Chapter 8. Invertebrate diversity

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

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

Summary

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

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

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

Introduction

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

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

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

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

Assessing the biodiversity value of invertebrate assemblages

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

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

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

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

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

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

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

Theoretical framework

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

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

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

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

Invertebrate utilisation of N. neesiana

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

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

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

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

Aims

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

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

Methods

Sampling

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

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

Direct search

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

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

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

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

Sweep net

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

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

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

Specimen processing and identification

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

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

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

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

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

Vegetation of the sampling sites

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

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

Statistical Analysis

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

Search samples

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

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

Sweep net samples

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

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

Grass utilisation

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

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

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

Results

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

Search samples

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

<u>Sweep net samples</u>

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

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

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

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

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

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

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

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

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

Utilisation of *N. neesiana*

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

Mollusca

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

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

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

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

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

Continued next page

Table 8.14 (continued)

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

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Table 8.14 (continued)

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

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

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

Orthoptera

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

Hemiptera

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

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

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

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

Coleoptera

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

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

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

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

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

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

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

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

Lepidoptera

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

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

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

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

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

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

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

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

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

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

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

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

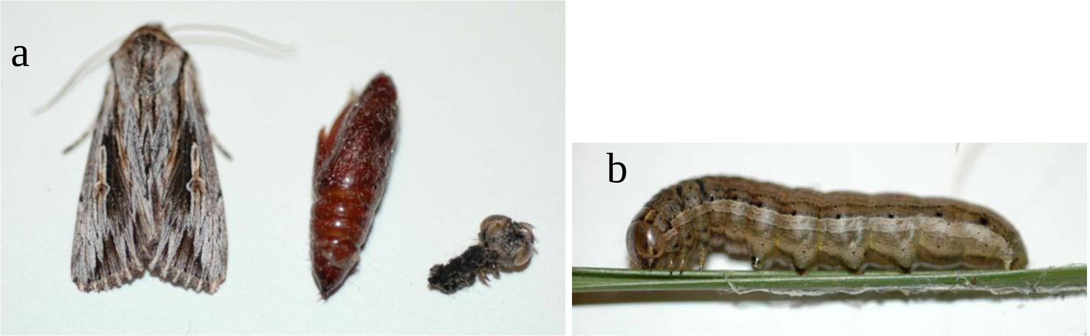

Figure 8.6. *Persectania ewingii*; a. adult, pupal case and final instar larval exuvium; b. larva; collected as a final instar larva in the base of an *N. neesiana* tussock at Iramoo on 10 August 2007 and reared on *N. neesiana*.

Hymenoptera

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

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

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

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

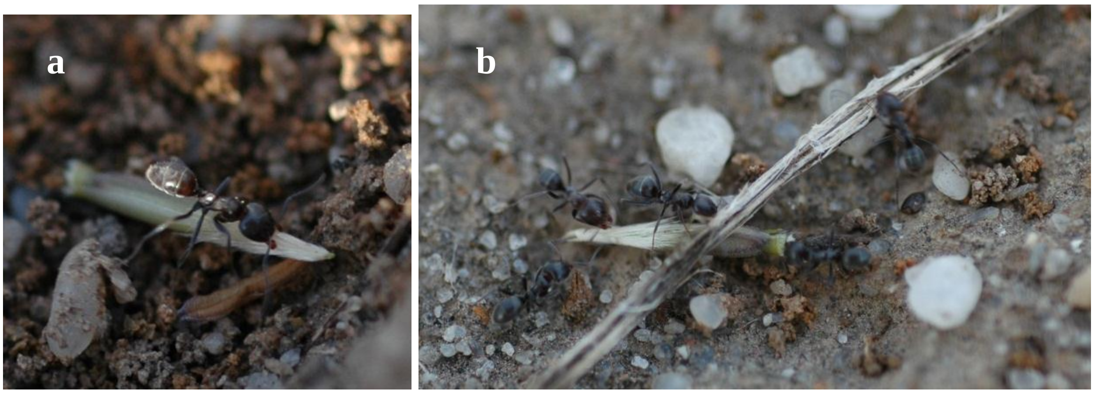

Figure 8.9. *Iridomyrmex* sp. removing artificially de-awned *N. neesiana* seeds dropped near a foraging trail at Laverton North Grassland, 29 November 2007. a. one method of carriage by an individual worker. b. workers cooperating to dislodge a seed wedged under plant debris.

Trophic web evidence

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

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

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

Discussion

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Invertebrate predators of *N. neesiana*

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

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

Mollusca

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

Orthoptera

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

Hemiptera

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

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

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

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

Coleoptera

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

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

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

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

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

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

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

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

Lepidoptera

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

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

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

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

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

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

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

Hymenoptera

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

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

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

Conclusions

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

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

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

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

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

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

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