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).
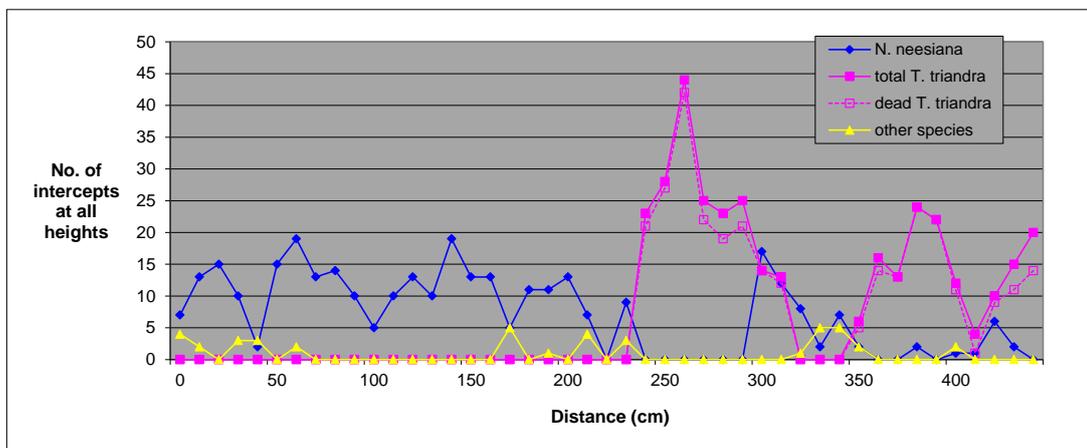

Figure 5.2. Distribution of *N. neesiana*, dead *T. triandra*, total *T. triandra* and other plant species along a pin transect at Yarramundi Reach, Patch G, 13 October 2007. The transect ran from dense, uniform *N. neesiana* into senescing *Themeda* (280 cm) to senescent *Themeda* (360-390 cm +) with small *N. neesiana* plants establishing underneath it.
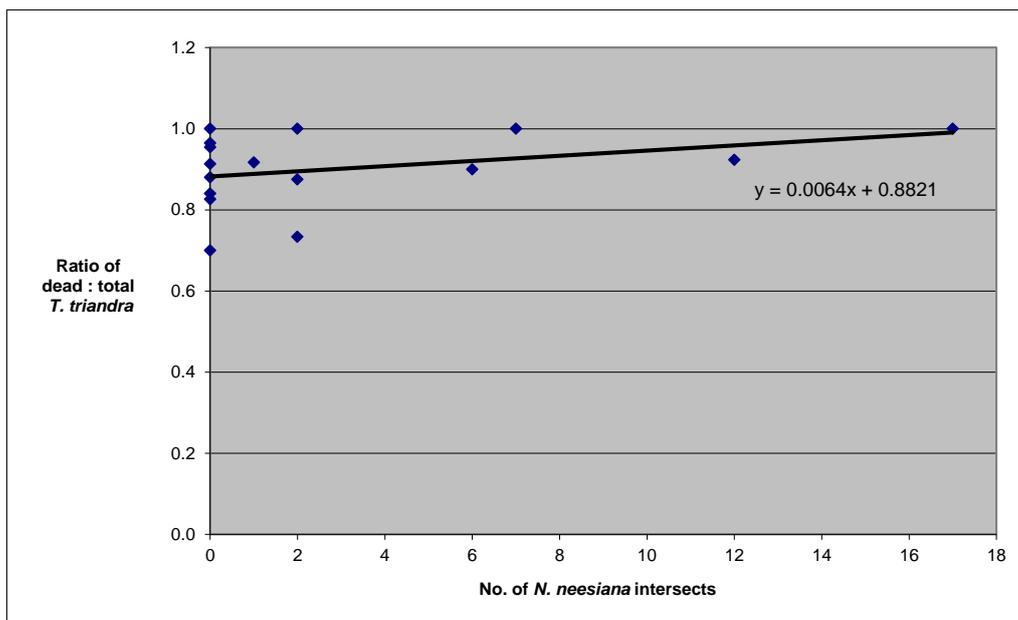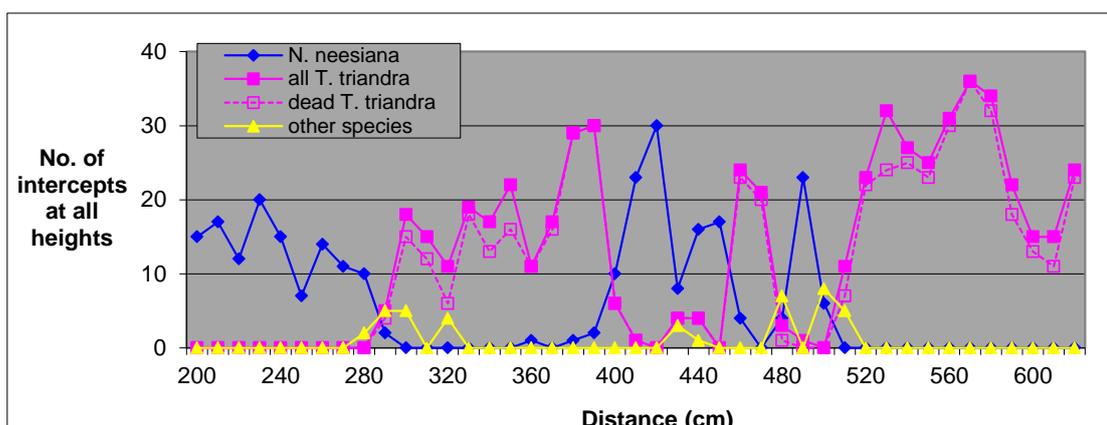
Figure 5.3. Relationship between the number of *N. neesiana* pin intersects at a transect point and the ratio of dead to living *T. triandra* pin intersects at that point, where the number of *T. triandra* pin intersects at the point was >9, at Yarramundi Reach patch G, 13 October 2007.

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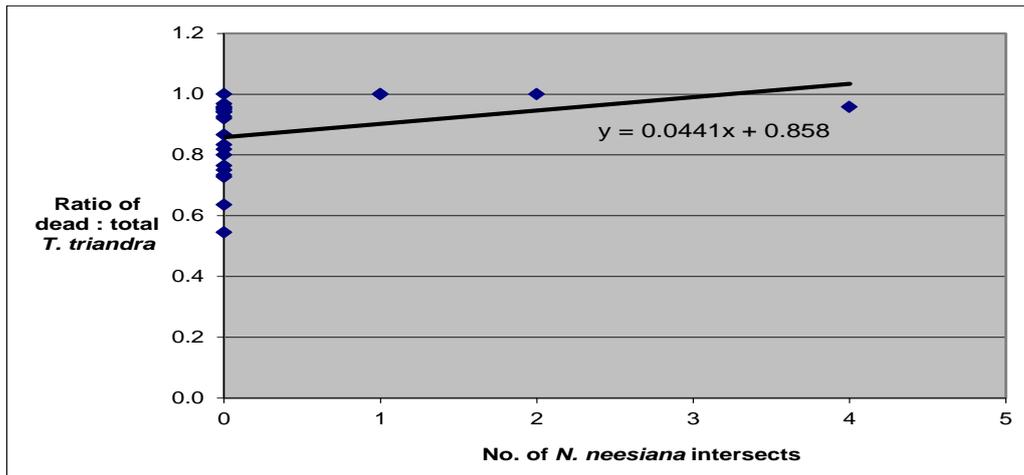
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Figure 5.5. Relationship between the number of *N. neesiana* pin intersects at a transect point and the ratio of dead to living *T. triandra* pin intersects at that point, where the number of *T. triandra* pin intersects at the point was >9, at Yarramundi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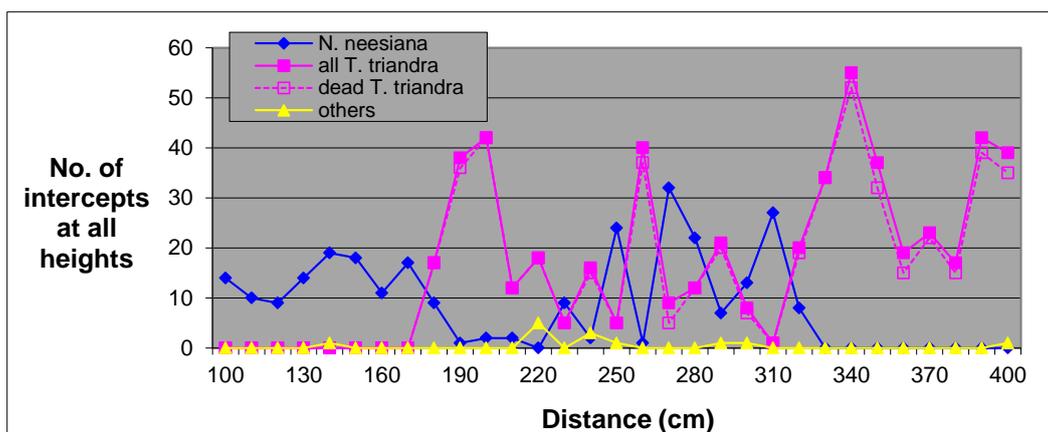

Figure 5.6. Distribution of *N. neesiana*, dead *T. triandra*, total *T. triandra* and other plant species along a pin transect at Yarramundi Reach peg 0885, 25 April 2008: transect from *N. neesiana* infestation through a complex zone of *N. neesiana* invasion (180-330 cm) into dense senescent *T. triandra*.
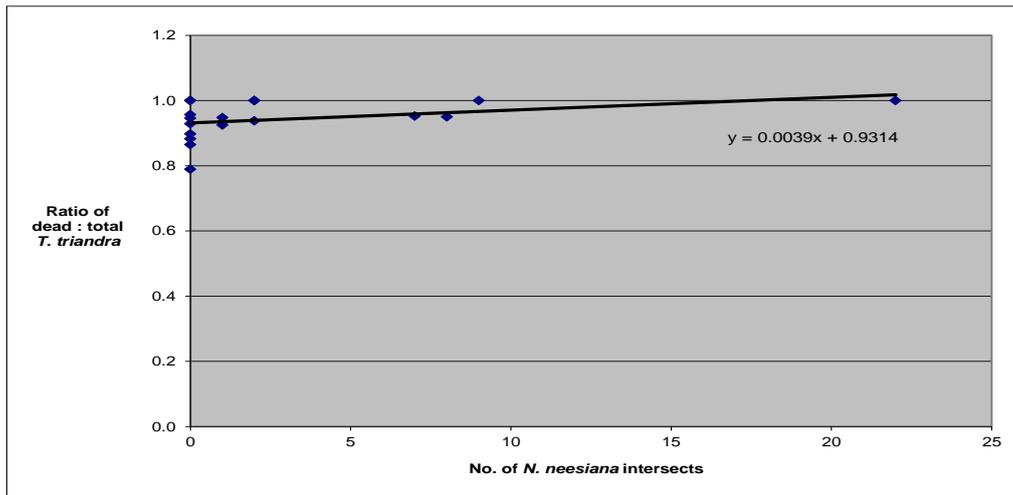
Figure 5.7. Relationship between the number of *N. neesiana* pin intersects at a transect point and the ratio of dead to living *T. triandra* pin intersects at that point, where the number of *T. triandra* pin intersects at the point was >9, at Yarramundi Reach peg 0085, 25 April 2008.

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).
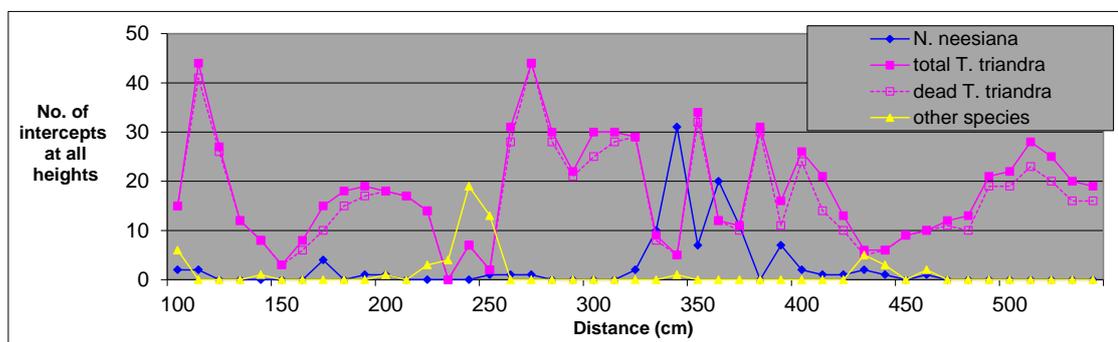

Figure 5.8. Distribution of *N. neesiana*, dead *T. triandra*, total *T. triandra* and other plant species along a pin transect at Dudley Street grassland peg 0886, 26-27 April 2008. Transect entirely in *T. triandra* grassland with variable incursions of *N. neesiana*.
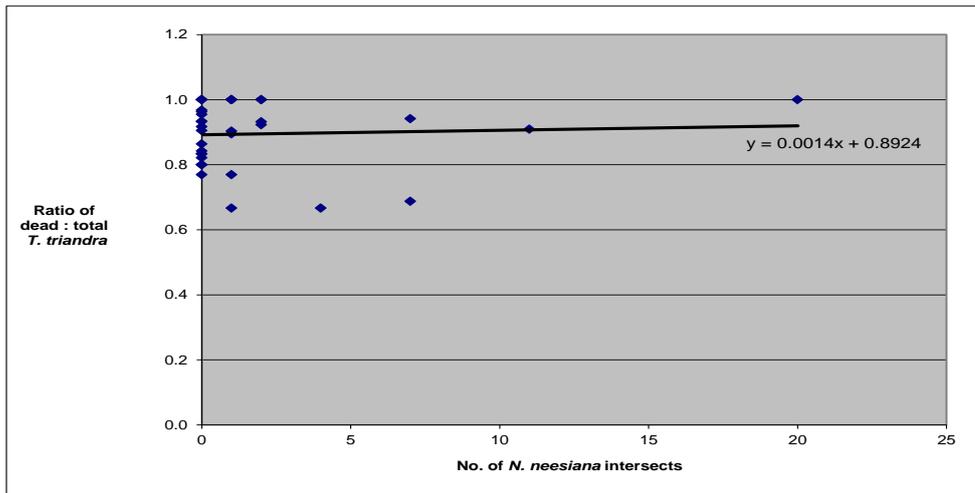
Figure 5.9. Relationship between the number of *N. neesiana* pin intersects at a transect point and the ratio of dead to living *T. triandra* pin intersects at that point, where the number of *T. triandra* pin intersects at the point was >9, at Dudley Street peg 0086, 26-27 April 2008.

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).
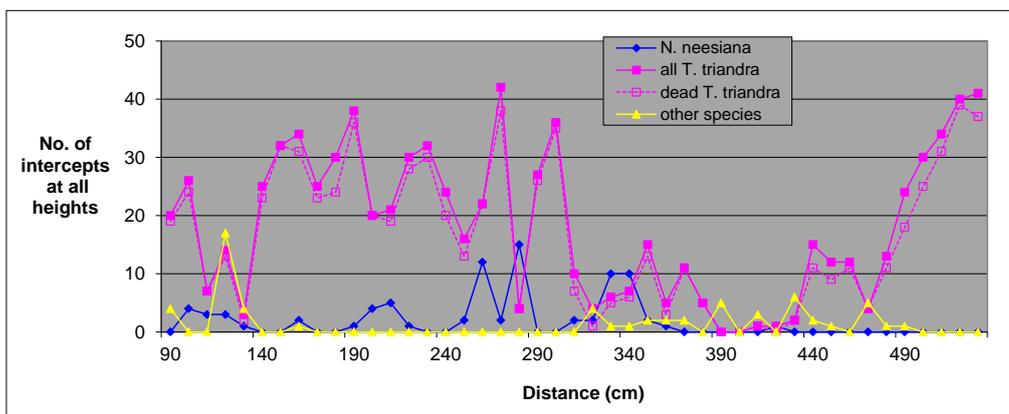

Figure 5.10. Distribution of *N. neesiana*, dead *T. triandra*, total *T. triandra* and other plant species along a pin transect at Dudley Street grassland peg 0887, 27-28 April 2008. The transect was entirely within a *T. triandra* sward of variable densities. Small *N. neesiana* were scattered amongst the *T. triandra*, particularly around highly senescent *T. triandra* tussocks.
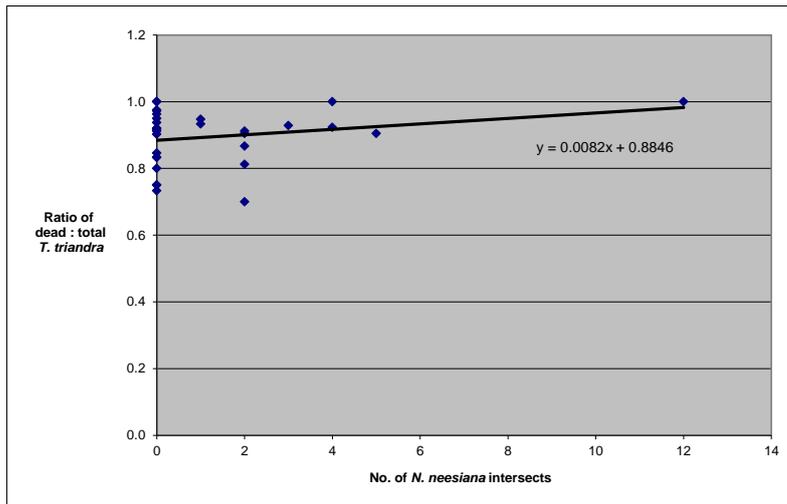
Figure 5.11. Relationship between the number of *N. neesiana* pin intersects at a transect point and the ratio of dead to living *T. triandra* pin intersects at that point, where the number of *T. triandra* pin intersects at the point was >9, at Dudley Street peg 0887, 27-28 April 2008.

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.
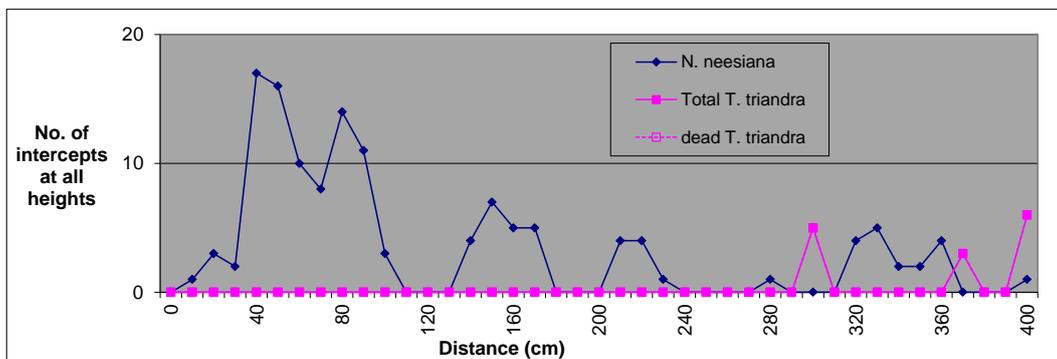

Figure 5.12. Distribution of *N. neesiana*, dead *T. triandra* and total *T. triandra* along a pin transect at Laverton North Grassland peg 0220, transect 11 March 2008. *T. triandra* was fully senescent and did not co-occur with *N. neesiana* at any point. No other species were detected.

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.
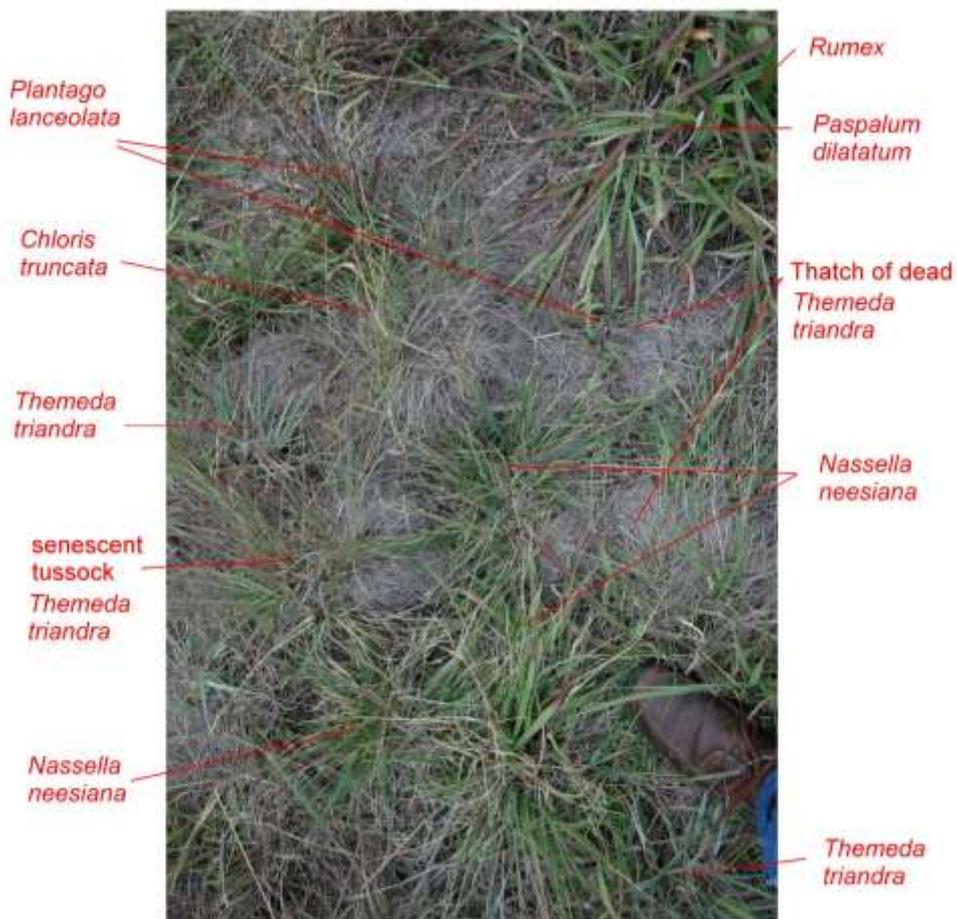

Figure 5.17. *Nassella neesiana* invasion zone in an area previously occupied by senescent *T. triandra* at Dudley Street grassland, 8 May 2007. A dense litter thatch of *T. triandra* foliage remains over much of the ground surface.

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

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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. triandra* 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.