benefit would be captured by wool and lamb producers who operate in that part of the Australian wool and lamb industries represented by the study area.

It must be emphasized that these results are preliminary because both the RPM and econometric modelling components require further refinement. In relation to the RPM, further work is required on refining the soils and rainfall digitized data and to incorporate elevations into the GIS model so as to be able to determine arable and non-arable country. Also, the livestock feed energy requirements in the model are preliminary values as the study is awaiting the inclusion in the model of energy requirements calculated by the GRAZFEED model. Further work is necessary in refining the econometric model's wool industry specification and in the integration of this component into the other livestock industry models.

Despite the recognized deficiencies in the analysis, the study represents a significant economic contribution to the study of serrated tussock. The 1997 survey represents the most accurate collection of data on the extent and distribution of serrated tussock in New South Wales. Having these data incorporated into a GIS model has made this information far more amenable to modelling, particularly for incorporation into an economic analysis.

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The biology of *Nassella* and *Achnatherum* species naturalized in Australia and the implications for management on conservation lands

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Summary

Several species of *Nassella* and *Achnatherum* are weeds of both conservation and pasture lands. These species have proven to be difficult to control and have continued to spread since their introduction to Australia. The impact of these species on conservation lands includes a perceived drop in biodiversity and a decrease in aesthetic value. Reasons for the ability of these species to out-compete native vegetation include effective dispersal mechanisms, the production of large amounts of aerial and clandestine seeds and large long-lived seedbanks. Management strategies must take these factors into account.

Introduction

Several species of *Nassella* (Barkworth 1990) and *Achnatherum* (Barkworth 1993) have become naturalized in Australia. They include *Nassella charruana* (Arech.) Barkworth, *N. hyalina* (Nees) Barkworth, *N. leucotricha* (Trin. & Rupr.) Pohl, *N. megapotamia* (Spreng. ex Trin.) Barkworth, *N. neesiana* (Trin. & Rupr.) Barkworth, *N. trichotoma* (Nees) Hackel ex Arech., *Achnatherum caudatum* (Trin.) S.W.L. Jacobs & J.Everett and *Achnatherum brachychaetum* (Godr.) Barkworth. These species are referred to as stipoid grasses. They are considered both environmental and pasture weeds. Carr *et al.* (1992) defines environmental weeds as exotic plants that invade native vegetation usually adversely affecting the survival of the indigenous flora. A potential impact of environmental weeds is a loss of biodiversity and a decrease in aesthetic value.

Stipoid grasses (in particular, *N. neesiana* and *N. trichotoma*) have proven to be difficult to control and have continued to spread in conservation lands. They are successful because they have many biological traits which allow them to outcompete native vegetation. Stipoid grasses generally invade plant communities which are already highly degraded and have a history of disturbance (G. Carr personal communication), and lands with higher fertility soil often previously used for grazing or farming. These communities may originally have been grasslands or grassy woodlands. Some conservation areas in Victoria with significant invasions of stipoid grasses include the Derrimut Grasslands Reserve, Organ Pipes National Park and Southern Plenty Gorge.

Anecdotal evidence suggests that there is a drop in biodiversity in stipoid grass-dominated grasslands because litter from the tall tussocks accumulates in the inter-tussock spaces and excludes shade intolerant species. However, thick stands of undisturbed *Themeda triandra* Forssk. have a similar inhibitory effect on other species (Stuwe and Parsons 1977). The diversity of cryptogams (e.g. mosses, lichens, bryophytes) is thought to decline in stipoid grass-dominated grasslands because the mosaic of substrates such as rocks and bare soil becomes covered with litter (V. Stajsic personal communication). Quantitative studies are needed to compare diversity of stipoid grass-dominated grasslands and adjacent native remnants. If there is reduced diversity, does it result from general degradation or is it specific to stipoid grass-dominated grasslands? Likewise, what effect do stipoid grasses have on the diversity of vertebrate and invertebrate species? The striped legless lizard (*Delma impar*) appears to prefer dense intact swards of native tussock grasses such as *T. triandra* and *Austrostipa* ssp., but can also use exotic species such as *Phalaris* spp. (Osbourne *et al.* 1993). How well do they exist in degraded stipoid grass-dominated grasslands?

Management of weeds in natural systems is often more difficult than in pastures or crops because there can be many more desirable species that need to be preserved. Different species have varying requirements for persistence such that one management strategy is unlikely to cover all species. The aim of a study by Phillips and Hocking (1996) was to distil a set of treatments that would allow a total replacement of *N. trichotoma* by *T. triandra* on the conservation-listed western basalt plains of Victoria. Is this achievable in the long term? Using the method detailed in Phillips and Hocking (1996), *N. trichotoma*-dominated grasslands were replaced by dense swards of *T. triandra* after four years (C. Hocking personal communication). Is this *T. triandra* dominance self perpetuating? What will prevent future recruitment from the presumably long-lived seed bank of *N. trichotoma* in these restored areas? Undoubtedly, a dense canopy of *T. triandra* inhibits the germination and survival of *N. trichotoma* seedlings. However, other species may also be affected by this inhibition such as the endangered daisy, *Rutidosis leptorrhynchoides* F.Muell., which requires gaps larger than 50 cm in diameter for recruitment and survival (Morgan 1997). Disturbance, such as the creation of gaps, is needed to maintain the frequency of native species but it also promotes growth of the exotic species that make up the bulk of the seedbank in degraded native grasslands (Lunt 1990a). Hence, in managing the whole community, not just stipoid grasses or the common native species, we need to consider strategies that will maximize biodiversity.

Understanding the ecology of both the native and exotic flora is necessary if successful long term management goals are to be achieved. Do we try to eradicate stipoid grasses or accept them as a permanent part of that community and try to manipulate the system to favour the native components? The aim of this paper is to discuss some of the biological attributes of *Nassella* and *Achnatherum* species which have resulted in their proliferation on conservation lands.

Dispersal

Long distance dispersal of the stipoid grasses is by adhering to the coats of animals, clothing or machinery via a sharp callus at the end of the seed (Table 1). Sheep can carry seed of *N. neesiana* in their wool for at least 166 days (Gardener unpublished data). Thus there would be ample opportunity for dispersal over large distances. Seeds probably also adhere to other animals such as kangaroos and rabbits.

Nassella trichotoma has tumbling inflorescences which detach at the base, and can be windblown for up to 10 km dispersing seeds as they go (Campbell 1982). *Jarava plumosa* (Spreng.) S.W.L.Jacobs and J.Everett can also be blown by wind but unlike most stipoid grasses the back of its lemma is also covered with long hairs (Burkart 1969). Heavy seeds without such hairs to assist in wind dispersal, e.g. *N. neesiana,* were found a maximum of 2.8 m away from the parent plant (Gardener unpublished data).

While the primary dispersal mechanism for *N. trichotoma* is wind, animals can inadvertently act as a secondary disperser after ingesting seeds. Campbell (1977) reported the excretion of 4600 seeds per wether in the 10 days after grazing infested paddocks. Healy (1945) found 70% seed germination from cows which had been fed *N. trichotoma.* On the other hand, very few seeds of *N. neesiana* survived passage through the guts of cows (e.g. 0.5% of panicle seeds and 2.7% of cleistogenes recovered from the faeces of Angus steers were viable). All seeds had passed through the animals within 4 days (Gardener unpublished data).

Stipoid grasses typically possess a geniculate, hygroscopically-active awn. Straightening and twisting of the awn occurs with wetting and drying events, enabling these seeds to move short distances and bury themselves in favourable microsites, thus increasing their probability of germination.

Reproduction

All stipoid grasses naturalized in Australia are cool season perennials which grow during autumn and winter and flower and set seed during the spring and early summer. They reproduce through self-pollination or outcrossing and bear seeds in terminal panicles (Connor 1987). Some also have axillary cleistogamous flowers (self-fertilized) which are extremely variable and morphologically different from those borne in the panicles. Seeds from these flowers, known as cleistogenes, originate from nodes on the flowering stem and are concealed under the leaf sheaths. In *N. neesiana* there is a progressive reduction in inflorescence length and number of spikelets and floral parts from panicle spikelets to spikelets at the base of the tillers (Connor *et al.* 1993). Five of the eight stipoid grasses in this study have axillary cleistogenes and four produce basal cleistogenes on the lowest node of the flowering tiller (Table 1).

Nassella neesiana and *N. trichotoma* have the potential to produce huge numbers of viable panicle seeds. In a dense, ungrazed infestation, seed production of *N. neesiana* ranged from 1584 to 22 203 seeds m^{-2} (Gardener *et al.* 1996). These differences were correlated with the amount of spring rainfall, the former being in a drought year and the latter being in an above average year. Fluctuation in seed production can be attributed mainly to the change in number of flowering tillers produced per unit area. Similar variability exists in seed production of *N. trichotoma* (Healy 1945). In a heavily infested paddock in New Zealand he found an average of 340 000 viable seeds m^{-2}, whereas Campbell (1977) estimated *N. trichotoma* produced 93 000 seeds m^{-2} in Australia.

Even if panicle seed production could somehow be reduced or stopped altogether, damaged tillers may still produce cleistogenes. Damaged flowering tillers of *N. neesiana* produced the same number of cleistogenes as undamaged tillers (Gardener unpublished data). It appears that if *N. neesiana* plants are sprayed with a mixture of paraquat (Gramoxone) and flupropanate (Frenock) just after tiller elongation, the basal cleistogenes still mature whereas most of the panicle seeds and axillary cleistogenes do not. Dyksterhuis (1945) found that clipping *N. leucotricha* twice weekly to 4 cm above ground level reduced the production of basal cleistogenes but did not prevent it.

Cleistogenes account for a considerable amount of total seed production in *N. neesiana* (e.g. 21.5% (6079) of 28 282 seeds m^{-2}) (Gardener unpublished data). On average, *N. neesiana* produced 7.2 cleistogenes per flowering tiller (Gardener *et al.* 1996). Sant *et al.* (1992) found that flowering tillers of *A. brachychaetum* produced up to 18 cleistogenes whereas *N. leucotricha* is capable of producing up to 12 (Dyksterhuis 1945).

In Argentina and the United States, *A. brachychaetum* is a serious weed in lucerne pastures where cleistogenes play a major role in the plant's persistence (Ares *et al.* 1970). Dyksterhuis (1945) found that cleistogenes in *N. leucotricha* are important in maintaining the species under adverse

Table 1. A summary of biological attributes of naturalized stipoid grasses in Australia from the literature and current research. Question marks indicate unknown information.

	Dispersal	Basal cleistogenes	Stem cleistogenes	Seed production (seeds m^{-2})	Seedbank (seeds m^{-2})	Seedbank longevity (years)	Seed dormancy
Nassella charruana	A	No	No	?	?	?	?
Nassella hyalina	A	No	Yes	?	?	?	?
Nassella leucotricha	A	Yes	Yes	?	0–75	?	Yes
Nassella megapotamia	A	No	No	?	?	?	?
Nassella neesiana	A	Yes	Yes	1584–22 203	681–11 307	>6	Yes
Nassella trichotoma	W,A	No	No	93 000–340 000	1755–42 930	>13	Yes
Achnatherum caudatum	A	Yes	Yes	?	?	?	Yes
Achnatherum brachychaetum	A	Yes	Yes	?	?	?	Yes

A = long distance dispersal via attachment to animals etc. W = wind dispersal.
Literature sources: Healy 1945, Ares *et al*. 1970, Campbell 1977, Campbell 1982, Joubert and Small 1982, Rosengurtt 1984, Kinucan and Smeins 1992, Vanauken 1997 and Gardener unpublished data.

conditions, particularly under heavy grazing or burning, because they still developed after flowering tillers were damaged. Basal cleistogenes, which are often below the soil surface, have at least two advantages. They are borne in a suitable habitat (as defined by the occurrence of their parent) and they are protected from extremes of climate, predation, grazing and fire.

In New Zealand, *N. neesiana* was found to develop basal cleistogenes in vegetative tillers prior to flowering (Connor *et al.* 1993). Similarly, Dyksterhuis (1945) found that plants of *N. leucotricha* commonly produced cleistogenes before panicles appeared on the plant.

Seedbanks

One reason for the proliferation of stipoid grasses is their long-lived seedbanks. Studies on seedbank size and longevity are only known for *N. neesiana* and *N. trichotoma*. Using direct counts of viable seeds (as opposed to germination counts (Gross 1990)) seedbanks ranged from 681 seeds m^{-2} in a medium infestation to 11 307 seeds m^{-2} in a dense infestation of *N. neesiana* on the Northern Tablelands of NSW (Table 1) (Gardener unpublished data). However, these values underestimated the total seedbank because only the seeds loose in the soil (mainly panicle seeds, but also some stem and basal cleistogenes) were counted. It was found that in the discarded tiller bases (the soil cores were passed through a 4 mm sieve to remove rocks and vegetation) there was an additional store of basal cleistogenes (e.g. a seedbank with 8335 panicle seeds m^{-2} had an additional 2963 basal cleistogenes m^{-2} or 35.5% extra).

Ares *et al.* (1970) suggested that there was a large store of *A. brachychaetum* seeds (predominantly cleistogenes) in the soil with 80–100% of seedlings being of cleistogene origin. Similarly, about 50% of the seedlings of *N. neesiana* consistently arose from cleistogenes (Bourdôt and Hurrell 1992).

After three years without seed input, the viable seedbank of *N. neesiana* (cleistogenes and panicle seeds) in bare soil declined from 4676 to 1286 seeds m^{-2} (Gardener unpublished data). If the seedbank continued to decline at this rate, it would take an estimated 11.4 years to reach 10 seeds m^{-2}. Bourdôt and Hurrell (1992) found that 17% of seeds buried at 5 cm in the ground were viable after six years. There is also anecdotal evidence of germination occurring after six years from continually bared ground.

In New Zealand, seedbanks of *N. trichotoma* have been found to range from 1755 seeds m^{-2} in light infestations to 42 930 m^{-2} in heavy infestations (Table 1) (Healy 1945). In Australia, 4784 seedlings m^{-2} have been recorded (Campbell 1958). Since only a small proportion of a seedbank usually germinates at any one time, the actual seedbank was probably much larger. Seed of *N. trichotoma* can remain viable for up to 13 years in the soil (Campbell 1982).

In their countries of origin, the seedbanks of stipoid grasses may not be so large. A survey of seven populations of *N. neesiana* on the Pampas Plains, Argentina, revealed that there was almost no seedbank present (Gardener *et al.* 1997). Kinucan and Smeins (1992) found *N. leucotricha* to be common in Texan rangelands (its native habitat), but it had a small seedbank of 75 seeds m^{-2} or less.

Seeds often have dormancy mechanisms that allow them to persist for a long time. Five of the eight stipoid grasses (Table 1) are known to possess dormancy mechanisms and it is likely that the others also do, since it is very common in the Stipeae. The hull or lemma around the seed may provide a barrier to gas and water exchange and also mechanically restrain the embryo. Before germination can occur, this barrier must be broken down. Freshly harvested seed of *N. trichotoma* and *N. leucotricha* both have after-ripening requirements to prevent them germinating in the summer after seed fall (Joubert and Small 1982, Vanauken 1997). Thus, seeds of *N. leucotricha* could remain dormant and viable in a seedbank for a considerable time, which is uncharacteristic of most grasses (Vanauken 1997).

Implications

Preventing the dispersal of stipoid grasses to new areas or 'restored weed-free areas' is very difficult because they effectively disperse by attaching to passing animals (researchers included) and machinery. In the case of *N. trichotoma*, it is almost impossible to prevent wind dispersal from nearby infestations.

The most important biological attribute to consider when making management decisions about weedy stipoid grasses is the potentially large, long-lived seedbank (at least for *N. neesiana* and *N. trichotoma*). If herbicides or other forms of disturbance are used to kill the adult plants, it is likely that recruitment will occur from the seedbank. Replacing the adult plant with competitive species such as *T. triandra* will reduce the probability of recruitment but it is unlikely that the seedbanks will be sufficiently exhausted to prevent some regeneration. Seeds have dormancy mechanisms that prevent them all from germinating even if ideal conditions exist and make them persist for many years.

In order to reduce the size of the seedbank, seed production must be prevented. However, unless plants are completely killed, it is difficult to prevent seed production because cleistogenes may still be produced in some species. Seed production is variable depending on environmental conditions but in *N. neesiana*, the seedbank can be maintained with low seed production. The overwhelming evidence that this species will persist no matter what, has led us to recommend utilizing it as a pasture plant on grazing lands but this option is not available on most conservation lands.

Conclusions

Evidence here suggests that *Nassella* and *Achnatherum* species have biological characteristics that enable them to proliferate in conservation lands. When management strategies are developed, they need to take into account the biology of both the weeds and the species to be conserved. Lunt (1990) says that 'ecologists face the formidable task of devising disturbance regimes that promote natives at the expense of exotics'. Research is required to identify such management strategies.

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