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).

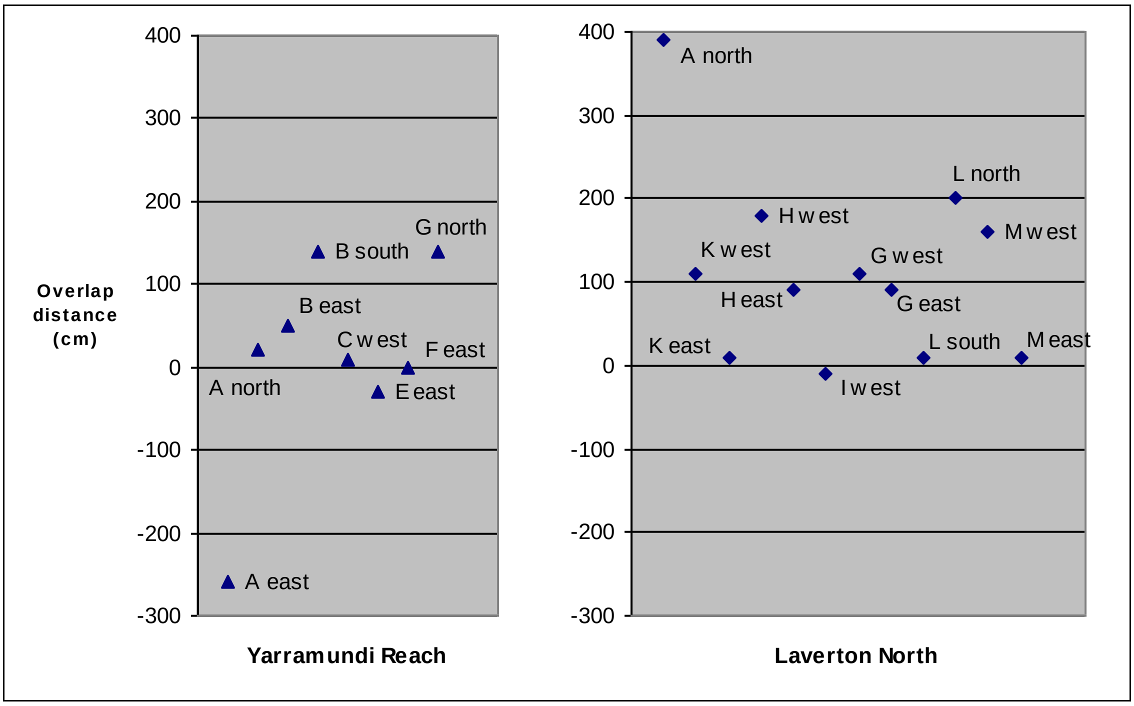

Figure 7.1. Overlap between *N. neesiana* and *T. triandra* at the margins of *N. neesiana* patches at Yarramundi Reach and Laverton North grasslands.

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 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 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 x 10^{-11}**
Major native grasses	7	68	3.1	**4.0 x 10^{-11}**
Total major grasses	64	74	3.1	**0.010**
All exotic grasses	60	8	2.7	**4.1 x 10^{-11}**
All exotic grasses excl. *N. neesiana*	7	7	5.3	0.931
All native grasses	7	68	3.1	**3.3 x 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 x 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 x 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).

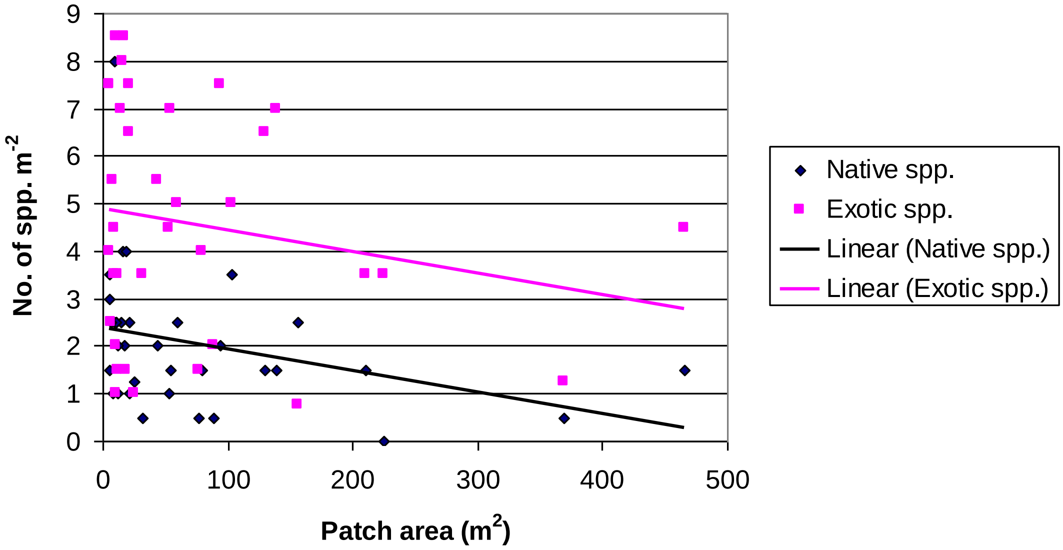

Figure 7.2. Relationship between the area (m^2) of *N. neesiana* patches and the mean number of native and exotic vascular plant species m^{-2} inside the patches for all patches assessed at the three grasslands.

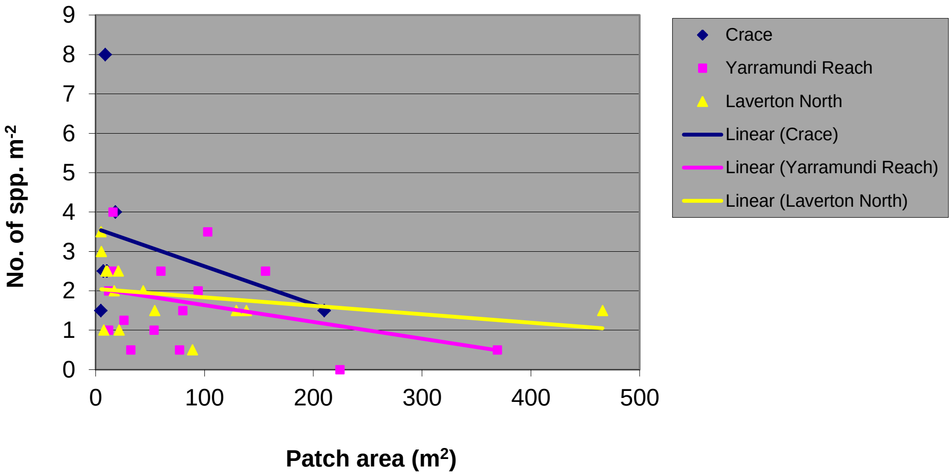

Figure 7.3. Relationship between the area (m^2) of *N. neesiana* patches and the mean number of native vascular plant species m^{-2} inside the patches for the three grasslands.

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.

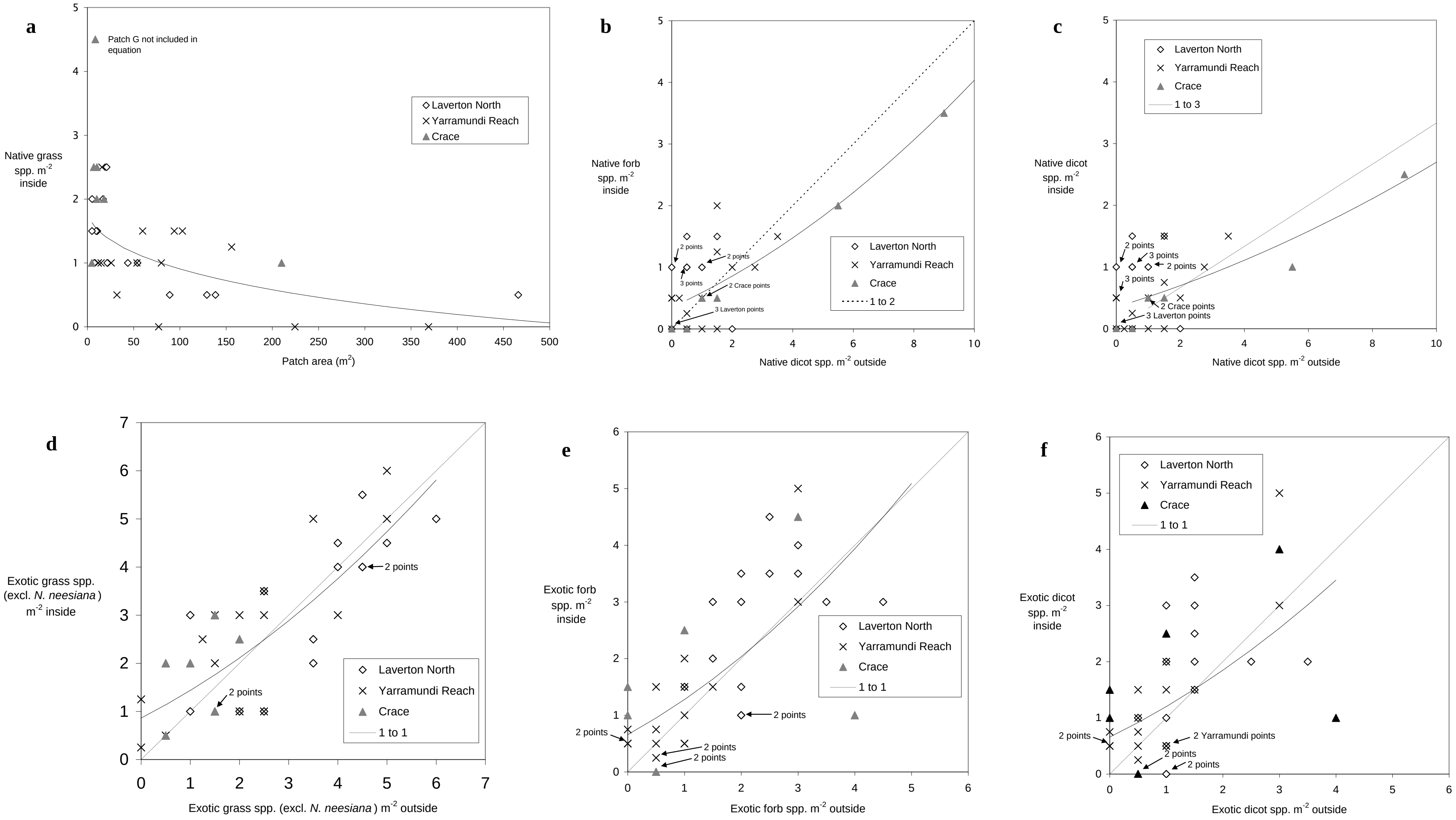

Figure 7.4. Chosen linear regressions of plant composition parameters inside *N. neesiana* patches: (a) relationship between the mean number of native grasses inside *N. neesiana* patches and patch area; (b) relationship between the mean number of native forb species inside *N. neesiana* patches and 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

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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]

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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*.