Nassella trichotoma (Nees) Arechav.: seedling recruitment and survival in New Zealand

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Summary As part of a long-term project on the ecology of *Nassella trichotoma* (Nees) Arechav. in New Zealand grasslands, the effect of aspect and soil disturbance/vegetation cover on seedling recruitment and survival was investigated. At each of three field sites in grazed grassland in North Canterbury, plots were established with the following treatments: (a) with and without added seed of *N. trichotoma* (1600 seeds m^{-2}), (b) disturbed pasture (soil bared by chipping away existing vegetation) at the beginning of the experiment vs. undisturbed pasture, and (c) northern (sunny) vs. southern (shady) aspects. Recruitment and survival were measured at 12 and 24 months after sowing respectively. Irrespective of aspect or disturbance, there was little recruitment in plots without added seed (<4 seedlings m^{-2}), whereas the average recruitment was 204 seedlings m^{-2} when seed was added. This suggests that recruitment is seed-limited at the experimental sites. Soil disturbance promoted recruitment but had no effect on survival rates indicating that the soil disturbances associated with chipping may contribute to population growth in this weed. Recruitment was higher on southern than on northern aspects but there was no evidence of a difference in survival during the 2-year period of the study, suggesting that the rarity of *N. trichotoma* on southern aspects in North Canterbury may be due to delayed mortality.
Keywords Disturbance, chipping, grubbing, nassella tussock, serrated tussock.

INTRODUCTION

In New Zealand *Nassella trichotoma* populations diminished dramatically during an intensive central government-funded control programme that began in the mid 1940s. In 1990, this funding stopped and the onus for on-going control was returned to rate payers in affected regions, governed by the provisions of local Regional Pest Management Strategies (RPMS) administered by the local Regional Council. In North Canterbury, the RPMS requires that affected land owners remove 98% of their *N. trichotoma* plants before 31 October each year. This is a time when on-farm commitments are high and time available for weed control is limited. As a result, the level of control required by the RPMS is not always achieved. Land managers have begun to question the ability of the current management regulations to maintain an ongoing decline in *N. trichotoma* populations but Regional Council officers require an objective scientific basis for any revision of the current management strategy. To help develop an optimal strategy, it is necessary to understand the regulating forces in population growth, spread and persistence, and how these might be affected by alternative management techniques. This is the rationale for a study of the population dynamics of the weed in New Zealand grasslands and a key component of this study is the exploration of the mechanisms regulating recruitment and survival of *N. trichotoma* seedlings.

In New Zealand, the main method of control for *N. trichotoma* is through manual chipping (grubbing) of plants. Chipping involves the digging up of plants and results in the formation of a bare 'cultivated' patch in the pasture. It has been suggested that such disturbance might enhance the recruitment of *N. trichotoma*, as has been shown in other species (McConnaughay and Bazzaz 1987, Moloney 1990, Panetta and Wardle 1992, Potvin 1993), and that this could explain why *N. trichotoma* populations persist despite the intensive annual chipping regime. In addition, an observation, for which an explanation may shed some light on the mechanisms regulating *N. trichotoma* populations, is the common absence of the species on south facing (shady) slopes in New Zealand grasslands despite a high seed rain onto these slopes from adjacent north facing slopes where the species may occur in prolific numbers. It has been hypothesised that this absence is due to greater competition from other pasture species on these slopes (Healy 1945).

Here we attempt to determine the effect of disturbance and aspect on recruitment and survival of *Nassella trichotoma* under natural and increased seed load to (1) establish whether populations in North Canterbury are seed-limited, (2) ascertain whether chipping promotes population growth and (3) provide an explanation for the rarity of the species on southern slopes.

MATERIALS AND METHODS

The trial was established in April 1999 on three sites in North Canterbury, New Zealand. *N. trichotoma* seed was collected in December 1998 from each site and combined to form a composite sample of genotypes from the field. The seeds were stored in paper bags until April 1999 when the experiment commenced. On each site four replicates of 32 25 × 25 cm permanent plots were established in which the following treatments were applied in a factorial manner:

- Aspect – north (sunny) or south (shady).
- Disturbance – nil or bared by chipping.
- Seed added – nil or +100 *N. trichotoma* seed (1600 seeds m^{-2}) randomly spread over plot.

Twice a year, in April and October, all new *N. trichotoma* seedlings within the plots were mapped and older seedlings were relocated with the aid of a 5 cm grid. The number of blades on each seedling was counted if their basal diameter was less than 1 mm otherwise their basal diameter and height were measured. Data on survivorship, growth, and reproduction of seedlings were obtained at each census following germination.

The total number of seedlings detected by April 2000, one year after the experiment was started, was analysed using a general linear model with a Poisson distribution. The number of new seedlings appearing after April 2000 was so low (less than 1% of the total up to April 2001) that only those appearing prior to the April 2000 census are considered here. The survival of these pre-April 2000 seedlings to April 2001, two years after sowing, was analysed using a generalised linear model with a binomial distribution; because there was no survival of seedlings in plots which had no added seed, the seed treatment was omitted from this analysis. Site was included in all analyses as a block effect and all analyses were carried out using Genstat 5 (Genstat 5 Committee 1993).

RESULTS

The mean number of seedlings recruited between April 1999 and April 2000 are shown in Table 1 and the results of the statistical analysis of the treatment effects are in Table 2. Fewer seedlings appeared in plots which had no additional seed added and recruitment was lower overall at the Highclare Downs site than at the other sites. Disturbance of the soil at the time of adding the seeds resulted in more recruitment overall than when the soil and its vegetation cover were left intact, and recruitment was higher on southern than on northern aspects. Disturbance promoted recruitment more on southern than on northern aspects.

The percentage of seedlings surviving on the plots to which seed had been added are shown in Table 3 and the corresponding statistical analysis is in Table 4. In contrast to seedling recruitment, there was no evidence that seedling survival was affected by either aspect or disturbance. Overall, survival was lower at the Highclare Downs site.

Table 1. Mean number (m^{-2}) of recruited *Nassella trichotoma* seedlings.

Site	Aspect	Nil seed		+ seed	
		Pasture	Bare ground	Pasture	Bare ground
Highclare	South	0	0	48	84
Downs	North	4	0	216	128
Sealrock	South	0	4	80	652
	North	0	0	60	156
Carvossa	South	4	0	164	712
	North	0	4	68	96

Table 2. Accumulated analysis of deviance for *Nassella trichotoma* seedling recruitment.

Source of variation	df	Mean deviance	F	P-value
Site	2	30.1	4.22	0.018
Aspect (A)	1	107.2	14.81	<0.001
Disturbance (D)	1	149.3	20.64	<0.001
Seed (S)	1	811.2	112.10	<0.001
A × D	1	59.4	8.21	0.005
D × S	1	1.1	0.15	0.703
A × S	1	0.3	0.04	0.840
A × D × S	1	0.5	0.08	0.784
Residual	86	7.4		
Total	95	19.1		

Table 3. Mean per cent survival of *Nassella trichotoma* seedlings in plots which had added seed.

Site	Aspect	Pasture	Bare ground
Highclare	South	8	0
Downs	North	0	26
Sealrock	South	0	33
	North	20	41
Carvossa	South	17	17
	North	6	10

Table 4. Accumulated analysis of deviance for *Nassella trichotoma* seedling survival.

Source of variation	df	Mean deviance	F	P-value
Site	2	20.1	4.92	0.015
Aspect (A)	1	0.2	0.06	0.811
Disturbance (D)	1	0.1	0.04	0.851
A × D	1	9.5	2.32	0.139
Residual	26	4.1		
Total	31	5.0		

DISCUSSION

The purposes of this study were:

(1) to determine if *N. trichotoma* is seed-limited in North Canterbury grassland,

(2) if the soil disturbances associated with the annual chipping of *N. trichotoma* in North Canterbury promote recruitment and survival in the weed, and

(3) to provide an explanation for the rarity of the species on southern slopes.

The extremely low densities of seedlings in unsown plots as compared to plots to which *N. trichotoma* seeds were added (Table 1), suggests that the natural reserve of viable seeds was small compared with the densities sown. This was verified in a pilot study on the density of *N. trichotoma* seed in the North Canterbury soil seed bank where we found very few seeds (<100 seeds m^{-2}; Lamoureaux, unpublished data). This suggests that current *N. trichotoma* populations at the study sites are seed-limited.

The higher recruitment on disturbed plots in the current study provides supporting evidence for the hypothesis that disturbance promotes recruitment in *N. trichotoma* (Tables 1 and 2). There are several possible explanations for this increase in recruitment on disturbed ground. First, the removal of vegetation promoted germination by increasing the available light at the soil surface. Supporting this idea, Joubert and Small (1982) found that seed germination in *N. trichotoma* was promoted by light particularly when the seed coat had been damaged. However, Healy (1945) observed that *N. trichotoma* readily germinated on the bare ground under the canopy of adult tussocks and suggested that the seed could readily germinate in low light. Secondly, the increased recruitment on bare ground could be in response to a higher red/far red ratio caused by removing the vegetation. Fenner (1980) and Silvertown (1980) found increases in germination in response to increases in this ratio in a large number of grassland species however, this aspect of *N. trichotoma* germination has not been investigated. Thirdly, the increased recruitment may be due to fluctuations in soil temperature. Thompson *et al.* (1977) showed that daily temperature fluctuations were enhanced within gaps created in vegetation and Joubert and Small (1982) found that the germination response of *N. trichotoma* seed varied with temperature. Finally, the increase in recruitment on soil bared by chipping may have been caused by improved seed moisture relations, although we have no evidence for this. While the hypothesis that chipping may promote recruitment in *N. trichotoma* is supported by this study, the mechanisms behind this response in recruitment remain obscure.

The rarity of *N. trichotoma* on southern aspects is not fully explained by the results of this study. Given the positive effects of southern aspect on seedling recruitment (Table 1), and the lack of any effect on seedling survival, southern slopes should support *higher* populations of the weed than northern slopes. However, this is not the case; the species is rare on southern slopes where vegetation cover is dense throughout the year and Healy (1945) found that the species did not occur in intact (undisturbed and ungrazed) native tussock or in dense swards of meadow grass, suggesting the *N. trichotoma* is a poor competitor. This conflict between field observations and our experiment may in part be due to a delay of competition-induced seedling mortality during the timeframe of this experiment. This could be due to a phenomenon called 'resistance to inanition' (Chippindale 1948) whereby grass seedlings in competition with other grasses remain in a suppressed state for long periods of time. The existence of such a phenomenon in our *N. trichotoma* populations will be verified or denied in future censuses.

In conclusion this study has:

(1) indicated that recruitment in current populations of *N. trichotoma* in North Canterbury grasslands is seed-limited,

(2) provided evidence that the disturbance associated with annual chipping operations promotes seedling recruitment and, as a consequence, can potentially promote population growth in the weed, and

(3) indicated that recruitment rates are higher on southern slopes than on northern slopes, and that the rarity of mature plants on southern slopes may be due to competition-induced mortality.

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