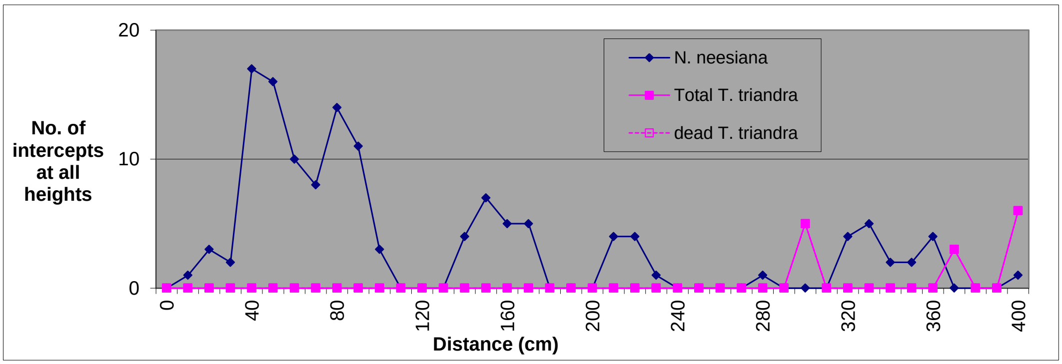

Figure 5.12. Distribution of *N. neesiana*, dead *T. triandra* and total *T. triandra* along a pin transect at Laverton North Grassland peg 0220, transect 11 March 2008. *T. triandra* was fully senescent and did not co-occur with *N. neesiana* at any point. No other species were detected.

The slopes of all fitted lines in the graphs was positive (Table 5.2), indicating that where the *T. triandra* sward was relatively dense there was an increasing presence of *N. neesiana* as the proportion of dead/total *T. triandra* in the sward increased. The two-sided sign test, that the slopes differed from 0, was affirmed, with a P value of 0.063. A P value <0.1 indicates significant evidence that where *T. triandra* was present and relatively dense, *N. neesiana* presence increased as the *T. triandra* became more senescent.

Table 5.2. Slopes of fitted lines relating the ratio of dead/total *T. triandra* pin intersects at a transect pin point to the number of *N. neesiana* pin intersects at that point, where the number of *T. triandra* pin intersects at a point was >9. 'Figure' refers to the figure in which the transect is illustrated.

Site	**Figure**	**Slope**
Yarramundi Reach Patch G	5.3	0.0064
Yarramundi Reach Peg 0884	5.5	0.0441
Yarramundi Reach Peg 0885	5.7	0.0039
Dudley Street Peg 0886	5.9	0.0014
Dudley Street Peg 0887	5.11	0.0082

Qualitative observations

Qualitative observations at Yarramundi Reach over the period from May 2007 to October 2008 indicated that active invasion of senescent *T. triandra* by *N. neesiana* was taking place throughout much of the grassland. Very high cover or closed swards of *T. triandra* were abundant. Simultaneous decline of *T. triandra* plants over areas of hundreds of square metres appeared to be occurring in large areas of the south-western part of the grassland, followed by broad scale occupation by *N. neesiana* (Fig. 5.13). In many cases areas of *T. triandra* dieback were invaded by annual grasses, notably *Avena* spp. (Fig. 5.13). In other areas senescence was more patchy and invasion by *N. neesiana* occurred as narrow bands (Fig. 5.14) or patchily.

At Dudley Street, observations over a similar period indicated that small areas of *T. triandra* senescence dieback were occurring in a mosaic pattern on the northern boundary of *T. triandra*-dominated areas in the west of the grassland (Fig. 5.15). *Nassella neesiana* invasions were occurring down slope from the edge of the *N. neesiana*-dominated area on the northern side of the site. *N. neesiana* was establishing around the bases of highly senescent but still living *T. triandra* tussocks, amongst dead tussocks with high standing litter and amongst collapsed, partially rotted-down tussocks (Figs. 5.16, 5.17). Nearby areas of still healthy *T. triandra* had high cover, with little intertussock space. The exotic weeds *Paspalum dilatatum*, *Avena* spp. and *Plantago lanceolata* also commonly invaded areas where *T. triandra* tussocks had died (Fig. 5.17).

Figure 5.13. **a.** A remnant island of senesced, dead *T. triandra* (in front of the *Callitris* sapling) surrounded by *N. neesiana* at Yarramundi Reach grassland, ACT, 21 October 2008; **b**. the dead *T. triandra* flowered strongly prior to dying, and **c.** the dead tussocks were initially invaded by *Avena* sp. (all the green growth), rather than *N. neesiana*.

Figure 5.14. *Nassella neesiana* intrusion into senescent *T. triandra*, Yarramundi Reach grassland, ACT, 24 October 2008, illustrating a typical mosaic pattern of *T. triandra* dieback.

At Laverton North senescence dieback of *T. triandra* was only apparent in long-unburnt areas to the west of the Reserve. Tussocks in this area generally were large, very widely spaced and over-run with dead material, and appeared to be very old; other plants were often tall and rank. Detached litter cover was extensive, and bare ground, unoccupied by other plant species was more prevalent than in burnt areas in the Reserve. Dieback was very patchy, occurring mostly with isolated tussocks. A sparse mosaic of *N. neesiana* invasion was apparent.

Figure 5.15. *Nassella neesiana* invasion front in the north-west section of Dudley Street grassland, 8 May 2007, looking approximately south-east, with Dudley Street in the far background. Dense cover of *T. triandra* in the background at right. Areas of dense dead *T. triandra* litter resulting from dieback are apparent in the foreground.

Figure 5.16. Remains of *T. triandra* tussocks after senescence dieback with seedlings of *N. neesiana* establishing in the centre, Dudley Street grassland, ACT, 13 October 2007.

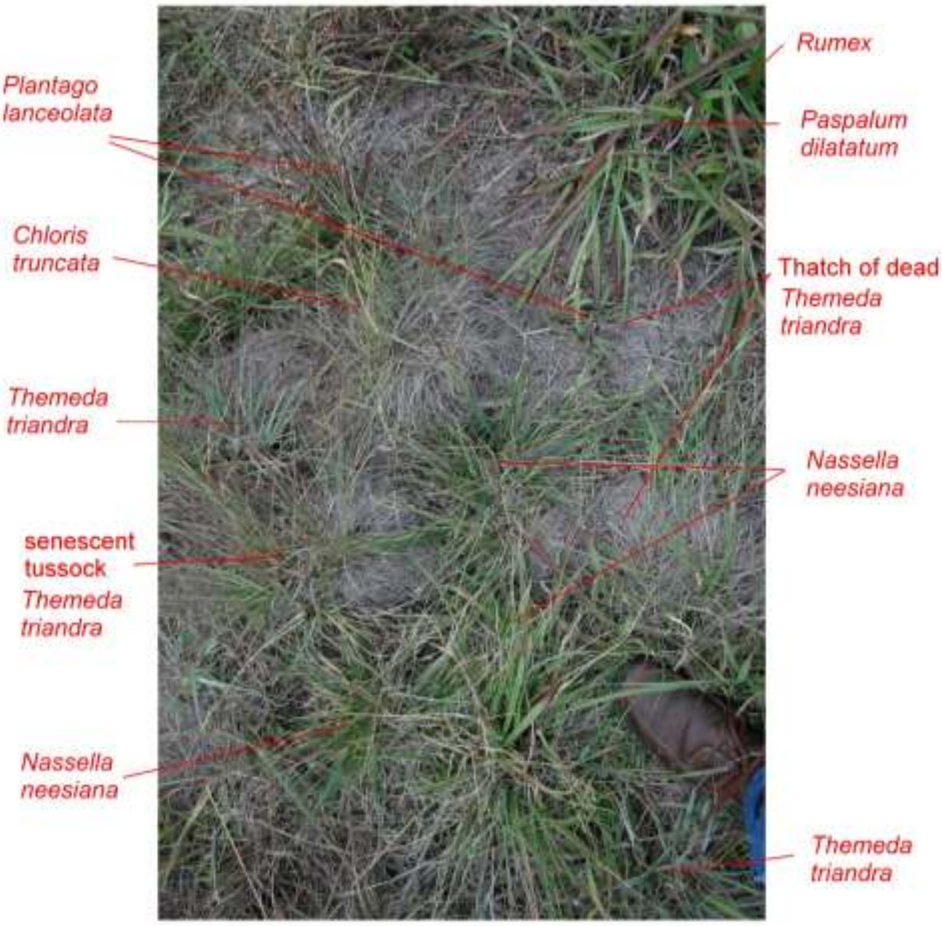

Figure 5.17. *Nassella neesiana* invasion zone in an area previously occupied by senescent *T. triandra* at Dudley Street grassland, 8 May 2007. A dense litter thatch of *T. triandra* foliage remains over much of the ground surface.

Discussion

Few other plant species were detected in the transects, which had been deliberately located in dense senescing *T. triandra,* and the areas dominated by *N. neesiana* that abutted such senescent stands. At Yarramundi Reach and Dudley Street these areas of *N. neesiana* occupied ground on which *T. triandra* senescence dieback had recently occurred (as evidenced from the aerial photography, Chapter 2). Other species in the areas with the highest levels of *T. triandra* senescence were commonly taxa typically associated with disturbed ground such as *Avena* sp., *Bromus* sp. and *Plantago lanceolata* (Kon and Blacklow 1995, Hussey *et al.* 1997, Jessop *et al.* 2006).

Fire-dependent C_4 Andropogoneae such as *T. triandra* typically disappear from swards, in higher productivity areas at least, in the absence of frequent fire (Bond *et al.* 2008). For example *T. triandra* cover decreased from >70% in frequently burnt South African grasslands to <10% when fires were excluded for 4 years or more (Uys *et al*. 2004). These fire-dependent grasses accumulate standing dead litter which shades out and kills shade-intolerant new tillers (Knapp and Seastedt, 1986; Everson *et al*. 1988), affecting the health of the plant, and this biomass accumulation can eventually result in sward collapse and dieback. At various times the frequency of fire in many temperate natural grasslands of south-eastern Australia has decreased without any alternative biomass reduction occurring.

Reduced fire frequency has resulted from deliberate fire suppression to protect urban and agricultural assets, fragmentation of larger tracts of native grassland into small parcels, so broad scale movement of fires is more limited, and from substitution of herbicidal management for fire (Williams 2007). In other cases burning for the benefit of the flora has been deliberately avoided so as to protect elements of the biodiversity thought to be susceptible to fire. In particular, fire has been deliberately excluded as a management tool in some grassland reserves because its effects on endangered species were not known. This was the case in relation to the Striped Legless Lizard *Delma impar* Fischer at Laverton North Grassland and Iramoo Wildlife Reserve in the past, and appears to be still a management consideration at Yarramundi Reach (Kukolic 1994, Hadden 1995, Frawley *et al.* 1995, Webster *et al.* 2003, O'Shea 2005). Fire frequency effects on this species are now better understood (O'Shea 2005), but for most other animal species the fire regimes that enable the retention of both plant and animal diversity have not been investigated.

The absence of management or constraints on the types of management possible has also resulted in fire regimes that have been inadequate to prevent senescence dieback. Lack of fire at Derrimut and Laverton North Grasslands led to significant documented *T. triandra* dieback, characterised as grassland 'collapse' in some sections of these Reserves. Based on the reported absence of senescence in 1986 (McDougall 1989) substantial senescence dieback must have occurred at Laverton North Grassland in the subsequent ten year period, by which time long unburnt areas had much reduced tussock density and were dominated by exotic species (Lunt and Morgan 1999a). This occurred prior to the imposition of regular ecological burning. Major invasions of *N. neesiana* in these grasslands appear to coincide with the excessively long fire-free periods.

The results and observations presented above support the proposition, and outcomes of other studies, that senescence dieback of *T. triandr*a enables *N. neesiana* invasion. Tussock and sward death evidently has a similar effect to that of herbicidal kill of the dominant grass (Chapter 5), enabling *N. neesiana* recruitment when there is propagule pressure. Replacement of the dominant native grass by *N. neesiana* must have significant biodiversity impact for species dependent upon *T. triandra*. However a major component of plant diversity has probably already been lost when senescence dieback occurs, because *T. triandra* swards have maintained very high cover over a prolonged period before the onset of dieback (McIntyre 1993, Kirkpatrick *et al.* 1995, Morgan 1998e, Prober *et al.* 2007).

Replacement of *T. triandra* by *N. neesiana* has continuing implications for the extent of grass litter accumulation. The C_3 *N. neesiana* also accumulates litter and is able to develop high biomass in many situations. Gardener (1998 p. 94) observed that production of large numbers of persistent culms often resulted in a “dense mat” of litter after the culms senesced and collapsed. Ens (2002a) found that infestations in Sydney woodlands formed dense litter mats. Bourdôt and Hurrell (1989b) found that uniform seedling swards resulted in cover of 53-69% and dry biomass of 2.7-3.4 t/ha after 13 months. On the Northern Tablelands of New South Wales annual biomass production was estimated to be 2.4 tonne ha^{-1} (Gardener 1998) similar to that found by Lunt and Morgan (1998a) for *T. triandra*. Gardener and Sindel (1998 pp. 76-77) stated that there is “anecdotal evidence” that *N. neesiana* causes loss of plant biodiversity in grasslands “because litter from the tall tussocks accumulates in the inter-tussock spaces and excludes shade intolerant species”. Diversity of bryophytes (mosses, liverworts) and lichens was also reported to decline following *N. neesiana* invasion “because the mosaic of substrates such as rocks and bare soil becomes covered with litter” (Gardener and Sindel 1998 p. 77, citing V. Stajsic pers. comm.). *Nassella neesiana* forms dense monocultures that can dominate pastures in southern New South Wales (Verbeek 2006), and dense clumps that exclude other pasture species in New Zealand (Bourdôt and Ryde 1986). Thus when senescence dieback of *T. triandra* is followed by *N. neesiana* invasion, the biodiversity impact of the senescence process may be intensified or continued by build-up of high litter levels by the exotic grass.

Dense grass litter in grasslands generally results in reduced plant biodiversity (Lenz *et al.* 2003) and absence of dense litter mats has generally been considered to be a requirement for maintenance of high plant diversity in Australian temperate grasslands (Wong and Morgan 2007). However, litter experiments in Dry *Themeda* grasslands in the ACT by Sharp (1997) over two growing seasons (18 months) found that litter retention resulted in higher native forb richness and cover than litter removal, with the opposite effect for exotic forbs, although there were individualistic responses for particular species. Generally plants with smaller seeds are inhibited more by litter because the germinants have inadequate energy reserves to penetrate the litter layer (Lenz *et al.* 2003). Manipulation of litter levels at finer temporal and spatial scales might therefore offer the potential to manipulate species composition in these systems (Sharp 1997). It would appear that the effects of grass litter accumulation on plant productivity differs seasonally and from site to site and species to species (Lenz *et al.* 2003), so widespread application of any findings may be difficult.

Implications for management

Management of *T. triandra* senescence requires regular monitoring of grass biomass, and biomass reduction of *T. triandra* in high biodiversity grassland dominated by this species is required to prevent loss of native plant diversity, including loss of the dominant grass, where *T. triandra* can achieve high cover. Historically, in the absence of exotic species, senescence dieback would once have resulted in regrowth of *T. triandra* or other native species, perhaps resulting in shifting patterns of dominant grasses and forb rich areas. But now that a diverse range of exotic species is universally present, senescence dieback frequently results in weed invasion and needs to be prevented. This type of management, in addition to protecting native biodiversity, is also likely to help minimise invasion by vigorous exotic perennial grasses such as *N. neesiana*.

Improved management might be facilitated by a guide that illustrates cover values and intertussock space values and the proportions of dead and living biomass of *T. triandra*. Any such guide would need to take account of site characteristics and climatic variations, which can result in widely different rates of biomass accumulation. Any guide would also have to acknowledge that some native grassland systems are not subject to senescence dieback.

Chapter 6. Soil moisture depletion in spring – a possible mechanism for *N. neesiana* impact

"Phenological complementarity promotes coexistence in ... plant communities".

Cleland *et al.* 2006 p. 13742.

Summary

Soil moisture content under swards of *N. neesiana* and *Themeda triandra* was measured at points spaced 0.1 m or 1 m apart along 6 transects with a total length of 69.9 m, with repeated measurement along two transects (37.9 m) at Yarramundi Reach Grassland in spring. All transects showed markedly lower sub-surface soil water content under *N. neesiana* than under *T. triandra*. The difference was highly significant. This was the case whether the *T. triandra* was senescent or healthy and when both species were either unmown or mown short, and appeared to be independent of micro-topographic position, surface soil features and time of day. Soil drying in spring probably contributes to ongoing losses of native vascular plants in areas invaded by *N. neesiana*, potentially consolidating the occupation of sites by *N. neesiana*, and may drive patch expansion by disadvantaging immediately adjacent native C_4 grasses. At a landscape scale, widespread replacement of native C_4 grasses by *N. neesiana* is likely to reduce runoff and increase deep drainage, resulting in increased salinity, soil acidification, and eutrophication downstream in the catchment. If these effects were happening, *Nassella neesiana* would have the potential to affect biodiversity far beyond the areas infested.

Introduction

Invasive plants can severely modify hydrological cycles (Vidler 2004). Competition for soil water may be a widespread mechanism by which invasive plants cause biodiversity impact, but few studies have provided firm demonstrations of this (Levine *et al.* 2003). Athel pine *Tamarix aphylla* (L.) H. Karst. (Tamaricaceae) in inland Australia lowers the water table, alters stream flow and flooding regimes and ultimately affects salinity levels (Griffen *et al.* 1989). Markedly increased rates of soil drying by high densities of the invasive annual *Bromus tectorum* L. have been found to adversely affect seedlings of a native perennial grass when the two were germinated simultaneously (Evans & Young 1972). Extending this work, Melgoza *et al.* (1990) demonstrated that *B. tectorum* significantly decreased the productivity of the co-occurring native grass *Heterostipa comata* (Trin. & Rupr.) Barkworth by reducing soil water content and the internal water potential of the grass. In contrast the C_4 grass *Andropogon virginicus* L., a native of the southern USA, is invasive in Hawaiian rainforest where it develops a high biomass of dead shoots that reduce evaporation rates from the soil, and also passes through an inactive senescent phase during which transpiration is reduced, resulting in excess water in the soil, increased runoff and accelerated erosion (Mueller-Dombois 1973).

Nassella neesiana is a C_3 or cool season grass that produces most of its vegetative growth from autumn to spring (April to October) and flowers mainly during spring and early summer (September to December) in south-eastern Australia (Snell *et al.* 2007). It produces substantial green biomass in winter but very little in summer (McLaren *et al.* 1998) when tussocks usually bear large numbers of persistent dead culms and leaves (Gardener *et al.* 2005).

Themeda triandra, the most important dominant native grass in the higher rainfall temperate lowland grasslands in the region, is a C_4 grass of the NADP-ME type (Hattersley 1986) that flowers and undertakes most of its growth from the middle of spring into summer (Groves and Whalley 2002). The optimum temperatures for *T. triandra* growth are in the range 25-35ºC (Wijesuriya and Hocking 1999). Below a threshold of 15°C the sward 'hays off' and the grass is dormant in winter and spring in southern Australia (Dunin 1999).

The phenology of *T. triandra* and the extent to which its growth is concentrated in summer is dependent to some extent on particular seasonal and site conditions. In the NSW Riverina *T. triandra* "commences new season's growth in late spring ... puts out new leaves until the soil moisture is depleted" and ceases growth "before the onset of heavy frosts" (Leigh and Mulham 1965 p. 30). In southern Victoria rapid growth commences in October, optimum growth rates occur in late spring and early summer if there is adequate soil moisture, growth continues in summer if soil moisture is not limiting, flowering and seed shed occurs mainly in mid-summer (January-February), and growth continues in autumn until constrained by cooler temperatures (Groves 1965, Morgan 1994, Lunt and Morgan 2002). Groves (1965) recorded inflorescences from early November to early December over two years in one Melbourne grassland. On the New England Tablelands (1060 m altitude) Trémont (1994) recorded flowering occurring in 'mid season' (any two months from November to February of December-January only) in grazed areas and late season (January to April) in ungrazed areas. Chan (1980) studied the phenology of *T. triandra* at Yarramundi Reach over the period of 9 months from September 1973: floral initiation was calculated to commence when day length reached 12 hr 33 min (36 minutes longer than for *Austrostipa bigeniculata* and *Austrodanthonia* spp.), head emergence commenced in mid October, anthesis occurred from c. 12 November to 9 January, and seed fall occurred over a period of c. 3 weeks to the end of

January. Leaf biomass production increased rapidly in early November, fell during December due to low rainfall and continued at levels of c. 30-40 g m^{-2} (dry weight) through until the end of April. Production of new reproductive stems reached a strong peak during mid November and monthly stem biomass production continued at high levels from January to April. Similar biomass production patterns were observed by Groves (1965) in southern Victoria. However McDougall (1989) reported flowering mainly in mid-spring corresponding with the period of highest productivity in Melbourne region grasslands, with seed shed between November and February, usually peaking in early January, but with an additional later peak if there was early summer rain. On the southern tablelands of NSW growth is limited by low temperatures between May and October and potentially by inadequate soil moisture when temperatures are favourable during the remainder of the year (Dunin and Reyenga 1978).

C_3 species as a general rule have lower water use efficiencies than C_4 species, that is they use more water per unit of carbon dioxide fixed (Radosevich and Holt 1984, Ghannoum 2009). C_4 grasses have greater stomatal resistance and greater stomatal control of transpiration than C_3 species (Dunin and Reyenga 1978) and are able to use greater amounts of water when vapour pressure deficits are high (i.e. in dry summer conditions) (Singh *et al.* 2003). Australian C_4 species use, on average, five times more soil water in summer than in winter, and have a summer water use efficiency twice that in winter (Singh *et al.* 2003). But the C_4 photosynthetic pathway is highly sensitive to water stress, equally or more so than the C_3 pathway (Ghannoum 2009).

Use of soil water by *T. triandra* is directly linked with its seasonal growth pattern, and reaches a maximum coincident with production of new leaf growth in summer (Dunin 1999). Swards of *T. triandra* are able to more effectively trap rainfall, reduce runoff and increase evaporation than swards of C_3 grasses (Singh *et al.* 2003). Dunin and Reyenga (1978) found that on an annual basis, 20% of water loss from a *T. triandra* grassland was by evaporation of dew and intercepted rainfall and 80% by evaporation from soil water and transpiration, and that plant control of evaporation was greater during the period of dormancy than during the growing period. During the dormancy period the standing dead biomass of *T. triandra* in ungrazed swards restricts evaporation to less than 50% of that in grazed swards, so conserving soil moisture prior to the growing period (Dunin 1999). McDougall (1989) found that total standing biomass (including substantial proportions of unattached litter) remained constant or fell slightly from the end of one growing period to the start of the next, although the proportion of green foliage declined from a mid spring peak of c. 85% to a June low of c. 35%. Conservative use of water by *T. triandra* during winter and early spring enables carry-over of soil moisture into its growing period, and this strategy is one factor that has enabled the species to be successful in temperate zones with unreliable summer rainfall (Dunin and Reyenga 1978). When the growth period commences again in summer, the conserved moisture is used, and soil moisture is depleted to a very low level by the end of the growing period (Dunin 1999). McDougall (1989) recorded soil moisture values ranging between c. 10 and 27% between September and January, and falls to c. 3-6% in February in burnt and unburnt swards at Laverton North Grassland.

Bolger *et al.* (2005) compared the drought tolerance of a range of native and exotic grasses widely present in south-eastern Australia in pot experiments. *Themeda triandra* had neither high nor low drought tolerance, having good dehydration tolerance and avoidance as the soil dries, but poor dehydration avoidance (high epidermal conductance) when transpiration reaches minimum levels. *Themeda triandra* folds its leaves to reduce dehydration. These findings may be misleading because there is some evidence that unlike the other native species tested, *T. triandra* may avoid dehydration by being deep rooted, and typically has good survival in a dormant condition during drought in south-eastern Australia (Bolger *et al.* 2005). Such experimental evidence also ignores other drought avoidance strategies such as litter accumulation.

Themeda triandra is phenologically complementary to the bulk of the native grassland flora, so largely avoids direct competition for resources with these other plants. *Themeda triandra* has a predominantly summer growing season, offset from the spring growing season characteristic of most of the native grasses and forbs (Patton 1935, Willis 1964, Groves 1965, Lunt *et al.* 1998, Groves and Whalley 2002). The major flowering period of the native grassland flora corresponds with the time that evaporation begins to exceed precipitation (Patton 1935, Willis 1964). As moisture levels decline, the flowering period rapidly ends and "most of the vegetation passes into a resting stage until the following autumn" (Patton 1935 p. 172), being practically dormant from December to April (Willis 1964). Chan (1980) recorded the flowering periods of 61 native species at Yarramundi Reach and found that 33 flowered in September, 51 in October, 49 in November, 32 in December, 28 in January and 7 or fewer species in every other month. Exotic species also showed a marked flowering peak in October and November. However particular conditions may alter this pattern: Davies (1997) found that some native perennials grow actively in summer if rainfall is significant, while Trémont (1994) recorded the peak flowering period was around one month later in ungrazed areas than in grazed areas, and considered native perennials to typically flower both in spring and autumn.

When *T. triandra* is replaced as the dominant grass by *N. neesiana* the phenological complementarity of soil water utilisation with the much of the native flora is presumably reduced: the spring growing and flowering *N. neesiana* would be expected to compete more strongly for soil resources with most of the native grasses and forbs during this critical period. Depletion of soil moisture during spring is one potential mechanism by which *N. neesiana* could have ongoing deleterious impacts on native plant diversity, including the exclusion of *T. triandra* and other native grasses from sites that it occupies. For example, continued soil moisture depletion during successive springs could result in lower fecundity and recruitment of native species in *N. neesiana* patches as patch size or patch age increases.

Depletion of soil moisture by *N. neesiana* prior to the growing period of *T. triandra* would also presumably have a negative impact on subsequent growth of *T. triandra* in areas close to or within *N. neesiana* infestations. Robertson (1985) argued that *T. triandra* was replaced by other grasses as a result of competition for water and McDougall (1989) concurred with this possibility, finding that *Austrostipa* and *Austrodanthonia* species took its place in ‘tree halo’ areas, where competition for water in the deeper layers of soil is presumably also important. Possibly *T. triandra* is most affected by this competition when the conditions it requires for growth are at their most marginal – for example when plants are in senescence, or subjected to shading.

To investigate these propositions, a series of simple measurements of soil moisture content near the surface were taken to determine whether soil moisture differences existed between areas where *N. neesiana* was the dominant grass and where *T. triandra* was dominant.

Methods

Soil moisture measurement

Soil moisture readings were taken with an MP406 moisture probe (ICT International Pty Ltd, no date). The probe is a battery powered, hand held device that measures the dielectric constant of the soil, giving values as direct volumetric soil water, from 0 to 100%. Measurement is based on the principle that the dielectric constant of water is approximately equal to 80, whereas that of soil is c. 3 or 4 and that of air is 1, so any change in the dielectric value of the soil matrix directly indicates a changed water content. The device uses high frequency radio techniques to measure soil capacitance. The probe consists of three stainless steel needles 60 mm long and 14 mm apart, that are pushed into the soil surface. It thus measures the capacitance of the volume of soil probed by the needles, from the surface to 60 mm depth.

Differences between laboratory-measured volumetric soil water content and the measurements obtained with the device are expected to be ±2-5% (ICT International Pty Ltd no date). However, in the work reported here, the absolute calibration of the device is unimportant, since the purpose was to determine relative differences between soils under *N. neesiana* and those under *T. triandra*. Nevertheless the absolute differences are useful, within the limits of measurement of the instrument, and the actual moisture values are valuable as data in their own right.

Sampling

Only near-surface soil moisture measurements were taken, i.e. at probe depth, without supplementary augering to greater depths. The probe was pushed into the soil until the needles were inserted for their full 60 mm length. This is likely to be in the broad vicinity of the primary root zone of the grasses under consideration. When present, litter mats or other objects were removed from the ground surface immediately before taking readings. Measurements were taken along straight line transects through the boundaries of *N. neesiana* patches, at intervals of 1 m in dense mature grassland, or at intervals of 0.1 m in short mown grassland where small tussocks provided less impediment to probe entry to the soil (Table 6.1). The short distances between probe readings also enabled better qualitative evaluation of the spatial variation of soil moisture levels. The cover and condition (*vis a vis* degree of senescence) of the *T. triandra* swards were subjectively assessed and the micro topographic positions of the grasses along the transect were recorded. Measurements were taken along transects through swards with different characteristics. Two transects (‘D’ and ‘mown zone’) were repeated a few days apart. The sampling was restricted to a relatively discrete portion of the grassland at intermediate topographic positions. Transects were deliberately located to avoid areas where there were indications of possible soil differences under the two vegetation types, such as hard pans, dumped soil or textural contrasts.

Transects were undertaken in six different areas and were repeated in two separate sections of Yarramundi Grassland Reserve, giving a total of eight sets of measurements (Table 6.1). Total lengths of transects was 69.9 m, or 107.8 m if the repeat sampling is included.

Table 6.1. Soil moisture transect samples at Yarramundi Reach grassland, October 2008.

Transect	Date	Time	Sampling interval (m)	Transect length (m)	Sward characteristics
Patch E transect 1	17/10/2008	5.15 pm	1	7	*N. neesiana* mature, dense 60-80% cover; *T. triandra* senescent, close to 100% cover
Patch E transect 2	17/10/2008	5.30 pm	1	8	
Patch B, centre	17/10/2008	5.45 pm	1	11	*T. triandra* variably senescent with cover of 100 or 90%
Patch B, west	17/10/2008	5.55 pm	1	6	*T. triandra* area mixed sward with *N. neesiana* 5 or 10%
Transect D	17/10/2008	6.20 pm	1	31	*T. triandra* mainly dense, senescent 90-100% cover
Transect D	22/10/2008	10.55 am	1	31	
Mown zone	19/10/2008	7:00 pm	0.1	6.9	Infrequently mown area, short turf with more diverse forb flora.
Mown zone	22/10/2008	12.30 pm	0.1	6.9	

Rainfall

Rainfall at the nearest measuring station, at the Australian National Botanic Gardens, c. 2.6 km north-east of the study area was below the long term average during the preceding two months, and during the month when soil moisture measurements were made was less than half the average (Table 6.2).

Table 6.2. Rainfall (mm) at the Australian National Botanic Gardens, Canberra, August to October 2008 and 1968-2010 averages (Source: Bureau of Meteorology, Australian Government).

	August	**September**	**October**	
Average 1968-2010	55.7	62.6	67.6	
Monthly totals 2008	24.4	48.0	33.4	
Daily totals 2008			9.4	4 October
			2.4	5 October
			9.0	7 October
			12.2	14 October
			0.4	22 October

Analysis

Sample soil moisture transects are presented as simple linear plots. For statistical analysis, means were calculated for moisture readings under areas dominated by either *T. triandra* or *N. neesiana*. Data points where neither grass was clearly dominant were excluded. For the purposes of significance testing, the data for the two Patch E transects and the two Patch B transects were combined, and the later sample for both Transect D and the mown zone were not considered independent from the earlier samples and were excluded. Data was analysed using general analysis of variance (ANOVA, F test). Means were $\log_{10}$ transformed.

Results

Samples of transect date are provided in Figures 6.1 and 6.2. Areas dominated by *T. triandra* consistently showed higher soil water contents than areas dominated by *N. neesiana* at Yarramundi Reach in October 2008 (Table 6.3).

For the selected and combined transects, the soil moisture difference under the two dominant grasses was highly significant (Table 6.4), and the overall ratio of soil moisture under *T. triandra* to that under *N. neesiana* was 4.7 (95% confidence interval = 3.0, 7.3). On average, *N. neesiana* depleted soil moisture to 27% of that under *T. triandra*.

Time of day did not appear to alter these relationships (e.g. Fig. 6.1), nor did upslope or downslope position appear to have much influence (Fig. 6.2). Within stands of *T. triandra*, measured soil moisture levels varied by large factors, sometimes 2-4 times.

Table 6.3. Mean soil moisture (%) under *N. neesiana* and *T. triandra* along transects at Yarramundi Reach grassland, October 2008.

Transect	**Date**	**Time**	**No. of soil moisture readings**		**Mean soil moisture (%)**		**Ratio of mean soil moisture *N.n.* : *T.t.***
			Nassella neesiana	***Themeda triandra***	***Nassella neesiana***	***Themeda triandra***	
Patch E transect 1	17/10/2008	5.15 pm	3	3	3.97	26.20	0.15
Patch E transect 2	17/10/2008	5.30 pm	3	3	5.43	26.53	0.20
Patch B, centre	17/10/2008	5.45 pm	4	8	4.25	13.18	0.32
Patch B, west	17/10/2008	5.55 pm	2	3	6.35	22.23	0.29
Transect D	17/10/2008	6.20 pm	12	19	4.84	19.84	0.24
Transect D	22/10/2008	10.55 am	12	19	0.61	12.66	0.05
Mown zone	19/10/2008	7:00 pm	33	29	0.41	2.55	0.16
Mown zone	22/10/2008	12.30 pm	33	29	0.11	1.09	0.10
Total			102	113			
Grand mean					**1.38**	**9.32**	**0.15**

Table 6.4. Significance testing of mean near-surface soil moisture under *N. neesiana* and *T. triandra* along selected transects at Yarramundi Reach grassland, October 2008.

	Log transformed mean	**SE**	**F pr**	**Back transformed mean (%)**
N. neesiana	0.424	0.0617	**0.0017**	2.65
T. triandra	1.093			12.39

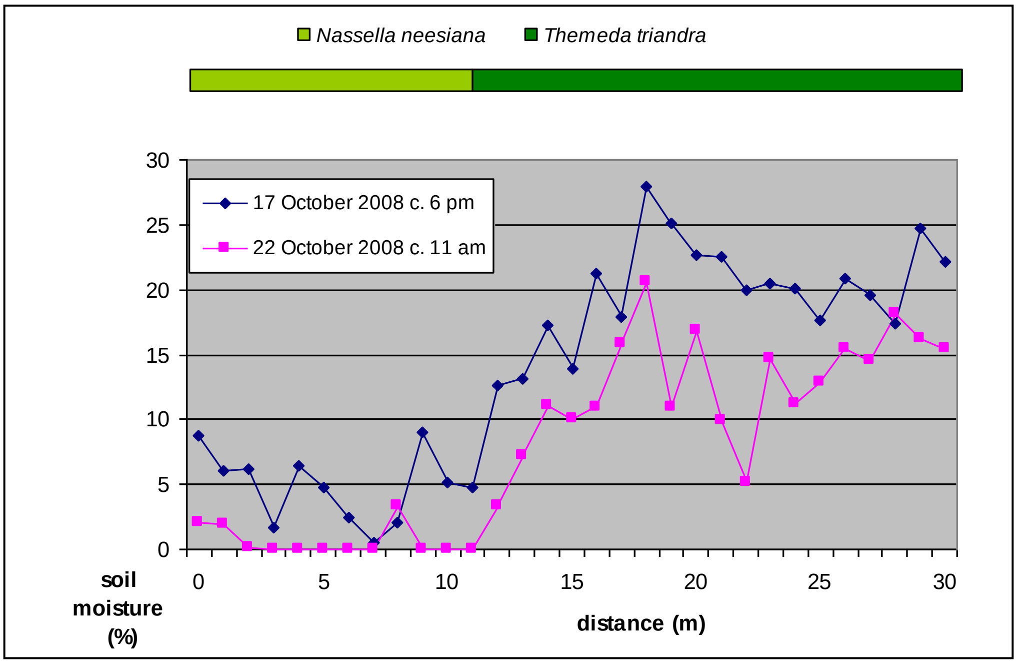

Figure 6.1. Near-surface soil moisture transect from *N. neesiana* into senescent *T. triandra*, Yarramundi Reach, ACT, 17 and 22 October 2008, Transect D. Despite light rain (1-2 mm) in the late evening of 21 October, the soils were drier during the late morning on 22 October than they were during the late afternoon of 17 October.

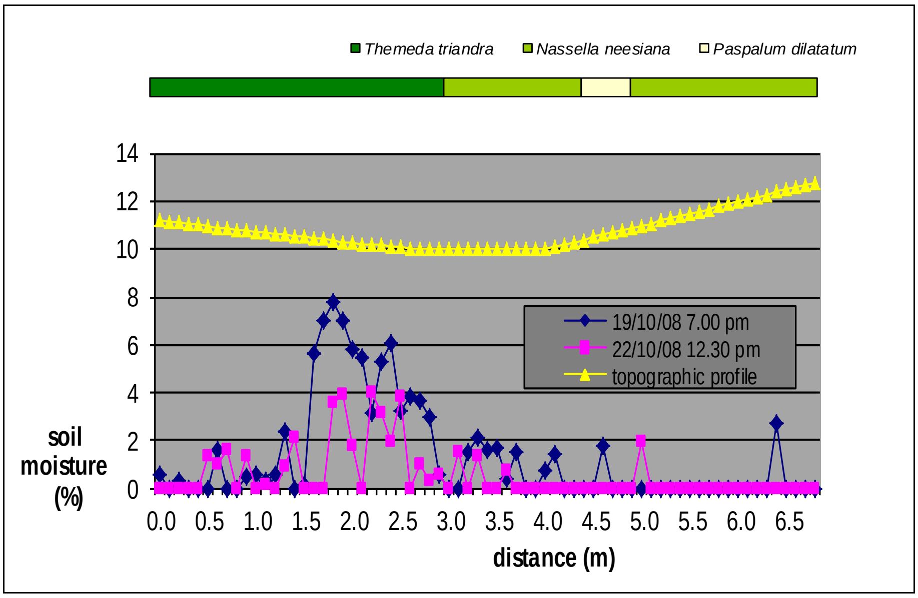

Figure 6.2. Near-surface soil moisture transect in a mown zone from *T. triandra* grassland into an *N. neesiana* patch at Yarramundi Reach, ACT, 19 and 22 October 2008. The "topographic profile" approximately illustrates the relative slopes and elevations along the transect.

Discussion

The data presented here are limited to a single grassland and a short period in October during a single year, but consistently shows that the near surface soil moisture levels under *N. neesiana* were markedly lower than those under *T. triandra*. The difference in soil moisture under the two grass types appeared to be independent of micro topographic position, aspect and time of day. There was no indication of soil differences along any of the short transects, and significant soil differences are unlikely to occur at the scale of investigation. *Nassella. neesiana* significantly depleted surface soil moisture in spring, often to very low levels, compared to the dominant native grass in the areas sampled.

Little information appears to be able available on the depth distribution of roots of *N. neesiana* and *T. triandra*. Groves (1965) found that only a small fraction by weight of roots penetrated below 15 cm in a *T. triandra* grassland at St Albans, Victoria. Dunin and Reyenga (1978) inferred that there was little root extraction of soil water at a depth of 78 cm in *T. triandra* grassland at Krawarree, New South Wales. Perennial grasses can extract soil moisture from depths below 1 m, but on basalt soils roots occur mostly in the top 80 cm of soil (Singh *et al.* 2003). Nie *et al.* (2008) found that the root "density" (roots per m^2) of a range of perennial grasses in the top 10 cm of soil was 2-4 times that in the 10-110 cm zone and that the deepest roots were usually not below 1.5 m, on a range of soil texture types.

Most of the root mass of *N. neesiana* and *T. triandra* is probably in the top 10 cm of soil, so measurements of soil moisture in the top 6 cm are likely to be a reasonable indicator of water content over the whole rooting profile.

Information is not available on the field capacities and wilting points of soils at Yarramundi Reach but values of volumetric soil water content close to zero suggest that soil water deficits under *N. neesiana* were common. Such conditions would create stress for co-occurring plants and impact upon their growth.

McDougall (1989) reported soil moisture values (at unstated depths) of c. 20-27% under *T. triandra* at Laverton North in October 1987. Many of the values reported here are within this range. The results are consistent with the findings of Dunin and Reyenga (1978) that conservative water use by *T. triandra* during its dormancy period results in higher soil water content under *T. triandra* swards than under C_3 dominated pasture in late spring. The results are also consistent with known characteristics of C_3 pasture grasses: they use soil water inefficiently, increase their water use in spring at the time when evaporation is increasing, and thus limit their own growth and that of summer growing species (Johnston *et al.* 1999). By depleting soil water in spring, *N. neesiana* could be controlling the resource available for the later-growing *T. triandra* and thereby disrupting one of the most fundamental hydrological patterns of the ecosystem.

It can be deduced that this pre-emption of soil water use by *N. neesiana* will impact on later growing *T. triandra* and may contribute to its replacement, or ongoing exclusion once *N. neesiana* has occupied previously disturbed sites. Competitive displacements of native grasses by exotic African grasses resulting from differential competitive responses to water stress have been found in Venezuelan savannahs by Baruch and Fernández (1993).

What has not been demonstrated is whether the soil moisture pattern reverses in summer when *N. neesiana* is dormant and *T. triandra* has entered its main phase of growth, as would be expected. Demonstration of this corollary should be one aim of a more thorough investigation of the significance of soil moisture depletion as a possible mechanism by which *N. neesiana* causes a biodiversity impact.

Impact on native plant diversity

The grasslands of temperate south-eastern Australia regularly suffer summer and early autumn droughts (Leeper 1964) and the early-mid spring growth peak of *N. neesiana* would appear to much better coincide with the usual periods of high precipitation than the late-spring and summer growing period of *T. triandra*. Under these conditions *N. neesiana* would *prime facie* appear to have superior competitive abilities to *T. triandra*. In years when rainfall is limiting to native grassland growth, and that may be most years, established *N. neesiana* presumably uses soil moisture reserves that would otherwise be available to the predominantly spring-growing native forbs, and sabotages the growth strategy of the later-growing *T. triandra* by limiting soil moisture accumulation during the period when rainfall is more reliable. A similar process has been recorded where annual pasture replaced an *Austrodanthonia*-dominated understorey in *Eucalyptus camaldulensis* Dehnh. woodland in the South-East of South Australia (Specht 2000). The seasonal growth pattern of the exotic Poaceae, *Trifolium* spp. and Asteraceae that dominated the pasture resulted in depleted surface soil water before the summer growth period of the native understorey species, and they used soil water at a greater rate than the native grasses. The increased evapotranspiration reduced the growth of the summer-growing native perennial grasses, and eventually led to their disappearance, along with native perennial herbs. These competitive advantages of exotic C_3 grasses, resulting from a phenology that enables maximum growth during cool-season wet periods, have been implicated in the major historical declines of *T. triandra* in Australian temperate grasslands (Mack 1989).

Soil moisture depletion in spring by *N. neesiana* impacts during the main growth and flowering period of the native grassland flora and therefore must detrimentally affect the productivity and fecundity of this flora. Depletion of spring moisture restricts the opportunities for establishment of spring germinating species (Johnston *et al.* 1999).

Since *N. neesiana* patches consist of proportionally more biomass generated from spring growth and spring soil moisture than areas dominated by *T. triandra*, these infestations must also deplete soil moisture prior to the main growing period of *T. triandra*, placing this dominant species under additional stress when summer rains are poor. The effect on existing plants would be expected to be greatest on remnant tussocks within *N. neesiana* patches and on plants close to patch edges. Similar effects would occur where *N. neesiana* was invading into disturbed areas within *T. triandra* dominated grasslands, reducing *T. triandra* opportunities for recruitment. The availability of seed and the presence of sufficient soil moisture are the major factors affecting seedling recruitment of *T. triandra* (O’Connor 1996). Reduced soil moisture reduces new growth and thus could be expected to reduce seed production and recruitment. Seeding is reportedly not prolific in dry summers (Leigh and Mulham 1965). *T. triandra* seeds usually germinate in spring in the Melbourne region (McDougall 1989, McDougall and Morgan 2005), and Stafford (1991) reported germination under experimental conditions in October in South Australia, while seedlings generally establish in spring and summer in temperate Australia when soils are moist (Virtue and Melland 2003). Soil moisture depletion by *N. neesiana* is thus likely to negatively affect both fecundity and recruitment of *T. triandra*.

Nassella neesiana tussocks have a centrifugal growth form, continually expanding their size, and growing outward. Experiments with *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex

Griffiths have demonstrated that such directional growth results in higher water use in the direction of expansion than in the trailing direction (Lauenroth and Aguilera 1998). Differential depletion of soil water at the edge of expanding *N. neesiana* fronts can thus be a mechanism driving further infestation expansion, and establishment and occupation in areas where *T. triandra* is dying away due to senescence, or has been removed by other disturbance mechanisms.

In south-eastern Australian natural grasslands where *T. triandra* is the dominant grass, the above scenario suggests that any negative impact on *T. triandra* growth and reproduction is effectively a positive feedback for *N. neesiana*, which may be partially propelling its own invasion through patch expansion via spring soil moisture depletion, or at least enable it to maintain occupation of sites it has invaded against re-establishment by *T. triandra*. Thus, increased early summer aridity created by C_3 grass water use has been cited as a likely cause of widespread decline of summer-active grasses throughout the region (Johnston *et al.* 1999). The effect is better characterised as phenological displacement (Cleland et al. 2006) than as competitive superiority.

Effects at the landscape scale

Dunin and Reyenga (1978) and Dunin *et al.* (1978) presented evidence that *T. triandra* grassland uses less water than sown pastures of exotic C_3 grasses, and has a water use pattern that results in greater runoff. Soil water under *T. triandra* is close to field capacity in late winter and spring is wholly depleted by the end of summer, and the soil remains dry longer into the autumn. Excess rainfall in *T. triandra* grasslands largely results in stream flow, whereas in areas dominated by C_3 species the excess results in deep drainage (recharge), particularly in winter (Dunin 1999, Johnston *et al.* 1999). A similar pattern was apparent in pastures dominated by the small- statured native C_4 *Bothriochloa macra* (Steud.) S.T. Blake compared to the large introduced C_3 *Phalaris aquatica* L. near Wagga Wagga, NSW (Johnston *et al.* 2003): the C_4 catchment produced 10 times more runoff than the C_3 pasture, dried the subsoil more frequently and more completely by greater water use from November to March, and probably prevented groundwater recharge (Johnston *et al.* 2003). Reduction of deep drainage requires increasing the soil water deficit before autumn rains (Singh *et al.* 2003). Replacement of C_4 dominant grasslands by summer dormant C_3 grasslands in south-eastern Australia has thus contributed to dryland salinity across large areas, by raising water tables and mobilising salts stored in the subsoil (Johnston *et al.* 1999, Singh *et al.* 2003, Reseigh *et al.* 2008).

When summer growing grasses are absent from temperate Australian grasslands the use of nitrogen mineralised from organic matter (nitrate and ammonium) in summer is reduced, which enhances its leaching in autumn and results in increased rates of soil acidification

(Johnston *et al.* 1999) and presumably of eutrophication at lower elevations in the catchment. Johnston et al. (2003) found that a C_3 pasture they studied at Wagga had higher nutrient (N and P) wash off risk than a matched C_4 *Bothriochloa macra* pasture.

The replacement of summer growing grasses by winter annuals and summer dormant perennials has already had major hydrological implications in the Murray Darling catchment (Johnston *et al.* 1999 2003) and the continued replacement of *T. triandra* by *N. neesiana* will add to these effects.

Conclusions

Surface soil moisture levels under *N. neesiana* swards in spring were consistently found to be significantly lower than under immediately contiguous swards of *T. triandra* in an ACT grassland, whatever the condition of the swards. Increased drying of the soil in spring may be one mechanism by which *N. neesiana* causes ongoing losses of native plant species once it is established, an effect likely to operate because a high proportion of the natives grow and flower during this period. Soil water depletion in spring probably disadvantages the later growing *T. triandra*, creating a positive feedback cycle for *N. neesiana* that may enable continued occupation of a site after the disappearance of *T. triandra*, and help propel invasion outward from infestation edges.

At a landscape scale, widespread replacement of summer growing native grasses by *N. neesiana* is likely to result in declines in runoff and stream flow and increased recharge, contributing to increased salinity, soil acidification and eutrophication at lower elevations in the catchment. *Nassella neesiana* populations may therefore impact on biodiversity far beyond the areas immediately invaded.

Further research

The review by Görgens and van Wilgen (2004) enables insight into necessary steps beyond the finding reported in this chapter of a difference in water use between an invasive species and indigenous vegetation in a single location and season. How does the effect vary under different rainfall regimes, and are effects measurable in runoff at the small catchment scale or in the groundwater via boreholes? What happens to water use at the plant community level when the alien is controlled or replaced, and are there demonstrable economic benefits in investment in weed management to deliver improved water supplies? Such questions should be addressed by further research.

Chapter 7. Diversity of vascular plants associated with *N. neesiana* patches

"So long as the natural vegetation covering, open though it be, is maintained, entrance to new-comers is denied."

Patton (1935 p. 175), on the resistance of Victorian basalt plains grasslands to invasion.

Summary

Species richness and composition of vascular plants within multiple *N. neesiana* patches, and in matched areas dominated by native grasses immediately outside the patches were compared at two grasslands in the ACT and one in Victoria. Areas occupied by *N. neesiana* were found to have significantly lower native species richness (spp. m^{-2}): between 24 and 65% at the three sites. Native grass richness was lower by 30-50%. Forbs (lower by 70% at two sites) and dominant or subdominant grasses were the most affected groups. Proportionately greater reductions were recorded at the two grasslands with relatively high native plant diversity. Exotic plant richness was similar inside and outside patches except at one ACT site where *N. neesiana* patches were enriched with exotic forbs. Native plant diversity was found to decrease with increasing patch size of *N. neesiana*. If larger patches are generally older than small patches, this indicates that *N. neesiana* presence has an ongoing negative impact on native diversity. Major loss of native diversity occurred even at the smallest patch sizes, suggesting that biodiversity loss may have preceded *N. neesiana* invasion. The likelihood that major disturbance is the common cause of the establishment of *N. neesiana* and the loss of native species diversity is discussed. Native species depauperation on disturbed ground can be explained by their poor colonising abilities compared with the exotic flora. The evidence supports the proposition that *N. neesiana* invasions are primarily facilitated by anthropogenic disturbances and that reduced native plant diversity correlated with *N. neesiana* presence is largely the result of such disturbances.

Introduction

Nassella neesiana has been portrayed as a serious cause of plant biodiversity loss in temperate native grasslands of south-eastern Australia. Carr *et al.* (1992) considered it to be a very serious threat to lowland grassland vegetation formations as a whole. Lunt and Morgan (2000 p. 98) rated it as "perhaps the most serious environmental weed in remnant native grasslands in southern Victoria”. McLaren *et al.* (1998) and Groves and Whalley (2002) rated it as the most significant weed threat to the temperate grasslands of south-eastern Australia, along with *N. trichotoma,* and Snell *et al.* (2007) considered it to be the worst environmental weed threat to these grasslands. Kirkpatrick (1995 p. 77) claimed that *N. neesiana* has “the potential to almost totally displace the native flora” and Kirkpatrick *et al.* (1995 p. 35) considered it apparently “capable of dominating grasslands across cool temperate south-eastern Australia”. Ens (2005) stated that it “swamps all other ground flora”.

These opinions are based, to various extents, on supposition, personal observations and various types of scientific study. Gardener and Sindel (1998 pp. 76-77) stated that there is “anecdotal evidence” that *N. neesiana* causes loss of plant biodiversity in grasslands “because litter from the tall tussocks accumulates in the inter-tussock spaces and excludes shade intolerant species”. However *T. triandra,* the major dominant native grass, has a similar inhibitory effect, which increases as the time since fire or thinning increases (as first reported by Stuwe and Parsons 1977). Diversity of bryophytes (mosses, liverworts) and lichens reportedly shows similar declines following *N. neesiana* invasion “because the mosaic of substrates such as rocks and bare soil becomes covered with litter” (Gardener and Sindel 1998 p. 77, citing V. Stajsic pers. comm.). But this also happens in dense stands of *T. triandra* (Scarlett 1994). Published evidence that demonstrates a plant diversity impact of *N. neesiana* is lacking, as is any adequate description of the plant species or groups supposedly affected.

Various authors have suggested that *N. neesiana* possesses superior competitive abilities to the dominant native grasses. For example Gardener and Sindel (1998) claimed that *N. neesiana* possesses many environmental traits that allow it to outcompete native vegetation, Wells *et al.* (1986) considered it to be competitive for space, light, water and nutrients and Cook (1999) thought it was very competitive when mature. Superior competitive abilities are generally imputed to be both the cause of *N. neesiana* invasions and the reason for its negative biodiversity effects. However, as Woods (1997) has pointed out, correlations of lower biodiversity with the presence of an invasive plant have often been accepted as evidence of the superior competitive abilities of the invader without there being an adequate understanding of causative mechanisms. There appears to be no detailed published evidence that *N. neesiana* is able to outcompete major native grasses for resources, and apart from high propagule pressure, the mechanisms by which it may invade native grasslands and cause biodiversity impacts have not been demonstrated.

There is an expectation from theory, and some published evidence, that greater species richness at the patch scale confers a degree of invasion resistance (Prieur-Richard and Lavorel 2000, Symstad 2000, Levine *et al.* 2004, Dunstan and Johnson 2006). More intense competition for resources and consequent fuller resource sequestration in more diverse communities is the explanation usually invoked, either due to a combined effect of all the species, or the greater likelihood that a species or functional group competitive with the invader is present in diverse communities (Symstad 2000, Dukes 2002, Stohlgren 2007, Prober and Lunt 2009). It might therefore by expected that the more diverse or functionally intact areas of temperate native grasslands of south-eastern Australia will be less subject to *N. neesiana* invasion and suffer smaller biodiversity impacts than species-poor areas.

Inappropriate disturbance regimes have had a profound negative impact on native plant richness in Australian temperate grasslands (e.g. Kirkpatrick *et al.* 1995, Dorrough *et al.* 2004) and resulted in major increases in exotic plant components (Moore 1973, Lunt *et al.* 1998), at least in part because the native and exotic components have a different response to such disturbances. The native species usually have poor abilities to colonise post-disturbance (Morgan 2001), while the exotic flora consists largely of ruderal and early successional species that are well adapted to disturbance (Trémont and McIntyre 1994, McIntyre and Lavorel 1994a). For these reasons, simultaneous correlation of *N. neesiana* infestation with both the presence of other exotic plants and reduced diversity of native species could be expected in cases where it has invaded in response to disturbance, rather than a result of superior competitive abilities. If this was not the case, the unlikely conclusion would have to be reached that *N. neesiana* is competitively superior to the native flora but not the exotic flora, despite the latter consisting largely of weeds, with supposedly good competitive abilities, and including a variety of life forms, biogeographical provenances, etc.

This study compares the native and exotic vascular plant diversity inside patches of *N. neesiana* with that in areas dominated by native grasses immediately outside the patches, at one degraded grassland in Victoria and two higher diversity grasslands in the ACT. The species richness per square metre of major plant categories (grasses, dicots and forbs; native or exotic) inside patches is compared with that in areas dominated by native species outside the patches. Comparisons are also made of the number of occurrences inside and outside patches of every species detected in samples. The relationship between the size (area) of *N. neesiana* patches and the native and exotic richness (spp. m^{-2}) of plant categories inside and outside the patches is next examined. Plant categories and species affected where *N. neesiana* is present are identified. This evidence is then evaluated in relation to potential mechanisms by which *N. neesiana* might cause such effects and in terms of the hypothesis that *N. neesiana* presence and the correlated biodiversity changes are both the result of prior disturbance.

Methods

Study sites

Field work for this component of the study was undertaken on the western side of Laverton North Grassland Reserve, in much of Yarramundi Reach grassland west of the bicycle path, and in the north-western section of the Crace Grassland Nature Reserve. Patches of *N. neesiana* of various sizes with areas >5 m^2, and a surrounding matrix dominated at least in part by native grasses were identified by ground inspections (Table 7.1).

Preliminary studies

A preliminary study of the plant diversity of three *N. neesiana* patches was undertaken at Yarramundi Reach on 25-26 May 2007 (Faithfull *et al.* 2008). The foliar cover of all vascular species present was estimated within four 1 x 1 m sampling areas inside each patch, four on the margins of each patch and four outside each patch. The data indicated that the presence of *N. neesiana* was correlated with reduced diversity of native vascular plants and increased diversity of exotic plants, but no overall statistical analysis of this data was undertaken. Examination of this small data set indicated that a more efficient sampling methodology involving two quadrats inside a patch and two quadrats outside a patch would provide sufficient resolution for statistical testing and enable the examination of a larger number of patches. In order to indicate how close to the margin of a patch the sampling of the native vegetation could be undertaken so as to minimise the presence of *N. neesiana* a series of pin transects were made across patch boundaries. Patches with visually discrete boundaries were examined at Yarramundi Reach (6 patches, 8 boundary transects) and Laverton North (7 patches, 12 boundary transects). Straight line transects that crossed the boundaries of the patches with pin samples at 10 cm intervals were assessed using the methods described in Chapter 5. *Themeda triandra* was the dominant native grass outside *N. neesiana* patches at each site and was therefore considered to represent the matrix in which the patches occurred. The number of pin intersects with foliage at all heights was calculated for each pin sample for the two grasses. A simple calculation was undertaken to obtain a standardised ‘overlap distance’ between *N. neesiana* and *T. triandra*. Absence of overlap, i.e. pronounced separation of the boundaries between invaded and uninvaded vegetation types was standardised in the same way:

- If *N. neesiana* and *T. triandra* occurred at the same pin point, then overlap occurred. The ‘overlap distance’ was defined as the distance between the first and the last co-occurrences, plus 10cm (10 cm being the interval between pin samples).

- If no overlap occurred then the 'overlap distance' equalled the negative of the distance between the last occurrence of *N. neesiana* and the first occurrence of *Themeda*, plus 10 cm.
- Readings of only 1 intercept at a particular pin point, and no other intercepts with *N. neesiana* within 20 cm, were ignored.

The overlap distances were graphed for each site (Fig. 7.1). Overlap distances for the two sites were compared using a Mann-Whitney U (Wilcoxon rank-sum) test. The overlap distances of the two grass species did not differ significantly between sites (U = 2.75, P (adjusted for ties) 0.118).

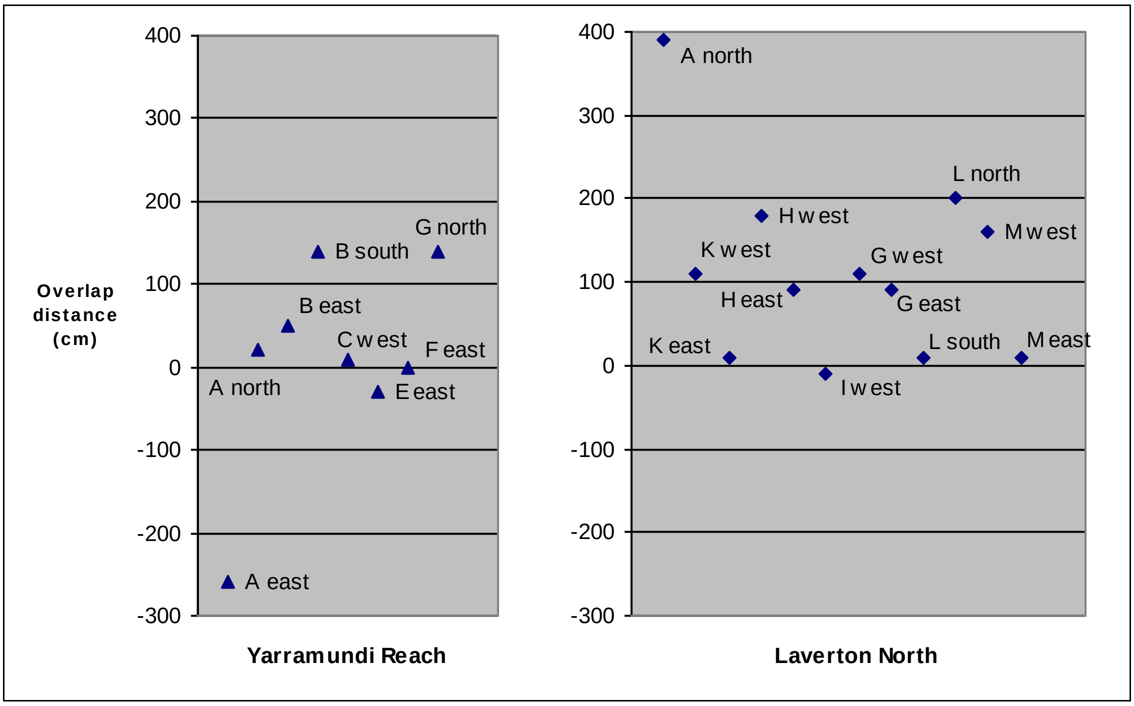

Figure 7.1. Overlap between *N. neesiana* and *T. triandra* at the margins of *N. neesiana* patches at Yarramundi Reach and Laverton North grasslands.

On the basis of this examination a distance of 2 m from the edge of a *Nassella neesiana* patch was identified to be sufficiently large to minimise the presence of *N. neesiana* in sampling undertaken in the native grassland matrix.

Vegetation sampling

A much expanded plant diversity data set was gathered by sampling at Laverton North and Crace, and additional sampling at Yarramundi Reach (Tables 7.1 and 7.2). At each site, *N. neesiana* patches were chosen to represent the range of situations in which they occurred at each grassland, and a range of patch sizes. Nominal patch centres were marked with pegs, their coordinates were recorded using a GPS device, and their distances and directions from prominent landmarks such as large trees or fence line corners were measured using a surveyor's tape and a magnetic compass.

Locations, areas and dates of assessment of areas sampled are shown in Table 7.1. Two contiguous 1 x 1 m sample areas were assessed within each patch, at or close to the nominal patch centre. The procedure for selecting sample areas outside patches was standardised, at least within the groupings presented in Table 7.1, to minimise biases.

In the native vegetation two contiguous 1 x 1 m sample areas were assessed, except for one patch at Yarramundi Reach where two sets of two contiguous 1 m^2 samples were assessed outside the patch because two strongly contrasting native grassland types (dominated either by *Austrostipa* sp. or *T. triandra*) were present close to the patch margin. Quadrats outside the patch were located in areas not dominated by exotic grasses, usually along a line to the east of the patch, generally 2 m from the patch edge or from outlier *N. neesiana* plants, unless this area was dominated by alien exotic grasses, in which case the line was moved south. In a few instances at Yarramundi Reach the location of 'outside' quadrats in areas without *N. neesiana* and not dominated by other exotic plants using this method was not possible and quadrats were assessed that were further from the patch edge (up to 7 m) or in another direction from the patch centre.

Projective foliar cover values (the proportion of ground covered by above-ground biomass, not including detached litter) were visually estimated to the nearest percent for all species present in each sample area. Estimates were made using a 1m x 1m steel frame quadrat subdivided into 10 cm x 10 cm cells. Cover <1% was recorded as presence only. A species was considered present in a quadrat on the basis of shoot presence, rather than rooted presence. Percent bare ground (including rocks) and cover of detached litter and animal dung were also recorded. All cover estimates were made by the one observer. Each patch was sampled on one occasion.

The area of each patch was determined using methods described in Chapter 2.

Statistical analyses

Species recorded was categorised as either exotic or native to Australia using standard floras and checklists, primarily Walsh and Stajsic (2007). The native or exotic status of a small proportion of species detected could not be confidently determined and these were excluded from analyses in which comparisons of native and exotic species categories were made. These were all monocots that occurred infrequently, with low cover (Table 7.3).

Table 7.1. Locations, areas and dates of assessment of *N. neesiana* patches used for vascular plant diversity studies. “Buildings” at Yarramundi Reach refer to the Aboriginal and Torres Strait Islander Cultural Centre. C designations for Crace are management zones specified in planning documents. Fences at Laverton North are the Kororoit Creek Road fence at the south and the low north-south fence along the western side of the Reserve.

Patch	**Lat/long (patch ‘centre’)**	**Location**	**Area (m^2)**	**Date assessed**
Yarramundi Reach, ACT				
A	35°17.367’ 149°05.047’	E of buildings	369	25/05/07
B	35°17.453’ 149°04.933’	SE of buildings	120	25/05/07
C	35°17.501’ 149°04.897’	S area, N of burn plot	156	26/05/07
D	35°17.443’ 149°04.812’	Far SW corner	225	11/10/07
D ext	35°17.448’ 149°04.812’	Far SW corner	54	11/10/07
E	35°17.430’ 149°04.955’	S of buildings	103	12/10/07
F	35°17.439’ 149°04.947’	S of buildings	77	12/10/07
H	35°17.432’ 149°04.886’	W of buildings, W of gully	90	17/10/07
I	35°17.512’ 149°04.911’	W, S of burn patch	12	17/10/07
J	35°17.509’ 149°04.904’	W, S of burn patch	12	17/10/07
K	35°17.451’ 149°04.835’	Far SW corner	16	18/10/07
L	35°17.528’ 149°04.842’	S, 100 m N of bike path	15	18/10/07
M	35°17.375’ 149°05.031’	NE, 37 m W of bike path	32	19/10/07
N	35°17.337’ 149°05.064’	Far NE, 37 m W of bike path	60	19/10/07
O	35°17.338’ 149°05.008’	N of buildings, nr Lady Denman Drive	94	19/10/07
Crace Grassland Reserve, ACT				
A	35°13.693’ 149°07.378’	C1, NW corner	210	16/10/07
B	35°13.621’ 149°07.426’	C1, NW	18	18/10/07
F	35°13.546’ 149°07.613’	C8, SW side	5	20/10/08
G	35°13.542’ 149°07.615’	C8, 5 m N of patch F	9	21/10/08
H	35°13.437’ 149°07.811’	C9 nr ridge top	10	22/10/08
I	35°13.388’ 149°07.808’	C9 N end	7	23/10/08
K	35°13.449’ 149°07.868’	C10, NW sector	10	24/10/08
Laverton North Grassland, Vic.				
A	37°50.709’ 149°47.397’	13 m E of W fence, 135 m N of S fence	279	25/11/07
B	37°50.744’ 149°47.390’	19 m E of W fence, 68 m N of S fence	5	25/11/07
C	37°50.686’ 149°47.400’	11 m E of W fence, 142 m N of S fence	44	29/11/07
D	37°50.641’ 149°47.415’	22 E of W fence, 57 m S of N fence	129	29/11/07
E	37°50.660’ 149°47.466’	100 m E of W fence, 134 m S of N fence	5	4/12/07
F	37°50.658’ 149°47.422’	35 m E of W fence, 96 m S of N fence	54	4/12/07
G	37°50.743’ 149°47.415’	55 m E of W fence, 79 m N of S fence	21	5/12/07
H	37°50.743’ 149°47.403’	34 m E of W fence, 75 m N of S fence	11	5/12/07
I	37°50.673’ 149°47.409’	42 m E of W fence, 116 m S of N fence	17	6/12/07
J	37°50.700’ 149°47.405’	26 m E of W fence, 162 m S of N fence	139	6/12/07
K	37°50.722’ 149°47.419’	51 m E of W fence, 114 m N of S fence	22	10/12/07
L	37°50.694’ 149°47.470’	116 m E of W fence, 180 m N of S fence	7	18/12/07
M	37°50.697’ 149°47.477’	122 m E of W fence, 180 m N of S fence	9	18/12/07
N	37°50.733’ 149°47.499’	171 m E of W fence, 110 m N of S fence	89	18/12/07

Table 7.2. Summary of the number of patches sampled, the number of 1 m^2 quadrats sampled inside and outside the patches, the patch designations, patch areas and sampling dates at the three grasslands sampled.

Site	**No. of patches**	**Quadrats per patch**		**Patch designations**	**Patch areas (m^2)**	**Sampling dates**
		Inside	**Outside**			
Laverton North	14	2	2	A-N	5-466	25/11-18/12/07
Yarramundi Reach	3	4	4	A-C	26-369	25-26/5/07
	11	2	2	D, Dext, E, F, H-K, M-O	12-225	11-19/10/07
	1	2	4	L	15	18/10/07
Crace	7	2	2	A-C, G, H, I, K	5-210	16-24/10/08

Table 7.3. Occurrence and cover of unidentified taxa detected in floristic sampling and excluded from some analyses.

Site	**Taxon**	**Patch**	**No. and location of quadrats**	**Cover (%)**
Laverton North	grass	F	1	<1
Yarramundi Reach	rhizomatous grass	H	1 outside	1
	?*Cyperus*	D ext	1 inside	<1
		H	1 inside	<1
		H	1 outside	<1
		J	1 outside	<1
Crace	*Carex* sp.	F	1 inside	<1

To assay the diversity present at each site, the total numbers of native grasses, exotic grasses, other native monocots, other exotic monocots, native dicots (eudicots), exotic dicots, native ferns, indeterminate species, native species, exotic species and total species that were detected in quadrats were determined for areas inside and outside patches. The ratios of grasses to other species, of native grasses to native forbs and of native species to exotic species for areas inside and outside *N. neesiana* patches for each site were also calculated.

To determine whether the sampling regime had actually sampled areas dominated by *N. neesiana* (within the patch) and areas dominated by native grasses (outside the patch), and to examine other differences between patches and areas outside patches, the mean percentage cover of *N. neesiana*, major exotic perennial grasses, major native grasses, all major grasses, all exotic grasses, all native grasses, litter, bare ground and dung inside and outside patches were calculated for each site. This included all exotic Poaceae that had moderate or high cover within one or more quadrats. ‘Major native grasses’ were found to be *T. triandra*, *Austrostipa* spp., *Austrodanthonia* spp., *Bothriochloa macra* and *Poa labillardierei*. Bare ground included rocks and gravel but excluded ground covered by readily visible cryptogam crusts. Animal dung included the dung of cattle, kangaroos, rabbits and hares. Mean values for these categories inside and outside of patches were compared using paired t-tests with pairs corresponding to patches and one inside value and one outside value per patch.

To examine the effect of *N. neesiana* presence on plant species diversity, the numbers of native, native grass, native forb, native dicot, exotic, exotic grass, exotic forb and exotic dicot spp. were recorded for each quadrat. The ‘exotic’ and ‘exotic grass’ categories did not include *N. neesiana*. All non-grass species, including the only fern, *Cheilanthes austrotenuifolia*, H.M. Quirk & T.C. Chambers detected in two outside quadrats at one patch, and the single individual of the exotic shrub *Rubus* sp., were grouped into the ‘forb’ category. The ‘dicot’ (Dicotyledonae) category included only eudicots. Thus, in this particular analysis, dicots are wholly a subset of forbs, and the non-dicot forbs include all non-grass Monocotyledonae plus the fern. The average number of species per quadrat inside and outside patches for each of these categories was then calculated for each site. These values can be interpreted as the number of species in a square metre area. These averages were square root transformed to reduce skewness, and then the values inside and outside patches were compared using a paired t-test. At Laverton North, one patch was deleted as the inside quadrats had an unrepresentatively low number of species.

Patches A-C at Yarramundi Reach were assessed in May and the other patches at the site were assessed in October. A factorial split plot comparison of the two data sets by date and quadrat showed no significant differences in cover values or the number of species in plant groups and no interaction effects, so the data were treated as a single set.

To investigate the influence of patch size on plant diversity, simplified summary graphs were constructed to indicate main trends.

To further investigate the effects associated with presence of *N. neesiana* and illuminate underlying processes, general linear regression was applied to the full data set (all three sites) to identify factors that influenced plant composition inside the patches. Parsimonious models relating the mean numbers of species/m^2 inside patches of native species, native grasses, native forbs, native dicots, exotic grasses (excluding *N. neesiana*), exotic forbs and exotic dicots, to corresponding quantities outside the patches, patch area and site were developed, using variance ratio F tests. The dependent variables were square root transformed, after the addition of 0.5, to reduce skewness.

Additional analysis was undertaken to investigate whether the occurrence of particular plant species was affected where *N. neesiana* was dominant. The occurrence of a species within at least one quadrat inside, or at least one quadrat outside a patch, was recorded for each patch within each site. These occurrences were then summed over all patches at a site, to determine the number of patches in which each species was observed inside the patch and outside the patch. The third and fourth of the four quadrats sampled at Yarramundi Reach patch L were excluded from this process, so that the inside and outside occurrence of a species at a patch was recorded using the same number of quadrats (i.e. for the same area). The number of occurrences of each species inside and outside patches at a site was compared using a sign test (Sokal and Rohlf 1969), with the pairing corresponding to patches. For the purpose of reporting and discussion, this data is referred to as 'incidence testing'.

Results

Site richness

At each site the majority of species in the uninvaded vegetation were either grasses or dicots, although 8 other native monocot species were observed at Yarramundi Reach (Table 7.4). The ratio of the number of grasses to other species in the uninvaded vegetation was 1.1 at Laverton North, 0.7 at Yarramundi Reach and 0.6 at Crace. The ratio of the number of native grasses to the number of native forbs in the uninvaded vegetation was 2.0 at Laverton North, 0.5 at Yarramundi Reach and 0.6 at Crace. The ratio of the number of native species to the number of exotic species in the uninvaded vegetation was 0.6 at Laverton North, 1.5 at Yarramundi Reach and 2.2 at Crace.

The ratio of grasses to other species within *N. neesiana* patches was approximately equivalent for all sites, but the ratio of native grasses to native forbs within patches was much lower at Yarramundi Reach than the other sites. The ratio of native to exotic species was highest at Crace, intermediate at Yarramundi Reach and lowest at Laverton North. No native monocots other than grasses were detected in quadrats at Laverton North and this grassland had low diversity of native grasses and native dicots. When the total number of species detected is compared to the area sampled ("ratio of spp. to area sampled" in Table 7.4), Laverton North had the lowest native richness and Crace had by far the highest, while Crace also had the highest exotic richness and Yarramundi Reach had the lowest.

Table 7.4. Total numbers of native and exotic vascular plant species detected in the sampled quadrats inside and outside *N. neesiana* patches at each grassland, total native and exotic species m^{-2}, and the ratios of grasses to other species, native grasses to native forbs and of natives to exotics inside and outside patches. Total area sampled is in parentheses.

Plant group		**Laverton North**		**Yarramundi Reach**		**Crace**	
		Inside (28 m^2)	Outside (28 m^2)	Inside (36 m^2)	Outside (38 m^2)	Inside (14 m^2)	Outside (14 m^2)
Grasses	Native	8	8	8	12	8	10
	Exotic	9	10	13	14	7	6
Dicots	Native	7	4	11	15	7	16
	Exotic	12	9	11	10	6	7
Other monocots	Native	0	0	5	8	1	2
	Exotic	2	2	0	0	1	0
Fern	Native	0	0	0	1	0	0
Indeterminate	-	0	1	1	2	1	0
All Groups	Native	15	12	24	36	16	28
	Exotic	23	21	24	24	14	13
	Total	38	34	49	62	31	41
Ratio of native spp. to area sampled		0.53	0.43	0.66	0.95	1.14	2.00
Ratio of exotic spp. to area sampled		0.82	0.75	0.66	0.63	1.00	0.93
Ratio of grasses to other species		0.8	1.1	0.8	0.7	0.9	0.6
Ratio of native grasses to native forbs		1.1	2.0	0.5	0.5	1.0	0.6
Ratio of natives to exotics		0.7	0.6	1.0	1.5	1.1	2.2

Type of grass cover inside and outside patches

Patches of *N. neesiana* were deliberately identified, and at all sites the cover of *N. neesiana* was high inside the patches and low outside them (Table 7.5). Conversely, the cover of native grasses was low inside the patches and high outside them. *N. neesiana* patches had low cover of other exotic grasses, and the cover of other exotic grasses (excluding *N. neesiana*) was low (< 10%), both inside and outside patches, at every site. The sampling method therefore effectively compared areas dominated by *N. neesiana* with areas dominated by perennial native grasses.

Total grass cover at a site was approximately equivalent inside and outside patches at all three sites (Tables 7.6-7.8). Laverton North had by far the lowest grass cover, very low litter cover and very high proportion of bare ground reflecting recent removal of biomass by fire (Table 7.8). Yarramundi Reach had high grass cover, the highest litter values and very little bare ground, reflecting the lack of recent fire and the absence of livestock and kangaroo grazing (Table 7.6). Crace had moderate levels of bare ground and significant amounts of cattle and kangaroo dung reflecting the moderate to intense grazing pressure mainly from kangaroos and livestock that is part of its active management regime (Table 7.7).

Table 7.5. Mean percent projective foliar cover of *N. neesiana*, all exotic grasses and native grasses in sampled quadrats inside and outside *N. neesiana* patches. Significant P values are indicated in bold.

	Inside patch	**Outside patch**	**sed**	**P value**
Nassella neesiana				
Crace	58	0	8.0	**0.00034**
Laverton North	37	0	2.3	**6.8×10^{-10}**
Yarramundi Reach	53	0	2.9	**1.5×10^{-10}**
Total exotic grasses				
Crace	62	3	7.2	**0.00019**
Laverton North	40	3	2.6	**3.6×10^{-9}**
Yarramundi Reach	60	8	2.7	**$4.1 \text{ x } 10^{-11}$**
Native grasses				
Crace	10	53	8.5	**0.0021**
Laverton North	7	33	2.1	**1.2×10^{-8}**
Yarramundi Reach	7	68	3.1	**$3.3 \text{ x } 10^{-11}$**

Species richness differences inside and outside patches

Nassella neesiana patches were found to have an impoverished native vascular plant flora compared with adjacent areas of native grassland (Tables 7.6-7.9). Mean native species richness (spp. m^{-2}) in *N. neesiana* patches was less than in areas immediately outside the patches at all three grasslands, and significantly lower ($P < 0.001$) at Yarramundi Reach (Table 7.6) and Crace (Table 7.7). Differences of 24%, 58% and 65% (back transformed data) were measured for Laverton North, Crace and Yarramundi Reach respectively.

Significantly lower mean native grass richness in *N. neesiana* patches occurred at all three grasslands. Differences of 31%, 37% and 49% were measured at Yarramundi Reach, Laverton North and Crace respectively. Lower richness at Laverton North could be completely explained by a reduction in the occurrence of *Austrostipa bigeniculata* (Hughes) S.W.L. Jacobs & J. Everett alone (Table 7.9).

Native forb richness was significantly lower inside patches at the two ACT grasslands (by 70 and 71%), but not at Laverton North where it was 25% higher, equivalent to 1sp. m^{-2} (Table 7.8). Species richness of native dicots, a subcategory of native forbs, was significantly lower inside patches only at Crace (by 78%) and was also lower at Yarramundi Reach (by 57%), but was slightly higher, again by 1 sp. m^{-2}, at Laverton North.

Proportionately larger differences in native species diversity were measured at the two grasslands with relatively high native plant diversity (Crace and Yarramundi Reach).

Table 7.6. Analysis of mean foliar cover and mean species diversity of major plant categories inside and outside patches of *N. neesiana* at Yarramundi Reach grassland, ACT. Fifteen patches were assessed in May (3 patches) and October 2007 (12 patches). Interaction and main effects are reported for plant categories where significant differences between the May and October groups were found. Major exotic grasses = *Nassella neesiana* + *Avena* sp. + *Phalaris aquatica* + *Paspalum dilatatum*. Major native grasses = *Themeda triandra* + *Austrostipa* spp. +*Austrodanthonia* spp. + *Bothriochloa macra* + *Poa labillardierei*.

Measurement	**Inside**	**Outside**	**SED**	**P value**
Cover %				
Nassella neesiana	53	0	2.9	**1.5×10^{-10}**
Major exotic grasses	58	5	2.5	**1.8×10^{-11}**
Major native grasses	7	68	3.1	**4.0×10^{-11}**
Total major grasses	64	74	3.1	**0.010**
All exotic grasses	60	8	2.7	**4.1×10^{-11}**
All exotic grasses excl. *N. neesiana*	7	7	5.3	0.931
All native grasses	7	68	3.1	**3.3×10^{-11}**
Total all grasses	67	76	2.9	**0.010**
Litter	24	15	2.6	**0.0065**
Bare ground	7	2	2.1	0.070
No. of species m^{-2}				
Square root of total spp.	2.51	2.76	0.108	**0.040**
Back transformed	6.3	7.6		
Square root of total spp. excl. *N. neesiana*	2.29	2.73	0.119	**0.0025**
Back transformed	5.2	7.5		
Square root of native spp.	1.19	1.99	0.153	**0.00017**
Back transformed	1.4	4.0		
Square root of native dicots	0.56	0.84	0.163	0.11
Back transformed	0.3	0.7		
Square root of native forbs	0.65	1.20	0.160	**0.0049**
Back transformed	0.4	1.4		
Square root of native grasses	0.89	1.53	0.160	**0.0013**
Back transformed	0.8	2.4		
Square root of exotic spp. (November 2007)	2.31	2.01	0.068	**2.3×10^{-5} (main effect)**
Back transformed	5.3	4.0		
Square root of exotic spp. (May 2007)	1.50	0.76	0.137	**0.014 (interaction)**
Back transformed	2.2	0.6		
Square root of exotic spp. excl. *N. neesiana*	1.88	1.71	0.077	**0.042**
Back transformed	3.5	2.9		
Square root of exotic dicots	1.06	0.82	0.100	**0.032**
Back transformed	1.1	0.7		
Square root of exotic forbs	1.06	0.83	0.101	**0.048**
Back transformed	1.1	0.7		
Square root of exotic grasses (November 2007)	2.01	1.68	0.082	**5.2×10^{-5} (main effect)**
Back transformed	4.0	2.8		
Square root of exotic grasses (May 2007)	1.28	0.40	0.165	**0.010 (interaction)**
Back transformed	1.6	0.2		
Square root of exotic grasses excl. *N. neesiana*	1.54	1.35	0.101	0.081
Back transformed	2.4	1.8		

Table 7.7. Analysis of mean foliar cover and mean species diversity of major plant categories inside and outside seven patches of *N. neesiana* at Crace Grassland, ACT, 16-24 October 2008. Major exotic grasses = *N. neesiana* +*Avena* sp. + *Phalaris aquatica* + *Paspalum dilatatum*. Major native grasses = *Themeda triandra* + *Austrostipa* spp. + *Austrodanthonia* spp. + *Bothriochloa macra* + *Poa labillardierei*.

Measurement	**Inside**	**Outside**	**SED**	**P value**
Cover %				
Nassella neesiana	58	0	8.0	**0.00034**
Major exotic grasses	62	2	7.1	**0.00016**
Major native grasses	8	49	9.2	**0.0047**
Total major grasses	70	50	10.0	0.097
All exotic grasses	62	3	7.2	**0.00019**
All native grasses	10	53	8.5	**0.0021**
Total all grasses	71	57	8.3	0.13
Litter[#]	8	8	1.8	0.97
Bare ground	11	21	5.8	0.14
Dung	4	2	1.0	0.11
No. of species m^{-2}				
Square root of total spp.	2.68	3.00	0.218	0.19
Back transformed	7.2	9.0		
Square root of total spp. excl. *N. neesiana*	2.47	2.99	0.220	0.058
Back transformed	6.1	8.9		
Square root of native spp.	1.67	2.56	0.109	**0.00021**
Back transformed	2.9	6.6		
Square root of native dicots	0.67	1.33	0.205	**0.019**
Back transformed	0.4	1.8		
Square root of native forbs	0.77	1.41	0.162	**0.0076**
Back transformed	0.6	2.0		
Square root of native grasses	1.42	1.98	0.184	**0.023**
Back transformed	2.0	3.9		
Square root of exotic spp.	2.00	1.51	0.243	0.093
Back transformed	4.0	2.3		
Square root of exotic spp. excl. *N. neesiana*	1.71	1.48	0.257	0.42
Back transformed	2.9	2.2		
Square root of exotic dicots	0.97	0.88	0.340	0.79
Back transformed	0.9	0.8		
Square root of exotic forbs	0.99	0.88	0.342	0.76
Back transformed	1.0	0.8		
Square root of exotic grasses	1.63	1.07	0.117	**0.0032**
Back transformed	2.7	1.1		
Square root of exotic grasses excl. *N. neesiana*	1.36	1.04	0.125	0.12
Back transformed	1.6	1.1		

[#] Not including patch I which was under a tree and had an extensive cover of tree litter.

Table 7.8. Analysis of mean foliar cover and mean species diversity of major plant categories inside and outside patches of *N. neesiana* at Laverton North Grassland, Vic., 25 November – 18 December 2007. 14 patches were assessed. Major exotic grasses = *N. neesiana* +*Avena* sp. + *Phalaris aquatica* + *Paspalum dilatatum*. Major native grasses = *Themeda triandra* + *Austrostipa* spp. + *Austrodanthonia* spp. + *Bothriochloa macra* + *Poa labillardierei*.

Measurement	**Inside**	**Outside**	**SED**	**P value**
Cover %				
Nassella neesiana	37	0	2.3	**6.8×10^{-10}**
Major exotic grasses	39	1	2.3	**6.2×10^{-10}**
Major native grasses	7	33	2.1	**1.7×10^{-8}**
Total major grasses	45	34	1.7	**2.0×10^{-5}**
All exotic grasses	40	3	2.6	**3.6×10^{-9}**
All native grasses	7	33	2.1	**1.2×10^{-8}**
Total all grasses	47	36	1.9	**0.00017**
Litter	3	2	0.5	0.13
Bare ground	47	57	1.8	**0.00018**
No. of species m^{-2}				
Square root of total spp.	3.04	2.92	0.091	0.20
Back transformed	9.2	8.5		
Square root of total spp. excl. *N. neesiana*	2.87	2.92	0.094	0.62
Back transformed	8.2	8.5		
Square root of native spp.	1.39	1.58	0.126	0.15
Back transformed	1.9	2.5		
Square root of native dicots	0.73	0.63	0.177	0.59
Back transformed	0.5	0.4		
Square root of native forbs	0.73	0.63	0.177	0.59
Back transformed	0.5	0.4		
Square root of native grasses	1.09	1.38	.125	**0.039**
Back transformed	1.2	1.9		
Square root of exotic spp.	2.69	2.42	0.094	**0.016**
Back transformed	7.2	5.8		
Square root of exotic spp. excl. *N. neesiana*	2.49	2.42	0.099	0.51
Back transformed	6.2	5.9		
Square root of exotic dicots	1.27	1.18	0.135	0.499
Back transformed	1.61	1.39		
Square root of exotic forbs	1.66	1.52	0.090	0.15
Back transformed	2.7	2.3		
Square root of exotic grasses	2.07	1.83	0.084	**0.014**
Back transformed	4.3	3.3		
Square root of exotic grasses excl. *N. neesiana*	1.80	1.83	0.089	0.76
Back transformed	3.2	3.3		

Table 7.9. Mean number of native vascular plant species per square metre inside and outside *N. neesiana* patches at three grasslands. Two set of Laverton North data for all native species and all native grasses are shown, either including or excluding *Austrostipa bigeniculata*. Significant P values are indicated in bold.

Species Category	**Square Root Transformed**			**Back transformed**		**P Value**
	Inside	**Outside**	**sed**	**Inside**	**Outside**	
All natives						
Crace	1.67	2.56	0.109	2.8	6.6	**0.00021**
Laverton North	1.39	1.58	0.126	1.9	2.5	0.15
Laverton North (excluding *A. bigeniculata*)	1.3	1.38	0.125	1.7	1.9	0.58
Yarramundi Reach	1.19	1.99	0.153	1.4	4.0	**0.00017**
Native grasses						
Crace	1.42	1.98	0.184	2.0	3.9	**0.023**
Laverton North	1.09	1.38	0.125	1.2	1.9	**0.039**
Laverton North (excluding *A. bigeniculata*)	0.97	1.14	0.150	0.9	1.3	0.27
Yarramundi Reach	1.07	1.25	0.157	1.1	1.6	**0.0013**
Native forbs						
Crace	0.77	1.41	0.162	0.6	2.0	**0.0076**
Laverton North	0.73	0.63	0.177	0.5	0.4	0.59
Yarramundi Reach	0.65	1.20	0.160	0.4	1.4	**0.0049**
Native dicots						
Crace	0.67	1.33	0.205	0.4	1.8	**0.019**
Laverton North	0.73	0.63	0.177	0.5	0.4	0.59
Yarramundi Reach	0.56	0.84	0.163	0.3	0.7	0.11

A significant difference between the number of exotic species m^{-2} inside and outside patches was apparent only at Yarramundi Reach (Tables 7.6 and 7.10). The mean numbers of exotic species, exotic forbs and exotic dicots per square metre were significantly higher ($P < 0.05$) inside the patches at Yarramundi Reach, and the exotic grasses were significantly higher at the $P = 0.08$ level. The mean species richness inside *N. neesiana* patches was 32% higher for exotic species, 45% higher for exotic grasses, 25% higher for exotic forbs and 13% higher for exotic dicots at this grassland. At Crace a similar trend was indicated, the mean species richness inside *N. neesiana* patches being 32% higher for all exotic species, 45% higher for exotic grasses, 25% higher for exotic forbs and 13% higher for exotic dicots, but few patches were assessed at this grassland and the differences were mostly far from significant. The differences detected at Laverton North were slight.

Table 7.10. Mean number of exotic vascular plant species (excluding *N. neesiana*) per square metre inside and outside *N. neesiana* patches at three grasslands. Significant P values are indicated in bold.

Species Category	**Square Root Transformed**			**Back transformed**		**P Value**
	Inside	**Outside**	**sed**	**Inside**	**Outside**	
All exotics						
Crace	1.71	1.48	0.257	2.9	2.2	0.42
Laverton North	2.49	2.42	0.099	6.2	5.8	0.51
Yarramundi Reach	1.88	1.71	0.077	3.5	2.9	**0.042**
Exotic grasses						
Crace	1.36	1.04	0.125	1.6	1.1	0.12
Laverton North	1.80	1.83	0.089	3.2	3.3	0.76
Yarramundi Reach	1.54	1.35	0.101	2.4	1.8	0.081
Exotic forbs						
Crace	0.99	0.88	0.342	1.0	0.8	0.76
Laverton North	1.66	1.52	0.090	2.7	2.3	0.15
Yarramundi Reach	1.06	0.83	0.101	1.1	0.7	**0.048**
Exotic dicots						
Crace	0.97	0.88	0.340	0.9	0.8	0.79
Laverton North	1.27	1.18	0.135	1.6	1.4	0.50
Yarramundi Reach	1.06	0.82	0.100	1.1	0.7	**0.032**

Effects of patch size on plant diversity

There was a general trend to lower numbers of species per square metre inside *N. neesiana* patches as the *N. neesiana* patch size increased, both for native and exotic species (Fig. 7.2). Assessed areas were close to patch centres, so it is possible that species richness was lower as the distance from the surrounding native vegetation matrix increased.

Native species richness trended towards zero at a patch size of around 500 m^2. There is approximately one less exotic sp. m^{-2} for each 200 m^2 increment in patch area.

The average number of native spp. m^{-2} outside patches for all sites was 3.9 and the average number of exotic spp. m^{-2} outside patches was also 3.9. Linear trend lines in Fig. 7.2 indicate an approximate halving of the native species richness inside patches for the smallest patch sizes compared to the native vegetation, and slightly higher exotic richness inside the patches at the smallest patch sizes.

The relationship between patch size and native diversity at the three grasslands is illustrated in Fig. 7.3. The slopes of the linear fitted curves suggest that the trend to lower native diversity with increasing patch size was more pronounced at the two richer grasslands (Crace and Yarramundi Reach). The trend was weakest at the weediest and most degraded grassland (Laverton North).

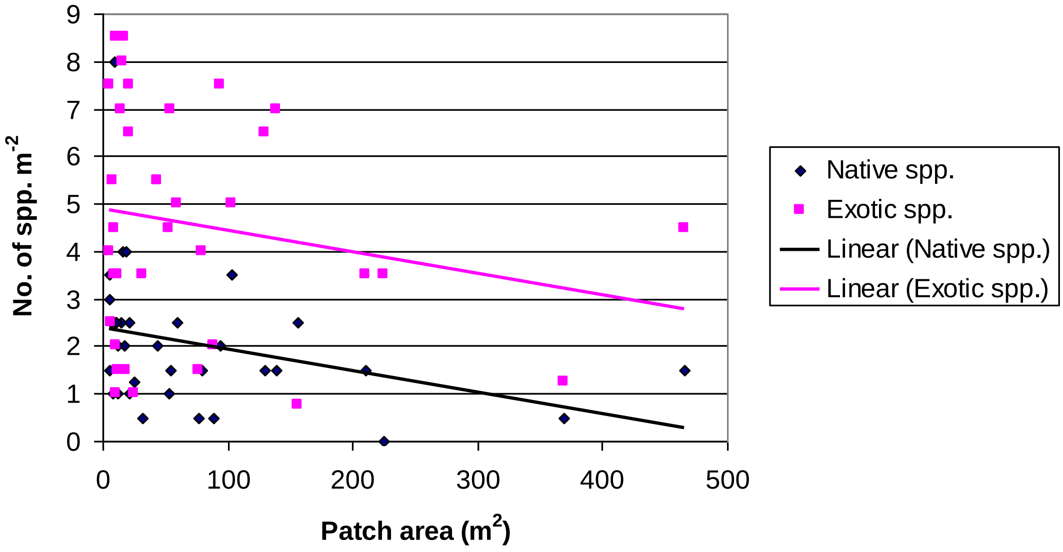

Figure 7.2. Relationship between the area (m^2) of *N. neesiana* patches and the mean number of native and exotic vascular plant species m^{-2} inside the patches for all patches assessed at the three grasslands.

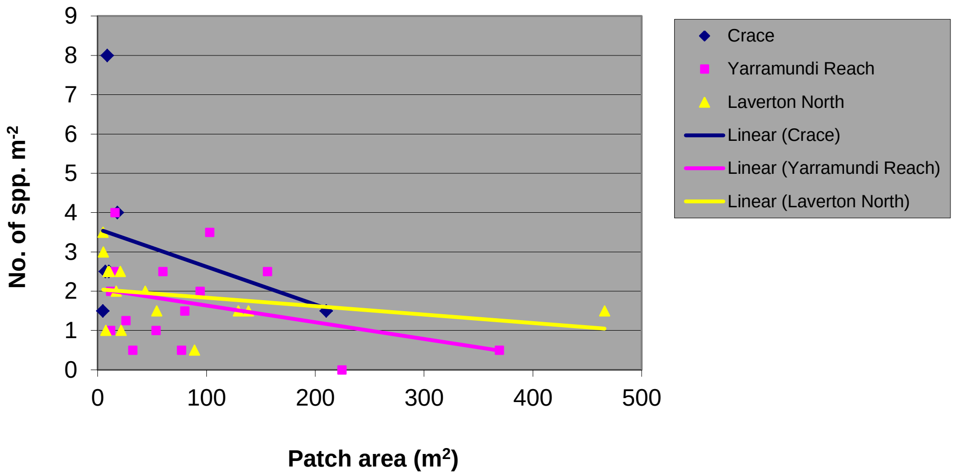

Figure 7.3. Relationship between the area (m^2) of *N. neesiana* patches and the mean number of native vascular plant species m^{-2} inside the patches for the three grasslands.

Linear regression analysis

With the exception of total number of native species, the most parsimonious models for the number of species in the various categories inside the patches were simple linear regressions of the number of species in particular classes, or of the square root of patch area (Tables 7.11 and 7.12). None of the relationships differed with site (Tables 7.11 and 7.12). There was no support for the proposition that the size of a patch was influenced by the mean number of species outside the patch: matrix vegetation richness was not influential in determination of patch area.

Table 7.11. The most parsimonious models identified by linear regression for the mean number of species m^{-2} inside *N. neesiana* patches. Models are in the form: $\sqrt{}$(Number of species m^{-2} inside + 0.5) = $\alpha \pm \beta \times$ (Variable), and the units of the variable are m^2 (patch area) or mean number of species m^{-2}. The exotic grass categories exclude *N. neesiana*.

Model	**% variance accounted for**	**Standard error of β**
$\sqrt{}$(Native Grasses Inside + 0.5) = 1.54 – 0.036 × $\sqrt{}$(Patch Area)	37.9	0.0077
$\sqrt{}$(Native Forbs Inside + 0.5) = 0.92 + 0.121 × (Native Dicots Outside)	42.6	0.0232
$\sqrt{}$(Native Dicots Inside + 0.5) = 0.92 + 0.087 × (Native Dicots Outside)	27.8	0.0228
$\sqrt{}$(Exotic Grasses Inside + 0.5) = 1.17 + 0.224 × (Exotic Grasses Outside)	60.8	0.0301
$\sqrt{}$(Exotic Forbs Inside + 0.5) = 1.08 + 0.258 × (Exotic Forbs Outside)	46.3	0.0462
$\sqrt{}$(Exotic Dicots Inside + 0.5) = 1.08 + 0.228 × (Exotic Dicots Outside)	28.6	0.0588

With increasing patch size there was a strong trend to lower average diversity of native grasses inside *N. neesiana* patches (Fig. 7.4a). On average, larger patches (> 100 m^2) had <1 native grass species m^{-2} (Fig. 7.4a). The response to area also indicates that, in small patches, the average diversity of native grasses inside the patches, about 1.5 spp. m^{-2} (Fig 7.4a), was substantially different to that outside the patches, which was 2.2 spp. m^{-2} across all sites (Table 7.9). On average, the number of native grass spp. m^{-2} inside even the smallest *N. neesiana* patches (5 m^2) was 0.7 spp. fewer than in the matrix of native vegetation outside the patches. At the Crace site the diversity of native grasses was substantially lower, even in small patches.

The diversity of native forbs and native dicots inside *N. neesiana* patches were positively related to the diversity of native dicots outside the patch (Figs. 7.4b and 7.4c). Except for patches with very few native dicots outside the patches, the number of native forbs inside the patch was less than one half the number of dicots outside the patch (Fig. 7.4b), and the number of native dicots inside the patch was less than one third the number of dicots outside the patch (Fig 7.4c).

The diversity of exotic grasses (excluding *N. neesiana*), exotic forbs and exotic dicots inside the patches were respectively similar to their diversity outside the patches (Fig 7.4d-f).

The effect of *N. neesiana* presence on the diversity of native species in total results from two factors: the linear response of native grasses to $\sqrt{}$(patch area), and the number of native dicots/m^2 outside the patches, which together explained 51% of the variance.

Table 7.12. P values for including and excluding terms in parsimonious linear regression models for each plant grouping.

	Native grasses	**Native forbs**	**Native dicots**	**Exotic grasses excl. *N. neesiana***	**Exotic forbs**	**Exotic dicots**
Terms Included						
√(patch area	0.000050	-	-	-	-	-
number of native dicot spp./m^2 outside	-	9.7×10^{-6}	0.00057	-	-	-
number of exotic grass spp. (excl. *N. neesiana*)/m^2 outside	-	-	-	1.2×10^{-8}	-	-
number of exotic forb spp./m^2 outside	-	-	-	-	3.0×10^{-6}	-
number of exotic dicot spp./m^2 outside	-	-	-	-	-	0.00046
Terms excluded						
site	0.13	0.21	0.099	0.63	0.40	0.85
√(patch area)	-	0.33	0.74	0.74	0.88	0.91
patch area	0.43	-	-	-	-	-
√number of native spp./m^2 outside	0.35	0.55	0.51	0.80	0.46	0.79
√number of native grass spp./m^2 outside	0.45	0.16	0.17	0.25	0.31	0.43
√number of native forb spp./m^2 outside	0.98	0.77	0.75	0.30	0.80	0.32
√number of native dicot spp./m^2 outside	0.37	0.75	0.68	0.24	0.53	0.19
√number of exotic spp. (excl. *N. neesiana*)/m^2 outside	0.64	0.28	0.090	0.94	0.55	0.59
√number of exotic grass spp. (excl. *N. neesiana*)/m^2 outside	0.79	0.78	0.45	0.76	0.27	0.58
√number of exotic forb spp./m^2 outside	0.85	0.13	0.072	0.36	0.045*	0.67
√number of exotic dicot spp./m^2 outside	0.67	0.21	0.16	0.29	0.72	0.90

* P value = 0.22 if one influential patch is excluded.

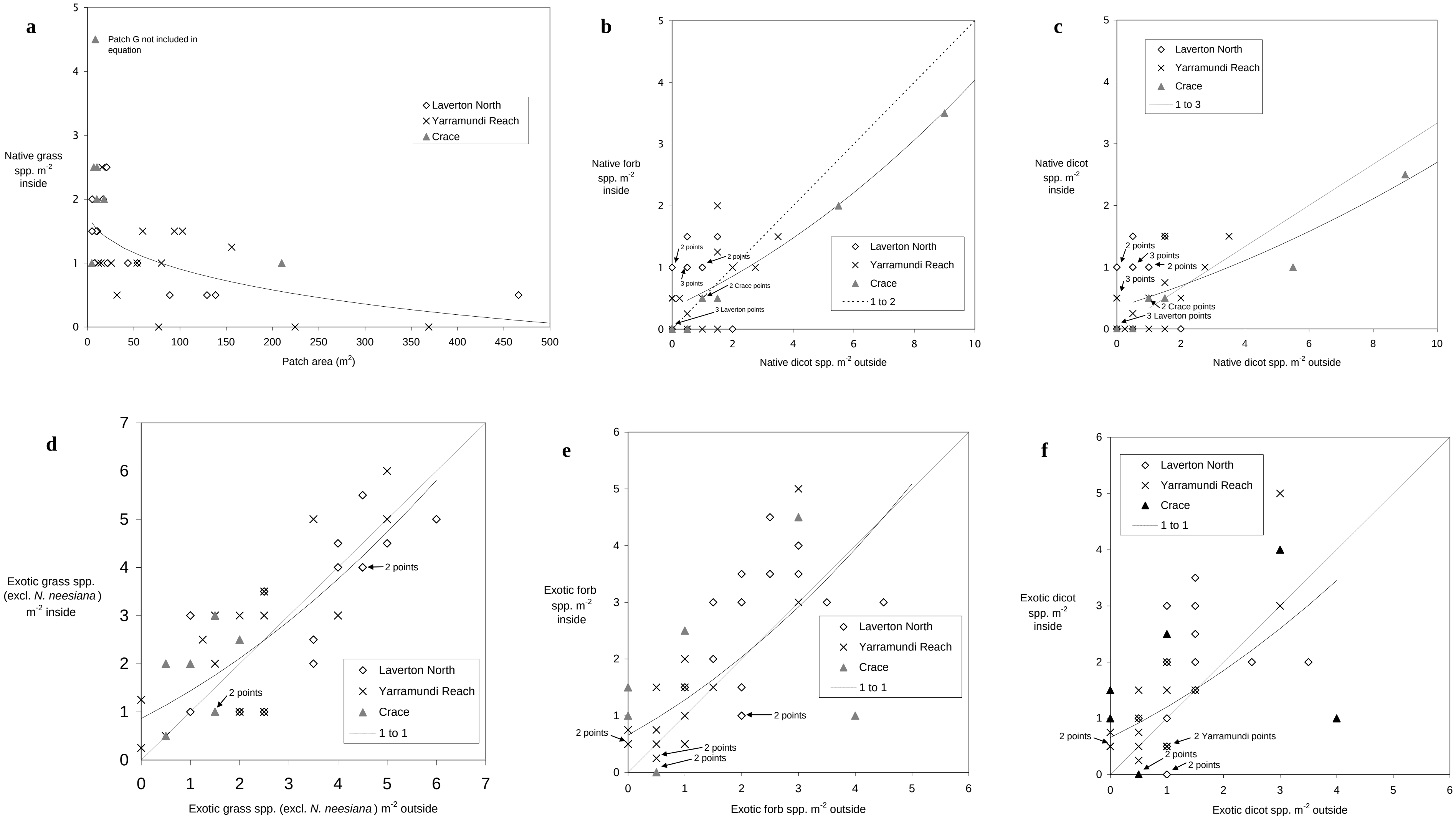

Figure 7.4. Chosen linear regressions of plant composition parameters inside *N. neesiana* patches: (a) relationship between the mean number of native grasses inside *N. neesiana* patches and patch area; (b) relationship between the mean number of native forb species inside *N. neesiana* patches and the mean number of native dicot species outside the patches; (c) relationship between the mean number of native dicots inside and outside *N. neesiana* patches; (d) relationship between the mean number of exotic grasses (excluding *N. neesiana*) inside and outside *N. neesiana* patches; (e) relationship between the mean number of exotic forbs inside and outside *N. neesiana* patches; (f) relationship between the mean number of exotic dicot species inside and outside *N. neesiana* patches.

Incidence of particular species inside and outside patches

The incidence of individual species detected in quadrats at the three grasslands is shown in Tables 7.13 (Crace), 7.14 (Yarramundi Reach) and 7.15 (Laverton North). These tabulations indicate clearly that the effect of *N. neesiana* presence is highly non-specific. Very few species were strongly affected.

Species other than *N. neesiana* that exhibited significant or close to significant differences in incidence inside and outside patches are listed in Table 7.16. Many exotic and native species occurred both inside and outside *N. neesiana* patches (e.g. Fig. 7.5), although the incidence of exotics was particularly large at Laverton North (Table 7.15).

No discernible differences were found in the incidence of particular grass species inside and outside patches except that there was a much greater incidence of *N. neesiana* inside the patches at all three sites (Tables 7.13-7.15), a lower incidence of the dominant native grass *T. triandra* inside the patches at Yarramundi Reach (Table 7.14), a lower incidence of the subdominant native *Austrostipa bigeniculata* inside the patches at Laverton North (Table 7.15) and possibly lower incidence (P = 0.0625) of the subdominant *Austrodanthonia carphoides* (Benth.) H.P. Linder inside the patches at Crace (Table 7.13) and of *Poa labillardierei* Steud. inside patches at Yarramundi Reach. Evidently the presence of *N. neesiana* is closely related to the absence of one or more of the dominant and subdominant grasses at a site.

Apart from *N. neesiana*, the only species for which there is evidence (P=0.0654) of higher incidence inside *N. neesiana* patches is the exotic daisy *Hypochoeris radicata* L. at Yarramundi Reach (Table 7.16, Fig. 7.5).

Figure 7.5. Forbs can survive in *N. neesiana* patches. Native *Bulbine bulbosa* in flower with rosettes of the exotic daisy *Hypochoeris radicata* in an *N. neesiana* patch at 35°17.427’ 149°04.921’ at Yarramundi Reach Grassland, 22 October 2008.

Table 7.13. Number of *N. neesiana* patches (out of 7) in which each vascular plant species was observed inside and outside the patch at Crace Grassland, ACT. The two dominant grasses are listed first, followed by other grasses, then other monocots, then dicots in alphabetical order. Exotic taxa are indicated with an asterisk (*). Significant P values are indicated in bold. 47 taxa were recorded, 30 native, 16 exotic and 1 undetermined (*Carex* sp.).

Species	**Inside**	**Outside**	**P-Value**
**Nassella neesiana*	7	1	**0.03125**
Themeda triandra	3	2	1.00
Other grasses			
**Aira elegantissima*	1	1	1.00
Austrodanthonia auriculata	2	2	1.00
Austrodanthonia caespitosa	4	4	1.00
Austrodanthonia carphoides	1	6	**0.0625**
Austrodanthonia sp.	0	4	0.125
Austrostipa bigeniculata	6	6	1.00
Austrostipa scabra	0	1	1.00
Austrostipa sp.	1	0	1.00
**Avena* sp.	1	1	1.00
Bothriochloa macra	2	3	1.00
**Bromus hordeaceus*	1	0	1.00
Elymus scaber	3	6	0.25
**Lolium rigidum*	1	1	1.00
**Phalaris aquatica*	6	4	0.625
Poa labillardierei	0	1	1.00
**Vulpia* sp.	4	3	1.00
Other monocots			
Carex sp.	1	0	1.00
Juncus filicaulis	0	1	1.00
Lomandra sp.	2	2	1.00
**Romulea rosea*	1	0	1.00
Dicots			
Acaena ovina	1	2	1.00
Asperula conferta	0	1	1.00
Brachyscome sp.	0	1	1.00
Calocephalus citreus	0	1	1.00
Chrysocephalum apiculatum	0	3	0.25
Convolvulus erubescens	1	2	1.00
Crassula sieberiana	1	2	1.00
Desmodium varians	1	1	1.00
Eryngium ovinum	0	1	1.00
Goodenia pinnatifida	0	1	0.50
Haloragis heterophylla	0	1	1.00
**Hypericum perforatum*	1	2	1.00
**Hypochoeris radicata*	2	2	1.00
**Lepidium africanum*	0	1	1.00
Oxalis 'perennans'	2	3	1.00
**Plantago lanceolata*	4	4	1.00
Plantago varia	0	3	0.25
Rumex dumosus	1	0	1.00
Solenogyne dominii	0	1	1.00
**Trifolium angustifolium*	0	1	1.00
**Trifolium dubium*	1	2	1.00
**Trifolium subterraneum*	3	2	1.00
**Trifolium* sp.	2	0	0.50
Vittadinia muelleri	1	1	1.00
Wahlenbergia sp.	0	1	1.00

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Table 7.14. Number of *N. neesiana* patches (out of 15) in which each vascular plant species was observed inside the and outside the patch at Yarramundi Reach grassland, ACT. Two of four quadrats assessed outside patch L were excluded from the results so that the inside and outside data apply to the same total area. The two dominant grasses are listed first, followed by other grasses, a fern, then other monocots, then dicots in alphabetical order. Exotic taxa are indicated with an asterisk (*). Significant P values are indicated in bold. 73 taxa were recorded, 41 native, 30 exotic and 2 undetermined (indet. rhizomatous grass and ?*Cyperus* sp.)

Species	**Inside**	**Outside**	**P-Value**
**Nassella neesiana*	15	5	**0.001953**
Themeda triandra	9	15	**0.03125**
Other grasses			
**Aira* sp.	2	2	1.00
**Aira elegantissima*	1	1	1.00
Austrodanthonia caespitosa	0	1	1.00
Austrodanthonia ?*duttoniana*	0	1	1.00
Austrodanthonia sp.	2	6	0.21875
Austrostipa bigeniculata	1	1	1.00
Austrostipa scabra	0	2	0.50
Austrostipa sp.	3	6	0.375
**Avena* sp.	8	9	1.00
Bothriochloa macra	4	5	1.00
**Briza maxima*	3	3	1.00
**Briza minor*	0	1	1.00
**Bromus diandrus*	1	2	1.00
**Bromus hordeaceus*	8	7	1.00
**Dactylis glomerata*	1	1	1.00
Elymus scaber	1	1	1.00
**Festuca arundinacea*	4	3	1.00
Microlaena stipoides	1	2	1.00
Panicum effusum	0	1	1.00
**Paspalum dilatatum*	10	7	0.5078
**Phalaris aquatica*	3	2	1.00
Poa labillardierei	2	7	**0.0625**
**Vulpia bromoides*	2	2	1.00
**Vulpia* sp.	9	7	0.50
unidentified rhizomatous grass	0	1	1.00
Fern			
Cheilanthes austrotenuifolia	0	1	1.00
Other monocots			
Bulbine sp.	0	2	0.50
Carex inversa	0	1	1.00
Carex breviculmis	1	2	1.00
?*Cyperus* sp.	2	2	1.00
Dianella longifolia	1	0	1.00
Juncus filicaulis	1	0	1.00
Juncus ?*homalocaulis*	0	1	1.00
Lomandra sp.	1	5	0.21875
Lomandra filiformis	2	1	1.00
Lomandra longifolia	0	2	0.50
Tricoryne elatior	0	4	0.125
Dicots			
Acaena ovina	0	1	1.00
Asperula conferta	1	0	1.00
Chrysocephalum apiculatum	1	1	1.00
Convolvulus erubescens	1	2	1.00

Continued next page

Table 7.14 (continued)

Species	**Inside**	**Outside**	**P-Value**
Crassula sieberiana	3	2	1.00
Cynoglossum suaveolens	3	2	1.00
Epilobium billardierianum	1	0	1.00
Eryngium ovinum	1	2	1.00
Euchiton involucratus	0	1	1.00
Goodenia pinnatifida	0	3	0.25
**Hirschfeldia incana*	0	1	1.00
**Hypericum perforatum*	1	4	0.25
**Hypochoeris glabra*	4	1	0.375
**Hypochoeris radicata*	11	4	**0.0654**
**Lactuca saligna*	0	2	0.5
**Lactuca serriola*	3	0	0.25
Leptorhynchos squamatus	0	3	0.25
Oxalis 'perennans'	1	1	1.00
**Petrorhagia* sp.	1	0	1.00
**Plantago lanceolata*	3	2	1.00
Plantago varia	1	4	0.25
**Rubus ‘fruticosus’*	1	0	1.00
Rumex brownii	1	1	1.00
Rumex dumosus	1	0	1.00
**Salvia verbenaca*	1	0	1.00
**Sanguisorba minor*	0	1	1.00
**Silene* sp.	0	1	1.00
**Sonchus oleraceus*	0	1	1.00
**Trifolium dubium*	2	1	1.00
**Trifolium subterraneum*	1	0	1.00
**Trifolium* sp.	4	2	0.5
Velleia paradoxa	0	1	1.00
Vittadinia cuneata var. *hirsuta*	0	1	1.00
Wahlenbergia sp.	0	2	0.50

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Table 7.15. Number of *N. neesiana* patches (out of 14) in which each vascular plant species was observed inside and outside the patch at Laverton North grassland. The two dominant grasses are listed first, followed by other grasses, then other monocots, then dicots in alphabetical order. Exotic taxa are indicated with an asterisk (*). Significant P values are indicated in bold. 45 taxa were recorded, 17 native, 27 exotic and 1 undetermined (grass sp.).

Species	**Inside**	**Outside**	**P-Value**
**Nassella neesiana*	14	1	**0.000244**
Themeda triandra	13	14	1.00
Other grasses			
**Aira* sp.	4	7	0.375
Austrodanthonia caespitosa	0	2	0.50
Austrodanthonia setacea	1	3	0.625
Austrodanthonia sp.	1	0	1.00
Austrostipa bigeniculata	5	12	**0.03906**
**Avena* sp.	10	10	1.00
**Briza maxima*	10	12	0.625
**Briza minor*	9	8	1.00
**Bromus hordeaceus*	5	4	1.00
Chloris truncata	0	1	1.00
Elymus scaber	1	0	1.00
Lachnagrostis filiformis	1	1	1.00
**Lolium rigidum*	4	5	1.00
**Nassella trichotoma*	0	1	1.00
**Phalaris aquatica*	5	4	1.00
Poa labillardierei	1	1	1.00
**Vulpia* sp.	11	13	0.50
Walwhalleya proluta	1	1	1.00
Poaceae sp.	0	1	1.00
Other monocots			
**Moraea setifolia*	1	2	1.00
**Romulea rosea*	14	12	0.50
Dicots			
Acaena ovina	1	0	1.00
**Anagallis arvensis*	6	5	1.00
**Arctotheca calendula*	1	0	1.00
**Cirsium vulgare*	0	1	1.00
Convolvulus erubescens	4	4	1.00
Euchiton sphaericus	1	0	1.00
**Helminthotheca echioides*	1	0	1.00
**Hypochoeris radicata*	1	0	1.00
Oxalis exilis	6	5	1.00
**Plantago lanceolata*	9	9	1.00
Plantago varia	1	1	1.00
**Rapistrum rugosum*	1	1	1.00
Rumex dumosus	2	0	0.50
Senecio quadridentatus	1	1	1.00
**Sonchus asper*	0	1	1.00
**Sonchus oleraceus*	9	8	1.00
**Trifolium dubium*	0	1	1.00
**Trifolium glomeratum*	2	2	1.00
**Trifolium scabrum*	1	0	1.00
**Trifolium striatum*	2	0	0.50
**Trifolium subterraneum*	1	0	1.00
**Trifolium* sp.	1	1	1.00

Table 7.16. Vascular plant species (except *N. neesiana*) whose frequency was significantly or close to significantly different inside *N. neesiana* patches compared to outside the patches at the three grasslands. Significant P values in bold.

Grassland	Species	No. of assessed patches	Occurrences inside	Occurrences outside	P value
Crace	*Austrodanthonia carphoides*	7	1	6	0.0625
Yarramundi Reach	*Themeda triandra*	15	9	15	**0.03125**
	Poa labillardierei	15	2	7	0.0625
	**Hypochoeris radicata*	15	11	4	0.0654
Laverton North	*Austrostipa bigeniculata*	14	5	12	**0.03906**

Discussion

Correlations of *N. neesiana* presence with plant diversity changes

The results from the examination of the effect of *N. neesiana* dominance on plant species diversity are clear (Tables 7.9 and 7.10). At the higher diversity sites (Crace and Yarramundi Reach) native species richness was substantially lower in the presence of *N. neesiana*, and this lower species richness occurred across floristic classes. At the already much degraded Laverton North site, apart from a reduction in *A. bigeniculata,* there was relatively little difference in native species richness between areas inside and outside patches. On the other hand there were only relatively small differences in exotic species richness between the inside and outside of patches, significant only at Yarramundi Reach (Table 7.10).

These results are similar to those found by McArdle *et al.* (2004) in a study of the invasive grass *Hyparrhenia hirta* (L.) Stapf. (Andropogoneae), in woodlands on the North West Slopes of New South Wales that were grazed up until 1994. McArdle *et al.* (2004) found a very marked reduction of native vascular plant species richness and no effect on exotic richness between invaded and uninvaded areas.

None of the parsimonious models for the number of species of different floristic classes inside patches included an effect of site. This implies that the response curves derived in the regression analysis are appropriate for sites of different states of degradation and preservation and that the relationships have reliability over a wide range of Australian situations where native grassland has been partially infested with *N. neesiana*.

Examination of historical aerial photos indicates that *N. neesiana* patches commonly increase in size over time (see Chapter 2), although the rates of change are very variable between sites and patches. Thus the finding that lower native grass richness is correlated with increased patch size suggests that the disappearance of native grass species is, at least in part, related to the age of the *N. neesiana* patches. It appears that this process can progress to a stage, at large patch sizes, where native grasses effectively disappear from within patches (Fig 7.4a). However this interpretation does not imply a particular mechanism for *N. neesiana* patch expansion, and results elsewhere in this thesis suggest that disturbance effects may be causing both biodiversity loss and *N. neesiana* establishment, and enabling patch expansion. Larger *N. neesiana* patches may be the consequence of more intense, longer running or more frequent anthropogenic disturbance.

The result from the regression analysis, that native forb richness is not related to patch size, indicates that there is no change in forb diversity after the initial establishment of *N. neesiana* patches. Thus all the reduction in native forbs and native dicots occurs prior to or at the time of establishment of patches. Also, the reduction in native species richness at (extrapolated) ‘zero patch size’ indicates a simultaneous reduction in native grass diversity prior to or at the time of establishment of *N. neesiana* patches. The regression analysis thus leads to the conclusion that, except when the surrounding grassland is already degraded with low native species richness, a large number of native grasses, forbs and dicots are lost prior to or at the time of establishment of *N. neesiana* patches (Figs. 7.2-7.4). This loss of native species richness includes about two thirds of native dicot species.

On the other hand, there appears to be little change in exotic species diversity after the establishment of *N. neesiana* patches. The diversity of exotic floristic classes inside a patch is generally similar to the diversity outside a patch (Figs. 7.4d-f).

Incidence of particular species inside and outside patches

Since there were many species present in each grassland, there is a high probability that the significance testing of the incidence of species inside and outside patches at a particular grassland will identify some species as having significantly different frequencies inside and outside *N. neesiana* patches when they were actually not significantly different. Up to one in 20 species can be expected to be identified as significant by chance if a probability of 0.05 is considered significant. Nevertheless each species identified as occurring at higher or lower incidence inside *N. neesiana* patches may provide clues to the potential mechanisms involved in the invasion and the related plant diversity changes.

Austrostipa bigeniculata was the subdominant native grass at Laverton North. It was frequently abundant in bands around the margins of *N. neesiana* patches and sometimes itself was the dominant grass in patches similar in shape and size to some *N. neesiana* patches. This perhaps suggests that whatever mechanisms have allowed establishment of the exotic may also have allowed establishment of a native congener. The dominant grass at Laverton North, *T. triandra*, was detected in quadrats inside almost all *N. neesiana* patches at that grassland (Table 7.15). Its cover exceeded that of *N. neesiana* in two quadrats in two small patches and was similarly high in another quadrat (30: 20%, 22: 20%, 18: 26%

respectively), but was ≤10% in other quadrats. The cause of these patterns is unclear, but they are suggestive of recolonisation of *N. neesiana* patches by native grasses under the prevailing burning regime.

Austrodanthonia carphoides was the dominant grass in the matrix vegetation outside two patches at Crace, subdominant to *T. triandra* in another and a minor component around two patches. If an undetermined *Austrodanthonia* species recorded in quadrats at this site was *A. carphoides* the level of significance is increased (Table 7.13). The subdominant *A. bigeniculata* was detected inside almost all patches sampled at Crace, however its cover was always much less than that of *N. neesiana*.

The species with significantly lower incidence inside *N. neesiana* patches at Yarramundi Reach was the native dominant *T. triandra*. Evidence presented in Chapter 5 demonstrates that senescence dieback of *T. triandra* is correlated with increased presence of *N. neesiana* in areas with *N. neesiana* propagule pressure at this grassland. Such dieback , with several characteristic traits, was obvious across wide areas and documented in Chapter 5. Lower incidence of *T. triandra* inside *N. neesiana* patches constitutes further evidence that senescence dieback of *T. triandra* enables invasion by *N. neesiana*. The tall subdominant *Poa labillardierei* was detected at close to significantly reduced incidence inside patches at this grassland.

All the affected grasses may be considered to be species that directly compete with *N. neesiana*. Apart from *T. triandra* they are C_3 species with a similar growing period.

The one species detected at greater incidence inside *N. neesiana* patches was the exotic *Hypochoeris radicata* L. (Asteraceae) at Yarramundi Reach. This perennial daisy is an old established alien in Australia, where it is abundant and very widely distributed in the south-east (Cameron and Richardson 1998), being a common component of suburban lawns and pastures. *Hypochoeris radicata* sometimes proliferates in long unburnt areas of native grassland: Lunt and Morgan (1999a) found that it obtained a mean cover of 33% in an area of Laverton North Grassland unburnt for 17 years, but reached only 1% cover in an adjacent area subject to frequent fire. The distribution of the species at Yarramundi Reach cannot be attributed directly to the absence of fire because the most recent fire burnt the whole grassland, and the earlier fire history is complex, with precise fire boundaries unknown, but fire has not been a component of deliberate management at this grassland for many years. The general abundance of *H. radicata* across a range of habitats, its long flowering period, wind-dispersed achenes, lack of seed dormancy and a light requirement for germination (Cameron and Richardson 1998) give it advantages in finding and occupying newly available ground. It can be considered a species that responds positively to disturbance.

Is *N. neesiana* a cause or a consequence of native plant diversity decline?

Clearly it is a critical issue whether the loss of native species diversity occurs prior to or during the initial establishment of *N. neesiana* patches. More specifically, the key question is whether the establishment of *N. neesiana* causes a reduction in native species diversity, or whether the establishment of *N. neesiana* and the loss of native species diversity have a common cause that results in their correlation. One way to address this issue is to compare the ecological characteristics of the native and exotic species in the native grasslands studied to determine if there are any systematic differences that might explain different responses to the presence of *N. neesiana* or to a prior event such as major disturbance.

Contrasting responses to disturbance of native and exotic species

The species indigenous to Australian temperate native grasslands in general have poor abilities to reoccupy areas in which severe disturbance causes their disappearance from the above-ground vegetation (Morgan 2001). This is mainly due to their perenniality, limited seed production, low and ephemeral soil seed banks and thus a dependence on the current year's seed production for regeneration, and possibly to more-limited propagule dispersal (Table 7.17). None of the native perennial intertussock species in existing native temperate grasslands are obligate seed regenerators, almost all being obligate resprouters, or resprouting and with limited seedling production, and mostly able to set, and actually setting, seed within 12 months of regeneration (Lunt 1990c, Morgan 1996, Lunt and Morgan 2002).

Resprouters in general allocate a smaller proportion of resources to seeds and a larger proportion to underground organs than plants with a non-resprouting strategy (Ramakrishnan and Vitousek 1989). Very few of the native grassland species have permanently established as weeds in other parts of the world (Randall 2002), despite massive exports of grassland-based products, including wool, grain, fodder and livestock, over a long historical period.

Natives are often replaced by exotics in disturbed areas of temperate native grasslands (Stuwe and Parsons 1977, McIntyre 1993, Wong and Morgan 2007). The exotics in general are common weeds found across the range of disturbed, open environments in south-eastern Australia. A large proportion of them have invaded temperate habitats around the world (Randall 2002). Many possess a set of characters that enable rapid colonisation of bare ground, and may be thought of as early successional species, pre-adapted to take advantage of major anthropogenic disturbances (Trémont and McIntyre 1994, Table 7.17) including increased soil nutrient concentrations (Smallbone *et al.* 2008).

Table 7.17. Abundance and distribution, soil seed bank and disturbance response characteristics of floristic components of the vascular plant floras of temperate natural grasslands of south-eastern Australia. ‘Disturbance’ in this context encompasses major anthropogenic disturbances such as livestock grazing, application of fertilisers, major soil disturbance etc. that did not occur prior to European occupation. Sources are indicated at the bottom of the table.

Plant category	**Abundance and distribution**	**Soil seed bank**	**Response to anthropogenic disturbance**
Annuals	variable exotic, few native; 76% exotic[15]; mostly exotic[9, 14]; 75-100% exotic[13];	90% of the spp. in above-ground veg.[1]; 80% of individuals, 59% of spp.[9]; tend to dominance along with longer-lived small-seeded forbs[25]	proportion significantly increased by grazing[13]; proportionately more in soil disturbed sites[19]
Perennials	high proportion of natives; 48% of the exotics, 90% of the natives[15]; largely native[9, 14]	20% of individuals, 41% of spp.[9]; transient[1]	richness significantly reduced by grazing[13]; no positive response to soil disturbance[19]
Monocots	variable proportion	92% of individuals, 37% of spp.[9]	
Dicots	variable proportion	8% of individuals, 63% of spp.[9]	
Forbs	variable proportion	Non-annual small-seed species tend to dominance along with annuals[25]	
NATIVES	variable proportion; sparseness[2]; about half the flora[9,14]; seedlings mostly rare or absent[20]	48% of the spp. in above-ground veg.[1]; most seed germinates or dies within 12 months[3]; minor component, 9% of individuals, 41% of spp.[9] few spp. not present in the above ground veg.[9]; mostly small or transient[18]; little ability to persist particularly in large-seeded spp., seeds often rapidly germinate or lose viability[25]	predominantly intolerant, some tolerant, few disturbance specialists[2]; none advantaged, proportionately disadvantaged[15]; grazing reduces persistence, simplifies complexity, age and size structure of community[21]
Annuals	relatively few[4]; lacking[5]; 10% of the natives[15];very few[9,14]		
Perennials	almost all the natives[5, 9,14]; 90% of the natives[15]; 85-90% native[13]; 90% of the common natives[17]	largely absent, mostly transient[1]; consistent paucity of herbaceous spp.[26]	
Hemicryptophytes		largely absent, mostly transient[1]	
Annual grasses	scarce-few[1]; none[13]; 1 of 14 native[15]; 10% of native grasses[9,14]	mod. to low[1]	
Perennial grasses	all the native grasses[13]; almost all the native grasses[9,14,15]	mostly absent or low[1]	intolerant[15]; sensitive – tolerant[6]; outcompeted by exotic annual grasses and forbs after soil disturbance and nutrient enrichment,[23]
Themeda triandra	widely dominant	v. low[1]; ≤1 year[7]	intolerant[6,15]

continued next page

Table 7.17 (continued).

Plant category	Abundance and distribution	Soil seed bank	Response to anthropogenic disturbance
Non-grass monocots	few, almost all natives[13]	v. high for Cyperaceae spp., otherwise mainly absent[1]; low – v. low persistence (3 spp.)[10]; Juncaceae and Cyperaceae prominent, Liliaceae often absent[25]	
Forbs	sparseness[2]; many[12]	absent – v. low[1]; large only for perennials with small seeds (e.g. *Hypericum gramineum*, *Juncus* spp., *Wahlenbergia* spp.)[3]; mostly transient[1]; persistent only for small seeded perennials (e.g. *Hypericum gramineum*, *Juncus*, *Wahlenbergia*.)[3]; persistence insufficiently known[10]	some intolerant[15]; intolerant[2, 4, 6]; taller species reduced and eliminated by grazing[21]
Dicots		mostly absent, otherwise low[1]; mod. – v. low persistence (3 spp.)[10]; nil persistence (1 sp.)[11]	some intolerant[15]
EXOTICS	variable proportion of the vegetation; about half the flora[14]; 27-32% [13]; dominate the seedling flora[20]	84% of the spp. in above-ground veg.[1]; dominant component, 91% of individuals, 59% of spp.[9]; overwhelming dominance when grazed[10]	most of the disturbance specialists, many tolerant[2]; proportionately advantaged, all of the advantaged species[15]; promoted by lack of fire[8]; many thrive on disturbed soils[17]; facilitated by grazing[21]; increased nutrient levels facilitate invasion[22,23, 24]; high levels - higher densities from larger disturbances[24]
Annuals	52% of the exotics[15]; most of the annuals[4]; v. high proportion of the annuals[9, 14]; 72% of the highly invasive weeds[17]	dominant component[9 10]	advantaged[15]; mostly regenerated profusely after fire[9, 14]; invasions facilitated by grazing[21]
Perennials	48% of the exotics[15]		
Annual grasses	common; one third of the exotic grasses[13]; two thirds of exotic grasses[15]; almost all the exotic grases[9,14]	mostly high, some low[1]; the dominant component, 69% of individuals, 15% of spp.[9]; major component of overwhelming dominance when grazed[10]	tolerant, advantaged[6]; mostly regenerated profusely after fire[9, 14]; dominate biomass after soil disturbance and nutrient enrichment[23]
Perennial grasses	two thirds of the exotic grasses[13]; one third of exotic grasses[15]; minor proportion of the exotic grasses[9,14]	absent to low[1]; much greater than for some native perennial grasses[6]	dominate more highly disturbed sites[16]
Annual monocots		dominant, high – very high[1]	
Non-grass monocots	almost absent[13]	high – v. high[1]; *Romulea rosea* a major component when grazed[10]; Juncaceae and Cyperaceae prominent[25]	regenerate profusely after fire[9,14]
Forbs	diverse[12]	v. high – low, rarely absent[1]; legumes and *R. rosea* a major component when grazed[10]	thistles and flatweeds proliferate and dominate after soil disturbance and nutrient enrichment[23]

[1] Morgan 1998c; [2] McIntyre and Lavorel 1994a; [3] Lunt and Morgan 2002; [4] Trémont and McIntyre 1994; [5] Sharp 1997; [6] Groves and Whalley 2002; [7] Virtue and Melland 2003; [8] Lunt and Morgan 1999c; [9] Lunt 1990b; [10] Lunt 1995a; [11] Lunt 1996, [12] Mott and Groves 1994; [13] Trémont 1994; [14] Lunt 1990a; [15] Stuwe and Parsons 1977; [16] McIntyre 1993; [17] Davies 1999; [18] Morgan 1999a; [19] McIntyre *et al.* 1995; [20] Morgan 2001; [21] Wong and Morgan 2007; [22] McIntyre and Lavorel 1994b; [23] Wijesuriya and Hocking 1999; [24] Wijesuriya 1999; [25] Lunt 1997a; [26] Morgan 1998a.

Reduction of soil nutrient concentrations to pre-disturbance levels using sugar in grassy woodlands significantly benefits the native components of the flora, including *T. triandra*, and reduces the growth of exotics (Prober *et al.* 2005, Smallbone *et al.* 2007, Prober and Lunt 2009). Based on studies of grasslands in the New England Tablelands of New South Wales, McIntyre and Lavorel (1994a) argued that under increasing levels of disturbance, species intolerant of disturbance are gradually replaced by 'disturbance specialists', predominantly exotics. McIntyre *et al.* (1995) found that of all life-forms present in the flora only therophytes responded positively to soil disturbance in these grasslands. Relatively little is known about soil seed banks in temperate grasslands of south-eastern Australia (Lunt 1997). The only detailed studies of soil seed banks in Victorian basalt plains grasslands dominated by *T. triandra* have both highlighted the major differences in the seed banks of the native and exotic components (Morgan 1998c, Lunt 1990b): simply put, all but a few native species have small, transient seed banks, while exotic species, particularly annual grasses, comprise the bulk of the seed bank and most of its non-transient components.

These observations lead to the conclusion that a major difference between the native and exotic species present in Australian native grasslands is their response to anthropogenic disturbance. Such disturbances include soil disturbance, water enrichment, nutrient addition, overgrazing and fire suppression. Most native species have poor abilities to reoccupy disturbed areas, while most exotics are good colonisers of disturbed areas (Table 7.17), although this depends on the nature of the disturbance.

There is strong evidence that anthropogenic disturbances that remove or damage the pre-existing vegetation enable *N. neesiana* to invade. Although Craigie (1993 p. 19) stated, in relation to infestations at Laverton North Grassland that "Prior disturbance does not seem to be necessary for invasion" she nevertheless noted that some of the worst infestations were on disturbed ground, and most infestations were in areas where *T. triandra* cover was sparse. Liebert (1996) reported that almost all of 13 newly discovered infestations of *N. neesiana* in central Victoria were on recently disturbed soils, mostly on roadsides and in railway sidings. Bruce (2001) found that sites with higher levels of soil disturbance in the ACT were overall more highly invaded. Lunt and Morgan (2000) found a strong negative correlation between the distribution of *N. neesiana* and the cover of the dominant native grass, *T. triandra*, the distribution of which was probably primarily limited by previous anthropogenic disturbance, namely ploughing and heavy grazing. Another form of disturbance, absence of fire resulting in senescence dieback of *T. triandra*, has also been implicated as a major cause of *N. neesiana* invasions (Morgan and Lunt 1999) (see Chapter 5).

The above considerations indicate that the establishment of *N. neesiana* and the loss of native plant diversity are likely to have the same common cause, namely localised anthropogenic disturbance of the grassland. It appears less likely that the loss of native species diversity is primarily caused by the competitive pressures within establishing *N. neesiana* patches. If this were the case, then one might expect that the stronger competition would have impacted also on other exotic species, yet the diversity of these was either maintained or increased inside *N. neesiana* patches. In addition, if *N. neesiana* was actively invading, one might expect to find larger areas on the borders between *N. neesiana* patches and native grassland areas that would exhibit a mix of *N. neesiana* and native forbs.

Degradation/preservation status of the three grasslands

The ratios of grasses to other species, native grasses to native forbs, and natives to exotics outside the patches (Table 7.4) are good indicators of the states of degradation and preservation of the sites. Native forbs are generally less tolerant to livestock grazing and trampling than native grasses (Lunt 1990a) and all sites have been subjected to grazing by livestock sometime in their history. Laverton North has much higher ratios of grasses to other species and of native grasses to native forbs and a much lower ratio of natives to exotics than Crace. Yarramundi Reach has intermediate levels except for the native grass to native forb ratio, which is lower than that for Crace. This implies the three sites cover a wide range of degradation states, with Crace being the best preserved (highest native plant richness), and Laverton North the worst. Craigie (1993) reported that most native forbs were eliminated from the Laverton North Reserve by continuous livestock grazing and trampling prior to its reservation in 1983.

It appears that even Crace is not a well-preserved native grassland. For instance, the proportion of the native flora consisting of grasses found at Crace (36%) is higher than any reported by Lunt (1990a) for grasslands at the eastern end of the Victorian basalt plains, indicating, since native forbs are generally the more sensitive component of the flora, that there has been major forb impoverishment. Furthermore the mean native species richness outside *N. neesiana* patches (Table 7.9) at this site was considerably lower than some species-rich remnants assessed by other workers: Patton (1935) calculated a species/area curve for Keilor basalt plains grassland in Victoria and found an average of c. 8-9 species/m^2, Stuwe and Parsons (1977) found species richness of c. 12-18/m^2 in Victorian basalt plains grasslands, while a rich remnant at Evans St., Sunbury, Victoria had c. 11-17 species/m^2 (Morgan 1998b). Nevertheless Crace was chosen to be a site that had both substantial *N. neesiana* infestation and relatively high native plant richness. Unfortunately no site could be found that had higher native plant diversity along with significant infestations of *N. neesiana* – one explanation for this is that high diversity sites have been relatively well managed, with reduced disturbance, and this in turn has limited opportunities for invasion by

N. neesiana. Nevertheless it is reasonable to assume that the three sites cover a good range of native grassland preservation in areas that have been partially infested with *N. neesiana*.

Disturbance regimes at the three grasslands

The Crace Grassland Reserve is highly disturbed, largely as a result of overgrazing (Cooper 2009) and the flora mainly consists of disturbance-tolerant species (ACT Government 2005). General observations at Crace suggest that *N. neesiana* infestations occur in areas subjected to major disturbance that has led to the destruction of the native grasses. These include areas at fence corners and gates subjected to intense animal traffic by kangaroos and cattle, kangaroo scrapes and camps, areas around rabbit warrens, areas that were closely mown, and areas around the former radio installations that were presumably subjected to heavy traffic of machinery etc. A recent review has found that livestock grazing is a degrading pressure on *T. triandra* grasslands that facilitates the dispersal and establishment of exotic plants, and that grazing for biomass reduction of *T. triandra* is a high risk strategy for biodiversity because it reduces the persistence of native species (Wong and Morgan 2007).

The Yarramundi Reach 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 managed by mowing several times a year until 1995 when mowing was greatly reduced in an attempt to protect the endangered Striped Legless Lizard *Delma impar* Fischer (Frawley *et al.* 1995 p.148). The whole site was burnt by wildfire in December 2000. Senescent stands of *T. triandra* were extensive at the site in late 2006 due to the absence of biomass reduction management. Extensive *T. triandra* stand death due to senescence is the main disturbance factor responsible for *N. neesiana* invasion at this site.

At Laverton North, grazing was the main land use for over 100 years prior to temporary reservation in 1983 and subsequent management has been largely by fire (Craigie 1993, Lunt and Morgan 1999a 1999b). Inspection of aerial photographs indicates that denudation due to grazing was severe before reservation and that a dense network of animal trails devoid of vegetation persisted for many years. The burning regime was irregular (described by Henderson (1999) as intermittent, ad hoc burning after reservation), high biomass levels of *T. triandra* occurred in the late 1980s and early 1990s (Craigie 1993) and senescence dieback of *T. triandra* occurred (Morgan and Lunt 1999, Lunt and Morgan 1999a 1999c) at the same time as major *N. neesiana* invasions (Bartley et al. 1990, Humphries and Webster 1992, Kirkpatrick *et al.* 1995), which appear to have been first noted by McDougall (1987). Concerns about the effects of fire on *D. impar* were also a concern at this site. Kukolic (1994) recommended that fire not be used to manage *D. impar* habitat, Hadden (1995) considered fire an unknown risk and Webster *et al.* (2003) noted that fires in spring represented a clear risk to Victorian populations because soil cracks were seasonally unavailable. These concerns were addressed and countered by the work of O'Shea (2005)). Areas denuded by earthworks in parts of the western end of the reserve in the 1980s were also occupied by *N. neesiana* (see Chapter 3). This mix of anthropogenic disturbances probably explains much of the invasion at this site.

Competitive effects of *N. neesiana*

The effects of disturbance that enable *N. neesiana* to occupy a particular area might persist over the longer term, and might explain the observed lower native plant diversity correlated with increased size of *N. neesiana* patches (Fig. 7.4a), if it is assumed that large patches are older than small patches. On the other hand the observed effect may be due to a continued or increasing negative impact of *N. neesiana* due to its greater cover and domination i.e. simplistically, to its competitive potential once it has occupied an area.

According to LeJeune and Seastedt (2001 p. 1572) a particular species is invasive when it "encounters habitats in which its particular suite of traits confers competitive advantage over the native dominants". Allegedly superior competitive abilities have been attributed to *N. neesiana* (e.g. Wells *et al.* 1986, Gardener and Sindel 1998, Cook 1999), but what exactly these consist of, and how they operate has generally not been indicated. Notable advantages possessed by *N. neesiana* in terms of competition for resources have not been described, and of course are dependent on the particular set of potential competitors and the environmental circumstances. Agricultural studies indicate that the plant is not particularly competitive in a mixture with major exotic pasture grasses (e.g. Grech 2007) and it has similar stature, habit, photosynthetic C fixation pathway and phenology to some native grasses. *Nassella neesiana* may possess competitive superiority due to release from co-evolved natural enemies and competitors in Australia, the so-called 'enemy release' hypothesis (Keane and Crawley 2002, Levine *et al.* 2004, Parker *et al.* 2006a), but on the other hand generalist native predators or "evolutionarily novel enemies" (Parker *et al.* 2006a) disproportionately attack exotic prey, which have not evolved specific defences against them (Parker and Hay 2005, Parker *et al.* 2006b). The competitive superiority of plant invaders to native species has "rarely been tested experimentally" (Seabloom *et al.* 2003 p. 13384) and is difficult to demonstrate. The known competitive advantages of *N. neesiana* are related to its high fecundity and possession of a diversity of seed types that can take advantage of a range of management regimes – in particular, it possesses two types of cleistogenes as well as panicle seeds (Gardener 1998). Bourdôt and Hurrell (1989a p. 415) considered the invasiveness of *N. neesiana* in New Zealand sheep pastures to be due to "adaptations that enable the plant to survive the hazards of semi-arid, low-fertility environments, rather than to high competitive ability".

One possible reason the establishment of *N. neesiana* patches might causes a reduction in native species diversity is potential allelopathy of *N. neesiana*. Allelopathic effects of grasses have been widely reported (e.g. Pratley 1996, Gill and Davidson 2000, Lemerle and Murphy 2000, Overbeck *et al.* 2007, Barbosa *et al.* 2008, Rout and Chrzanowski 2009) and all plants are probably more or less allelopathic (Gill and Davidson 2000). Allelopathy has rarely been investigated in the Stipeae, although the leaf leachate of *Stipa pulcherrima* C. Koch has been found to reduce recruitment and slow the growth of co-occurring species (Ruprecht *et al.* 2008). There appears to be no existing evidence of allelopathic effects of *N. neesiana*. If they exist, such effects might be expected to impact over longer periods, and so might possibly explain the lower prevalence of other grasses in larger *N. neesiana* patches. Allelopathy of *N. neesiana* might be expected to have evolved to cause greatest impact upon its main competitors, which in the core of its native range, the Pampas grasslands of Argentina, are other grasses. Such allelopathy, transferred into an environment with an entirely different flora, would constitute a “novel weapon” (Callaway and Maron 2006) against that flora. However there is no good reason to believe that a set of exotic species that has not evolved in the presence of *N. neesiana* and is assembled from a number of different continents should be better adapted to such possible allelopathic effects than the set of native species present in the Australian grasslands. Thus allelopathy, resulting in competitive exclusion of native species, is unlikely to be the cause of the lower native species diversity correlated with its presence.

Forbs and other small plants of the intertussock spaces gradually disappear from *T. triandra* grassland as the density of the sward increases (Wong and Morgan 2007). Similar increase in cover as an *N. neesiana* stand consolidates may explain lower species richness in larger patches. Soil moisture depletion in spring (Chapter 6) is another potential mechanism of ongoing impacts of *N. neesiana* on native plant biodiversity.

Conclusions

The dominance in patches of *N. neesiana* was clearly correlated with major loss of dominant and/or subdominant native grass species and a decline of >50% in the number of native forb species, including a decline of >30% in the number of native dicots. In contrast, the presence of *N. neesiana* did not significantly affect the diversity of any category of exotic species: the diversity of exotic grasses, forbs and dicots inside patches was approximately equivalent to their diversity outside the patches, except at Yarramundi Reach where exotic forb richness was higher inside patches. Species richness of native grasses was strongly negatively correlated with patch size, suggesting that *N. neesiana* has an increasing impact on native grass diversity as its residence time increases. The absence of a site influence on the native species declines is a robust finding, indicating that these effects can be expected in the presence of *N. neesiana* wherever it occurs in native grasslands.

These correlations alone are poorly informative about the mechanisms that may be responsible for the biodiversity effects. But the data, along with evidence provided in earlier chapters and knowledge of the past management of the different grasslands, enable sound inferences to be made about the likely extent to which *N. neesiana* infestation is the cause or the consequence of the biodiversity changes.

On balance there was no evidence that higher plant diversity in these grasslands resulted in vegetation more resistant to *N. neesiana* invasion. Significantly lower native plant diversity occurred in *N. neesiana* patches whatever the species richness of the surrounding uninvaded matrix. However there are indications that dominant native grass components constitute an invasion barrier, and damage to them enables *N. neesiana* invasion. In many cases these biodiversity changes are probably largely or partly a result of prior degradation, including death of native grass due to senescence, overgrazing and soil disturbance. Substantially lower native plant diversity than the native grass dominated matrix at even the smallest patch sizes clearly suggests that *N. neesiana* presence and lower native diversity have a common cause that results in their correlation. Major biodiversity loss appears commonly to precede invasion, affecting most completely the native forb component, the species richness of which declines dramatically whatever the size of the *N. neesiana* patch. Native grass diversity is less dramatically affected.

Despite the strong effect on native species, the presence of *N. neesiana* has little effect on the species richness of exotics, including grass, forb and dicot components. The suggested explanation for this effect involves relatively unselective prior destruction of all species by disturbance, the greater abilities of the exotics to survive in the soil seed bank and to recolonise disturbed areas, along with the general very poor recruitment abilities of the native flora.

Once established, the presence of *N. neesiana* appears to have ongoing negative impacts that lead to gradual disappearances of additional native Poaceae from the areas invaded. These changes occur as patches expand or as the residence period of *N. neesiana* increases. However they might arise from ongoing disturbance of some type (e.g. anthropogenic nutrient enrichment) rather than competitive exclusion by *N. neesiana*.

Chapter 8. Invertebrate diversity

“The plant-herbivore interface may be the major zone of interaction responsible for generating terrestrial organic diversity”.

Paul R. Ehrlich and Peter Raven, 1964, *Butterflies and Plants: A Study in Coevolution*.

Summary

Data are presented on the number of invertebrate species and their abundance in 19 sets of search samples and 23 sets of sweep net samples inside *N. neesiana* patches and in immediately adjacent, native-grass dominated areas for three Victorian and four Australian Capital Territory sites. Sweep net samples indicated consistently lower mean invertebrate species richness and mean total invertebrate individuals inside *N. neesiana* patches in both spring and autumn, with significantly lower mean invertebrate species richness inside *N. neesiana* patches in autumn (12.9 compared to 16.9 spp. or -24%), and significantly lower mean numbers of invertebrate individuals inside *N. neesiana* patches in spring (40 compared to 63, or -37%). The much less speciose search samples showed no consistent or significant differences between the mean numbers of native or exotic species or their total mean abundance inside and outside *N. neesiana* patches, except for the number of exotic individuals in the ACT in spring 2007, where searches in *N. neesiana* patches yielded significantly more exotic individuals (2 spp. compared to 1 sp.), due to larger numbers of the Portuguese Black Millipede *Ommatoiulus moreletii* Lucas. Areas dominated by *N. neesiana* usually had lower invertebrate diversity than areas dominated by native grasses, but disturbance prior to *N. neesiana* occupation may have caused or contributed to the effects. A range of species occurred more frequently and commonly in swards dominated by *N. neesiana* than adjacent *T. triandra* swards and vice-versa, but the mechanisms causing these differences are mostly difficult to identify and rarely due to grass host specificity.

Almost nothing is known about invertebrate exploitation of *N. neesiana* for food or shelter, either in areas where it is native, or in its introduced range and there are no previously published records of invertebrates feeding on the grass in Australia. Details are provided in this Chapter of numerous invertebrates that inhabit *N. neesiana* in Australian temperate native grasslands. *Nassella neesiana* is utilised as food by a wide range of generalist grass-eating insects, including species of Pseudococcidae, Acrididae, Anthribidae, Curculionidae, Anthelidae, Psychidae and Noctuidae, and the fallen seeds are harvested by *Pheidole* ants. The ecology of these insects is generally very incompletely known.

Observations of parasitoids and predators of a few of the insects indicate that *N. neesiana* supports at least simple food webs.

Introduction

Alterations to the composition, structure and functioning of natural ecosystems by invasive plants can have a major impact on native invertebrates but knowledge of how this occurs and what is affected, is very limited (Samways 2005). Weed impacts on animal diversity can be harmful or beneficial. Weeds can provide food, building materials, nectar, shade and numerous other benefits for associated organisms (Richardson and van Wilgen 2004). Low (2002) provided numerous Australian examples of native animals, including endangered species, benefiting from alien plant invasions, by utilising the resources that weeds provide. Weeds can contribute to conservation of biodiversity, for example by protecting other plants from herbivory and acting as refuges or 'nurse' plants for other species.

Does *N. neesiana* have an impact on invertebrate biodiversity? The only previous attempt to assess the impact of *N. neesiana* on faunal diversity (Ens 2002a 2002b) found that insect diversity was lower in areas occupied by the plant than in comparable native dominated areas in Cumberland Plain woodlands (Sydney), although some groups and species benefited. Ens (2002a) reported significant quantitative impacts, with a negative effect of *N. neesiana* on Formicidae (ants) and three Formicidae species, reportedly "by altering the ground cover composition", and on mean abundance of Thysanoptera, and Cicadidae moults, but a beneficial effect ("significant habitat") on Blattodea (cockroaches) and two unidentified Coleoptera spp. Abundance of Collembola, Hemiptera, Gastropoda, Lepidoptera larvae and Araneae was significantly reduced in invaded areas. These results were attributed to altered habitat structure and "change in plant architecture" i.e. the scale, complexity and heterogeneity of plants in the invaded community, and "indirect effects on the trophic hierarchy". Ens (2005) summarised her results as "reduced ant abundance" and alteration of "the entire invertebrate community composition".

Ens' (2002a) study compared effects on invertebrates in one invaded and one uninvaded area at each of two sites. There was no clear description of the vegetation differences between invaded and uninvaded areas, and little indication that the significant correlations detected were not chance results given the large number of possible correlations that were tested for. Similar habitat differences might well have been detected by comparing two different uninvaded areas, e.g. high cover *T. triandra* with low cover *T. triandra*. The factors that explained the presence of *N. neesiana* in the invaded sampling areas and its absence in the uninvaded area were not clearly explained, so there was little indication that the effects were caused by *N. neesiana*, as opposed to prior disturbance.

Any attempt to determine the biodiversity impact of invasive species in a particular habitat is dependent to a large extent on existing knowledge of the biodiversity of the habitat. Yen (1995, 1999) highlighted the lack of baseline invertebrate survey data for Australian temperate native grasslands, and although excellent basic survey work in Victoria is available (Yen *et al.* 1994a 1994b 1995) and there have been numerous subsequent or contemporaneous studies in ACT and Victorian grasslands (e.g. Farrow 1999 2006, Gibson and New 2007, Greenslade 1994, Hadden 1997 1998, Hadden and Westbrooke 1999, Melbourne 1993, Melbourne *et al.* 1997, New 2000, Rowell and Crawford 1995, Sharp 1997), knowledge is still very inadequate for biodiversity assessment purposes. Definitive baseline survey data for invertebrates is lacking for all Australian terrestrial habitats (Neville and Yen 2007).

Assessing the biodiversity value of invertebrate assemblages

As with plants, the abundance or rarity of an invertebrate, its ecological role (e.g. keystone or minor species), its detrimental/pest or beneficial value and its native or exotic status are critical considerations in the assessment of its biodiversity value. However the task of assigning such values to the components of a local fauna is beset with difficulties. Five main factors complicate attempts to assess the impact of plant invasions on invertebrate diversity:

1. '**Taxonomic impediments**' – invertebrate faunas contain large numbers of species, often many undescribed, and often difficult to identify (New 1984, Samways 2005). The problem is magnified by the high proportion of the fauna that have juvenile stages with a different form to the adult. Eggs, larvae, nymphs and pupae of insects are frequently impossible to identify without rearing to the adult stage. Dimorphism or polymorphism in the adult stage is also problematic, e.g. the males and females of flower wasps (Tiphiidae: Thynninae) are highly dimorphic and difficult to associate unless captured in copulo.

2. 'E**cological impediments**' – knowledge of the biology of a species is required to achieve any insight into the ecological mechanisms that might connect it to the impact of the weed. An ecological impediment may arise from the taxonomic impediment, although identification to family or genus level may provide sufficient ecological resolution, e.g. of the likely food plants, habitat or functional role of the organism. Lack of identification necessarily prevents access to any previously published ecological knowledge, so for example the native or exotic status of a species may not be determinable. Even for described taxa, little ecological information usually exists and in a high proportion of cases only the adult has been described.

3. **Highly variable mobility** of a large proportion of the fauna at the scales of interest – e.g. crypis and general immobility may make many species difficult to detect, flying species typically move distances greater than the size of infested areas, and mass dispersal into unsuitable habitats is common. An unknown, but probably high proportion of the fauna present may occur incidentally. These difficulties are compounded by typically seasonal activity patterns and general stochasticity in populations (Cranston and Trueman 1997).

4. A high proportion of species are **small in size** (<5 mm) and some occur in **large numbers,** so processing the sampled material is slow, exacting and requires considerable knowledge and skill.

5. **Sampling methods suitable to the purpose have not been developed or are difficult to apply**. Commonly used methods to assess species diversity such as sweep net sampling are unselective and typically collect large numbers of taxa and individuals. They also tend to damage some taxa making them more difficult to identify. More importantly, such methods provide little or no insight into the microhabitats of collected taxa, and so are disconnected from the objective of weed impact assessment. More refined sampling methods that avoid some of these problems tend to be unproductive; e.g. direct searching of individual plants frequently detects no organisms or organisms that are incidentally present. The spatial area sampled by a particular method may be influenced by the physical or biotic characteristics of the area, e.g. sweep netting will contact less vegetation where the vegetation cover is more open. Such biases in sampling methods need to be understood and ideally standardised across sampling areas (Southwood 1994) and cautious interpretation is required when differing habitats, or habitats with the same composition but different structure (e.g. before and after burning in grasslands) are sampled and compared (New 1984).

Basic knowledge deficiencies mean that even simple measures of faunal values, such as the proportion of an assemblage that consists of common taxa with general habitat requirements or rare taxa with specialised requirements, are difficult to determine. The fauna of an area may appear rich because it contains numerous common species that inhabit disturbed sites, while another area may appear impoverished but contain a high proportion of rare, specialised taxa (New 2010).

Theoretical framework

A complex range of biotic and abiotic factors influence invertebrate community structure, including plant species composition, vegetation structure and landscape composition. Schaffers *et al.* (2008) found that local plant species composition best predicted arthropod assemblages in a range of semi-natural grassland types in the Netherlands and that vegetation structure was a poor predictor. Plant species composition “integrates and synthesises across … causal factors … over time”: it is largely determined by environmental conditions, has a strong influence on vegetation structure, and has direct, “bottom-up” trophic effect likely to be carried upward to higher trophic levels (Schaffers *et al.* 2008 p. 791).

Trophic effects are likely to be of particular importance where an invasive exotic grass displaces native grasses in grassland vegetation. Two complementary theories seek to explain the effects of faunal community composition that may occur in such situations. The enemy release hypothesis, a foundation of classical weed biological control, predicts that an exotic plant in its introduced environment lacks native natural enemies and that where it replaces native vegetation it therefore reduces diversity by eliminating fauna dependent on the plants displaced (New 1989, Wajnberg *et al.* 2001, Keane and Crawley 2002, Levine *et al.* 2004, Parker *et al.* 2006a). In contrast, the biotic resistance hypothesis posits that native generalist plant predators prefer the exotic plant because it lacks co-evolved defences to them (Levine *et al.* 2004, Parker *et al.* 2006a 2006b, Parker and Hay 2005). Both effects may occur concurrently, so that taxa that are host-specific on native plants disappear from invaded areas, while taxa that are generalists, or otherwise possess adaptations that enable them to utilise the introduced species, may increase in abundance or occur where they were previously absent.

Food webs are another conceptual basis for comprehending the interactions of invasive species on the invaded community (Strong and Pemberton 2002). Those that develop around animals introduced for biological control "are simpler than in natural communities" (Strong and Pemberton 2002 p. 57) and similar simplification may be expected at higher trophic levels when an exotic plant invader displaces native plants. The effects on herbivores should determine the faunal composition at higher trophic levels (Schaffers *et al.* 2008).

The net negative effect on invertebrate species diversity might therefore be expected to be low if *N. neesiana* simply replaces a native grass, but will presumably increase, potentially to high levels, if *N. neesiana* invasions actually cause the loss of diverse native floras. Large losses of invertebrate biodiversity would also be expected if *N. neesiana* infestations are the result of prior losses of native floristic diversity due to disturbance. Some native generalist herbivores and their dependents at higher trophic levels can be expected to spread into infestations but many specialist herbivores and their dependents can be expected to disappear.

Invertebrate utilisation of N. neesiana

The existing literature appears to contain no records of invertebrate utilisation of *N. neesiana* in Australia, nor have any records of utilisation in the native range been located. Infestations of unidentified aphids (Hemiptera: Aphidae) and mealybugs (Hemiptera: Pseudococcidae) have been found on *N. neesiana* cultivated in the Department of Primary Industries glasshouses at Frankston (Julio Bonilla pers. comm.).

An extensive literature survey detected few detailed records of invertebrate utilisation of grasses found in the temperate native grasslands of south-eastern Australia. In particular there are few records of insect species that attack native grasses, except for butterflies (Lepidoptera) (Braby 2000). The only records of invertebrate predation on *Nassella* spp. are for *N. trichotoma*, which is the food plant of Australian amycterine weevils (Coleoptera: Curculionidae) (Zimmerman 1993) and is damaged by two species of underground grass grubs, *Oncopera* spp. (Lepidoptera: Hepialidae) (Campbell 1998). Records of nematodes from native grasses also appear to be limited and none have been found that relate to *Nassella* spp., however unidentified "*Stipa*" spp. are colonised by three species (McLeod *et al*. 1994). Lowe (1954) recorded the root-feeding larvae of *Chlorochiton* sp. (Coleoptera: Scarabaeidae), a New Zealand endemic, killing large patches of *N. trichotoma*. Slay (2001) recorded that the Black Field Cricket *Teleogryllus commodus* (Walker) (Orthoptera: Gryllidae), a species commonly found in temperate grasslands in Victoria, hollows out the fallen seeds of *N. neesiana* in New Zealand. This appears to be the only published record of invertebrate utilisation of *N. neesiana*.

Based largely on Northern Hemisphere knowledge, the basic insect phytophage fauna of the smallest grasses generally consists of one species each of Eurytomidae (Hymenoptera), Cecidomyiidae (Diptera) and Pseudococcidae (Hemiptera) (Tscharntke and Greiler 1995). These may be species-specific, narrowly oligophagous on several grass species or genera, or widely polyphagous. The phytophage assemblage of a grass is dependent on many factors, but larger faunas are associated with wider geographical range, large size, predictable occurrence and perenniality (Lawton and Schroder 1977). Thus the large, cosmopolitan Common Reed, *Phragmites australis* (Cav.) Trin. ex Steud., is the most speciose grass host known, attacked by c. 100 insect species (Tscharntke and Greiler 1995) and has a total of over 160 associated arthropods, approximately half of which are endophages (Witt and McConnachie 2004). Its diverse flora may be largely a result of a long evolutionary history, it being a "Palaeogenic relict" belonging to the "most ancient of modern grasses" the Arundineae (Tsvelev 1984 p. 59).

In Australia, *N. neesiana* can therefore be expected to host a range of native oligophagous or polyphagous herbivorous invertebrates and to lack species-specific and narrowly oligophagous herbivores from its native range. The makeup of these two groups is difficult to predict since guilds of grass-feeders have not yet been identified for the native grasses of Australian temperate grasslands or for *Nassella* species, either here or in their native ranges. Existing knowledge of the faunas of south-eastern Australian native grassland forbs is also rudimentary, so it is not possible to predict changes to the fauna resulting from forb displacement.

Aims

The primary aim of the invertebrate studies was to compare the species diversity and abundance of invertebrates in areas occupied by *N. neesiana* with immediately adjacent, otherwise similar, areas dominated by native grasses, at a range of sites at which floristic data was collected. Based on the known difficulties of invertebrate sampling and biodiversity assessment techniques it was determined that an attempt should be made to assess as large a part of the macroinvertebrate fauna as feasible, using a range of sampling methods. The second aim was to examine the invertebrate fauna of *N. neesiana* and native grasses, particularly *T. triandra*, with a focus on herbivorous insects feeding on the grasses. The expectation was that no specialist *N. neesiana* herbivores would be found, but that the plant would be attacked by native generalists. A subsidiary objective was to gather evidence that *N. neesiana* herbivores form at least part of the basis of food webs in invaded communities.

A deductive process was then followed to attempt to identify trends in these data that might make sense in terms of established theories. Data were interpreted in the context of the reduced floristic diversity associated with invaded areas and potential cause and effect relationships.

Methods

Sampling

To compare the invertebrate species richness and species population sizes of invaded areas with those of the native grassland matrix, invertebrates were sampled at three sites in Victoria and four sites in the ACT by direct searching and sweep netting (Table 8.1). Matched samples were obtained at each site on each date in areas dominated by *N. neesiana* and in immediately adjacent areas dominated by native grasses. Nominal centres of areas of native grass sampled were within 30 m of the nominal centres of the matched *N. neesiana* areas sampled. To avoid edge effects and minimise presence of *N. neesiana* plants, the areas of native grass sampled were always more than 2 m beyond the outer boundaries of the *N. neesiana* patches. The locations and general features of these sites have been provided in Chapter 1 and their botanical compositions verified by sampling reported in in Chapter 7.

This invertebrate sampling data provided no direct evidence of any functional relationship between the invertebrates collected and the two grass types. To gather data on invertebrate utilisation of *N. neesiana* and native grasses, additional observations were made opportunistically in the field when invertebrate feeding or other close association was noticed. Specimens found were in many cases held in captivity for rearing and further study. Records were made of any predation or parasitism of grass-utilising species to provide basic information on food webs.

Direct search

Search samples were undertaken on hands and knees and involved 15 minutes of systematic searching of the soil surface, litter, bases and upper parts of plants along irregular transects no less than 2 m from perceived boundaries with native grass or *N. neesiana* dominated areas.

Invertebrates detected were collected by hand, without the aid of any equipment. Collected specimens were placed directly into vials of 75% ethanol, except for some material not requiring preservation, such as skeletal parts of beetles, which were sometimes held in vials without fluid. Search samples were standardised by a set period of search time. Variation in the vegetation density and other characteristics of the sample areas meant that equivalent areas or volumes were not sampled.

Material collected included skeletal parts lying on the ground or litter surface and within spider webs. Specimens were mostly of moderate to large size, the size range largely determined by what could be picked up in the fingers. Small and rapidly moving insects such as leafhoppers (Hemiptera: Cicadellidae), ants and small moths were largely ignored. Invertebrate artefacts including mollusc shells and spider egg sacs that were found were included in the samples and counted along with living individuals.

A total of 212 individuals were collected in Victoria and 537 in the ACT.

Sweep net

Sampling was undertaken with a standard hoop net with a 38 cm diameter circular hoop (Australian Entomological Supplies E31), a funnel-tapered, white polyester net bag, 74 cm long with 0.9 x 0.3 mm mesh (Australian Entomological Supplies E563) and a 1.2 m handle. Each sample consisted of 15 horizontal sweeps through the standing vegetation, with one sweep per pace, and was undertaken in less than one minute. Sweeps were selectively targeted at denser patches of the sample grass, avoiding as far as possible areas of mixed species in the canopy. Sampling was undertaken under conditions of no or light winds, and when the canopy was not wet due to precipitation. Approximately equivalent spatial areas, defined by the net size are considered to have been sampled in native grass and *N. neesiana* dominated areas.

Samples were emptied into zip-lock plastic bags and killed with household aerosol insecticide. If large, strong insects such as adult grasshoppers were collected they were separated and killed by immersion in 75% ethanol. Some juvenile individuals were separated for attempted rearing and a few adults were kept alive for tests of potential food plants. Zip-lock bags of specimens were stored in a freezer until processing.

A total of 1096 individuals were collected in Victoria and 2060 in the ACT.

Specimen processing and identification

Direct search specimens preserved in alcohol were sorted using forceps in a shallow plastic saucer. Sweep net sample material was sorted in white plastic trays using forceps and fine paint brushes. Invertebrate artefacts including spider egg cases and hatched eggs were also separated and treated as part of the sample yield.

Table 8.1. Sample site locations, dates and times of sampling and weather data for invertebrate search and sweep net samples. Times are clock times at the start of the sampling period. The search sample period was 15 minutes; sweep net samples were undertaken in less than 1 minute. Temperatures were at ground level with an unshaded thermometer at the time of the sampling.

Site		**Location**	**Dates**	**Search start time**		**Sweep net start time**		**Temp (°C)**	**Weather**
				Nassella neesiana	***Themeda triandra***	***Nassella neesiana***	***Themeda triandra***		
Woodlands		*N.n.* 37°38.240' 144° 50.153'	3/11/06	-	-	14:10	14:05		
		T.t. 37°38.231' 144° 50.153'	8/03/07	11:22	11:37	12:33	12:40	21-23	clear, light-moderate SW wind, recent light rain
			8/03/08	15:07	16:29	16:10	16:05	30-31	overcast, light-moderate SSW wind
Iramoo		N.n. 37°45.233' 144°47.461',	9/11/06	-	-	18:37	18:55		no cloud, cool, S breeze
		T.t. 37°45.221' 144°47.457'	27/11/06	17:29	17:42	17:06	17:00		sunny, warm, light SW breeze
			8/03/07	15:17	15:00	14:50	14:45	24-26	50-60% cloud, light-moderate SW wind
			10/08/07	14:45	15:05	14:30	14:25	15	overcast, cool, N. wind
			6/03/08	14:23	14:47	15:52	15:55	28-30	no cloud, light-moderate S wind
Laverton North	Patch A	*N.n.* 37°50.710' 144°47.394'	22/4/07	-	-	14:59	15:07	22	80% cloud, light-moderate S wind, rain previous day
		T.t. 37°50.700' 144°47.397'	7/03/08	14:15	14:40	15:08	15:12	35	near cloudless, light S breeze
Constitution Avenue		*N.n.* 35°17.450' 149°08.523' *T.t.* 35°17.462' 149°08.512'	14/10/07	15:52	15:41	15:19	15:12	29	5% cloud, light-very light NW breeze, dry vegetation, dry ground
			24/04/08	15:25	14:45	14:40	14:33	26-30	20-40% cloud, still to light SE breeze, mild-warm
			20/10/08	11:28	11:00	10:50	10:43	33-35	cloudless, warm, very light W breeze
Dudley Street		*N.n.* 35°18.844' 149°05.480' *T.t.* 35°18.851' 149°05.471'	15/10/07	15:45	15:22	15:15	15:11	34	no cloud, 25□ in shade, mild-warm, light-moderate W breeze, dry vegetation, dry ground
			24/04/08	11:43	12:37	11:12	11:16	33-35	little high cloud, still-very light air from S, mild-warm
			19/10/08	15:40	15:11	15:00	14:56	32-38	40% cloud, light W breeze, dry
Crace Grassland	Patch A	*N.n.* 35°13.693' 149°07.378',	14/10/07	12:34	12:12	12:00	12:05	24-38	10% high cloud, mild, light NW wind, dry
		T.t. 35°13.682' 149°07.368'	23/04/08	12:35	12:08	11:54	11:50	28-38	50% cloud, mild-warm, windless
	Patch B	*N.n.* 35°13.621' 149°07.426' *T.t.* 35°13.622' 149°07.432'	24/10/08	15:34	15:11	14:59	14:54	23-27	light overcast (high cloud), very light N wind, cloud thickened to almost rainy, wind cooled
Yarramundi Reach	Patch A	*N.n.* 35°17.367' 149°05.047' *T.t.* 35°17.366' 149°05.028'	25/5/07	-	-	13:32	13:25	21	cloudless, still to very light breeze, mild
	Patch D	*N.n.* 35°17.441' 149°04.814' *T.t.* 35°17.444' 149°04.821'	15/10/07	12:45	13:10	12:32	12:38	36-38	no cloud, warm, light-moderate W wind, vegetation dry, ground dry
			23/04/08	14:52	15:13	14:22	14:30	24-29	little cloud, light E wind
			19/10/08	16:59	17:21	16:40	16:43	29-35	15% cloud, light W breeze, dry

Specimens were preserved, mounted and labeled in accordance with standard practices. Material was either pinned (directly with large specimens, or glued to card triangles or rectangles with entomological glue, or PVA glue for skeletal fragments of larger Coleoptera) or preserved in 75% ethanol in screw-topped, glass vials. Multiple specimens of small species were generally mounted together on large cards. Specimen and vial data labels were generated on computer, photo reduced using a photocopier and printed on acid-free paper.

Identifications were obtained by comparison with specimens in institutional collections (Museum of Victoria, Victorian Agricultural Insect Collection), using keys and descriptions in a wide range of literature and on web sites, and by referral to specialist taxonomists. Identification of specimens from sweep net samples was affected by the poor condition of many individuals due to abrasion in the net. Identification of species was also impaired by the lack of adults of some taxa. Various other taxonomic difficulties impeded analysis. However a large proportion of species from the search samples was identified to sufficient taxonomic level to determine their exotic or native status. A much more limited proportion of species collected in the sweep net samples could be identified to such a level.

Vegetation of the sampling sites

Sweep net and search sampling at Laverton North, Crace and Yarramundi Reach was undertaken in and around patches of *N. neesiana* that were botanically sampled as part of floristic quadrat studies. Separate botanical assessments of invertebrate sampling areas were undertaken at Woodlands (Vic.), Iramoo (Vic.), Constitution Avenue (ACT) and Dudley Street (ACT). Presence and cover of all vascular species present was assessed in each sampling area using the same technique as in the floristic studies (Chapter 7). At the Victorian sites three 1m x 1m quadrats were assessed in the *N. neesiana* area and three in the matched area dominated by native grasses. At the ACT sites two quadrats were assessed, except at Yarramundi Reach where four quadrats were assessed.

Vegetation of the areas sampled by sweep net and direct searching is summarised in Table 8.2. *N. neesiana* was the dominant grass in all *N. neesiana* areas sampled and ranged in cover from 27% to 80%. *Themeda triandra* was the dominant grass in matched areas of native grasses except for Crace patch B, where *Austrodanthonia carphoides* cover was 43% and *T. triandra* 15%. Except for that site *T. triandra* cover ranged from 38% to 91%.

Statistical Analysis

The total number of species and total number of individuals in each search and sweep net sample were calculated. Each of these samples was a unique combination of site x visitation date x dominant grass type x sampling method. For search samples, data was analysed for the number of exotic species, native species and total species, and for the number of exotic, native and total individuals. Exotic/native contrasts were not possible with the sweep net data.

Search samples

Matched samples from the four sites in the ACT were taken on three occasions: October 2007, April 2008 and October 2008. These were first analysed individually for each period, then as a combined data set. Victorian data consisted of five sets collected in March in either 2007 or 2008, and these were analysed as a set. Two Victorian samples in August and November were not analysed as a set. Paired T tests using ANOVA were applied to data for the number of exotic species, native species and total species per sample, and the number of exotic individuals, native individuals and total individuals for the various periods for the ACT and Victorian sites.

An average of each measurement was calculated for all autumn samples (ACT – April, Victoria – March), and all ‘spring’ samples (ACT – October, Victoria – August and November), from each combination of site and dominant grass type (*N. neesiana*/*T. triandra*). These averages were used as the unit of analysis for each measurement. Spring measurements and autumn measurements were analysed using two treatment split plot analyses of variance with site representing the main plots and State (ACT or Victoria) and dominant grass type being the treatments.

Sweep net samples

An average of each measurement was calculated for all autumn (ACT - April and May, Victoria - March and April) samples, and all ‘spring’ (ACT – October, Victoria – August and November) samples, from each combination of site and dominant grass type (*N. neesiana* or *T. triandra*). These averages were used as the unit of analysis for each measurement. ‘Spring’ measurements and autumn measurements were analysed using two treatment split plot analyses of variance, with site representing the main plots, and State and dominant grass type being the treatments. The counts of the number of individuals were logarithmically transformed before analysis.

Further analysis was undertaken on the frequency of occurrence of taxa that occurred frequently or commonly in two or more samples.

Grass utilisation

The data presented is a compendium of *ad hoc* observations of direct utilisation and information from the search and sweep net sampling. Statistical analysis was not undertaken. Records were qualitatively assessed in regard to the known biology of the taxa in relation to utilisation of Poaceae.

Table 8.2. Vegetation of the invertebrate sampling areas. Means of three 1 m^2 quadrats at Woodlands, Iramoo and Laverton North, means of two 1 m^2 quadrats at Yarramundi Reach patch D, Constitution Avenue, Dudley Street and Crace, and of four 1 m^2 quadrats at Yarramundi Reach patch A.

Site		**Date**	**Sample area**	**Sward height (cm)**	***N. neesiana* cover (%)**	***T. triandra* cover (%)**	**Total vascular plant cover (%)**	**Cover of other major species (%)**	**Cover of detached litter (%)**	**Bare ground (%)**	**Vascular plant species m^{-2}**
Woodlands		12/3/08	*N. neesiana*	11	38	0	45	*Holcus lanatus* 4 *Microlaena stipoides* 3	29	24	4.7
			T. triandra	7	0	49	49	-	6	43	2.7
Iramoo		16/4/08	*N. neesiana*	22	72	0	82	*Nassella trichotoma* 8 *Themeda triandra* 2	12	5	3.7
			T. triandra	11	3	88	92	*Lolium rigidum* 2	4	3	7.0
Laverton North		18/4/08	*N. neesiana*	12	27	0	37	*Austrostipa bigeniculata* 3 *Romulea rosea* 3 *Plantago lanceolata* 2	3	60	6.0
			T. triandra	13	0	38	45	*Romulea rosea* 4	5	50	6.3
Constitution Ave		17/10/07	*N. neesiana*	13	44	3	100	*Trifolium subterraneum* 40 *Hirschfeldia incana* 6.5 *Bromus hordaceus* 4, *Vulpia* sp. 3	0	0	7.0
			T. triandra	13	0	91	98	*Hypericum perforatum* 5	2	0	5.0
Dudley St.		17/10/07	*N. neesiana*	10	71	0	78	*Plantago varia* 6	18	4.5	3.5
			T. triandra	7.5	0	90	99	*Poa labillardierei* 2.5 *Plantago varia* 2.5 *Goodenia pinnatifida* 2	1.5	0	5.0
Crace	Patch A	16/10/07	*N. neesiana*	1	36	2	45	Dung 7, *Trifolium* spp. 2.3 *Austrostipa* sp. 2 *Phalaris aquatica* 2	12	36	6.5
			T. triandra	2.5	0	61	79	*Austrodanthonia* sp. 18	6.5	14	4.0
	Patch B	18/10/08	*N. neesiana*	6.5	80	6.5	87	Dung 11	5.5	2	6.5
			T. triandra	14	0	15	69	*Austrodanthonia carphoides* 43	10	16	14.0
Yarramundi Reach	Patch A	25/5/07	*N. neesiana*	8.5	48	0	54	*Paspalum dilatatum* 4	38	8	3.0
			T. triandra	20	0	78	80	-	20	0	2.5
	Patch D	16/10/07	*N. neesiana*	20	72	0	79	Cryptogam crust 4 *Paspalum dilatatum* 3	14	3	8.0
			T. triandra	13	0	69	72	Cryptogam crust 17	5	6.5	9.0

Results

Species richness and population size: *N. neesiana* vs native grassland

Search samples

No significant differences were found between the mean number of invertebrate species or the mean number of invertebrate individuals in search samples inside *N. neesiana* patches and outside the patches where *T. triandra* was the dominant grass (Tables 8.3-8.9) except for the number of exotic individuals in the ACT in October 2007 (Table 8.3), where searches in *N. neesiana* patches yielded significantly more exotic individuals. The Portuguese Black Millipede *Ommatoiulus moreletii* Lucas (Julidae) alone explains the difference in exotic species at each site (Table 8.10). No significant differences were detected for April 2008 ACT samples (Table 8.4), October 2008 ACT samples (Table 8.5), ACT samples as a whole (Table 8.6), March Victorian samples (Table 8.7), all autumn samples (Table 8.8) and all 'spring' samples (Table 8.9). No significant differences in total numbers were found between sites.

Table 8.3. Effect of dominant grass type on the mean number of invertebrate species and individuals in search samples in the ACT in October 2007. Significant P value in bold.

Measurement	***Nassella neesiana***	***Themeda triandra***	**sed**	**P-Value**
Number of Species				
Native	5.5	6.5	1.96	0.65
Exotic	1.0	0.5	0.29	0.18
Total	7	7	2.2	0.84
Number of Individuals				
Native	18	30	17.6	0.55
Exotic	2	1	0.3	**0.014**
Total	20	31	17.4	0.59

Table 8.4. Effect of dominant grass type on the mean number of invertebrate species and individuals in search samples in the ACT in April 2008.

Measurement	***Nassella neesiana***	***Themeda triandra***	**Sed**	**P-Value**
Number of Species				
Native	7.5	7.3	1.03	0.82
Exotic	1.0	0.8	0.48	0.64
Total	8.5	8.0	1.19	0.70
Number of Individuals				
Native	15	15	2.2	0.92
Exotic	4	5	2.0	0.65
Total	19	20	2.8	0.81

Table 8.5. Effect of dominant grass type on the mean number of invertebrate species and individuals in search samples in the ACT in October 2008.

Measurement	***Nassella neesiana***	***Themeda triandra***	**Sed**	**P-Value**
Number of Species				
Native	6.3	6.0	0.63	0.72
Exotic	1.5	1.3	0.25	0.39
Total	7.8	7.3	0.65	0.50
Number of Individuals				
Native	25	14	10.2	0.36
Exotic	3	4	1.0	0.39
Total	28	18	10.4	0.41

Table 8.6. Effect of dominant grass type on the mean number of invertebrate species individuals in search samples in the ACT, averaged over three sampling occasions (October 2007, April 2008, October 2008).

Measurement	***Nassella neesiana***	***Themeda triandra***	**Sed**	**P-Value**
Number of Species				
Native	6.4	6.6	0.89	0.86
Exotic	1.2	0.8	0.14	0.092
Total	7.6	7.4	0.83	0.85
Number of Individuals				
Native	19	20	3.0	0.94
Exotic	3	3	0.4	0.73
Total	22	23	3.3	0.91

Table 8.7. Effect of dominant grass type on the mean number of invertebrate species and individuals in search samples in Victoria, averaged over March sampling occasions.

Measurement	***Nassella neesiana***	***Themeda triandra***	**Sed**	**P-Value**
Number of Species				
Native	6.3	6.8	0.76	0.58
Exotic	1.5	1.7	0.17	0.42
Total	7.8	8.5	0.83	0.51
Number of Individuals				
Native	10	12	1.6	0.29
Exotic	3	6	1.6	0.24
Total	13	17	3.4	0.33

Table 8.8. Effect of dominant grass type on the mean number of invertebrate species and individuals in search samples, averaged over all autumn (April and May) sampling occasions in Victoria and the ACT.

Measurement	***Nassella neesiana***	***Themeda triandra***	**sed**	**P-Value**	
				Grass type	**State by grass type interaction**
Number of Species					
Native	7.0	7.1	0.68	0.92	0.61
Exotic	1.2	1.1	0.29	0.81	0.51
Total	8.2	8.2	0.78	1.00	0.49
Number of Individuals					
Native	13	14	1.4	0.58	0.42
Exotic	3	5	1.3	0.25	0.56
Total	16	19	2.2	0.34	0.45

Table 8.9. Effect of dominant grass type on the mean number of invertebrate species individuals in search samples, averaged over all ‘spring’ (ACT – October, Victoria – August and November) sampling occasions.

Measurement	***Nassella neesiana***	***Themeda triandra***	**sed**	**P Value**	
				Grass type	**State by grass type interaction**
Number of Species					
Native	5.4	5.4	1.07	1.00	0.53
Exotic	1.1	0.8	0.11	0.075	0.27
Total	6.5	6.2	1.11	0.81	0.63
Number of Individuals					
Native	18	18	3.9	1.00	0.81
Exotic	2	2	0.4	1.00	0.29
Total	20	20	3.8	1.00	0.90`

Table 8.10. Number of individuals of the Portuguese Black Millipede *Ommatoiulus moreletii* and the native millipede *Onocladosoma* sp. detected by search sampling in grassland dominated by *N. neesiana* or *T. triandra* at Dudley Street and Constitution Avenue, ACT, October 2007 and April 2008.

Site	**Date**	***N. neesiana***		***T. triandra***	
		O. moreletii	*Onocladosoma* sp.	*O. moreletii*	*Onocladosoma* sp.
Constitution Ave	14/10/07	2	0	0	0
Dudley St	15/10/07	3	0	1	1
Constitution Ave	24/4/08	2	0	8	5
Dudley St	24/4/08	9	0	6	1
Total		16	0	15	7

Sweep net samples

Sweep net samples showed significant differences between the mean number of invertebrate species inside and outside *N. neesiana* patches, averaged over all autumn samples (Table 8.11), and the mean number of invertebrate individuals inside and outside *N. neesiana* patches over all ‘spring’ samples (Table 8.12). The mean number of species in *N. neesiana* samples in autumn was 76% of that in *T. triandra* autumn samples (Table 8.11). The mean number of species in *N. neesiana* samples in 'spring' was 85% of that in *T. triandra* samples (18.2 compared to 21.4 spp.), but the difference was not statistically significant at the $p<0.05$ level. The mean number of individuals in 'spring' *N. neesiana* samples was 64% of that in the matched *T. triandra* samples (Table 8.12). The mean number of individuals in autumn *N. neesiana* samples was half of that in the matched *T. triandra* samples (Table 8.11) but the difference did not approach statistical significance.

A near significant State/grass-type interaction for the number of species in autumn sweep net samples (Table 8.11) indicates a pronounced difference in the richness of the ACT sites, with Victorian sites being more impoverished (14.1 versus 11.2 spp./sample in *N. neesiana* patches, 19.5 versus 13.5 spp./sample outside patches).

Table 8.11. Effect of dominant grass type on the mean number of invertebrate species and individuals in sweep net samples, averaged over all autumn (ACT – April and May, Victoria – March and April) sampling occasions.

Measurement	***Nassella neesiana***	***Themeda triandra***	**sed**	**P Values** **Grass type**	**State by grass type interaction**
Number of Species					
Total	12.9	16.9	0.69	**0.0020**	0.082
Number of Individuals					
(back transformed)	30	58	0.153	0.13	0.77

Table 8.12. Effect of dominant grass type on the mean number of invertebrate species and individuals in sweep net samples, averaged over all 'spring' (ACT – October, Victoria – August and November) sampling occasions.

Measurement	***Nassella neesiana***	***Themeda triandra***	**sed**	**P Values** **Grass type**	**State by grass type interaction**
Number of Species					
Total	18.2	21.4	2.07	0.19	0.58
Number of Individuals					
(Back transformed)	40	63	0.071	**0.049**	0.49

The occurrence of some taxa found relatively frequently in samples is indicated in Table 8.13. While these more common and abundant species contributed to the differences in species richness between the two different vegetation types, most of the variation is accounted for by many uncommon species of small Diptera and microhymenoptera.

Table 8.13. Some commonly occurring taxa in sweep net samples inside and outside *N. neesiana* patches, showing the number of samples in which the taxon occurred and the total number of individuals of the taxon. Taxa are listed in rough order from those with strong preference for *N. neesiana* to those with strong preference for *T. triandra*.

Taxon	**Family**	**Order**	**No. of samples**		**No. of individuals**	
			N. neesiana	***T. triandra***	***N. neesiana***	***T. triandra***
Stenophyella macreta	Lygaeidae	Hemiptera	7	1	34	1
Euciodes suturalis	Anthribidae	Coleoptera	4	1	23	2
Nysius vinitor	Lygaeidae	Hemiptera	6	4	17	7
various	Coccinellidae	Coleoptera	5	3	8	4
Halotydeus destructor	Penthaleidae	Acarina	4	4	148	67
Cortinacara & *Cortinaria*	Lathridiidae	Coleoptera	5	6	7	7
Anthicus spp.	Anthicidae	Coleoptera	4	4	4	10
Phalacridae spp.	Phalacridae	Coleoptera	3	3	3	54
various green midges	Chironomidae	Diptera	11	14	87	636
Runcinia elongata	Thomisidae	Araneida	6	15	9	133
Hispellinus multispinosus	Chrysomelidae	Coleoptera	0	4	0	6

Utilisation of *N. neesiana*

A tabulation of non-orthopteran species observed utilising *N. neesiana* for food, as shelter or as a substrate in the field, or consuming *N. neesiana* in captivity is provided in Table 8.14. A tabulation of Orthoptera and their *Nassella* or native grass hosts is provided in Table 8.15. Some records of these species on *T. triandra*, the main native grass displaced by *N. neesiana*, or on other grasses are also tabulated for comparison.

Mollusca

The only mollusc species found on *N. neesiana* was the Small Pointed Snail *Cochlicella barbara* (L.), a specimen of which was found firmly attached to a dead leaf of *N. neesiana* at Laverton North Grassland on 12 February 2008 (Fig. 8.1).

Figure 8.1. A living individual of the exotic Small Pointed Snail *Cochlicella barbara* cemented to a dead leaf of *N. neesiana* at Laverton North Grassland, 12 February 2008.

Table 8.14. Observations of invertebrates, excluding Orthoptera, on *Nassella neesiana*, *Themeda triandra* and associated native and exotic grasses.

A. b. = *Austrostipa bigeniculata* *A. c.* = *Austrodanthonia caespitosa* *A. cu.* = *Austrostipa curticoma* *Ad.* = *Austrodanthonia* sp. *A. m.* = *Austrostipa mollis*
A. s. = *Austrostipa scabra* *Au.* = *Austrostipa* sp. *B. h.* = *Bromus hordaceus* *C. t.* = *Chloris truncata* *E. c.* = *Eragrostis curvula*
N. n. = *Nassella neesiana* *N. h.* = *Nassella hyalina* *N. t.* = *Nassella trichotoma* *T. t.* = *Themeda triandra*

Species	Family	Host	Location	State	Date	Notes
Mollusca						
**Cochlicella barbara* (L.)	Helicidae	*N. n.*	Laverton North Grassland	Vic	12/2/08	live animal cemented on to dead leaf, no evidence of feeding
Hemiptera						
mealy bug	Pseudococcidae	*N. n.*	Iramoo	Vic	27/11/06	on lower stem, one only
			Iramoo	Vic	10/8/07	search sample, on lowest leaf, on inner side and lowest part of leaf
Cicadetta waterhousei (Distant)	Cicadidae	*N. t.*	Iramoo	Vic	19/10/06	adult specimen
		N. n.	Iramoo	Vic	2/11/07	nymphal exuviae loose at bases of tussocks, no emergence holes apparent
		A. b.	Iramoo	Vic	5/11/08	adult calling from panicle
Dictyotus caenosus (Westwood)	Pentatomidae	*N. n.*	York Park, Barton	ACT	9/5/07	in tussock
Dictyotus conspicuus Gross	Pentatomidae	*N. n.*	Laverton North Grassland	Vic	30/10/06	proboscis inserted into leaf sheath over inflorescence
			Derrimut	Vic	31/3/07	
		.	Greenvale	Vic	24/12/03	ex bag of seed collected by Charles Grech
		A. m.	Frankston North	Vic	9/2/07	c.6 adults around & emerging from tussock 6.15 pm
Eribotes ?*reconditus* Bergroth	Pentatomidae	*N. n.*	Oaklands Park	Vic	22/11/06	nymph & adult separately on panicles, early afternoon
			Iramoo	Vic	31/7/07	4 on ground at base of plant, c. 4.30 pm
		.	Iramoo	Vic	12/11/08	1 on panicle 1.30 pm, not feeding
		A. s.	Yarramundi Reach	ACT	18/10/07	2 skeletal in dense spider web in centre of tussock with many other skeletal insects
		T. t.	Frankston North	Vic	6/2/06	1 in dense leafy base of small tussock
Nysius vinitor Bergroth	Lygaeidae	*N. n.*	Sunshine	Vic	23/11/06	1 on panicle
Parcephaleus dobsonensis Evans	Cicadellidae	*N. n.*	Laverton North	Vic	30/10/06	1 on node of culm, c. 2 pm
		Lolium sp.	Laverton North	Vic	30/10/06	seen

Continued next page

Table 8.14 (continued)

Species	Family	Host	Location	State	Date	Notes
Stenophyella macreta Horváth	Lygaeidae	*N. n.*	Iramoo	Vic	11/12/07	hind body only, harvested in paper bag with seed heads
		C. t.	Iramoo	Vic	18/1/08	numerous on panicles
		-	Laverton North	Vic	27/1/07	1 swept from grasses
		A. c.	Laverton North	Vic	27/1/07	1 on green panicle 4.05 pm
		A. b./A. c.	Laverton North	Vic	30/1/08	ex collection of above ground parts
		N. n.	Laverton North	Vic	7/3/08	4 adults, 10 nymphs, sweep net sample, 3.08 pm
		E. c.	Frankston North	Vic	6/2/06	1 on flowering stem, mid afternoon
		N. n.	Dudley Street, Yarralumla	ACT	15/10/07	sweep net sample
			Constitution Avenue, Campbell	ACT	14/10/07	12, sweep net sample 3.19 pm
Coleoptera						
Dicranolaius conicicornis (Blackburn)	Melyridae	*A. cu.*	Laverton North Grassland	Vic	27/1/08	1, mandibles closed around awn on fruiting panicle, ?feeding, ?ovipositing
		N. n.	Iramoo	Vic	14/2/07	1 on dry panicle 1.40 pm
		N. h.	Iramoo	Vic	11/12/07	1 on flowering panicle, appeared to be eating the glumes or possibly ovipositing
Euciodes suturalis Pascoe	Anthribidae	*N. n.*	Laverton North Grassland	Vic	30/10/06	culms
		N. n.	Woodlands Historic Park	Vic	3/11/06	sweep net sample 17 adults, 1 adult parasitoid gen. nr. *Triaspis*
		N. n.	Iramoo	Vic	9/11/06	sweep net sample, 2 adults, 1 adult gen. nr. *Triaspis*
		T. t.	Iramoo	Vic	9/11/06	sweep net sample, 2 adults
		T. t.	Derrimut	Vic	31/3/07	oviposition scars on culms
		N. n.	Iramoo	Vic	8/11/07	fresh oviposition scars on stems, adult on stem, adults gen. nr. *Triaspis* on scarred stems
			Iramoo	Vic	5/11/08	oviposition scars and adults on stems, adults gen. nr. *Triaspis* searching scarred stems
		N. h.	Iramoo	Vic	5/11/08	oviposition scars and adults on stems
Cubicorhynchus maculatus Macleay	Curculionidae	*N. n.*	Dudley Street, Yarralumla	ACT	25/4/08	dead on ground in uniform, mowed area of *N. n.*
		various	Yarramundi Reach	ACT		*N.n.*, *T.t.*, *A.s.* tussocks
Cubicorhynchus sordidus Ferguson	Curculionidae	*N. n.*	Crace	ACT	various	search samples
Eurymetopus birabeni Kuschel	Curculionidae	*N. n.*	Crace	ACT	19/10/08	pupa in soil under plant.
			Dudley Street, Yarralumla	ACT	18/10/07	larva exposed while digging up plants, pupated c. 20/11, adult 3/12
Talaurinus confusus Ferguson	Curculionidae	*N. t.*	Iramoo	Vic	6/11/08	teneral specimen, collected with part of clay pupation cell, dead or nearly dead on soil surface c. 2 hr after digging up a tussock of *N. n.*
?*Talaurinus howitti* Macleay /"*Prophalidura* sp. 2"	Curculionidae	*N. n.*	Greenvale	Vic	23/11/06	mandibles attached to leaf tip 12.32 pm, ate green & dry leaves, stems, green seed etc. in captivity, dead 26/1/07
Phalidura abnormis (Macleay)	Curculionidae	*N. n.*	Yarramundi Reach	ACT	9/5/07	skeletal, amongst dense dry thatch

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Table 8.14 (continued)

Species	Family	Host	Location	State	Date	Notes
Lepidoptera						
Anthela denticulata (Newm.)	Anthelidae	*N. n.*	Iramoo	Vic	5/7/07	V instar larva eating *N. n.*, reared on *N. n.*, moulted 14/7, cocoon completed 3/8, adult 26/1/08
Anthela denticulata (Newm.)	Anthelidae	*N. n.*	Iramoo	Vic	10/8/07	V instar larva on *N. n.*, reared on *N. n.*, moulted 12/8, cocoon completed 6/9, female adult 18-19/2
Anthela ferruginosa Walker	Anthelidae	*N. n.*	Yarramundi Reach	ACT	19/10/08	search sample, 1 larva in 15 min, tussock centre, reared on *N. n.*, cocoon 4/1/09, adult 23/1
Anthela ocellata (Walk.)	Anthelidae	*A. m.*	Frankston North	Vic	21/11/06	5 moults, reared entirely on *A. m.*, cocoon 22/2/07, adult 18/3/07
		N. n.	Woodlands Historic Park	Vic	3/11/06	4 moults, reared entirely on *N. n.*, cocoon 3/1/07, adult 29/2/07
Anthela ocellata (continued)	Anthelidae	*N. n.*	Laverton North	Vic	24/4/07	II? instar larva on dead leaf of isolated tussock, reared on *N. n.*, 4 captive moults, adult 1/9/07
					5/12/07	larva on *N. n.*, reared on *N. n.*, moulted 3 times, cocoon 22/1/08, adult female 11/2
		T. t.	Laverton North	Vic	5/12/07	III? larva on leaf, produced frass on *T.t.* food 5-6/12, dead 7/12
Pterolocera sp.	Anthelidae	*N. n.*	Crace	ACT	12/10/06	on ground amongst dense *N.n.*, reared on *N.n.*, cocoons 22/10, 27/10, adults c. 22/2, 6/3/07
			Crace	ACT	13/10/07	larvae eating leaf (1), stem (1), 7 other larvae on plants
		Au sp.	Crace	ACT	13/10/07	larvae on plants
		Ad sp.	Crace	ACT	13/10/07	larva seen eating leaf
		B. h.	Crace	ACT	13/10/07	1 larva seen on plant
		T. t.	Crace	ACT	13/10/07	5 larvae seen on plants
Mythimna convecta (Walker)	Noctuidae	*N. n.*	Carrum Downs	Vic	various	larvae eating potted plants
		T. t.	Frankston North	Vic	23/11/07	early VI instar larva on panicle, leaf and flower feeding damage, ate *T.t.* leaves & flowers in captivity, 6/12 ‘cocoon’, 7/12 pupa, 24/12 adult
Persectania ewingii (Westwood)	Noctuidae	*N. n.*	Iramoo	Vic	21/7/07	larva on soil at tussock base, reared on *N.n.*, pupa 25/8, died
			Iramoo	Vic	10/8/07	larva in base of tussock, reared on *N.n.*, adult 24/9; larva ?V on soil surface under dense *N.n.*, failed to thrive, diseased; larva ?III in base of *N. n.* tussock, ate *N. n.* in captivity, diseased.
?*Psychanisa baliodes* (Meyrick)	Psychidae	*T. t.*	Laverton North	Vic	25/11/07	larva active on *T.t.*, reared on *T.t.*, stopped feedings c. 31/12/07, adult 17/2/08
			St Albans Rd Grassland	Vic	23/11/06	one old case on *T.t.* panicle leaf
		N. n.	St Albans Rd Grassland	Vic	23/11/06	three old cases on *N. n.* stems
			Iramoo	Vic	5/11/08	apparent feeding damage on panicle, 2 reared on *N. n.*, ate leaves and flowers, adults failed to emerge
Grass case moth sp. 2	Psychidae	*N. n.*	Crace	ACT	19/10/08	larva climbing and attaching to *N. n*
Hymenoptera						
Pheidole sp.	Formicidae	*N. n.*	Laverton North, Iramoo	Vic		numerous observations harvesting fallen seeds

Table 8.15. Observations of field host grasses of Orthoptera and grasses eaten in captivity. Insects were adults unless otherwise specified. Sweep net and search samples were in matched pairs on each occasion, one area dominated by *N. neesiana* and one by *T. triandra*.

Species	**Locality**	**Date**	**Host plant in field (No. of individuals)**	**Association with host**	**Plants eaten in captivity**	**Notes**
Acrida conica (Fabricius) nymph	Laverton North Grassland	29/11/2007	*N. neesiana* (1)	on the plant	-	
A. conica nymph	Laverton North Grassland	4/12/2007	*N. neesiana* (1)	on the plant	-	
A. conica	Iramoo	Often	*T. triandra* (several)	on the plant	-	
Austroicetes sp. nymphs	Woodlands Historic Park	3/11/2006	*N. neesiana* (2), *T. triandra* (14)	prob. on the plant	-	sweep net samples
Austroicetes sp. nymph	Crace Grassland	14/10/2007	*N. neesiana* (1)	prob. on the plant	-	sweep net sample
Austroicetes sp. nymph	Crace Grassland	24/10/2008	*N. neesiana* (1)	prob. on the plant	-	sweep net sample
Austroicetes vulgaris (Sjöstedt)	Woodlands Historic Park	8/3/2008	*N. neesiana* (1)	prob. on the plant	-	sweep net sample
Caledia captiva (Walker)	Laverton North Grassland	19/2/2008	- (1)	-	*N. neesiana*	
Fipurga crassa (Sjöstedt)	Yarramundi Reach	11/10/2007	*N. neesiana* (1)	on the plant	*N. neesiana* not eaten	
Gastrimargus musicus (Fabricius) nymph III	Laverton North Grassland	4/12/2007	- (1)	-	*N. neesiana*	
G. musicus nymph IV	Laverton North Grassland	25/11/2007	*T. triandra* (1)	on the plant	*T. triandra* – reared to adult	
G. musicus	Yarramundi Reach	23/4/2008	*N. neesiana* (1)	on the plant	-	search sample
Macrotona sp. nr. *modesta* Sjöstedt final instar	Iramoo	21/1/2008	*N. trichotoma* (1)	on the plant	*N. trichotoma*	
Macrotona australis (Walker) nymph	Crace Grassland	14/10/2007	*T. triandra* (1)	prob. on the plant	-	sweep net sample
M. australis nymphs	Dudley Street	10/10/2008	*N. neesiana* (1), *T. triandra* (2)	prob. on the plant	-	sweep net samples
M. australis nymph	Yarramundi Reach	15/10/2007	*T. triandra* (1)	prob. on the plant	-	sweep net sample
M. australis	Yarramundi Reach	23/4/2008	*N. neesiana* (1)	on the plant	-	search sample
M. australis nymphs	Yarramundi Reach	19/10/2008	*N. neesiana* (2), *T. triandra* (4)	prob. on the plant	-	sweep net samples
Oedaleus australis (Saussure)	Woodlands Historic Park	8/3/2007	*N. neesiana* (2)	prob. on the plant	-	sweep net sample
Phaulacridium vittatum (Sjöstedt)	Crace Grassland	23/4/2008	*N. neesiana* (1)	prob. on the plant	-	sweep net sample
Praxibulus sp. small nymph	Yarramundi Reach	11/10/2007	*N. neesiana* (1)	on the plant	*N. neesiana* – three moults	
Schizobothrus flavovittatus Sjöstedt nymph III	Laverton North Grassland	22/4/2007	*T. triandra* (1)	on the plant	*T. triandra* but not *N. neesiana*	
S. flavovittatus	Laverton North Grassland	24/4/2007	- (1)	-	*N. neesiana* – but died 1/5/2007	
S. flavovittatus	Laverton North Grassland	20/4/2007	- (1)	-	*N. neesiana, T. triandra*	
Teleogryllus commodus (Walker) nymph	Laverton North Grassland	24/4/2007	*N. neesiana* (1)	on the plant	*N. neesiana* – but died 28/4/2007	
?Tettigoniidae sp.	Frankston North	9/2/2007	*T. triandra* (several)	eggs in culm stems	-	

Orthoptera

A number of species were commonly present in areas dominated by *N. neesiana*, and were commonly found on the grass (Table 8.15). Five Orthoptera species were recorded eating *N. neesiana* in captivity.

Hemiptera

The Smoky Buzzer *Cicadetta waterhousei* (Distant) (Cicadidae) was a prominent species at Iramoo from mid-October through November. An adult was captured on *Nassella trichotoma* on 19 October 2006. Adults were numerous and many nymphal exuviae were found loose on the ground at or near bases of *N. neesiana* tussocks on 2 November 2007, although no emergence holes were evident amongst the grass. On 5 November 2008 an adult was observed calling from an *Austrostipa bigeniculata* panicle c. 35 cm above the ground.

Unidentified mealybugs (Pseudococcidae) were found on *N. neesiana* at Iramoo, generally in leaf axils, between the stem and the leaf of lower leaves, and colonies were often partly concealed beneath the leaf sheaths. Infestations were also found on *Austrostipa* and *Austrodanthonia* spp. in other grasslands.

Dictyotus conspicuus Gross (Pentatomidae: Pentatominae) was observed on *N. neesiana* at Laverton North on 30 October 2006 on a sheathing leaf of an inflorescence from which awns and one flower were protruding. It moved over the sheath actively sensing the substrate with antennae and proboscis, then appeared to insert its proboscis into the leaf and remained in that position for several minutes. Later examination of the leaf and flowers beneath failed to reveal any feeding scar. Similar plant material provided to the captive specimen failed to illicit comparable behaviour, although the insect appeared to preferentially rest on the leaf sheath over the inflorescence. A dead individual was also found in a bag of *N. neesiana* panicle seed collected at Greenvale.

Eribotes ?*reconditus* Bergroth (Pentatomidae: Pentatominae) was found on *N. neesiana* on a few occasions but was never observed feeding. It was also found amongst other grasses. In the ACT it was collected in sweep net and search samples in *T. triandra* grassland at three sites.

Coleoptera

Dicranolaius conicornis (Blackburn) (Melyridae: Malachiinae) was found twice on the panicles of grasses at Iramoo and once at Laverton North. At Iramoo one was found on a dry panicle of *N. neesiana* on 14 February 2007, and one on a flowering head of *N. hyalina* on 11 December 2007 where it appeared to be eating glumes. A specimen from Laverton North Grassland was found on 27 January 2008 on a seed-bearing panicle of *Austrostipa curticoma* with its mandibles closed on an awn at 3.50 pm, where it was possibly feeding. It was common at Crace on 21 October 2008 where it was observed eating petals of *Goodenia pinnatifida* Schldtl.

Oviposition scars and adult activity of the Grass-stem Anthribid, *Euciodes suturalis* Pascoe, (Anthribidae) were observed on the culms of *N. neesiana* on several occasions. Evidence was obtained that it attacks a wide range of native and exotic grasses in Australia: 28 grass species (15 exotic) were recorded as hosts or probable hosts, mainly on the basis of the presence of oviposition scars on culms. An undescribed new genus of Braconidae (Heliconinae) near *Triaspis* Haliday (A. Austin pers. comm.) was commonly found associated with the beetle and observed apparently ovipositing into *E. suturalis* oviposition scars.

A larva and a pupa of *Eurymetopus birabeni* Kuschel (Curculionidae) were found amongst roots of *N. neesiana* in the ACT suggesting a probable trophic relationship.

Five species of Amycterini (Curculionidae: Amycterinae) were found associated with *Nassella neesiana*. *Cubicorhynchus maculatus* Macleay was a common species at Yarramundi Reach, where adults were consistently and readily found in the centres of dense Stipeae tussocks, including *N. neesiana* and *Austrostipa scabra* along with characteristic piles of frass that retained the morphological features of the grasses. On 15 October 2007 a search sample amongst *N. neesiana* yielded four live and two skeletal adults, while the matched sample in *T. triandra* yielded four skeletal adults. In a separate deliberate search of tussocks in a nearby area, one adult was found in the 20 *N. neesiana* tussocks searched and two adults in 20 tussocks of *A. scabra*. On 18 October five skeletal adults were found in dense spider web in the centre of an *A. scabra* tussock. A search sample on 23 April 2008 yielded 2 live and 5 skeletal adults amongst *N. neesiana* and 2 skeletal adults amongst *T. triandra*. *Cubicorhynchus maculatus* was the only amycterine detected at Dudley Street grassland. Two dead adults were found on the ground in an area of uniform, mowed *N. neesiana* on 24 and 25 April 2008, a skeletal abdomen was found in the *N. neesiana* search sample on 24 April and a skeletal head in the 19 October 2008 *N. neesiana* search sample.

A second amycterine, *Phalidura abnormis* (Macleay) was found at Yarramundi Reach. A skeletal adult was found amongst dense *N. neesiana* on dry thatch on 9 May 2007 and a skeletal hind body in *N. neesiana* patch D on 22 April 2008. The search samples of 23 April 2008 yielded two skeletal adults, both in the *N. neesiana* area. *Phalidura abnormis* was also detected at Crace, a skeletal abdomen found on the ground on 18 October 2007.

Cubicorhynchus sordidus Ferguson was common at Crace. Skeletal remains of adults were found in search samples, four individuals in the *N. neesiana* sample on 14 October 2007, two individuals amongst *N. neesiana* and two amongst *T. triandra* on 23 April 2008 and two abdomens were found in the samples of 24 October 2008, both from the *N. neesiana* area.

A fourth amycterine, *Talaurinus confusus* Ferguson, was found at Iramoo. A teneral adult was found on the soil surface with part of its clay pupation cell after digging up a plant of *N. neesiana* plant on 6 November 2008, indicating that the larva had pupated in the root mass.

A species tentatively identified as *Talaurinus howitti* Macleay (and equivalent to "*Prophalidura* sp. 2" in the Victorian grassland survey work of Yen *et al.*1994a 1994b 1995) was found at Greenvale on 23 November 2006 with its mandibles attached to the dead tip of an *N. neesiana* leaf. It was kept in captivity, and ate *N. neesiana*, leaving many small chewed up shreds. Material eaten or damaged included parts of lemmas and awns of green seed, stems both green and dry, and dry leaf sheath material.

Lepidoptera

A Psychidae species, possibly *Psychanisa baliodes* (Meyrick), with a cylindrical case covered with pieces of grass stems (1 cm + long) arranged longitudinally in parallel, was observed at Iramoo (Fig. 8.2), along the railway line at St Albans, at Laverton North and at Dudley Street grassland in the ACT. Two larvae were found on *N. neesiana* panicles just prior to flowering at Iramoo on 5 November 2008. At least one had apparently fed on glumes. Another individual was seen nearby on *Lolium rigidum*. The two individuals from *N. neesiana* were reared on *N. neesiana*, eating leaves and newly emerging flowers and producing very pale frass. Feeding continued in captivity until late December when the larvae probably died. No adults had emerged by December 2009. The St Albans railway line individuals were found on *T. triandra* but no adults emerged from the cases. A larva collected at Laverton North Grassland on 25 November 2007 was active on *T. triandra* and was reared on *T. triandra*, with an adult emerging c. 17 February 2008. A specimen from Dudley Street grassland was found feeding on *T. triandra* on 19 October 2008 and ate *T. triandra* in captivity until c. 20 December when the larva may have died. No adult was reared.

Figure 8.2. Larval case of a grass case moth, Psychidae sp. on *N. neesiana* at Iramoo, Vic., 5 November 2008.

A second Psychidae species, probably also a grass-feeder was found in the ACT. The case of this species is ornamented with short pieces of grass stem (2-3 mm long) untidily arranged but mainly at right angles to the axis of the case and sometimes additionally with numerous small plant fragments possibly derived from litter. A specimen found climbing and attaching to *N. neesiana* at Crace on 19 October 2008 was offered *T. triandra* in captivity but failed to feed and had apparently died by c. 16 December. An old case was found on the litter in an *N. neesiana* patch at Yarramundi Reach on 15 October 2007. Several old cases were observed on *Poa labillardierei* at Yarramundi Reach, ornamented with *P. labillardierei* stems.

Larvae of a grass anthelid, *Pterolocera* sp. (Anthelidae) species were abundant on the ground amongst low (<5 cm high), dense, grazed, *N. neesiana* lacking culms in the far north west of Crace Grassland on 12 October 2006. Many were in the process of moulting. Three specimens were collected and reared on *N. neesiana* in the laboratory, producing copious quantities of frass. One died and two formed cocoons, both of which produced females, which are wingless and currently impossible to identify to species. In the same area at Crace on 13 October 2007 late instar larvae were again abundant, and were observed eating an *Austrodanthonia* leaf (1 larva), an *N. neesiana* leaf (1) and an *N. neesiana* stem (1). The plants on which larvae occurred were counted for 10 minutes: larvae occurred on *N. neesiana* (7), *Bromus hordaceus* (1) *T. triandra* (5) and *Austrostipa* sp. (3). One larva was reared on *N. neesiana* and pupated in early December but failed to hatch. On 17 October 2008 at Crace, a larva was observed eating *Austrostipa* sp. (Fig. 8.3a). On 19 October at Crace a larvae was seen eating a leaf of *Austrodanthonia carphoides*.

Figure 8.3. *Pterolocera* sp.; a. larva on *Austrostipa,* Crace, 17 October 2008; b. adult female and eggs, from Crace 12 October 2006 larva, collected and reared on *N. neesiana*.

On 20 October 2008 larvae were again abundant at Crace, with dense populations in the very shortly grassed areas infested with *N. neesiana* in the far north-west of the Reserve, as in the two previous years. It was found to be widespread in the Reserve as a whole. One was observed eating a stem of *Austrostipa bigeniculata*. It lopped the top 7 cm and ate down the stem. On 21 October 2008 at 6.18 pm ESST, larvae were observed feeding on *Austrodanthonia carphoides* and *Phalaris aquatica*.

A larva of the Rusty Anthelid, *Anthela ferruginosa* Walker was found in the centre of an *N. neesiana* tussock at Yarramundi Reach on 19 October 2008. It ate *N. neesiana* in captivity, moulted c. 27 October and c. 29 November, pupated c. 4 January and emerged c. 22 January.

Larvae of *Anthela denticulata* (Newman) (Fig. 8.4) were common on *N. neesiana* at Iramoo, being apparent for example, throughout the winter of 2007. A fifth instar larva observed on a leaf tip and eating *N. neesiana* on 5 July 2007 was reared to the adult stage on *N. neesiana*. A fifth instar larva found in a search sample on *N. neesiana* on 10 August 2007 was also reared to adulthood on *N. neesiana*. Numerous larvae observed on 12 August 2008 were eating leaves of *N. neesiana* and *N. trichotoma* but larvae were never found on *Themeda triandra*.

Figure 8.4. Larva of *Anthela denticulata* eating *N. neesiana*, Iramoo grassland, Cairnlea, Victoria, 13 August 2008.

A larval Eyespot Anthelid *Anthela ocellata* (Walker) collected on *N. neesiana* at Woodlands Historic Park on 3 November 2006 was reared on *N. neesiana*, moulted four times, and constructed a cocoon in early January 2007 from which an adult emerged on 29 February. Larvae of this species were observed on several occasions at Laverton North Grassland, but were not common. A larva, probably in the second instar, found on a dead leaf of an isolated *N. neesiana* tussock on 24 April 2007 was reared on *N. neesiana* in the laboratory, moulted four times in captivity and emerged as an adult female on 1 September (Fig. 8.5). Larvae were also found on *N. neesiana* on 5 December 2007. One was reared on *N. neesiana*, moulted three times, constructed a cocoon on 22 January 2008 and emerged as an adult female on 11 February. Another larva, provided solely with *T. triandra* in captivity, produced frass on 5-6 December but was dead by 7 December. A larva collected in the *N. neesiana* search sample at Crace on 23 April 2008, probably feeding on *N. neesiana*, was reared on the grass and produced a cocoon in May which was parasitised by tachinid flies which emerged on 23 April 2008. Two larvae were found in the *N. neesiana* search sample at Dudley Street grassland on 24 April 2008, but none in the matched sample in *T. triandra*. A first instar larva found at Frankston North on *Austrostipa mollis* on 21 November 2006 was reared entirely on this plant, constructed a cocoon on 22 February and emerged as an adult female probably on 17 March.

Figure 8.5. *Anthela ocellata* collected at Laverton North Grassland, 24 March 2007. a. larva after 14 weeks of rearing on *N. neesiana*; b. cocoon with *N. neesiana* leaves loosely attached.

Larvae of the Southern Armyworm *Persectania ewingii* (Westwood) (Noctuidae) were collected amongst *N. neesiana* at Iramoo and ate the plant in captivity (Fig. 8.6). A final instar larva found on the soil surface at the base of *N. neesiana* tussock on 21 July 2007 avidly ate *N. neesiana* leaves in captivity, pupated on 25 August, but died as a pupa sometime before 18 September. A final instar larva found in the base of *N. neesiana* tussock on 10 August 2007 fed on the plant in captivity and was reared to the adult stage on 24 September. Two larvae detected during the *N. neesiana* search sample at Iramoo on that day were diseased and died in captivity. One, probably a third instar, found in the base of tussock, ate *N. neesiana* for four days but then succumbed. The other, possibly fifth instar, found on the soil surface, ate *N. neesiana* in captivity but did not thrive and died on 29 August. This species and larvae of the Common Armyworm *Mythimna convecta* (Walker) were found eating the leaves of potted *N. neesiana* plants at Carrum Downs, Victoria.

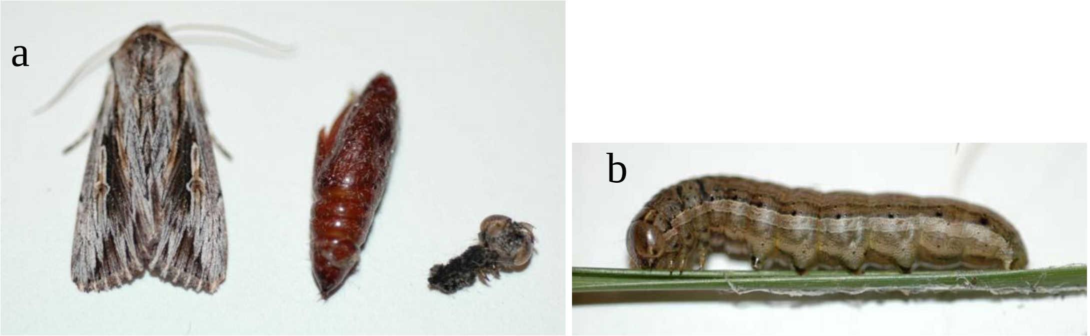

Figure 8.6. *Persectania ewingii*; a. adult, pupal case and final instar larval exuvium; b. larva; collected as a final instar larva in the base of an *N. neesiana* tussock at Iramoo on 10 August 2007 and reared on *N. neesiana*.

Hymenoptera

Observations at Laverton North Grassland Reserve and Iramoo Grassland indicated that a high proportion of shed *N. neesiana* seed was collected by the harvester ant *Pheidole vigilans* (Smith) (Mymicinae) and delivered to the nest. During periods of seed fall, bare ground was cleared of all fallen seeds over areas of tens of square metres in the vicinity of *Pheidole* nests. Minor workers undertook much of the harvest (Fig. 8.7), but major workers participated in difficult harvesting tasks, notably the removal of *N. neesiana* seeds firmly stuck upright in the soil, and negotiating the entry of seeds through the nest entrance hole. Fragments of *N. neesiana* seeds were found to be common at times in debris middens around nest entrances, indicating that the nutritive contents of seeds were removed within the nest.

Figure 8.7. *Pheidole* sp. minors working on excavations of awnless *N. neesiana* seeds solidly stuck upright in the ground at Iramoo grassland, 21 January 2008. Excavated soil particles are prominent in the foreground. a. cooperative effort by three workers; b. single worker, previously removing soil has moved to the top of the seed in an attempt to lever it free from the ground.

Pheidole ants were probably responsible for removal of a large proportion of the *N. neesiana* seeds applied in the disturbance experiment (Chapter 4). They also harvested high proportions of the fallen seeds of other grasses and some forbs (Fig. 8.8). A small dark *Iridomyrmex* species was observed to collect artificially de-awned *N. neesiana* green seeds and take them into their nests at Laverton North (Fig. 8.9).

Figure 8.8. *Pheidole* minor workers moving *Nassella trichotoma*, *Themeda triandra* and *Romulea rosea* seeds along a foraging trail towards the nest at Iramoo, 19 January 2008.

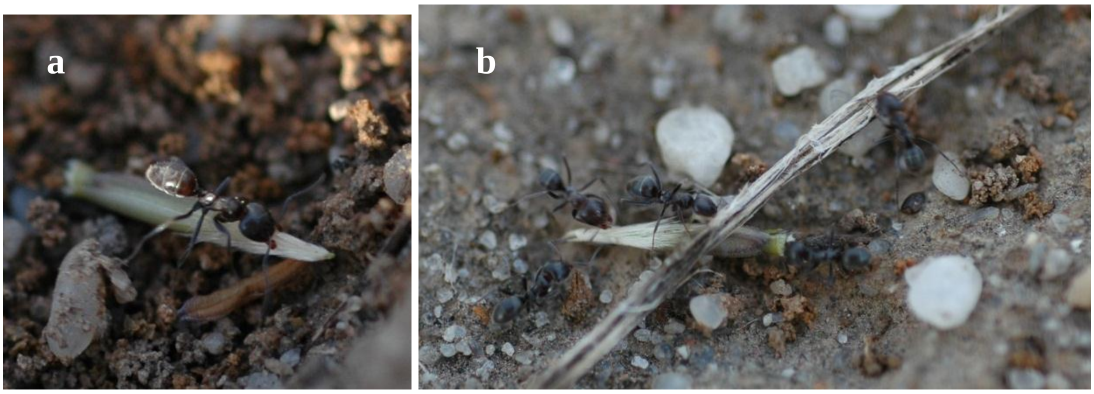

Figure 8.9. *Iridomyrmex* sp. removing artificially de-awned *N. neesiana* seeds dropped near a foraging trail at Laverton North Grassland, 29 November 2007. a. one method of carriage by an individual worker. b. workers cooperating to dislodge a seed wedged under plant debris.

Trophic web evidence

Larval *Pterolocera* were seen to be eaten by birds at Crace, namely the Pallid Cuckoo *Cucuclus pallidus* (Latham) (17 October 2008, two larvae in two minutes), which repeatedly massaged larvae through its bill before consumption, and the Australian Magpie *Cracticus tibicen* (Latham) (21 October 2008), which rubbed the larvae on the ground to remove the spines before consumption.

A larva of *Anthela ocellata* collected in the *N. neesiana* search sample at Crace on 23 April 2008, probably feeding on *N. neesiana*, was reared on the grass and produced a cocoon in

May which was parasitised by *Cuphocera* sp. (Tachinidae: Tachini) which emerged as adults on 23 April 2008. Frequent association of the heliconine braconid gen. near *Triaspis* Haliday with Euciodes suturalis indicates another parasitoid association with an invertebrate herbivore of *N. neesiana*.

Discussion

Invertebrate species richness and population size: *N. neesiana* vs native grass

The only significant difference in the invertebrate faunal numbers detected by search sampling was at the ACT sites in October 2007 where the number of exotic species inside *N. neesiana* patches was higher than outside patches, due to larger numbers of Portuguese Black Millipedes. This pest species has also spread into Victorian basalt plains grasslands (Yen 1995). There is no evidence that this exotic millipede competitively excludes native millipedes, but it may influence litter decay rates (Yen 1995, Griffin and Bull 1995). Although found only in low numbers in search samples and co-occurring with *O. moreletii* the native millipede *Onocladosoma* sp. was not detected in search samples in *N. neesiana* areas (Table 8.12). The two species appear to have similar ecological requirements and overlapping niches, both being generalist detritivores (Griffin and Bull 1995). Further investigation of *Onocladosoma* sp. is required to determine if its absence from *N. neesiana* areas is a general effect and to examine possible mechanisms.

Significant differences were detected in the invertebrate faunas of standing vegetation of areas dominated by *N. neesiana* and *T. triandra* sampled by sweep net. Areas inside *N. neesiana* patches had a significantly impoverished fauna in autumn and significantly fewer individuals in spring compared with areas dominated by *T. triandra* outside the patches. Some taxa appear to be more abundant in *N. neesiana* areas, some taxa were detected with no apparent difference in frequency between grassland types and many taxa were detected so infrequently that it was not possible to infer any differences in occurrence inside and outside *N. neesiana* patches. The findings of lower species richness, lower total numbers of individuals in invaded areas, and both detrimental and beneficial impacts on particular species in invaded areas are in general agreement with the conclusions of Ens (2002a, 2005) that *N. neesiana* infestations alter habitat parameters for invertebrates and change the composition of invertebrate communities.

As with the vascular plant diversity data (Chapter 7), implicating *N. neesiana* as the primary cause of the differences is problematic. Evidence presented in earlier chapters indicates that *N. neesiana* replaces other grassland vegetation where there has been significant anthropogenic disturbance at the $1m^2$+ scale that has led to death of the native grasses. The difficulty is to determine whether any change in the invertebrate fauna is a result of the disturbance or of the presence of *N. neesiana* which follows the primary disturbance. *Nassella neesiana* infestations typically occur in the grasslands studied in patches less than 30 m in diameter, interspersed with native vegetation or infestations of other exotic grasses. Patches may be sparsely or densely vegetated. A range of other native and exotic plants occur in varying densities in both the *N. neesiana* patches and the other vegetation. Studies reported in Chapter 7 indicate that no plant species, native or exotic, appears to be preferentially impacted by *N. neesiana* presence, except some dominant or subdominant native grasses. Theoretical expectations of likely invertebrate impacts of *N. neesiana* in relation to phytophagous species appear to have a poor fit with these findings. In part this is probably due to the highly generalised nature of the sampling, in which many taxa were collected that are not grassland habitat specific. Species detected that were remote from their source habitats included *Acizzia* sp. (Hemiptera: Psyllidae), which is almost certainly an *Acacia* feeder, eucalypt-feeding psyllids at Iramoo, and *Apion* nov. sp. 2, the host plant of which is supposedly the small forest tree *Pomaderris aspera* Sieber ex DC. (Rhamnaceae) (Zimmerman 1994b).

Displacement of the native plants with their co-adapted phytophagous faunas by the introduced grass, with a less diverse fauna of generalist predators, was hypothesised to be a likely primary cause of lower invertebrate diversity in areas dominated by *N. neesiana*. The study has provided little evidence that that is the case: most of the differences in species richness and abundance cannot be explained by feeding associations. When the known biologies of individual invertebrate taxa affected by the presence of *N. neesiana* are examined in detail it is clear that explanation of the differences in occurrence and abundance cannot usually be linked directly to characteristics of the dominant grasses. In only one case is there a clear explanation for the differences in abundances between *N. neesiana* patches and areas of *T. triandra*. The leaf beetle *Hispellinus multispinosus* Germar was detected only in *T. triandra* samples (Table 8.13), and was the only species with a known trophic relationship (a *T. triandra* feeder) that determined a notable difference in occurrence. It was one of the most abundant beetles detected by Yen *et al.* (1994) in *T. triandra* grasslands in the western region of Melbourne. Adult *Hispellinus* Weise are small, black, spiny, grass-eating beetles with larvae that are flattened, legless, leaf-miners (Matthews and Reid 2002) that “consume the mesophyll parenchyma leaving longitudinal white streaks” and *Themeda* is a known host of the genus (Jolivet and Hawkeswood 1995 p. 141). Four Australian species have been described including *Hispellinus australicus* (Motschulsky), which occurs throughout South Australia and feeds on “grasses” (Matthews and Reid 2002). In the ACT and southern Victoria this species is generally only found upon *Themeda triandra* and not on any neighbouring grasses (personal records). A narrow host plant range, not including

Stipeae (Jolivet and Hawkeswood 1995) accounts for the absence of this beetle from samples dominated by *N. neesiana*.

A variety of direct and indirect mechanisms must be invoked to explain other differences. The crab spider *Runcinia acuminata* (Thorell) (Thomisidae) was found commonly in native grass samples in both Victoria and the ACT, but detected at much lower frequency in *N. neesiana* samples (Table 8.13). A possible explanation for the paucity of individuals in areas dominated by *N. neesiana* may be the superior camouflage afforded by dead or browned-off glumes in the panicles of *T. triandra*, a very important requirement for a predator that hunts by waiting and seizing prey that comes into range. Another factor may be the greater availability of prey on *T. triandra*. Thomisidae build no snare webs but seize prey with their elongate, spiny fore legs (hence the name ‘crab’ spiders), and hunt by stealth and ambush (Barrion and Litsinger 1995). Mascord (1970 p. 48 as *Runcinia elongata*) considered it common in NSW and “usually found in grass-seeding heads and low herbage”. Yen *et al.* (1994) failed to detect it in samples across a range of vegetation types including *Poa* and *T. triandra* grasslands in the western region of Melbourne. It reportedly feeds on “small insects ... attracted to grass heads, predominantly small moths” and the females construct egg sacs in grass panicles and sit upon them (Mascord 1970 p. 48).

The grass bug *Stenophyella macreta* Horváth (Hemiptera: Lygaeidae) was detected almost entirely in *N. neesiana* samples, both in autumn and spring (Table 8.13), possibly due to the superior camouflage the plant provides. It is a pale brown, elongate species (c. 6-7 mm long, 1 mm wide), similar in form to the glumes of *N. neesiana* or *Austrostipa* spp. Only the driest panicles of *T. triandra* would appear to offer appropriate concealment. Most Lygaeidae feed on seeds, but some are phloem feeders or predators (Slater 1991). *Stenophyella macreta* “is often common in seed heads of grasses” (Slater 1991 p. 502) and “appears to feed on a number of grasses even when they are completely dry” (Slater 1976 p. 135). The native Rutherglen Bug, *Nysius vinitor* Bergroth was found more frequently and in larger numbers in *N. neesiana* samples (Table 8.13), but the differences were not significant. It is a highly polyphagous fruit and vegetable pest which feeds on many broadleaved weed species (Hely *et al.* 1982) and avidly on weed seeds, but in plague years may seriously damage and breed in the heads of cereals (Gellatly and Forrester 1985).

The category “green midges” (Diptera: Chironomidae) includes at least two species with variably bright green bodies. Of the individuals collected, 707 of 723 were obtained in the ACT, and a very high proportion of these appear to be *Chironomus* (*Dicrotendipes*) *conjunctus* Walker, widely distributed in eastern Australia (Freeman 1961). Green midges were found in nearly as many *N. neesiana* as *T. triandra* samples, but the total number of individuals (636) detected in samples outside *N. neesiana* patches was >7 times that detected inside patches (Table 8.13). Knowledge of Australian Chironomidae is “sparse” (Edward 1986 p. 159). Chironomids are mostly small, delicate flies, with larvae (some known as ‘bloodworms’) that “with few exceptions” are aquatic, and adults that are mainly crepuscular or nocturnal and may occur in very large swarms (Colless and McAlpine 1991) but probably live for no more than a few days (Pinder 1986). The difference is not related to the closer proximity of *N. neesiana* sample areas to water bodies, but the striking differences in numbers between areas with different dominant grasses was most pronounced at the three ACT sites located not far from Lake Burley Griffin, where the largest numbers were obtained. Possibly the relationship is again a case of camouflage, with the midges preferentially resting during the day on the foliage of *T. triandra*, rather than the yellowish or paler foliage of *N. neesiana*.

Another feature of the areas dominated by native grasses is an apparently greater diversity of fungus-associated Coleoptera, Phalacridae in particular. Phalacridae are mostly fungal feeders (Matthews 1992) and the adults and larvae of *Phalacrus* Paykull feed on rusts and smuts on grasses and sedges (Booth *et al.* 1990). Many (15) individuals of a *Phalacrus* sp. obtained in the sweep net sample at Yarramundi Reach on 19 October 2008, were apparently associated with heavy smutting on *Bothriochloa macra* by *Sporisorium tenue* (Syd. & P. Syd.) Vánky, the only smut recorded from this grass (Vánky and Shivas 2008). The matched sample in the *N. neesiana* area (which had little or *B. macra*) yielded only a single individual. The native grass sample also yielded an adult of the accidentally introduced *Leucohimatium arundinaceum* Forskål (Languriidae), believed to feed on smut spores (Matthews 1992). *Themeda triandra* has a rich smut flora, and four species are known from *Austrostipa* spp. in south-eastern Australia, whereas none are known from Australian *N. neesiana* (Vánky and Shivas 2008). Lathridiidae (Coleoptera) are probably all spore-feeders, mostly on moulds but also on fructifications of larger fungi (Booth *et al.* 1990), but only a few individuals were obtained in sweep net samples and no difference was apparent between *N. neesiana* and native grasses.

Larval Anthicidae (Coleoptera) are mostly generalist scavengers or predators that feed on decaying vegetation, fungi or tiny arthropods (Booth *et al.* 1990). Their abundance in native grass assessed by sweep netting was about 2.5 times that in *N. neesiana* (Table 8.13).

Euciodes suturalis Pascoe (Coleoptera: Anthribidae) is an interesting native generalist grass phytophage that was found to attack the stems of a wide range of grasses including *N. neesiana*, *T. triandra* and *Austrostipa* spp. Its higher abundances in *N. neesiana* areas (Table 8.13) possibly relates to the better synchronisation of *N. neesiana* stem development with the phenology of the beetle, adults of which appear to have an activity period concentrated in November, before major flowering of *T. triandra*.

Crisp *et al.* (1998) presented evidence that the assumption that native invertebrate diversity is reflected by native plant diversity is often correct: sites with the highest beetle species richness were those with the highest species richness of plants, both exotic and native. If such an effect is operating in the comparison of *N. neesiana*-dominated areas with those dominated by *T. triandra*, it could be considered a confounding factor, since *N. neesiana* sample areas were sometimes richer in plant species than *T. triandra* areas (Table 8.2, last column). There are two other major confounded factors: sampled sites included both burnt and unburnt areas, and grazed and ungrazed areas. Absence of fire in south-eastern Australian *T. triandra* grasslands results in increased populations of pest invertebrates (Wong and Morgan 2007). Increasing levels of livestock grazing reduce grassland insect diversity (Samways 2005) and impacts on the persistence of native fauna in *T. triandra* grasslands in south-eastern Australia (Wong and Morgan 2007). Disentangling the impacts of fire and grazing from the impacts of *N. neesiana* requires more detailed experimental studies, beyond the present study, in which these factors are controlled.

Variations in the abundance of particular insects may have ramifications at higher trophic levels i.e. of predators, parasitoids and top predators. For example, adult midges are important foods of birds (Pinder 1986), so *T. triandra* areas may provide superior food resources when green midges are abundant. Similarly grass-feeding invertebrates may develop large populations that enable increased diversity at higher trophic levels. So, the impact of *N. neesiana* on biodiversity also depends on the productivity of the invaded and uninvaded areas, in terms of their invertebrate ’outputs’.

Structural change in the habitat may have limited influence, since *N. neesiana* patches are similar in their gross morphology to grasslands consisting of native tussock grasses. Litter build-up has sometimes been inferred to be a major alteration in *N. neesiana* areas (Gardener and Sindel 1998), of special significance for invertebrates (Ens 2002a), but litter accumulation by *T. triandra* (Trémont and McIntyre 1994) probably has similar effects. The phenological differences between *N. neesiana* and the major native dominant *T. triandra* resulting from their different photosynthetic C fixation systems, may be important, since the synchronisation of the phenology of a grass host and its inhabitants may be a critical factor for their survival and fecundity. However any such contrasts would presumably be less when the native grassland consists of other C_3 species such as *Austrostipa* and *Austrodanthonia* species.

In evolutionary time, the interaction of invasive species with other species in the invaded community changes selection pressures, and ultimately results in evolutionary change, with existing species adapting to better exploit the modified environment, the invader counter-adapting and coevolving, and new species arising (Cox 2004). In the longer term invasive species tend to become integrated into the invaded community in such a way that their initial impacts, often largely negative, are softened, and the ecological adjustments resulting in better integration tend to precede the evolutionary (Cox 2004).

Invertebrate predators of *N. neesiana*

The invertebrate fauna of *N. neesiana* in Australia was previously completely unknown. *Nassella neesiana* has been found in the study reported in this chapter to host a wide range of generalist grass-eating insects in Australia, including species of Pseudococcidae, Acrididae, Anthribidae, Curculionidae, Anthelidae, Psychidae and Noctuidae, and the fallen seeds are harvested and destroyed by ants. No invertebrates were found that prevent seed formation or destroy seed on the plant, and heavy damage to the plant was observed only with *Pterolocera* sp. at Crace on plants kept short by grazing mammals.

Ecological explanations of why various other invertebrates were found on *N. neesiana* were not established: some may be phytophagous or predatory on smaller organisms on the plant, others may use it for shelter, or be casual visitors.

Mollusca

Native molluscs are thought to be naturally rare in native grasslands of south-eastern Australia (Holland *et al.* 2007) and none were identified in the grasslands investigated. Various exotic slugs and snails were observed but were usually in low numbers. Smith and Kershaw (1979) noted that *C. barbara* can be a crop and pasture pest, and Kershaw (1991) listed grasslands as habitat, and stated that it can be found on grass stems “low and inside tussocks”, but it is not clear if it ever damages grasses, which are thought be generally unpalatable to molluscs (Barker 2008).

Orthoptera

Published information on host preferences of the grasshoppers (Acrididae) found on *N. neesiana* is generally vague. Feeding by grasshoppers is difficult to observe in the field because they flush readily when closely approached, and captive rearing is difficult because of requirements for sunlight and other precise environmental conditions, although most species “can be raised on grass” (Rentz *et al.* 2003 p. 22). According to Rentz (1996 p. 173) “most grasshoppers seem to be very selective about the plants they eat. A few are general feeders, but the majority have definite host plant associations.” *G. musicus* “prefers grasses of medium height rather than short grass” and “feeds mostly on grasses” (Rentz 1996 p. 177). *Austroicetes cruciata* is a pest of winter wheat (Rentz 1996) and other cereals, while *Austroicetes vulgaris* “frequently damages crops and pastures” (Rentz *et al.* 2003). *Acrida conica* is “especially fond of disturbed areas such as playing fields or over grazed pastures where there are introduced European grasses” (Rentz *et al.* 2003 p. 348). *Schizobothrus* *flavovittatus* “lives in short grasses” and “has a habit of diving into deep grass at the end of escape flights” (Rentz *et al.* 2003 p. 346). *Phaulacridium vittatum* consumes a wide range of native and introduced forbs and does not eat grasses (Rentz *et al.* 2003). *Praxibulus* spp. cause significant pasture damage (Rentz *et al.* 2003).

Hemiptera

Concentrations of nymphal exuviae around *N. neesiana* plants suggest that *Cicadetta waterhousei* may be a nymphal host plant. Many Australian cicadas utilise Poaceae, and the family probably supports more cicada species than any other plant family (Moulds 1990). The nymphs feed on the roots and the adults may feed on the stems and oviposit into stems. Several *Cicadetta* species appear to be specific to grasses, but few host plants have been recorded (Moulds 1990) and generalisations about host-specificity cannot yet be made. The habitat of *C. waterhousei* has been recorded as grasses of “several species; usually long and partly or completely browned” and it has often been found on dried out seed-bearing *Avena* spp. in South Australia (Moulds 1990 p. 167). The nymphs feed on grass roots (Moulds 1990).

Mealybugs (Pseudococcidae) are generally polyphagous (Witt and McConnachie 2004) and can generally be expected to occur in the phytophage assemblage of even the smallest grasses (Tscharntke and Greiler 1995). No published records of Pseudococcidae attacking the grasses of temperate south-eastern Australian grasslands have been found.

Dictyotus conspicuus is a common species in south-eastern Australia “often found in colonies”, recorded on *Beyeria leschenaulti* (D.C.) Bail., “clover” in an orchard, and moist sand under a native *Goodenia* (Gross 1975 p. 209). Its Victorian distribution includes St Albans, Meredith, Morrisons, Clarkefield, Tallarook and Wallan (Gross 1975) suggesting an association with grasslands and grassy woodlands. No details of food plants were recorded by Gross (1975) but species in the genus are “most frequently seen on the ground” (Gross 1975 p. 100).

The food plants of *Eribotes* ?*reconditus* (Pentatomidae) appear to be unrecorded. Gross (1975) reported that several South Australian specimens of the very similar *Eribotes hobartensis* Distant were obtained by sweeping grassland and that one was found on *Atriplex paludosa*. *E. reconditus* was said to occur “in much the same type of habitat”.

Coleoptera

The plant associations of *Dicranolaius conicornis* (Melyridae: Malachiinae) and related beetles are very poorly understood. Malachiinae larvae and adults are generally considered to be predators with the adults often feeding on pollen (Booth *et al.* 1990, Moore 1990, Matthews 1992). According to Moore (1990) adult *Dicranolaius* are pollen feeders, most often seen on flowers *Wahlenbergia* and of yellow-flowered daisies such as *Hypochoeris*.

Evidence suggests that a wide range of invertebrate prey is attacked, but there is also evidence of more general adult phytophagy. Larvae of *Dicranolaius villosus* (Lea) are predators of egg pods of the Australian Plague Locust *Chortoicetes terminifera* (Walker), a single larva consuming all or most of the eggs in a pod, however the abundance of adults in the field greatly exceeds the number that could have arisen from locust pods alone (Farrow 1974). Horne *et al.* (2000) found in laboratory tests that adult *Dicranolaius bellulus* (Guérin-Méneville) is a general predator and scavenger, feeding on eggs and first instar Lepidoptera larvae and scavenging dead crickets. *Dicranolaius cinctus* (Redtenbacher)) reportedly damages rice in New South Wales (Booth *et al.* 1990). Hely (1958 as *D. bellulus*) reported that adult beetles are attracted into flowering crops in February, “may attack the anthers and flowering organs, but ... mainly feed on the newly-set grain through the “milk” and “dough” stages and may even continue to feed on the chalky grain as it ripens” (Hely 1958 p. 29). Adult beetles push the glumes of the rice flower apart, “working their mandibles along the suture at the overlapping margins and with the body holding the glumes apart feed on the developing grain” or, if this approach is unsuccessful “gnaw out the side of the husk” (loc. cit.). Hely (1958 p. 30) stated that the flowers of sedges, rushes and aquatic grasses “of the millet type” are the normal foods of adults. The observations of *D. conicornis* on three Stipeae species suggest that the flowers and fruit may sometimes be eaten, as is the case with rice and *D. cinctus*. Observations of feeding on *Goodenia* petals contradict existing understanding. Clearly much remains to be learnt about the ecology of *Dicranolaius* spp. in Australia.

Host plants of the native *Euciodes suturalis* (Anthribidae) in Australia have not previously been documented, although in New Zealand, where the beetle is an introduced species, a few grasses introduced from the northern hemisphere have been recorded as hosts (Zimmerman 1994a).

Eurymetopus birabeni Kuschel, like *N. neesiana* itself, is native to Argentina and Uruguay, and is an accidental introduction to Australia (Scataglini *et al.* 2005, Barriga-Tuñón 2011). Its food plants and habitat in the area of origin are not recorded in the accessed literature.

Five species of Amycterini (Curculionidae: Amycterinae) were found associated with *N. neesiana*. Amycterini is a highly diverse Australian endemic tribe of primitive, flightless, ground weevils, the members of which, as far as is known, are confined to grasses or other monocots, with larvae that are free-living in the soil and feed on root crowns, adults eating grass leaves including, unusually, dead, dry grass, and the eggs are deposited directly into the substrate, rather than in a prepared site in a host plant (Howden 1986, Zimmerman 1993, May 1994, Porch 2009). The tribe is considered to be a Gondwanaland relic but has no known closely related group in South America (Zimmerman 1993). Adults of the species that feed on wiry grass stems have stout, blunt mandibles and gular roll (‘lip’), while species that feed on soft tissues have a different mouthpart morphology (Howden 1986). Short sections of grass stems “as whole as when digested” are passed as faeces by adults of the grass-feeding species, nutrients being extracted by digestive fluids while the material is held in the proventriculus (Zimmerman 1993 p. 285). Such characteristic adult frass piles, consisting of consumed *N. neesiana* fragments were observed for both *C. maculatus* and *T. howitti*. Apart from the two species of *Oncopera* (Lepidoptera: Hepialidae) recorded damaging *Nassella trichotoma* by Campbell (1998), the Amycterini contains the only species of insects in Australia for which published records of *Nassella* feeding appear to exist.

Zimmerman (1993 p. 262) recorded *N. trichotoma* and “some other” unstated grasses” as host plants of *C. sordidus*, evidently an identification of Howden’s (1986) “*Cubicorhynchus* sp.” observed near Yass, NSW (see also May 1994). The finding that *N. neesiana* and *A. scabra* are also hosts suggests that the species is at least narrowly oligophagous on a range of Stipeae. Adults and a larva of *Cubicorhynchus calcaratus* Macleay of eastern and southern Australia have been found in a clump of “*Stipa*” in South Australia, while *Austrostipa nitida* and *A. nodosa* along with other grasses are hosts of another eastern and southern species *C. taurus* Blackburn, the larvae of which have been found in the crowns and root masses (Howden 1986, Zimmerman 1993, May 1994). Other species in the genus also have grass hosts including *Microlaena stipoides* and “*Stipa*” for the Western Australian *C. bohemani* (Boheman) (Zimmerman 1993) and unidentified grass for *C. crenicollis* (Waterhouse) (May 1994). Howden (1986 p. 100) noted that all *Cubicorhynchus* species “collected to date have been associated with either native or introduced species of Poaceae” and recorded that larvae collected from grass crowns “often regurgitated green material, indicating that they fed on underground stems and not the roots” (Howden 1986 p. 100). *Sclerorinus* spp. (Amycterini) have also been recorded from undetermined “*Stipa* sp.” (May 1994 p. 495).

Phalidura abnormis feeding on *N. neesiana* was not observed but the species appeared to be strongly associated with the grass. Zimmerman (1993 p. 359) noted that B.P. Moore had found both larvae and adults of this species feeding on *N. trichotoma*, the native host plants being “unknown”. Howden’s (1986) listing of *Phalidura assimilis* Ferguson feeding on *N. trichotoma* near Yass are treated by Zimmerman as *P. abnormis*, and May (1994) listed *P. abnormis* as the only *Phalidura* known to feed on *N. trichotoma*. However larvae of *Phalidura elongata* (Macleay) feed on underground parts of *N. trichotoma*, and other grasses (Zimmerman 1993), while adults consume *N. trichotoma* and pupae are also found in association with it (Howden 1986). The frequent presence of *P. abnormis* skeletal material in *N. neesiana* swards at Yarramundi Reach suggests that a second *Nassella* sp. is included in its diet.

Extremely little is known about the biology of *Talaurinus* species: Zimmerman (1993) listed only the type localities (Melbourne, Vic. for *T. howitti*) and no food plant information. *Nassella neesiana* appears to be the first recorded host plant for *T. howitti*.

Lepidoptera

The small Psychidae species close to *Psychanisa baliodes* (Meyrick) found on *N. neesiana* appears to be a generalist grass feeder. *Psychanisa* Walker is represented by two described Australian species (Nielsen and Edwards 1996). Common (1990) stated that *P. baliodes* feeds on *Brachyloma* (Epacridaceae) at Canberra, a plant not present in the grasslands in which cases were found in this study, so possibly the species is very broadly phytophagous. Chadwick (1966) reviewed the little that was then known about the larval feeding habits of Australian Psychidae, only one species of which had been recorded consuming grasses, '*Plutorectis*' *caespitosae* Oke (*Lomera caespitosae* in Common 1990), blamed for extensive patch death of *Poa* spp. snowgrasses in the Australian Alps. This species cuts grass blades for attachment to its case and also consumes plants in a range of other families (Chadwick 1966). Edwards (2002 p. 61) recorded that the *Poa* snow grass feeding larvae live in "tightly silked, neat, cases incorporating grass blades in longitudinal orientation resting among the leaves of the vegetation and feed on grass blades". Chadwick (1966) provided detailed descriptions of the life history, all the life stages, case building, and the case itself, described as bearing "a remarkable resemblance to the stubble of snow grass" (p. 18) when mature. Edwards (2002) noted that the extensive damage attributed to the moth was caused by an underground grass caterpillar, *Oncopera alpina* Tindale (Lepidoptera: Hepialidae), as had earlier been concluded by Chadwick. Green and Osborne (1994) illustrated the case, with its somewhat untidy array of grass pieces of differing lengths. They erroneously stated that the larvae feed exclusively on "Snow grass" in the Australian Alps, causing damage to large areas in the subalpine zone, especially below the treeline, when in large numbers.

At least several Australian anthelid species are known to feed on grasses (Common 1990, Marriott 2008). In addition to those detected feeding on *N. neesiana*, these include *Anthela oressarcha* Turner, an alpine species known from Kosciuszko National Park, *A. euryphica* Turner from central New South Wales (Common 1990) and the inland *A. basigera* (Walker) (Marriott 2008). The semi-arid area *A. ochroptera* Lower is probably grass feeding (Marriott 2008). *Pterolocera* Walker contains eight described spp., but unpublished studies have identified many more (Edwards and Fairey 1996), with estimates of the total ranging up to 30 (Marriott 2008). Except for one species, *Pterolocera* have brachypterous females (Edwards and Fairey 1996) and their flightlessness means that sedentary colonies are formed, presumed to be a significant cause of speciation. According to Common (1990 p. 491) the food plants of larval *Pterolocera* are grasses, including cereals, and some species occasionally cause damage to native pastures (Edwards and Fairey 1996). According to Marriott (2008) an undescribed member of the “lined group” of *Pterolocera*, found in open grassland, is grass feeding, with larvae accepting “*Poa* spp. and many introduced grasses”. The larva of this species is very similar to the material collected in the ACT. The observations indicate that a wide range of grasses including *N. neesiana* are acceptable to larvae.

Anthela ferruginosa is known from Queensland to Victoria, South Australian and Tasmania, inland as well as on the coast (Common 1990). Larvae reportedly feed on “grasses” (Common 1990, Marriott 2008). *Nassella neesiana* is a newly recorded host.

Common (1990 p. 396) stated that larvae of *Anthela denticulata*, found in inland New South Wales south from Trangie “feed on grass”, but that similar moths found in Victoria were believed by E.D. Edwards to be a separate (undescribed) species. Marriott (2008) treated the Victorian populations as *A. denticulata*, considered them to be “grass feeding” and suggested that the species is “probably” found “across the western grasslands” of the State. The grass food plants include cereals (Common 1990 pp. 490-1) and periodic damage to crops has been reported (Edwards and Fairey 1996). Froggatt (1910) reported *A. denticulata* larval remains as common on damaged *Atriplex* in the Hay district of NSW. His identification may have been erroneous, since Common (1990 p. 485) listed no Anthelidae as chenopod feeders. The *Nassella* spp. are newly recorded host plants.

Anthela ocellata larvae were commonly found on *N. neesiana* and were successfully reared on it. French (1911 p.123) stated that this species is a “very common and destructive pest ... especially destructive to grasses on pasture land as they eat the grass as well as defile the pastures when they are numerous.” He noted that the larvae may be seen in thousands in late spring, and that there were two generations per year, with larval feeding in June-September and December-January and adults in November and March-April. Coupar and Coupar (1992 p. 27) stated that the larvae “rest on the base of the food plant during the day” and feed at night on “various introduced grasses” including *Ehrharta erecta*. According to Common (1990 p. 396) the larvae are “frequently found feeding on grasses in gardens” and (p. 491) the food plants are grasses, including cereals.

The noctuids *Persectania ewingii* and *Mythimna convecta* are serious pests of pasture grasses, grass forage crops and cereals, consuming the stems, leaves and seed heads (Common 1954, Goodyer 1983, McDonald 1991). In Victoria *M. convecta* is much more common in cereal crops and *P. ewingii* in pastures (McDonald and Smith 1986). *Persectania ewingii* has been recorded defoliating *Austrostipa pubinodis* (Trin. & Rupr.) S.W.L. Jacobs & J. Everett in a tussock grassland in South Australia, eating “practically all the current season’s growth” (Lower 1954 p. 161, as *Stipa pubescens* R.Br.). Apart from cereals, *M.*

convecta attacks maize and *Setaria* (Common 1990). McDonald (1991) demonstrated differential development and survival rates of these species on different cereal grasses, and of *M. convecta* on three exotic pasture grasses (*Hordeum leporinum* Link, *Lolium perenne* L. and *Pennisetum clandestinum* Hochst. ex Chiov.) and native *Astrebla pectinata* (Lindl.) F. Muell. ex Benth., with the latter two grasses resulting in significantly lower growth rates. The larvae of the two species are similar and are mainly nocturnal feeders, which hide in litter or at the base of grass plants during the day (Goodyer 1983). As highly polyphagous grass pests it is no surprise to find they also eat *N. neesiana*.

Hymenoptera

Seed harvesting ants generally collect seeds from the ground surface, carry them to the nest, store them in underground granaries, feed the nutritive parts to their larvae and discard the seed remains, including awn fragments and lemmas of grasses, in refuse middens outside nest entrances. Ants often prefer the seeds of grasses to those of other plants, possibly because they have low levels of toxins or are easier to hull, and because they are easy to store without deterioration (Buckley 1982). *Pheidole* species are often the dominant component of the harvesting fauna in Australia and are highly opportunistic foragers which gather large quantities of seed, respond strongly to pulses of seed availability and are largely dependent on the seed they have stored during periods when fallen seed are unavailable (Briese and Macauley 1980 1981). *P. vigilans* has been called “the most familiar *Pheidole* species in the better-watered parts of south-eastern Australia” and “a common, moderately variable species” (Brown 1971 p. 13).

Gardener *et al.* (1996a) stated that ant predation of *N. neesiana* seeds appeared to be lacking in pastures of the New England Tablelands of New South Wales and suggested that this might be due to the impenetrability of the lemma providing good protection to the edible caryopsis. Gardener (1998) set up experiments in pasture to investigate removal of de-awned *N. neesiana* seeds and found in one experiment that around one third of unburied seed disappeared. The experimental results were considered inconclusive and no ant species was implicated in seed removal.

The observations reported in this chapter indicate that *Pheidole* ants are a major predator of *N. neesiana* seeds. The activity of harvester ants may partly explain the small soil seed banks reported for most plants in Victorian natural temperate grasslands.

Conclusions

Some areas occupied by *N. neesiana* in temperate native grasslands were found to have significantly reduced mean invertebrate species richness or mean total abundance at particular times compared to matched areas of native grassland. *Nassella neesiana* areas never had greater mean invertebrate species diversity than native grassland areas.

Various species were found to be more common in *N. neesiana* areas, while others were less common. The mechanisms responsible for the changes for each affected species mostly remain speculative and may be classed as indirect floristic effects, without known phytophagy-related explanations. Theoretical frameworks that are founded on invertebrate food plant relationships alone are not adequate for explaining the differences detected; instead structural, phenological and other explanations are clearly required. Patches of *N. neesiana* may be enriched with species such as amycterine weevils that feed upon it, but not upon the dominant native grass *T. triandra*, but only one species, *Hispellinus multispinosus*, was detected that has a direct trophic dependency on *T. triandra* and was absent in *N. neesiana* patches.

The extent to which differences in invertebrate assemblages in invaded and un-invaded areas can be attributed to prior disturbance that enabled *N. neesiana* to occupy an area, or to direct effects dependent on the presence of *N. neesiana* or the displacement of particular native plants is very uncertain. Understandings developed in other experiments and surveys and reported in previous chapters in relation to the plant diversity effects of prior disturbance that enable *N. neesiana* occupation suggest that much of the lower invertebrate diversity in occupied areas could be attributed to disturbance that precedes *N. neesiana* occupation of sites. More sophisticated sampling and specimen processing techniques than used in this study are required to determine cause and effect relationships between invertebrate composition and *N. neesiana*.

Nassella neesiana is inhabited by a range of invertebrates and commonly eaten by some native invertebrate species. As far as is known, the invertebrates that utilise *N. neesiana* as food in Australia are native species that are oligophagous on grasses or widely polyphagous. Invasions of *N. neesiana* are therefore occurring despite pronounced biotic resistance from native invertebrates. The host range of the only South American native invertebrate found associated with *N. neesiana*, the weevil *Eurymetopus birabeni*, has not been determined. Thus it appears that *N. neesiana* in temperate Australian native grassland has been broadly released from the invertebrate predation to which it is presumed to be subject to in its native habitats. Available literature records indicate that fewer species are recorded from most of the common grass species than have now been recorded from *N. neesiana*. This suggests that *N. neesiana* in temperate Australian grasslands supports faunas of similar biodiversity value to those of the dominant native grasses. The data is not adequate to test the theoretical prediction that generalist native phytophages preferentially attack *N. neesiana* in comparison with native hosts (predator release theory).

Observations of birds eating larval Anthelidae that feed on *N. neesiana* , the emergence of parasitoids from one *N. neesiana* phytophage and the discovery of a new braconid species that is apparently a parasitoid of the *N. neesiana* culm-borer *Euciodes suturalis*, provides evidence that the plant supports simple food webs in native grasslands.

Evolutionary theory and evidence from community ecology studies of other weeds suggest that the fauna utilising *N. neesiana* in Australia can be expected to grow with increased residence time, and the plant is likely to increasingly become better integrated into, and less of a weed problem in the native grassland environment. Nevertheless the displacement of native flora associated with the presence of *N. neesiana* almost certainly results in large net declines in native invertebrate diversity in the areas it occupies, due to the disappearance of a diverse fauna of specialist phytophages dependent on native plants and their specialist predators and parasitoids.

Studies of this type are highly dependent on the extent of baseline knowledge, which remains at a relatively low level for Australian invertebrates as a whole, and for temperate grassland invertebrates in particular. Further more detailed study of the material collected will assist in improving this situation.

Chapter 9. Conclusions

"The consequences of biological invasions in disturbed sites and secondary succession represent at once the most difficult and important area of research. It is here that the effects of invasion are most easily confounded with those of the massive, prolonged, or novel disturbances which often form the invaded habitat ... here that changes in ecosystem-level characteristics are rapid even in the absence of biological invasions."

Ramakrishnan and Vitousek, 1989, p. 282.

Summary

Nassella neesiana has been widely portrayed as a major cause of biodiversity loss in the temperate native grasslands of south-eastern Australia. The studies reported here demonstrate that markedly lower native vascular plant and invertebrate diversity are correlated with the presence of *N. neesiana* in these systems, but that the correlations are probably in part the result of prior loss of biodiversity, due to anthropogenic disturbances that enable *N. neesiana* to invade, and that areas of intact, well managed native grassland are highly resistant to invasion. In short, disturbance processes may have caused much of the biodiversity loss in the areas studied, and *N. neesiana* then opportunistically invaded these disturbed, low biodiversity areas.

The changes in biodiversity correlated with *N. neesiana* presence include large reductions in the species richness of native forbs, smaller reductions in the species richness of native grasses, little change or small increases in the richness of exotic vascular plants, a significant reduction in invertebrate species richness in autumn and a significant reduction in the number of invertebrate individuals in spring. *Nassella neesiana* has been found to have some positive effects on biodiversity as a host plant for a range of native insects, but there is no indication that this compensates for the biodiversity losses that occur when there is disturbance that results in subsequent *N. neesiana* establishment in these areas. *Nassella neesiana* alters ecohydrological features of grasslands with probable positive feedbacks on its own success, and these changes also probably have off-site biodiversity impact.

The findings of the study require cautious interpretation and have implications for current management strategies. The consequences for native grassland management that have been determined align with other reported studies and reviews – grasslands need active, appropriate ecological management, and where this occurs they are resistant to major weed invasion. A set of future research priorities is provided that addresses the problems of exotic perennial grass invasions, major lacunae in the understanding of native grassland ecology, and the areas in which an increased understanding of *N. neesiana* biology would be beneficial.

Introduction

This chapter reiterates the major findings reported in earlier chapters and attempts to further synthesise them and integrate them with the general knowledge reported in the literature. The key findings are presented first. These need to be interpreted with caution, since they are derived under limited spatial, temporal and climatic conditions, or are perhaps results that relate to the specificity of the sites studied, and may not be generally applicable to the range of grassland conditions in which *N. neesiana* occurs. Some cautionary considerations are detailed and discussed. The significance and implications of the findings are then briefly discussed. Implications for the management of temperate grasslands are then briefly elaborated. The thesis concludes with a set of recommendations for future research that would improve understanding of the ecology and management of native grasslands, particularly in relation to *N. neesiana*, and increase the potential to minimise its negative biodiversity effects.

Major findings

The major findings from this study may be summarised as follows:

1. Major reductions in native plant biodiversity are correlated with the presence of *N. neesiana* patches including reductions of dominant or sub-dominant native grasses. Direct competitive impact of the grass in invaded areas may be less important in loss of plant diversity than prior degradation, including senescence dieback of *T. triandra*, damage by livestock grazing and soil disturbances that enable *N. neesiana* to invade. Loss of native plant diversity in invaded areas may commonly *precede N. neesiana* invasion. However the competitive impacts of *N. neesiana* and the ongoing biodiversity effects of anthropogenic disturbance are intricately confounded in all the grasslands studied, and the contribution of each factor to the biodiversity changes that were detected has not been determined.
2. *Nassella neesiana* invasions appear to be largely enabled by anthropogenic disturbance that results in the death of the pre-existing dominant perennial grasses. In the absence of such disturbance *N. neesiana* seedlings and juvenile plants do not survive. Areas dominated by healthy growing native tussocks are resistant to invasion. Severe

disturbance does not necessarily result in invasion because coincident propagule pressure is required.

3. Gap sizes of c. 1 m^2 enable significant establishment, while gaps of c. 10-30 cm largely disallow establishment. Biomass of *N. neesiana* plants that establish in areas with larger gaps is much greater than areas with small gaps.
4. Fertilisation with nitrogen or phosphorus does not enhance *N. neesiana* recruitment, but immobilisation of nutrients using sugar significantly reduces establishment. However nitrogen fertilisation significantly reduces productivity of the dominant native grass *Themeda triandra* and therefore would preferentially benefit *N. neesiana* when the two species are in competition.
5. Establishment of *N. neesiana* on the boundaries between existing patches of *N. neesiana* and areas dominated by the major native grass *Themeda triandra* is higher where *T. triandra* is more senescent, i.e. when *T. triandra* swards have a higher proportion of dead foliage. Uninvaded areas have consistently higher proportions of living *T. triandra* leaves. In areas subject to *N. neesiana* propagule pressure *N. neesiana* invasion accompanies *T. triandra* senescence dieback, which occurs as a natural process when biomass reduction (by fire or grazing) fails to occur over periods greater than c. 5 years.
6. *Nassella neesiana* infestations in native grasslands have an impoverished native vascular plant flora compared with immediately adjacent areas of native grassland. Native plant species richness (spp. /m^2) in *N. neesiana* patches is significantly less than in comparable areas immediately outside patches. Differences of 32-65% (back transformed data) were measured at three grasslands. Native forb diversity was 54-68% lower and native grass diversity 71-85% lower in infested areas. Larger differences were found in the more species rich grasslands.
7. The larger the *N. neesiana* patch, the greater the reduction in native vascular plant species richness.
8. If larger patches are older than smaller, this indicates that *N. neesiana* may be having a significant, but smaller, negative impact on native plant diversity after it has established.
9. Soil moisture under *N. neesiana* stands appears to be much depleted in spring compared to stands of the dominant native grass *T. triandra*. Most of the vascular plant diversity in Australian temperate native grasslands consists of spring-growing species, so the spring-growing *N. neesiana* competes directly with them for water. In contrast *T. triandra* is mainly summer growing and competes with other native plants for water to a more limited extent. Thus, soil water depletion in spring may be one mechanism for ongoing losses of native plant diversity after *N. neesiana* establishment. Widespread displacement of *T. triandra* by *N. neesiana* is likely to have negative ecohydrological

effects at the catchment scale including reduced runoff and increased deep drainage that potentially affect biodiversity far beyond the areas infested.

10. Species richness of exotic vascular plants (not including *N. neesiana*) inside *N. neesiana* patches was not significantly different to comparable areas immediately outside patches, except at one site where *N. neesiana* infestations were mainly the result of recent senescence dieback of the dominant native grass. This is explained if infestations result from disturbance that indiscriminately kills the existing vegetation, by the lesser ability of the native flora to re-colonise after disturbance and the by the better adaptation of the exotic flora to higher nutrient concentrations that result from disappearance of the dominant native grass *T. triandra*.
11. Analysis of historical aerial photographs and satellite images, in association with on-ground measurements, demonstrates that *Nassella neesian*a invasions into native grasslands tend to be slow, except where the native grassland is in poor ecological condition. Where infestations abut areas of senescent *T. triandra*, linear expansion rates >1 m per year can be expected, although much higher rates are apparent in severely disturbed areas. Where native grasslands are kept healthy by biomass reduction, the expansion of *N. neesiana* infestations and associated losses of plant biodiversity are kept low. There is some indication that areal coverage of *N. neesiana* can be reduced when the management regime consists of frequent burning.
12. Overall invertebrate diversity and abundance is significantly negatively correlated with the presence of dense *N. neesiana*. The mechanisms responsible for these differences are complex and difficult to determine, and are not generally attributable to loss of native food plants. A number of native insect species were found to be more abundant and frequent in infested areas than in uninvaded grasslands.

Cautionary considerations

The conclusions have been reached largely from studies at a fine scale (e.g. square metre plots and small to moderate sized *N. neesiana* patches) in open native grasslands, but the findings about mechanisms of invasion and impact can be generalised to some extent to the landscape and regional scales. They align with a range of other studies at different scales of analysis (e.g. Lunt and Morgan 1998a 2000, Morgan and Lunt 1999) and using different techniques for study (e.g. Dunin and Reyenga 1978, Wijesuriya and Hocking 1999). This gives these conclusions some robustness beyond their application to the actual sites studied.

Disturbances that kill the native vegetation have been demonstrated to facilitate *N. neesiana* invasions. But as observed by Hierro *et al.* (2006) disturbance may operate in association with other mechanisms that increase the fitness of the invader in the invaded environment, including superior competitive abilities, release from natural enemies and possession of ‘novel weapons’ such as allelopathic properties. Release from natural enemies has been demonstrated for some pathogens (fungi) by biological control studies, but release of invertebrate enemies has not (Hierro *et al.* 2006). The studies reported here (Chapter 8) provide little illumination on the question of natural enemy release or a possible role of phytophagous animals in providing biotic resistance to invasion: a wide range of macroscopic native insects was found to inhabit and feed upon *N. neesiana* in Australia, but no observations or records were found of invertebrate natural enemies in the native range, and there was no indication that the few native vertebrate herbivores detected consuming *N. neesiana* preferred it to native grasses. Nor has investigation revealed much evidence of the possibility that *N. neesiana* possesses special characteristics that assist it to invade, apart from its possession of clandestine cleistogenes. To most intents and purposes it appears to be just another invasive exotic grass that is given advantage through disturbance that removes dominant native grasses.

Dominance by an invader in some but not other areas, that is suggestive of competitive superiority, may actually be just a priority effect: the exotic may not be able to outcompete an equilibrium population of competitors, but is the first to invade after strong disturbance and establishes dominance, leading to “multiple stable equilibria” (Seabloom *et al.* 2003 p. 13384). The widespread perception that *N. neesiana* is able to actively invade grasslands appears to be based in part on this misunderstanding. However, “it is the impact of invaders and not their establishment *per se* that threaten native communities” (Levine *et al.* 2003 p. 775). In this regard the advances in the understanding of invasion mechanisms reported in this thesis need to be balanced by an improved understanding of the ability of *N. neesiana* to persist in invaded areas, and exclude native floral and other biodiversity. This is particularly relevant for temperate lowland native grassland biodiversity conservation because remaining biodiversity-rich areas are small in size and fragmented across the landscape, so any occupation by exotic species is significant as a proportion of area available for conservation, and as an additional degrading and fragmenting process. Evidence suggests that infestations can continuously occupy a small area for many years if no control activity is undertaken. Persistence of infestations is most likely enhanced by production of basal and stem cleistogamous seeds that provide a temporal, ‘priority’ advantage in comparison with native grasses when an *N. neesiana* tussock dies. These seeds are immediately available for reestablishment at the microsite occupied, while native species, which generally have minimal soil seed banks and very limited ‘turnover’ must produce and disperse their seeds to that site.

Nassella neesiana infestations exist because at some time there were appropriate conditions for establishment and recruitment. This study has determined that such conditions include the removal of the pre-existing dominant grasses at a scale of ≥1 m. This area requirement is likely to be variably dependent on environmental and site conditions, because establishment requires absence of significant competition (which is likely to be below-ground competition for nutrients and water), and competition only develops under conditions related to resource scarcity and resource limitation. Competition for water appears likely to be of more importance than that for soil nutrients, so recruitment events may occur commonly when there is coincidence of good rainfall and disturbance that creates gaps of <1 m.

The study examined only some of the grosser and most easily investigated mechanisms that may explain the ability of *N. neesiana* to invade and influence the biodiversity of invaded areas. Important areas awaiting investigation include the role of fungal and bacterial symbionts, including endophytes, and of pathogenic microbes, in the alteration of the fitness of native plants and *N. neesiana*, and of soil biogeochemistry and nutrient cycling. It might well be suspected for example that the different litter qualities of *N. neesiana* and the dominant native grass, derived in part from their different C fixation pathways, result in more rapid nutrient cycling in the invaded system, and that this in turn would enable the development of a markedly different flora.

Studies of the invertebrates were almost entirely focused on the vegetation above the ground and inhabitants of the soil surface. However, as with the vegetation, a high proportion of the invertebrate biomass is underground, with many species spending most of their lives beneath the soil surface, particularly as larvae. Many species detected undoubtedly feed on the subterranean organs of grasses. This unexplored realm has largely been neglected because it is difficult and inconvenient to study, but major insights into grassland biology will undoubtedly proceed from simple excavation of tussocks and rearing of juvenile stages of the invertebrates that are found. All invertebrate sampling was undertaken during daylight. Nocturnal sampling would likely reveal markedly different sets of species, including many that emerge from the soil and litter into the canopy during conditions of darkness.

A final caution needs to be made in regard to the temporal scale of studies. Since very few plant invaders are ever eradicated, ultimately both the invader and the invaded system adapt to accommodate each other, and since there is more adaptive potential in the community than in the single invader, the impact will eventually decay (Whitney and Gabler 2008), or, if these adaptive changes are themselves considered to be impacts, may continue to slowly increase but include a higher proportion of evolved, ‘accomodatory’ change. Future attempts to evaluate *N. neesiana* impact on biodiversity should seek to integrate this longer term, ecological and evolutionary time perspective, and attempt to evaluate the extent and pace of the accommodation. Perhaps, for example, the lack of published record of invertebrates eating *N. neesiana* reflects a real absence, and the herbivory detected in this study results from very recent adaptation.

Significance and implications of the findings

When meshed with the other studies, the patch diversity study of vascular plants (Chapter 7) revealed two important effects. Major disturbances cause the loss of native plant species and allow *N. neesiana* invasion, sometimes along with other exotic species. After invasion, further losses of native species occur in the presence of *N. neesiana* as patches expand or as the period since *N. neesiana* established increases. Larger patches of *N. neesiana* have lower species richness of native vascular plants (spp. /m^2) than small patches, so the plant evidently has some continuing negative impact after establishment.

Replacement of *T. triandra* by *N. neesiana* removes the most important “phenological complementarity” (Cleland *et al.* 2006) in the system: a dominant C_4 grass with a summer flowering and growth period (*T. triandra* flowers once per year in summer - Groves and Whalley 2002) complementary to a very high proportion of the rest of the native vascular flora, is replaced by a C_3 species which potentially competes directly for limiting resources with this bulk of native plant diversity during its spring growing period. Phenological complementarity “promotes coexistence in multispecies plant communities” (Cleland *et al.* 2006 p. 13741) and its removal probably precipitates cascading detrimental effects including ongoing losses of native plant species.

The effects of prior management and the actual impacts of invasive plants are always confounded and frequently interact. This study has partially enabled their disaggregation and independent evaluation. *Nassella neesiana* may be more a symptom of prior degradation than a cause of biodiversity loss. The conditions that favour its invasion are primarily those that remove the competition provided by the native vegetation, particularly the dominant grass *T. triandra*. *Nassella neesiana* certainly occupies sites previously occupied by native grassland. Where there is propagule pressure from *N. neesiana*, any disturbance that kills the native grass sward over areas in excess of c. 1 m^2 probably enables invasions, but intact swards are highly resistant to invasion, even when propagule pressure is high. *Nassella neesiana* invades bare areas and can maintain its place, possibly due to its larger soil seed banks and the possession of stem and basal cleistogenes. Once it occupies a site, it too is resistant to invasion.

Mowing and slashing probably kill many native grasses which have higher mortality when cut short, so *N. neesiana* often invades grasslands initially via mown areas and along human thoroughfares. Fertile conditions are required for establishment, but these can be met by decay of the biomass of dead native grasses in the typical temperate grassland systems of south-eastern Australia, which occupy some of the least nutrient impoverished lands in the country.

Nassella neesiana patch margins have greater native plant diversity than patch centres, but patches nevertheless tend to have 'hard' edges: there is a sharp contrast over a short distance with the native vegetation matrix, with strongly reduced native plant diversity on one side, and reduced invertebrate diversity. *Nassella neesiana* therefore can be viewed as creating habitat fragmentation and infestations can be viewed as a barrier to biotic movement with implications for plants, and for animals: "for maximal insect diversity conservation the aim is to reduce the contrast between patch and matrix" (Samways 2005 p. 97).

Initial establishment of *N. neesiana* is strongly dependent on the extent and availability of ground (including below-ground) not occupied by other living plants. It is invasive in disturbed grassland habitats but appears largely unable to overcome environmental barriers in undisturbed habitats. When propagule pressure is applied, areas of intact grassland are resistant to invasion. Further invasion on the margins of infestations may be propelled by the ability of *N. neesiana* to deplete soil water in spring, prior to the growth period of *T. triandra*. This may impact on the vigour and productivity of adjacent areas of *T. triandra* and make them more invasible. Such a positive feedback, in which *N. neesiana* would drive its own spread, would be likely to have a landscape-scale threshold determined by the abundance of the invader and above which the impacts rapidly increase (Levine *et al.* 2003), so that increased presence of the invader accelerates its own invasion. *Nassella neesiana* may in part maintain its dominance by preventing spring soil water storage required for optimum growth of *T. triandra*, a form of resource pre-emption that enables the maintenance of multiple stable states (Seabloom *et al.* 2003). The ability of *Nassella neesiana* to continue to occupy for extended periods the ground where it establishes is partly explained by it being long-lived and may be enhanced by its ability to replace itself in situ from cleistogenes.

McIntyre (1995) argued that general declines in the abundance of many native grassland forbs, which comprise the overwhelming majority of plant diversity in all well preserved grasslands, must result from the failure of current management regimes to provide for their highly specific ecological requirements for regeneration, and that many of these requirements might possibly be met by the types of exogenous disturbances often considered to be harmful management practices. The dilemma for grassland managers is that the conditions that facilitate the establishment of *N. neesiana* and of other weeds appear to be similar to those required for establishment of native forbs (Morgan 1997b 1998b 1999b, Robinson 2003 2005, Reynolds 2006) and probably for the recruitment of native grasses, i.e. soil disturbance, large canopy gaps (≥1 m) associated with reduced shade and below-ground competition, and the absence of competition, particularly from established dominant perennial grasses. Although not tested in this study, soil disturbance that creates more areas of rough ground is likely to benefit *N. neesiana* by allowing the natural seed drilling to be more effective, increasing the availability of suitable germination sites (Peart 1979 1984), and via a temporary nutrient flux (Wijesuriya 1999, Wijesuriya and Hocking 1999).

Populations expand when niche space becomes available through death of native grasses and there is propagule rain. *Nassella neesiana* appears to have similar competitive abilities to native grasses, but superior fecundity (possibly because specific pre-dispersal seed predators and pathogens are lacking in the invaded range: none being detected in this study) and dispersal capability, including the ability, when tussock mortality occurs, to re-establish at the same point from basal cleistogenes.

Implications for grassland management

Understanding of the mechanisms of impact is important in determining improved methods of management (Levine *et al.* 2003). The findings of this thesis largely reinforce the messages of current best-practice grassland management doctrines (e.g. Wong and Morgan 2007): this involves active management to maintain the native tussock matrix, reduce *T. triandra* biomass accumulation by frequent burning, and where necessary, reduce livestock grazing to minimise biodiversity losses and disturbances that drive weed invasion.

The main message for grassland managers resulting from this study is that *N. neesiana* infestations are probably largely the consequence of bad management decisions in the past, and that ongoing management should avoid the same mistakes. The core management principles can now been considered to be long-standing – frequent biomass reduction of *T. triandra,* minimisation of soil disturbances and disturbances that kill the native grasses including livestock grazing and close mowing, and minimisation of propagule pressure by control of infestations at grassland edges and along thoroughfares. But there are continual problems in ensuring the application of these fundamentals, as the recent massive *N. neesiana* invasions at Yarramundi Reach amply demonstrate. The impacts of *N. neesiana* on biodiversity can be minimised by minimising prior degradation such as *T. triandra* senescence and soil disturbance and by strengthening invasion resistance by maintenance of a healthy cover of non-senescent *T. triandra*.

It is too late to save the biodiversity in areas already occupied by *N. neesiana* stands, since most of the damage to plant biodiversity that can occur has already occurred by the time infestations exceed 5 m^2. Control activities should therefore be prioritised for very small infestations and isolated tussocks, to reduce *N. neesiana* propagule pressure, and perhaps directed at somewhat larger infestations if they have large boundary: area ratios, so that natural recolonisation by major native grasses can occur more readily and quickly. Theory predicts that high perimeter to area ratios increase vulnerability to invasion (Byers *et al.* 2002), so similarly enhances the probability of recolonisation by elements from the native matrix.

The findings indicate that management activity directed at controlling *N. neesiana* should be prioritised for those infestations occurring in areas with a range of severe, ongoing anthropogenic disturbances and that infestations in well-managed grasslands tend to be relatively stable. It is better to remove the causes of degradation, but if for some reason this is impossible, then treatment of the symptoms, such as *N. neesiana* infestations, is better than no action at all. However infested areas retain some native plant diversity which could be imperilled by control activities.

The lack of cost-effective, consistently reliable rehabilitation treatments for infested areas of grassland after herbicidal kill of *N. neesiana* implies that established infestations with stable margins may be better left untreated until rehabilitation techniques are improved, or conditions for rehabilitation by such methods as ‘spray and hay’ (i.e. wet years) (Phillips and Hocking 1996, Dare and Hocking 1997, Hocking 1998, Mason 1998, Mason and Hocking 2002, Mason 2004, Hocking 2005b) are likely to become suitable.

Many herbicides used to control *Nassella* spp. have severe impacts on native vegetation and can result in major weed invasion (Hocking 1998). Whatever the herbicide used, cleistogenes that have already matured but remain attached to the plant, concealed beneath leaf sheaths are not killed (Hurrell *et al.* 1994). Furthermore, when a large *N. neesiana* seed bank is present, baring the ground with herbicides encourages seedling recruitment and may lead to rapid re-establishment and an ultimate increase in density and cover (Hartley 1994, Gardener *et al.* 1996b, Gardener *et al.* 1999, Lunt and Morgan 2000, Slay 2002a, Storrie and Lowien 2003). Herbicidal management in agricultural situations has often resulted in the expansion of *N. neesiana* populations and exacerbation of spread due to the elimination of competition (Slay 2001 2002a 2002c). In areas of native grasslands where there is *N. neesiana* propagule pressure, recruitment of *N. neesiana* is probably facilitated when herbicidal kill of pre-existing vegetation in areas exceeding 1 m^2. Such management is currently routinely applied to control *N. neesiana* in grasslands but is counterproductive if the most likely outcome is reoccupation by *N. neesiana* from the soil seed bank. Such understandings are rarely incorporated into management planning (Buckley *et al.* 2007) but need to be.

Nassella neesiana infestations are readily identifiable from aerial photographs in some grasslands at particular times of year, if some ground-truthing is undertaken. This finding opens the way to better infestation mapping and more reliable long term evaluation of the outcomes of *N. neesiana* management programs.

Recommendations for future research

The studies undertaken suggest a number of areas where further research may yield instructive insights, information for improved grassland management and techniques or knowledge that would be useful to minimise the biodiversity impacts of *N. neesiana*. These include:

1. Further investigations of potential mechanisms of invasion, in particular allelopathic effects of *N. neesiana*, the extent to which grazing of livestock creates suitable conditions for invasion, and the requirements for *N. neesiana* establishment at a small spatial scale (gap size) under a variety of conditions. Pot studies to investigate competitive interactions of *N. neesiana* with native species are also needed. The mechanisms by which *N. neesiana* causes biodiversity impact remain poorly explored.
2. Potential differential effects of fire intensity, frequency and seasonal timing on the mortality, fecundity and recruitment of *N. neesiana* and native plants. There are some indications that *N. neesiana* may suffer higher mortality when grassland management regimes include frequent fire.
3. The differential effects of cutting regimes on native and invasive grasses, particularly on their mortality and fecundity. There is strong evidence that invasion corridors are created by mowing and slashing and that the disturbance effects of these activities (e.g. mowing at low levels which may preferentially kill native tussocks) may be of greater importance than their effects on propagule dispersal.
4. Long term herbicide impact studies in which infestations of various small sizes are killed and the patterns of *N. neesiana* reestablishment and of native species recolonisation are assessed. In order to properly determine baseline conditions these trials would need to be predicated upon seed bank studies that included attached *N. neesiana* stem and basal cleistogenes. The aim of such studies would be to determine if current herbicidal management strategies have an effective outcome in terms of revegetation or are counterproductive and perpetuate the *N. neesiana* infestation.
5. More thorough studies to determine the effects of *N. neesiana* on seasonal soil water content, and research to determine the impact on catchment water yield and other ecohydrological factors. The impacts of *N. neesiana* on soil moisture were examined only during a single season at one site, but the potential implications appear alarming.
6. Basic studies of microbial symbionts and antagonists of *N. neesiana* and native grasses, particularly soil fungi and endophytes. Evidence is increasing that ecological

understanding may be inhibited by treating plant invasions as single organism problems, and that management techniques can be improved by understanding their biotic dependencies of invasive plants.

7. Detailed studies of the role of seed harvesting ants on the dynamics of soil seed banks in native grasslands. Evidence suggests that ant seed predation may be a major cause of the impoverishment and ephemerality of native seed banks, which in turn contributes to the very limited native plant recruitment commonly reported in native grasslands – probably the most critical current problem in ensuring their ongoing survival. Furthermore, the large, persistent *N. neesiana* seed banks recorded in some areas, notably agricultural grasslands, might be related to reduced ant activity.
8. Investigation of the potential and actual dispersal of *N. neesiana* seeds in running water. If moving water is an effective vector, then priorities for regional *N. neesiana* management require realignment.
9. Intensified exploration of the invertebrate faunas and soil biology of native grasslands. Knowledge of the former remains extremely fragmentary and would benefit from a large desk study that integrates the existing scattered knowledge with data trawled from museum collections. Almost nothing is known about the soil biology of Australian temperate native grasslands. Basic studies of invertebrate species and faunas are required to advance grassland invertebrate ecology and provide a sound basis for sustainable use of native pastures and the management of biodiversity in conservation reserves.
10. Intensified study of the autecology of native grassland plants. The major paucity of basic knowledge of the biology of Australian native plants found in grassland ecosystems needs to be redressed.
11. Cross-disciplinary investigation of the ecological history of native grasslands to better understand the factors resulting in their original formation, and their subsequent evolution and dynamics. Palaeoecological and palaeoanthropological studies focused on fire regimes, plant species composition, vertebrate grazing influences, including the role of the extinct megafauna and the recently extinct macrofauna, and the relationships between climate and grassland distribution appear eminently feasible.

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