ESTIMATING THE FATE OF SEEDS IN A *NASSELLA TRICHOTOMA* POPULATION

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ABSTRACT

A previously-developed model for a nassella tussock (*Nassella trichotoma*) population suggests that 97% of the seeds produced do not enter the soil seed bank. To determine the extent to which seeds are lost from the soil surface, an experiment was conducted over 1 year at three sites in North Canterbury pastures. In January 2007, soil cores with intact pasture in open-topped containers were buried to ground level at each of the sites. Three treatments (no seed, 25 awned or 25 de-awned seeds scattered onto the core surface) were applied. The number of intact seeds recovered by monthly exhumation of cores declined linearly and at an average rate of 48% over the year. Assuming the model is correct this rate of loss implies that only 5% of the seeds produced reach the soil surface and that 95% are therefore lost before deposition through wind dispersal or through pre-dispersal predation.

Keywords: *Nassella trichotoma*, nassella tussock, seed bank, tetrazolium, population growth rate.

INTRODUCTION

Nassella trichotoma (Nees) Arechev. (nassella tussock), is a perennial tussock grass native to South America. It is unpalatable to stock, drought tolerant and considered a serious threat to pastoral agriculture in New Zealand, Australia and South Africa. It was first recorded in New Zealand in the early 1900s, but because it was easily confused with native tussocks, it was not recognised as a serious problem until it reached high population densities around 1940 (Leonard 1956). Through a central government-funded programme, population densities were substantially reduced by the late 1980s to stable levels of 5 and 2 plants/ha on "undeveloped" and "developed" pastures respectively, which have no economic impact on pasture production (Bourdôt et al. 1992). However, ongoing management (manual removal of plants [grubbing] before seeding each year) is considered necessary by pastoral farmers in Marlborough and North Canterbury to ensure that this weed does not return to densities that impact on pasture production (ECan 2005; MDC 2008). Current research is aimed at understanding the population dynamics of nassella tussock to inform its ongoing management in pastoral agricultural systems (Lamoureaux et al. 2006; Smith & Lamoureaux 2006).

As part of this research, a matrix model (Caswell 2001) has been developed and parameterised using demographic data from local populations of nassella tussock in North Canterbury pastures (Lamoureaux & Bourdôt 1999). These data were collected from four sites over 4 years from populations consisting of 5-21 plants within 3 × 3 m plots. In the process of validating this model it was found that the predicted plant population growth rate in the absence of grubbing greatly exceeded rates measured in field plots (S.L. Lamoureaux, unpubl. data). This was due to an unrealistically high accumulation of seeds in the model's soil seed bank, despite it having accounted for losses due to seedling recruitment and the decay of seeds in the soil (Lamoureaux et al. 2006). The model suggests that 97% of the seeds produced each year are lost from a population and do not enter its soil seed bank. This loss could occur (1) before the seeds fall to the soil surface (by emigration of panicles on wind currents or seed predation) and/or (2) after the seeds reach the soil surface but before entering the soil seed bank (by predation, disease, germination or physical removal by wind, water or animals). In this paper the relative importance of (1) and (2) were estimated using an experiment that determined the rate of loss of seed from the soil surface during the 12 months immediately following deposition.

METHODS

The experiment was carried out from January 2007 until February 2008 at three sites on sheep- and cattle-grazed pasture in North Canterbury: Highclere Downs (S 43° 1.5', E 172° 44.2'), Sealrock-hill (S42° 59.4', E172° 43.4') and Sealrock-valley (S42° 59.1', E172° 44.0'). At each site, on 15 January 2007, 51 soil cores of intact pasture measuring 100 mm in diameter by 80 mm deep were extracted from each of two replicate plots. The cores from each plot were taken from three concentric circles of 3 m, 4 m and 5 m radius with 17 cores equally spaced around each circle (inner, middle and outer) and lined up along each radius. The soil cores and resulting holes left by the extracted soil cores were numbered in a clockwise direction 1-17.

Each soil core was trimmed at its bottom end to 75 mm long and inserted into a tightly fitting open-topped 80 mm length of 100 mm-diameter PVC drain pipe, leaving a 5 mm raised edge. The bottom end of each container was capped with 420 micron stainless steel mesh to contain the core and allow drainage. The turf layer of each soil core was cropped to 3 cm length and the cores in their containers were buried to ground level back into their originating holes. One of three treatments was then applied to each of the 51 cores: no nassella tussock seeds added, 25 seeds added with awns attached or 25 seeds added with awns removed, providing for 17 sampling occasions. The 25 seeds were scattered onto the soil core surface. Treatments and sampling times were assigned to core positions in a completely random design.

Three soil cores (one from each treatment) were exhumed monthly from each of the six plots for 12 months with the last batch being dug up in January 2008. Each core was separated into a soil and a litter layer by cutting off the litter layer using a sharp knife. Each layer was then washed separately, first through a 2 mm sieve to remove large soil and plant matter, and then through a 500 micron sieve to remove finer particles whilst still retaining seeds. After drying overnight at room temperature, the organic matter was again sieved and the remainder searched for nassella tussock seeds using a laboratory magnifier.

All intact seeds (those with the lemma unbroken) found during the search were tested for viability firstly by leaving them for a month to germinate in a 25ºC incubator (Joubert & Small 1982) in Petri dishes. The seeds in each dish were placed on filter paper moistened with distilled water and dusted with a 50/50 w/w mix of benomyl (Benlate, 500 g ai/kg) and captan (Captan, 800 g ai/kg) fungicides. After 1 month, any un-germinated seeds were bisected laterally with a scalpel and immersed in a 1% solution of tetrazolium salt solution (2,3,5-triphenyl tetrazolium chloride) for a further 24 hours. At the end of the staining period the seeds were assessed for viability using the criteria for small grasses (2002 supplement for Poaceae in Peters 2000).

Data were analysed by fitting a regression line to the number of intact seeds as a percentage of the number sown versus time for each of the two replicates at each site, then analysing the resulting six slope estimates by analysis of variance (three sites by two replicates) (GenStat 10th Ed). The latter analysis of variance was also used for a second variable, the percentage of the intact seeds that were viable averaged over the 13 sampling occasions for each plot at each site.

RESULTS

Nearly all of the 25 seeds were found and were intact at the first sampling time, and fragments of seeds were readily found at later times indicating that the seed extraction methodology was reliable.

Eight intact seeds in total (10/m^2) were retrieved from 78 sampled cores (13 occasions × 2 reps × 3 sites) that had not had seeds added, compared with 1408 and 1443 seeds (1758 and 1801/m^2 respectively) for the awned and de-awned seed addition treatments. The seeds in "no-seed added" cores represent the natural background level of nassella tussock seeds in the soil seed bank at these sites. Because they were so few in number the data were not adjusted to account for them.

At the first sampling occasion, 100% of the seeds extracted from the cores were in the litter layer. By the end of the experiment, 365 days after the seeds were sown, 25% of the seeds extracted were from the litter layer and 75% from the soil.

The number of intact seeds (as a % of seeds sown) averaged over "awned" and "de-awned" (presence of awns was not significant) declined linearly at all three sites (Fig. 1). On average, about 48% of the seeds had disappeared after 1 year and there was no evidence for a site effect (Table 1). On average, 70.8% of the intact seeds were viable and there was no evidence for a site effect (Table 1).

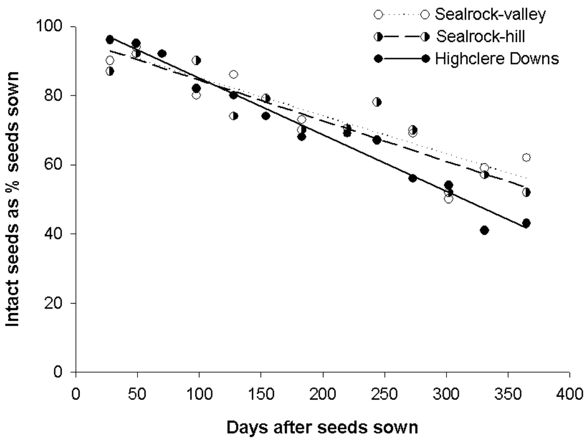

FIGURE 1: The number of intact nassella tussock seeds at each of the three sites averaged over "awned" and "de-awned" seed treatments, expressed as a percentage of the number sown at the beginning of the experiment. The fitted regression lines (y=*a*+*b*x, where *x* is days after seeds were sown) are shown: Highclere Downs, *a*= 101.29, *b*= -0.1635; Sealrock-hill, *a*= 96.19, *b*= -0.1174; Sealrock-valley, *a*= 96.14, *b*= -0.1099.

The mechanism(s) of these losses were not ascertained in this experiment. However, the occurrences on all sampling occasions of rotting seeds, small invertebrates (weevils, slaters, ants and earthworms), germinated seeds, broken seeds and empty seed coats, suggest multiple mechanisms.

TABLE 1: Reduction in the numbers of intact nassella tussock seeds (% per year) estimated from six individual regression lines, and the proportion of the intact seeds that were viable (%) averaged over the 13 sampling occasions at three sites in North Canterbury.

	Reduction in no. intact seeds	Viability of intact seeds
Highclere Downs	59.7	67.6
Sealrock-hill	42.8	73.5
Sealrock-valley	40.1	71.4
LSD 5%	40.8	12.9
Mean ± 95% CI[1]	47.5±26.3	70.8±7.4

[1]The 95% confidence interval for the true mean for North Canterbury, treating the three sites as a random sample of North Canterbury farms.

DISCUSSION

The current version of the population model for nassella tussock in North Canterbury pastures, predicts a population growth rate, in the absence of grubbing, of λ=1.875. By contrast, the average measured growth rate of the populations used to parameterise this model, assuming exponential growth, is λ=1.136 (S.L. Lamoureaux, unpubl. data). For such a population growth rate to be achieved in the model, the proportion of seeds that contribute to this growth must be reduced from 1.0 to 0.026. This implies that 0.974 (1-0.026) of the seeds produced by the modelled population do not enter the soil seed bank, and are lost either before or after deposition on the soil. Based on the results of the present experiment, the relative importance of these two sources of seed loss in a nassella tussock population can now be estimated. In the experiment reported here, an average of 0.475 of the seeds deposited on the soil was lost after 1 year (Fig. 1, Table 1). Assuming that of the seeds remaining after 1 year, the proportion 0.525 (1-0.475) enters the seed bank, then 0.05 (0.026/0.525) of the seeds produced by the modelled population would need to be deposited on the soil to result in 0.026 entering the seed bank, and 0.024 (0.05-0.026) would be lost after deposition before entering the soil. The balance, 0.95 (1-0.05) of the seeds produced would be lost before deposition.

In summary, this analysis suggests that 95% of the seeds produced in a particular year by a nassella tussock population are lost before reaching the soil surface, 2.4% are lost after deposition on the soil surface, and the remaining 2.6% enter the soil from where they can contribute to population growth. This leads to the hypothesis that most of the seeds produced annually by a nassella tussock population never contribute to its population growth. This hypothesis is supported by earlier speculation that most of the seeds of nassella tussock are dispersed away from the parent plant as tumbling panicles (Taylor 1987). Research on other plant species also shows that only a small fraction of seeds produced may contribute to population growth, in these cases the majority being rapidly lost to predation, disease and senescence (Jansen & Ison 1995).

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