

Chapter 9. Conclusions

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

Ramakrishnan and Vitousek, 1989, p. 282.

Summary

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

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

The findings of the study require cautious interpretation and have implications for current management strategies. The consequences for native grassland management that have been determined align with other reported studies and reviews – grasslands need active,

appropriate ecological management, and where this occurs they are resistant to major weed invasion. A set of future research priorities is provided that addresses the problems of exotic perennial grass invasions, major lacunae in the understanding of native grassland ecology, and the areas in which an increased understanding of *N. neesiana* biology would be beneficial.

Introduction

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

Major findings

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

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

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

3. Gap sizes of c. 1 m² enable significant establishment, while gaps of c. 10-30 cm largely disallow establishment. Biomass of *N. neesiana* plants that establish in areas with larger gaps is much greater than areas with small gaps.
4. Fertilisation with nitrogen or phosphorus does not enhance *N. neesiana* recruitment, but immobilisation of nutrients using sugar significantly reduces establishment. However nitrogen fertilisation significantly reduces productivity of the dominant native grass *Themeda triandra* and therefore would preferentially benefit *N. neesiana* when the two species are in competition.
5. Establishment of *N. neesiana* on the boundaries between existing patches of *N. neesiana* and areas dominated by the major native grass *Themeda triandra* is higher where *T. triandra* is more senescent, i.e. when *T. triandra* swards have a higher proportion of dead foliage. Uninvaded areas have consistently higher proportions of living *T. triandra* leaves. In areas subject to *N. neesiana* propagule pressure *N. neesiana* invasion accompanies *T. triandra* senescence dieback, which occurs as a natural process when biomass reduction (by fire or grazing) fails to occur over periods greater than c. 5 years.
6. *Nassella neesiana* infestations in native grasslands have an impoverished native vascular plant flora compared with immediately adjacent areas of native grassland. Native plant species richness (spp. /m²) in *N. neesiana* patches is significantly less than in comparable areas immediately outside patches. Differences of 32-65% (back transformed data) were measured at three grasslands. Native forb diversity was 54-68% lower and native grass diversity 71-85% lower in infested areas. Larger differences were found in the more species rich grasslands.
7. The larger the *N. neesiana* patch, the greater the reduction in native vascular plant species richness.
8. If larger patches are older than smaller, this indicates that *N. neesiana* may be having a significant, but smaller, negative impact on native plant diversity after it has established.
9. Soil moisture under *N. neesiana* stands appears to be much depleted in spring compared to stands of the dominant native grass *T. triandra*. Most of the vascular plant diversity in Australian temperate native grasslands consists of spring-growing species, so the spring-growing *N. neesiana* competes directly with them for water. In contrast *T. triandra* is mainly summer growing and competes with other native plants for water to a more limited extent. Thus, soil water depletion in spring may be one mechanism for ongoing losses of native plant diversity after *N. neesiana* establishment. Widespread displacement of *T. triandra* by *N. neesiana* is likely to have negative ecohydrological

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

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

Cautionary considerations

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

Disturbances that kill the native vegetation have been demonstrated to facilitate *N. neesiana* invasions. But as observed by Hierro *et al.* (2006) disturbance may operate in association with other mechanisms that increase the fitness of the invader in the invaded environment,

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

Dominance by an invader in some but not other areas, that is suggestive of competitive superiority, may actually be just a priority effect: the exotic may not be able to outcompete an equilibrium population of competitors, but is the first to invade after strong disturbance and establishes dominance, leading to “multiple stable equilibria” (Seabloom *et al.* 2003 p. 13384). The widespread perception that *N. neesiana* is able to actively invade grasslands appears to be based in part on this misunderstanding. However, “it is the impact of invaders and not their establishment *per se* that threaten native communities” (Levine *et al.* 2003 p. 775). In this regard the advances in the understanding of invasion mechanisms reported in this thesis need to be balanced by an improved understanding of the ability of *N. neesiana* to persist in invaded areas, and exclude native floral and other biodiversity. This is particularly relevant for temperate lowland native grassland biodiversity conservation because remaining biodiversity-rich areas are small in size and fragmented across the landscape, so any occupation by exotic species is significant as a proportion of area available for conservation, and as an additional degrading and fragmenting process. Evidence suggests that infestations can continuously occupy a small area for many years if no control activity is undertaken. Persistence of infestations is most likely enhanced by production of basal and stem cleistogamous seeds that provide a temporal, ‘priority’ advantage in comparison with native grasses when an *N. neesiana* tussock dies. These seeds are immediately available for reestablishment at the microsite occupied, while native species, which generally have minimal soil seed banks and very limited ‘turnover’ must produce and disperse their seeds to that site.

Nassella neesiana infestations exist because at some time there were appropriate conditions for establishment and recruitment. This study has determined that such conditions include the removal of the pre-existing dominant grasses at a scale of ≥ 1 m. This area requirement is likely to be variably dependent on environmental and site conditions, because establishment requires absence of significant competition (which is likely to be below-ground competition for nutrients and water), and competition only develops under conditions related to resource scarcity and resource limitation. Competition for water appears likely to be of more importance than that for soil nutrients, so recruitment events may occur commonly when there is coincidence of good rainfall and disturbance that creates gaps of < 1 m.

The study examined only some of the grosser and most easily investigated mechanisms that may explain the ability of *N. neesiana* to invade and influence the biodiversity of invaded areas. Important areas awaiting investigation include the role of fungal and bacterial symbionts, including endophytes, and of pathogenic microbes, in the alteration of the fitness of native plants and *N. neesiana*, and of soil biogeochemistry and nutrient cycling. It might well be suspected for example that the different litter qualities of *N. neesiana* and the dominant native grass, derived in part from their different C fixation pathways, result in more rapid nutrient cycling in the invaded system, and that this in turn would enable the development of a markedly different flora.

Studies of the invertebrates were almost entirely focused on the vegetation above the ground and inhabitants of the soil surface. However, as with the vegetation, a high proportion of the invertebrate biomass is underground, with many species spending most of their lives beneath the soil surface, particularly as larvae. Many species detected undoubtedly feed on the subterranean organs of grasses. This unexplored realm has largely been neglected because it is difficult and inconvenient to study, but major insights into grassland biology will undoubtedly proceed from simple excavation of tussocks and rearing of juvenile stages of the invertebrates that are found. All invertebrate sampling was undertaken during daylight. Nocturnal sampling would likely reveal markedly different sets of species, including many that emerge from the soil and litter into the canopy during conditions of darkness.

A final caution needs to be made in regard to the temporal scale of studies. Since very few plant invaders are ever eradicated, ultimately both the invader and the invaded system adapt to accommodate each other, and since there is more adaptive potential in the community than in the single invader, the impact will eventually decay (Whitney and Gabler 2008), or, if these adaptive changes are themselves considered to be impacts, may continue to slowly increase but include a higher proportion of evolved, 'accomodatory' change. Future attempts to evaluate *N. neesiana* impact on biodiversity should seek to integrate this longer term, ecological and evolutionary time perspective, and attempt to evaluate the extent and pace of

the accommodation. Perhaps, for example, the lack of published record of invertebrates eating *N. neesiana* reflects a real absence, and the herbivory detected in this study results from very recent adaptation.

Significance and implications of the findings

When meshed with the other studies, the patch diversity study of vascular plants (Chapter 7) revealed two important effects. Major disturbances cause the loss of native plant species and allow *N. neesiana* invasion, sometimes along with other exotic species. After invasion, further losses of native species occur in the presence of *N. neesiana* as patches expand or as the period since *N. neesiana* established increases. Larger patches of *N. neesiana* have lower species richness of native vascular plants (spp./m²) than small patches, so the plant evidently has some continuing negative impact after establishment.

Replacement of *T. triandra* by *N. neesiana* removes the most important “phenological complementarity” (Cleland *et al.* 2006) in the system: a dominant C₄ grass with a summer flowering and growth period (*T. triandra* flowers once per year in summer - Groves and Whalley 2002) complementary to a very high proportion of the rest of the native vascular flora, is replaced by a C₃ species which potentially competes directly for limiting resources with this bulk of native plant diversity during its spring growing period. Phenological complementarity “promotes coexistence in multispecies plant communities” (Cleland *et al.* 2006 p. 13741) and its removal probably precipitates cascading detrimental effects including ongoing losses of native plant species.

The effects of prior management and the actual impacts of invasive plants are always confounded and frequently interact. This study has partially enabled their disaggregation and independent evaluation. *Nassella neesiana* may be more a symptom of prior degradation than a cause of biodiversity loss. The conditions that favour its invasion are primarily those that remove the competition provided by the native vegetation, particularly the dominant grass *T. triandra*. *Nassella neesiana* certainly occupies sites previously occupied by native grassland. Where there is propagule pressure from *N. neesiana*, any disturbance that kills the native grass sward over areas in excess of c. 1 m² probably enables invasions, but intact swards are highly resistant to invasion, even when propagule pressure is high. *Nassella neesiana* invades bare areas and can maintain its place, possibly due to its larger soil seed banks and the possession of stem and basal cleistogenes. Once it occupies a site, it too is resistant to invasion.

Mowing and slashing probably kill many native grasses which have higher mortality when cut short, so *N. neesiana* often invades grasslands initially via mown areas and along human thoroughfares. Fertile conditions are required for establishment, but these can be met by

decay of the biomass of dead native grasses in the typical temperate grassland systems of south-eastern Australia, which occupy some of the least nutrient impoverished lands in the country.

Nassella neesiana patch margins have greater native plant diversity than patch centres, but patches nevertheless tend to have 'hard' edges: there is a sharp contrast over a short distance with the native vegetation matrix, with strongly reduced native plant diversity on one side, and reduced invertebrate diversity. *Nassella neesiana* therefore can be viewed as creating habitat fragmentation and infestations can be viewed as a barrier to biotic movement with implications for plants, and for animals: "for maximal insect diversity conservation the aim is to reduce the contrast between patch and matrix" (Samways 2005 p. 97).

Initial establishment of *N. neesiana* is strongly dependent on the extent and availability of ground (including below-ground) not occupied by other living plants. It is invasive in disturbed grassland habitats but appears largely unable to overcome environmental barriers in undisturbed habitats. When propagule pressure is applied, areas of intact grassland are resistant to invasion. Further invasion on the margins of infestations may be propelled by the ability of *N. neesiana* to deplete soil water in spring, prior to the growth period of *T. triandra*. This may impact on the vigour and productivity of adjacent areas of *T. triandra* and make them more invulnerable. Such a positive feedback, in which *N. neesiana* would drive its own spread, would be likely to have a landscape-scale threshold determined by the abundance of the invader and above which the impacts rapidly increase (Levine *et al.* 2003), so that increased presence of the invader accelerates its own invasion. *Nassella neesiana* may in part maintain its dominance by preventing spring soil water storage required for optimum growth of *T. triandra*, a form of resource pre-emption that enables the maintenance of multiple stable states (Seabloom *et al.* 2003). The ability of *Nassella neesiana* to continue to occupy for extended periods the ground where it establishes is partly explained by it being long-lived and may be enhanced by its ability to replace itself in situ from cleistogenes.

McIntyre (1995) argued that general declines in the abundance of many native grassland forbs, which comprise the overwhelming majority of plant diversity in all well preserved grasslands, must result from the failure of current management regimes to provide for their highly specific ecological requirements for regeneration, and that many of these requirements might possibly be met by the types of exogenous disturbances often considered to be harmful management practices. The dilemma for grassland managers is that the conditions that facilitate the establishment of *N. neesiana* and of other weeds appear to be similar to those required for establishment of native forbs (Morgan 1997b 1998b 1999b, Robinson 2003 2005, Reynolds 2006) and probably for the recruitment of native grasses, i.e. soil disturbance, large canopy gaps (≥ 1 m) associated with reduced shade and below-ground

competition, and the absence of competition, particularly from established dominant perennial grasses. Although not tested in this study, soil disturbance that creates more areas of rough ground is likely to benefit *N. neesiana* by allowing the natural seed drilling to be more effective, increasing the availability of suitable germination sites (Peart 1979 1984), and via a temporary nutrient flux (Wijesuriya 1999, Wijesuriya and Hocking 1999).

Populations expand when niche space becomes available through death of native grasses and there is propagule rain. *Nassella neesiana* appears to have similar competitive abilities to native grasses, but superior fecundity (possibly because specific pre-dispersal seed predators and pathogens are lacking in the invaded range: none being detected in this study) and dispersal capability, including the ability, when tussock mortality occurs, to re-establish at the same point from basal cleistogenes.

Implications for grassland management

Understanding of the mechanisms of impact is important in determining improved methods of management (Levine *et al.* 2003). The findings of this thesis largely reinforce the messages of current best-practice grassland management doctrines (e.g. Wong and Morgan 2007): this involves active management to maintain the native tussock matrix, reduce *T. triandra* biomass accumulation by frequent burning, and where necessary, reduce livestock grazing to minimise biodiversity losses and disturbances that drive weed invasion.

The main message for grassland managers resulting from this study is that *N. neesiana* infestations are probably largely the consequence of bad management decisions in the past, and that ongoing management should avoid the same mistakes. The core management principles can now be considered to be long-standing – frequent biomass reduction of *T. triandra*, minimisation of soil disturbances and disturbances that kill the native grasses including livestock grazing and close mowing, and minimisation of propagule pressure by control of infestations at grassland edges and along thoroughfares. But there are continual problems in ensuring the application of these fundamentals, as the recent massive *N. neesiana* invasions at Yarramundi Reach amply demonstrate. The impacts of *N. neesiana* on biodiversity can be minimised by minimising prior degradation such as *T. triandra* senescence and soil disturbance and by strengthening invasion resistance by maintenance of a healthy cover of non-senescent *T. triandra*.

It is too late to save the biodiversity in areas already occupied by *N. neesiana* stands, since most of the damage to plant biodiversity that can occur has already occurred by the time infestations exceed 5 m². Control activities should therefore be prioritised for very small infestations and isolated tussocks, to reduce *N. neesiana* propagule pressure, and perhaps directed at somewhat larger infestations if they have large boundary: area ratios, so that

natural recolonisation by major native grasses can occur more readily and quickly. Theory predicts that high perimeter to area ratios increase vulnerability to invasion (Byers *et al.* 2002), so similarly enhances the probability of recolonisation by elements from the native matrix.

The findings indicate that management activity directed at controlling *N. neesiana* should be prioritised for those infestations occurring in areas with a range of severe, ongoing anthropogenic disturbances and that infestations in well-managed grasslands tend to be relatively stable. It is better to remove the causes of degradation, but if for some reason this is impossible, then treatment of the symptoms, such as *N. neesiana* infestations, is better than no action at all. However infested areas retain some native plant diversity which could be imperilled by control activities.

The lack of cost-effective, consistently reliable rehabilitation treatments for infested areas of grassland after herbicidal kill of *N. neesiana* implies that established infestations with stable margins may be better left untreated until rehabilitation techniques are improved, or conditions for rehabilitation by such methods as 'spray and hay' (i.e. wet years) (Phillips and Hocking 1996, Dare and Hocking 1997, Hocking 1998, Mason 1998, Mason and Hocking 2002, Mason 2004, Hocking 2005b) are likely to become suitable.

Many herbicides used to control *Nassella* spp. have severe impacts on native vegetation and can result in major weed invasion (Hocking 1998). Whatever the herbicide used, cleistogenes that have already matured but remain attached to the plant, concealed beneath leaf sheaths are not killed (Hurrell *et al.* 1994). Furthermore, when a large *N. neesiana* seed bank is present, baring the ground with herbicides encourages seedling recruitment and may lead to rapid re-establishment and an ultimate increase in density and cover (Hartley 1994, Gardener *et al.* 1996b, Gardener *et al.* 1999, Lunt and Morgan 2000, Slay 2002a, Storrie and Lowien 2003). Herbicidal management in agricultural situations has often resulted in the expansion of *N. neesiana* populations and exacerbation of spread due to the elimination of competition (Slay 2001 2002a 2002c). In areas of native grasslands where there is *N. neesiana* propagule pressure, recruitment of *N. neesiana* is probably facilitated when herbicidal kill of pre-existing vegetation in areas exceeding 1 m². Such management is currently routinely applied to control *N. neesiana* in grasslands but is counterproductive if the most likely outcome is reoccupation by *N. neesiana* from the soil seed bank. Such understandings are rarely incorporated into management planning (Buckley *et al.* 2007) but need to be.

Nassella neesiana infestations are readily identifiable from aerial photographs in some grasslands at particular times of year, if some ground-truthing is undertaken. This finding

opens the way to better infestation mapping and more reliable long term evaluation of the outcomes of *N. neesiana* management programs.

Recommendations for future research

The studies undertaken suggest a number of areas where further research may yield instructive insights, information for improved grassland management and techniques or knowledge that would be useful to minimise the biodiversity impacts of *N. neesiana*. These include:

1. Further investigations of potential mechanisms of invasion, in particular allelopathic effects of *N. neesiana*, the extent to which grazing of livestock creates suitable conditions for invasion, and the requirements for *N. neesiana* establishment at a small spatial scale (gap size) under a variety of conditions. Pot studies to investigate competitive interactions of *N. neesiana* with native species are also needed. The mechanisms by which *N. neesiana* causes biodiversity impact remain poorly explored.
2. Potential differential effects of fire intensity, frequency and seasonal timing on the mortality, fecundity and recruitment of *N. neesiana* and native plants. There are some indications that *N. neesiana* may suffer higher mortality when grassland management regimes include frequent fire.
3. The differential effects of cutting regimes on native and invasive grasses, particularly on their mortality and fecundity. There is strong evidence that invasion corridors are created by mowing and slashing and that the disturbance effects of these activities (e.g. mowing at low levels which may preferentially kill native tussocks) may be of greater importance than their effects on propagule dispersal.
4. Long term herbicide impact studies in which infestations of various small sizes are killed and the patterns of *N. neesiana* reestablishment and of native species recolonisation are assessed. In order to properly determine baseline conditions these trials would need to be predicated upon seed bank studies that included attached *N. neesiana* stem and basal cleistogenes. The aim of such studies would be to determine if current herbicidal management strategies have an effective outcome in terms of revegetation or are counterproductive and perpetuate the *N. neesiana* infestation.
5. More thorough studies to determine the effects of *N. neesiana* on seasonal soil water content, and research to determine the impact on catchment water yield and other ecohydrological factors. The impacts of *N. neesiana* on soil moisture were examined only during a single season at one site, but the potential implications appear alarming.
6. Basic studies of microbial symbionts and antagonists of *N. neesiana* and native grasses, particularly soil fungi and endophytes. Evidence is increasing that ecological

understanding may be inhibited by treating plant invasions as single organism problems, and that management techniques can be improved by understanding their biotic dependencies of invasive plants.

7. Detailed studies of the role of seed harvesting ants on the dynamics of soil seed banks in native grasslands. Evidence suggests that ant seed predation may be a major cause of the impoverishment and ephemerality of native seed banks, which in turn contributes to the very limited native plant recruitment commonly reported in native grasslands – probably the most critical current problem in ensuring their ongoing survival. Furthermore, the large, persistent *N. neesiana* seed banks recorded in some areas, notably agricultural grasslands, might be related to reduced ant activity.
8. Investigation of the potential and actual dispersal of *N. neesiana* seeds in running water. If moving water is an effective vector, then priorities for regional *N. neesiana* management require realignment.
9. Intensified exploration of the invertebrate faunas and soil biology of native grasslands. Knowledge of the former remains extremely fragmentary and would benefit from a large desk study that integrates the existing scattered knowledge with data trawled from museum collections. Almost nothing is known about the soil biology of Australian temperate native grasslands. Basic studies of invertebrate species and faunas are required to advance grassland invertebrate ecology and provide a sound basis for sustainable use of native pastures and the management of biodiversity in conservation reserves.
10. Intensified study of the autecology of native grassland plants. The major paucity of basic knowledge of the biology of Australian native plants found in grassland ecosystems needs to be redressed.
11. Cross-disciplinary investigation of the ecological history of native grasslands to better understand the factors resulting in their original formation, and their subsequent evolution and dynamics. Palaeoecological and palaeoanthropological studies focused on fire regimes, plant species composition, vertebrate grazing influences, including the role of the extinct megafauna and the recently extinct macrofauna, and the relationships between climate and grassland distribution appear eminently feasible.