THE FAILURE OF MANAGEMENT TECHNOLOGY FOR REPRODUCTIVELY EFFICIENT GRASSY WEEDS: THE CHILEAN NEEDLE GRASS EXAMPLE

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Summary A study of the biology of *Nassella neesiana* showed its ability to dramatically increase seed production during favourable environmental conditions yet produce sufficient seed to maintain the seedbank in unfavourable years. The incorporation of seeds into the seedbank is very efficient. The seedbank is large in established infestations and can persist for many years. Control methods which create disturbance such as herbicide application and cultivation remove desirable competitive species and produce ideal conditions for *N. neesiana* germination. A high survival rate of these seedlings may result in a subsequent increase in the dominance of *N. neesiana* in pastures. Cleistogenes produced at the nodes of flowering tillers provide an alternative mode of reproduction.

INTRODUCTION

Why have perennial grassy weeds proliferated when there is a diverse array of management techniques available? Possible answers to this question can be found in a study of their biology. Much of their success results from their ability to produce large numbers of viable seeds, a long lasting store of seeds in the soil, a perennial life-cycle and flexibility of reproductive mechanisms.

Common examples of these grassy weeds in Australia include serrated tussock (*Nassella trichotoma* (Nees) Hack. ex Arechav), African lovegrass (*Eragrostis curvula* (Schrad.) Nees), giant Parramatta grass (*Sporobolus indicus* var. *major* (Buse) Baaijens) and Chilean needle grass (*Nassella neesiana* (Trin. & Rupr.) Barkworth). There are no widely successful management techniques which result in the eradication or long term reduction in the abundance of these grasses. The failure of current management techniques primarily stems from a lack of understanding of seedbank dynamics. Auld *et al*. (1987) stated, 'the fact that many weeds have long term propagules which may be inaccessible (buried) and widely dispersed *militates against* the success of an eradication policy for well established species'. Management strategies based on a thorough understanding of the seedbank dynamics of the target species are more likely to be successful that those in which the seedbank is ignored.

Many avenues for weed management are available. Possibilities such as biological control (e.g. pathogens to reduce seed production of *Sporobolus indicus* var. *major*; Hetherington 1992) or a system of grazing management (e.g. control of *Aristida ramosa* R.Br. by grazing; Harradine and Whalley 1980) may be useful in maintaining a balance between desirable and undesirable species. However, these technologies are either not available or are difficult to apply for most of these grasses. In most pasture systems the two forms of management most readily available for perennial grassy weeds are physical and chemical control.

Physical control includes manual weeding, cultivation, mowing and burning. Many different types of chemical control exist, but in a pasture system, residual and pre-emergent herbicides have limited application because they are generally not specific enough, killing many desirable species. Hence, herbicides are limited to post-emergent foliar applications. Both physical and chemical methods often involve high costs and may be ineffective in the long term.

Nassella neesiana (synonymous with *Stipa neesiana*) is a native of South America and was first identified in Australia in the 1940s. Its spread and the realisation of its threat went unnoticed until about 15 years ago. This grass now dominates large areas of highly productive pastures on the Northern Tablelands of NSW and the Volcanic Plain of Victoria. It is becoming increasingly common in the Central and Southern Tablelands of NSW and also has been collected in the Adelaide Hills. Its weed status in pastures is due to its invasive nature and its production of large amounts of unpalatable flower stalks during summer which result in a significant reduction in stock carrying capacity.

The recommended treatment of large infestations of *N. neesiana* is herbicide application followed by sowing pasture seeds and fertiliser spreading (M. Duncan personal communication). The approximate cost of this treatment is \$A268 ha^{-1} (herbicide \$A123, contract sprayer \$A25, pasture seed mix \$A50, contract sowing \$A14, fertiliser \$A56). Furthermore, the paddock needs to be spelled for a minimum of one year resulting in a loss of between \$A150 and \$A360 ha^{-1} for prime lamb enterprises (M. Duncan personal communication). This approach is expensive and the infestations of *N. neesiana* have continued to expand despite these recommendations. This paper focuses on particular aspects of the biology of *N. neesiana* which make it difficult to control with traditional management techniques.

MATERIALS AND METHODS

The study site was situated 50 km north of Armidale on the Northern Tablelands of NSW (30° 03'N 152° 36'E, elevation 1300 m, average annual rainfall 881 mm) in a pasture heavily infested with *N. neesiana*. Reproductive efficiency was quantified in the following ways:

Fecundity Potential seed production was measured by multiplying the mean number of flowering tillers m^{-2} (40 × 0.25 m^2 quadrats) by the mean number of glumes per tiller (100 tillers). The effect of this seed input on the seedbank was measured by taking random soil cores (50 × 5.3 cm diameter × 5 cm deep) before and after seed fall. The seeds were removed from the soil cores using a dry sieving technique (1 mm mesh). Stock were excluded from the experimental areas.

Seed bank decline and longevity Five exclosures (4 m × 4 m) were surrounded with shade cloth to prevent seed from adjacent plants entering the seedbank. Inside the exclosures, the last seed input occurred in the summer of 1993–94 with all subsequent seeds of panicle origin being removed by hand. Inside the exclosures there were two treatments—ground kept bare with bi-annual herbicide application and ground with original vegetation remaining. A total of 120 soil cores were taken for each treatment in November of 1994 and 1995. Seeds were again removed using a dry sieving technique.

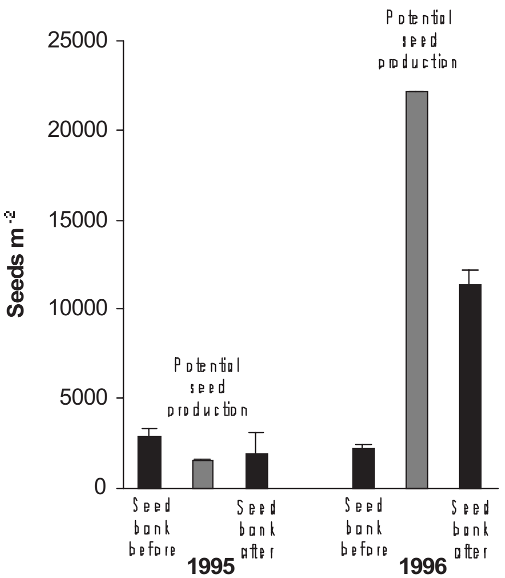

Figure 1. The number of viable seeds in the seedbank before and after seed input (expressed as potential production) in 1995 and 1996.

Seedling emergence and survival Emergence of seedlings was compared in bare and vegetated plots (20 × 0.3 m^2 plots for each treatment) in the above mentioned exclosures. In adjacent plots (20 × 0.3 m^2 plots for each treatment) seedlings were marked with coloured pins and the survival of each cohort was recorded at subsequent sampling times. Sampling was undertaken at six month intervals in the autumn and spring.

Flexibility of reproductive mechanisms *N. neesiana* has clandestine seeds or cleistogenes which are concealed beneath the leaf sheath at each node on the flowering tillers. These seeds are morphologically different from seeds of panicle origin. The cleistogene of the first node above the root is not always present and is generally singular. One hundred flowering tillers were removed from an ungrazed stand of *N. neesiana*, leaf sheaths were removed and the cleistogenes were counted at each node. Corresponding seeds of panicle origin were also counted. Four replicates of 50 cleistogenes (pooled from all the nodes) were incubated on germination pads with 12 hours of light at 25°C and 12 hours of dark at 15°C. Germination was recorded daily.

Error bars on all graphs represent standard error.

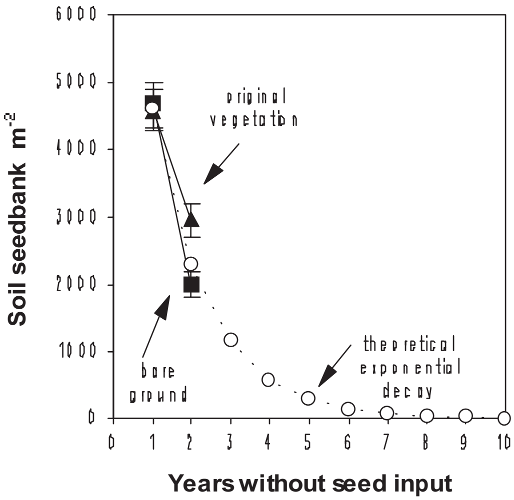

Figure 2. The decay of the seedbank in vegetated and bare plots.

RESULTS

The summer of 1995 was very dry which resulted in poor seed production whilst 1996 had good rain resulting in high seed production (Figure 1). Although potential seed production was low in 1995 (1550 seeds m^{-2}) there was no significant decrease in the seedbank. Conversely, potential seed production in 1996 was 22 122 m^{-2}. The proportion of these seeds incorporated into the seedbank was 41.6%. The seedbank had a greater rate of decay when the vegetation was removed (Figure 2). After two years without seed input the seed banks had declined annually at 35.7% and 57.3% respectively for the vegetated and bare plots. The dotted line represents a theoretical exponential decay.

Negligible emergence occurred in vegetated plots (Figure 3). Emergence for autumn and spring of 1995 on bare ground was 51.1 and 135.9 seedlings m^{-2} respectively. Of the 1434 seedlings that had germinated by 12 April 1995, 79.6 ± 5.5% were still alive on 13 April 1996. The mean total number of cleistogenes (Figure 4) produced per tiller was 7.3 ± 0.5 compared with a total seed production of panicle origin of 26.6 ± 0.7. Of the pooled cleistogenes, 84 ± 6 % were found to be viable.

DISCUSSION

These results demonstrate that *N. neesiana* is a very adaptable and reproductively efficient species. The seedbank can be maintained with very low inputs of seed in poor years, whereas in a good year, a large proportion (41.6%) of seeds produced on the panicles are incorporated into the seedbank. Although seed production did not appear as high as that of other grassy weeds, the seedbank is still large (11 122 seeds m^{-2}). Healy (1945) found that heavy infestations of *N. trichotoma* produced approximately 340 000 seeds m^{-2} with an underlying seedbank of 48 238 seeds m^{-2}. *S. indicus* var. *major* had a potential seed production of 668 000 seeds m^{-2}, yet over two years the seedbank only increased from 3800 to 8300 seeds m^{-2} (Andrews 1995). Similarly, Dowling and Nicol (1993) reported *Vulpia bromoides* (L.) Gray as having a seed production of 265 092 m^{-2} with a viable seedbank of only 4817 seeds m^{-2}. One possible explanation for the large proportion of *N. neesiana* seed being incorporated into the seedbank is the apparent lack of seed predation by ants (personal observations).

The seedbank in bare ground had a more rapid rate annual depletion (57.3%) than that with existing vegetation (35.7%). This could have been due to several factors; there is a much higher rate of germination from the bare ground causing a loss from the seedbank, the adult plants may have been adding seeds from the basal cleistogenes even though all seeds of panicle origin had been removed, and the rate of seed decomposition could be faster when the soil is exposed. These rates of seedbank depletion compare to those found in a study of *N. neesiana* by Bourdôt and Hurrell (1992). Annual rates of depletion for a mowed treatment (which prevented panicle seed input) and a bare ground treatment (glyphosate) were 37.6% and 60.6% respectively. Using

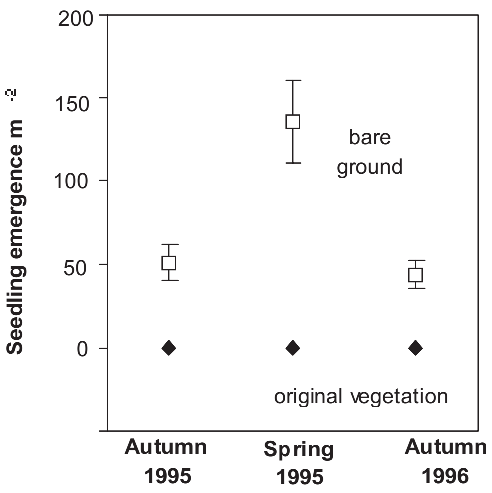

Figure 3. The emergence of seedlings in bare and vegetated plots.

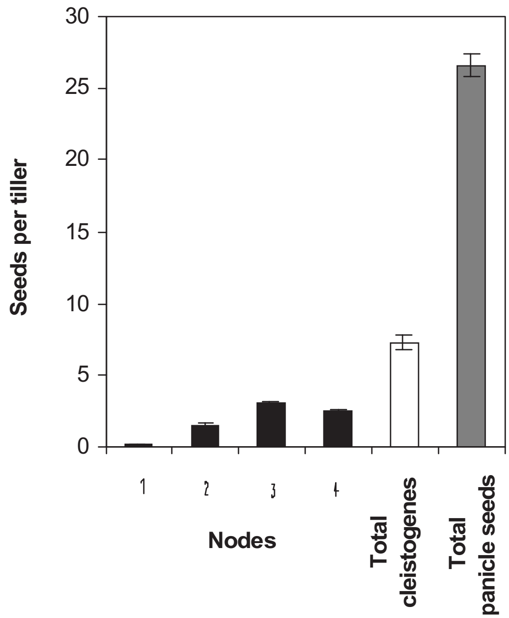

Figure 4. The number of cleistogenes produced at each of the nodes in ascending order from the base of the flowering tillers.

a predictive model based on three years of seedbank depletion data, they calculated that the 95% confidence limits for depleting a seed bank of 15 000 seeds m^{-2} to 1 seed m^{-2} would take between 5 and 12 years. This is a long time to keep a piece of land completely unproductive without a guarantee of reinfestation. Similarly, Campbell (1982) reported an 8% viability of a *N. trichotoma* seedbank after 13 years.

The fact that *N. neesiana* only germinates in bare areas suggests that triggers for germination may include disturbance and availability of light. However, only a very small number of the viable seeds in the seedbank (approximately 4600 seeds m^{-2}) actually emerged in 1995 (187 seedlings m^{-2} $year^{-1}$). This suggests that *N. neesiana* may have complex seed dormancy mechanisms. Bourdôt and Hurrell (1992) found a similar trend of germination in the autumn and spring but a much higher rate of emergence (about 1350 seedlings m^{-2} $year^{-1}$). The low densities of seedlings found in this study, may have assisted their high survival rate (79.6%) in spite of the drought experienced during their development. In contrast, Campbell (1982) found that after three years, only 20 *N. trichotoma* plants remained from an initial seedling density of 4000 m^{-2}.

A further adaptation of *N. neesiana* which aids in its reproductive success is its ability to produce cleistogenes or clandestine seeds. Cleistogenes develop independently of the panicle and can contribute up to 25% of the total seeds produced by a plant. These seeds were found to have similar viability rates and germination cues as panicle derived seeds. Dyksterhuis (1945) found that cleistogenes of the related *Stipa leucotricha* Trin. & Rupr. could develop without the production of flowering culms during heavy grazing. Several possible advantages may exist for this alternate mode of reproduction. Firstly, the propagules develop 4–6 weeks after the normal seeds have dropped, extending the reproductive period. Secondly, the storage of seeds in the upright dead stems may afford a different dispersal mechanism such as ingestion by stock later in the season (normally seeds are dispersed on the coats of animals or on machinery). Thirdly, since the basal cleistogene is produced underground it is incorporated directly into the seedbank, independent of normal flowering.

In summary, the failure of chemical and physical management techniques on *N. neesiana* results from a combination of biological attributes. The plant has the ability to dramatically increase its seed production during favourable environmental conditions yet can produce sufficient seed to maintain the seedbank in unfavourable years. The incorporation of seeds into the seedbank is very efficient. The seedbank is large in established infestations and can persist for many years. It is unlikely that any control method could exhaust the seedbank and in the long term eradicate the species. Control methods which create disturbance such as herbicide application and cultivation remove desirable competitive species and produce ideal conditions for *N. neesiana* germination. A high survival rate of these seedlings may result in a subsequent increase in the dominance of *N. neesiana* in pastures. An alternative mode of reproduction independent of the panicle seed production exists. If the adult plant is killed by herbicides, ideal germination conditions are created for the cleistogenes, which are surrounded by the organic matter of their dead parent. *N. neesiana* can be described as a reproductively efficient grassy weed.

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