



Original article

Population growth of *Nassella trichotoma* in grasslands in New Zealand slower today than in the pastShona L. Lamoureaux^{a,*}, Graeme W. Bourdôt^a, David J. Saviile^b^aAgResearch Limited, Private Bag 4749, Christchurch 8140, New Zealand^bSaviile Statistical Consulting Limited, P.O. Box 69192, Lincoln 7640, New Zealand

ARTICLE INFO

Article history:

Received 1 November 2010

Accepted 24 June 2011

Available online 29 July 2011

Keywords:

Demography

Fecundity

Grubbing

Nassella tussock

Serrated tussock

Soil seed bank

ABSTRACT

Nassella trichotoma established in modified tussock-grasslands in New Zealand from about 1860. Management programmes since 1946 have reduced populations to levels no longer impacting pastoral production. Optimising future management requires knowledge of the trajectory of population growth and its regulating demographic processes. To that end, four long-term field experiments were conducted. Net reproductive rate varied from 1.021 to 1.237 year⁻¹ and growth in plant basal diameter from 8.1 to 16.6 mm year⁻¹. The probability of flowering increased with basal diameter and was essentially unity above 50 mm diameter. Populations grubbed annually declined abruptly but recruitment was unaffected and extinction did not occur. Of seeds sown into disturbed and intact pastures, 0–51% produced seedlings and more arose on sunny slopes and from disturbed than intact pasture. Death rates were high; 7 years after sowing, surviving plants represented only 0–9% of the seed sown. Seeds buried 25 mm deep in the pasture litter on two occasions declined in viability at rates of 74 and 89% in the first year and first three months respectively and 26 and 0% year⁻¹ thereafter. Seed production plant⁻¹ (square root scale) increased linearly with plant basal diameter; for example, plants of 11 and 100 mm diameter are predicted to produce 0 and 11,092 spikelets (each with one seed) respectively. We estimate that a *N. trichotoma* population today will, in the absence of management, take 210 years to increase to 90% of its carrying capacity supporting the hypothesis that population growth in this species is slower than occurred historically. We show that the rates of some demographic processes may be much lower than in the past and suggest this is due to more competitive vegetation resulting from improved management. The size-dependence of many processes supports the need for a size-structured model to explain population growth in this weed.

© 2011 Elsevier Masson SAS. All rights reserved.

1. Introduction

Nassella trichotoma (Nees) Hack. ex Arechav. invaded indigenous tussock-grasslands in the eastern parts of the Marlborough and Canterbury regions of New Zealand following their modification for pastoral farming by the early colonists in ca. 1860 (Healy, 1945). The aggressiveness of this exotic grass, a species of low digestibility to sheep (Campbell, 1982), has been attributed to the degradation of the native vegetation cover as a result of burning, heavy stocking, grazing by rabbits and the native grass-grub (*Costelytra zealandica* White), and the species' high seed output and tolerance of drought (Healy, 1945). By the early 1900s near monocultures had developed in both regions, particularly on the northerly hill slopes that are exposed to the sun and drying north-west "foehn" wind (Healy,

1945). Since the wide-scale renovation of these infested grasslands (by improving soil fertility and sowing pasture grasses and legumes) in the mid 20th century (Leonard, 1956), re-invading *N. trichotoma* plants have been removed annually (by manually digging them out; a process known as grubbing) in regionally-coordinated management programmes (Dingwall, 1962). This effort, sustained until the present day, has resulted in the weed falling to densities that no longer reduce live-weight gains of sheep and other grazing animals (Bourdôt et al., 1992).

The extent to which ongoing management of this weed is worthwhile remains a topic of debate. Denne (1988) developed a population model for the weed based on demographic data and anecdotal information available at the time (Campbell, 1982; Healy, 1945) and integrated this with economic principles. Whilst a cost-benefit analysis indicated that the annual grubbing programmes conducted until the late 1980s provided positive net benefits, and an economic threshold analysis supported management of the weed at the current low population densities, an optimisation analysis

* Corresponding author. Tel.: +64 3 325 9951; fax: +64 3 325 9946.

E-mail address: shona.lamoureaux@agresearch.co.nz (S.L. Lamoureaux).

suggested that grubbing once every 3 years would maximise the net benefit to New Zealand (Denne, 1988). A reduced grubbing frequency was not adopted due to concern that the 30–40 years to reach the saturation density of 40,000 plants ha⁻¹ assumed by Denne underestimated the population growth rate in the absence of management. Burning is no longer practised and rabbit populations are smaller and generally stable compared to the “plague” populations of the late 19th century (Bell and Douglas, 1992; Lough, 2009) so it is probable that the population growth of *N. trichotoma* may be lower than in the past through constraining effects of inter-specific plant competition.

To realistically model population growth in *N. trichotoma*, thereby enabling comparison of potential future grubbing strategies (Smith and Lamoureaux, 2006), a model valid under current farming conditions, that accounts for the contributions plants of different size make to population growth in the absence of grubbing is necessary (Lamoureaux and Bourdôt, 1999). Existing accounts of *N. trichotoma* provide little of the data necessary to develop such a model (Beggs, 1958; Dingwall, 1962; Healy, 1945; Leonard, 1956, 1962; Milne, 1954; Taylor, 1987). To redress this deficiency we report on four long-term field experiments conducted in sheep- and cattle-grazed modified tussock-grasslands in New Zealand. Experiment 1 examines the relationships of death and reproductive maturity to plant size, Experiment 2 the effect of sward disturbance on recruitment and survival of seedlings, Experiment 3 the longevity of buried seeds, and Experiment 4 the effect of plant size on seed output. Experiment 1 also provides an empirical test of the hypothesis that population growth in *N. trichotoma* is slower than in the past.

2. Materials and methods

All experimental sites were in cattle/sheep-grazed modified tussock-grassland containing *N. trichotoma*. Site details are provided in Table 1.

2.1. Experiment 1 – demographic effects of “grubbing”

At each of two sites (Highclere Downs and Sealrock 1) (Table 1) four treatments (not grubbed [control], grubbed in autumn, grubbed

in spring, grubbed autumn and spring) were allocated to 5 × 5 m plots on a southwest (shady) and an opposing northeast (sunny) hill slope. A randomised complete block layout with four replicates (16 plots) was used. Two other sites (Sealrock 2 and Carvossa) (Table 1) were included as additional controls with a single “not grubbed” treatment replicated four times on a southwest, and once on a northeast slope. At least 5 plants (0.55 plants m⁻²) of *N. trichotoma* occurred in the central 3 × 3 m area of each plot.

At 6-month intervals (April [autumn] and October [spring]), a census of the *N. trichotoma* plants on the central 3 × 3 m area of the plots was made by mapping each plant using a 0.5 × 0.5 m string grid, beginning December 1998 (nominally an October census) and ending October 2003 on the grubbed plots and in April 2006 on all but one control plot. At Sealrock 2 four additional censuses were made ending May 2008. At each census the 3 × 3 m area was searched to locate new recruits and record the fates of all plants present at the previous census. Mortalities were “natural” (non-anthropogenic), “grubbed” (accidental and as per treatment) or “coalesced plants”. Basal diameter (measured in two directions using a digital calliper) and reproductive status (presence of panicles) were recorded. After each census, all of the *N. trichotoma* plants on the treatment plots were grubbed simulating a thorough commercial operation. To prevent dispersal of *N. trichotoma* seeds, as required under the Environment Canterbury Regional Pest Management Strategy (ECan, 2005), all plots were covered with a 30 mm mesh from October to February each year.

Five analyses were conducted. Firstly, population growth rates (weighted by number of years of data) were estimated for the “control” plots at each of the four sites assuming exponential growth between the start and end values of the (mean) net population size (initial population size + recruits – deaths).

Secondly, the relationships between the probability of dying within a six-month period and plant basal diameter at the beginning of the period (also restricted to the “control” plots) were determined by binomial regression using a logit link function (a) for each plot at each site with the data pooled over all years, (b) for each site with the data pooled over all plots and years, (c) for each year with the data pooled over all sites, and (d) with the data pooled over all sites and years. To check for differences between

Table 1

Details of the experimental sites used in four experiments to determine the key demographic processes regulating populations of *Nassella trichotoma* in modified tussock-grasslands in New Zealand.

Site name	Aspect	Soil group ^a	Natural nutrient status ^a	Latitude & longitude ^b	Altitude (m.a.s.l.)	Exp. 1	Exp. 2	Exp. 3		Exp. 4	
								1999 a	2001 b	2001	2002
Highclere Downs	SW	YGE	Med.	43 01 10 S 172 44 14 E	180	✓	✓	✓	✓		
	NE	YGE	Med.	43 01 11 S 172 44 06 E	180	✓	✓	✓	✓		✓
Sealrock 1	SW	REND	Med.–High	42 59 12 S 172 43 54 E	340	✓	✓	✓	✓		
	NE	REND	Med.–High	42 59 15 S 172 43 50 E	360	✓	✓	✓	✓		✓
Sealrock 2	SW	REND	Med.–High	42 59 30 S 172 43 27 E	290	✓					
	NE	REND	Med.–High	42 59 28 S 172 43 25 E	290	✓				✓	
Carvossa	SW	YGE	Med.	42 57 45 S 172 44 44 E	300	✓	✓	✓			
	NE	YGE	Med.	42 57 46 S 172 44 34 E	290	✓	✓	✓			
Greta Valley	NE	YGE	Med.–High	42 57 48 S 173 02 36 E	360					✓	
Waipara River	Flat	River gravel	–	43 04 32 S 172 46 05 E	60					✓	✓

^a Gibbs (1980); YGE = Yellow grey earth, REND = Rendzina.

^b World Geodetic System 1984.

sites, two features of the curve fitted to each plot in (a), the slope and the diameter corresponding to 10% death (LD_{10}), were subjected to separate analyses of variance.

Thirdly, the average rate of growth in plant diameter was estimated for the plants on the “control” plots at each site by fitting parallel lines, one plant⁻¹ that survived for the duration of the experiment, using analysis of covariance with the response variable being diameter, “treatments” being individual surviving plants, and the covariate being time (parallel lines provide a good approximation to the data, as can be seen from the appropriate figure in the Results section).

Fourthly, the relationships between the probability of flowering and plant basal diameter (also restricted to the “control” plots) were determined using the same methodology as for death above, but using diameter corresponding to 50% flowering in place of the LD_{10} .

Finally, the effects of the grubbing treatments on the recruitment rate averaged across all years were analysed separately for each site using analysis of variance.

2.2. Experiment 2 – seedling recruitment and survival

This experiment was conducted over the seven years from April 1999 until April 2006 at three of the four sites in Experiment 1 (Table 1). *N. trichotoma* seeds collected in December 1998 were bulked across sites, and stored in a paper bag at room temperature. On 21 April 1999, four blocks of four 25 cm × 25 cm plots, spaced 0.5 m apart, were marked out on each of the three sites on the northeast and southwest slopes. Four treatments (+seed + disturbance, +seed – disturbance, – seed + disturbance, – seed – disturbance) were randomly assigned to the four plots in each block. On 21 April 1999, the “+disturbance” treatment was applied by removing all vegetation with a grubber, and the “+seed” treatment was applied by hand-spreading 100 seeds of *N. trichotoma* seeds (1600 seeds m⁻²) across the plots. Overall, the experiment consisted of 96 plots = 4 Blocks × 2 Disturbances × 2 Seed Additions × 2 Aspects × 3 Sites.

In April and October each year, until April 2006, all new *N. trichotoma* seedlings within each plot were mapped, and all previously mapped seedlings were examined with the aid of a wire grid divided into 25.5 × 5 cm cells, measuring their basal diameters and noting presence/absence of panicles. A plant was “dead” if no longer present (on two consecutive census dates) or if present but completely desiccated.

The cumulative recruits, cumulative deaths, and recruits–deaths (net population size) were calculated and their final values (April 2006) for the “+seed” plots were analysed for the effect of disturbance using analysis of variance (a) within each aspect (SW and NE) and site, and (b) combined over aspect and site with the 2 aspects × 3 sites treated as 6 blocks and the treatment means from (a) as input.

The effect of site and aspect on the plant diameter growth rate was evaluated using the average basal diameter for each census for those plants surviving to the end of the experiment for each site and aspect.

2.3. Experiment 3 – buried seed longevity

For Experiment 3a, conducted from April 1999 until April 2004 at three sites (Table 1), seeds were collected in December 1998 from *N. trichotoma* at each site, mixed in about equal numbers and stored in a paper bag at room temperature. The proportion viable was determined in January 1999 as the sum of those germinating and those dormant but staining positive with 2,3,5-triphenyl tetrazolium chloride (TTC). Fifty seeds, dusted with a 1:1 mixture of

benomyl (Benlate containing 500 g/kg benomyl, Du Pont) and captan (Captan 80 W containing 800 g/kg captan, Nufarm) were placed on a moistened filter paper in each of four Petri dishes (50 × 4 = 200 seeds). Seedlings were removed daily, and after 30 days at 25 °C those not germinated were bisected laterally. The embryo section was placed in a TTC solution (1 g TTC/100 ml sterile distilled water) at 25 °C for 24 h. A seed was classified viable if the embryo was stained red (Peters, 2000).

In April 1999, 40 lots of 50 of the stored seeds were each mixed with 250 ml of steam-sterilised soil from each of the three experimental sites. Each of the 120 lots of seeds was then enclosed in a mesh bag (made from Weedtex; 97 g m⁻² UV stabilised woven polypropylene tape, Donaghys Industries, Box 20449, Christchurch, New Zealand) allowing passage of water, roots and small soil organisms. On 15 April 1999, 40 bags were buried (25 mm deep at the litter layer–soil interface) at each site; 20 on each of a northeast and southwest hill slope allowing for four replicates of five retrieval occasions. Overall, there were 120 bags of seed = 4 Replicates × 5 Retrieval times × 2 Aspects × 3 Sites. A bag was retrieved from each of the replicates at each site in April 2000, 2001, 2002, 2003 and 2004; the contents of each were sieved and the intact seeds of *N. trichotoma* were removed and subjected to the TTC viability test.

For Experiment 3b, conducted from April 2001 until April 2006 at two sites (Table 1) used for Experiment 3a, seeds collected in December 2000 were stored separately for each site in paper bags at room temperature until April 2001. The proportion viable was determined as before, but using 100 seeds in each of four Petri dishes (100 × 4 = 400 seeds).

In April 2001, 64 lots of 100 of the seeds from each of the two sites (provenances) were each mixed with sterilised soil (from each of the two burial sites) and enclosed in mesh bags as in Experiment 3a. On 17 April 2001, 128 of these bags (64 of each seed provenance) were buried at both sites. Overall, the experiment consisted of 256 bags of seed = 4 Replicates × 2 Seed provenances × 8 Retrieval times × 2 Aspects × 2 Sites. Two bags were retrieved from each of the replicates (one of each provenance) at each site in July and October 2001, January 2002 and April 2002, 2003, 2004, 2005 and 2006. All intact seeds of *N. trichotoma* were removed and tested for viability using TTC.

For each of Experiments 3a and 3b, the percentage viability data were re-expressed as a percentage of the initial percentage viability (85.5% for Experiment 3a and 40.5% for both seed provenances for Experiment 3b).

For years 0–1, the decay rates (from 100% viability at year 0) of the re-expressed data were calculated using the difference in percentage viability between 100 and the value at year $t = t_1$ where t_1 is the sampling time closest to $t = 1$. The three 3-monthly samples in Experiment 3b were excluded to standardise the decay rates to an annual basis. For Experiment 3a, the mean decay rates for each site and aspect were subjected to an analysis of variance using the site by aspect interaction as the error term. For Experiment 3b a similar analysis was carried out, except that provenance was included as a factor, nested within site and aspect, using the site by aspect interaction as the “higher level” error term and all other interactions (pooled) as the “lower level” error term.

The data from years 1 to 5 were analysed by fitting the exponential model

$$y = Ae^{-b(t-t_1)} \quad (1)$$

to the data for each aspect within each site for Experiment 3a, and to the data for each aspect and provenance within each site for Experiment 3b, using a binomial error distribution and an identity link function; y (eq. (1)) is the observed percentage viability of the seeds in year t relative to the initial percentage viability at $t = 0$, A

was constrained to be the mean relative percentage viability at $t = t_1$, and b is a slope parameter. Parameter b (eq. (1)) was subjected to an analysis of variance (as for years 0–1).

In addition, for each experiment the unadjusted viability data were bulked over sites and “overall” curves were fitted as follows. Firstly, a straight line decay was fitted to the bulked data for the initial ($t = 0$) and first subsequent assessment (at $t = 1.0219$ and $t = 0.2548$ years for Experiments 3a and 3b respectively). Secondly, an exponential decay model (eq. (1)) was fitted to the data for the remaining assessments, with parameter A constrained to be the viability at $t = 1.0219$ and $t = 0.2548$ years respectively. Lastly, all four fitted curves were re-expressed in terms of viability relative to the initial percentage viability at $t = 0$ (by dividing each equation by the latter constant).

2.4. Experiment 4 – plant size and seed yield

In 2001 and 2002, during peak flowering (December), at least thirty *N. trichotoma* plants of varying size were located at each of three sites (Table 1). The basal diameter of each plant was measured and they were then grubbed and taken back to the laboratory where the panicles on each were counted. The number of spikelets was then counted on ten panicles chosen at random from a subset made up of every 10th panicle counted on larger plants, and every 2nd on smaller plants; all spikelets were counted on plants with less than 10 panicles. The number of spikelets on each plant was estimated by multiplying the number of panicles by the mean number of spikelets panicle⁻¹. In *N. trichotoma*, there is one floret spikelet⁻¹ and therefore potentially one seed spikelet⁻¹. For analysis, the number of panicles plant⁻¹, mean number of spikelets panicle⁻¹, and the estimated number of spikelets plant⁻¹ were square root transformed and a linear regression against plant size was performed for each site. The slopes of the three regressions within each of the two years were compared using a *t*-test. A regression was also fitted to all the data across sites for each of the three variables.

3. Results

3.1. Experiment 1 – demographic effects of “grubbing”

N. trichotoma plants were not found in any of the plots on the southwest (shady) slopes at any of the sites. These plots are therefore excluded from our analyses.

Where grubbing was withheld on the northeast (sunny) slopes, gains and losses of plants occurred at all four sites (Fig. 1). Plants were lost from the populations either by death, coalescence, or as occurred on one occasion at each of Highclere Downs and Sealrock 1, by accidental grubbing. Gains mainly exceeded losses so that net population size increased at each of the sites but the rate varied between the sites. It was greatest at Highclere Downs (before the plots were accidentally grubbed) with a 23.7% year⁻¹ increase and lowest at Carvossa with a 2.1% year⁻¹ increase (Table 2). Deaths occurred predominantly among smaller plants (Fig. 2), e.g., for 1 mm-diameter plants, the probability of death is 0.13 from the pooled overall curve in Fig. 2. By contrast, for 20 mm-diameter plants it is only 0.01 (Fig. 2). Growth in basal diameter proceeded linearly at all four sites but varied between the sites, with values of 8.1, 11.6, 13.4, and 16.6 mm plant⁻¹ year⁻¹ at Highclere Downs, Sealrock 1, Carvossa and Sealrock 2 respectively (Fig. 3). The probability of a *N. trichotoma* plant flowering increased sigmoidally with basal diameter, being 0.5 at 28 mm overall, and essentially unity above 50 mm diameter (Fig. 4a–d). There was evidence that this relationship varied between the four sites, with the slope being significantly greater at the Carvossa than at the Highclere Downs site ($P < 0.05$) (Fig. 4a c.f. d).

At both sites where grubbing treatments were imposed, population size declined following the first grubbing but extinction did not occur because the recruitment gains balanced the losses (Fig. 1). Recruitment occurred in the autumn–winter and spring–summer periods at both sites. At Sealrock 1 recruitment during the autumn–winter periods (mid April to mid October) was greater on the plots grubbed in spring (Table 3). This increase occurred mainly prior to the first spring grubbing (Fig. 1) and therefore cannot be attributed solely to the grubbing. The overall annual rate of recruitment was not affected by grubbing at either site. Losses due to natural death and coalescence occurred in both the autumn–winter and spring–summer periods at both sites but did not vary between the two six-month periods and were not affected by the grubbing treatments (Table 3).

3.2. Experiment 2 – seedling recruitment and survival

On the plots where *N. trichotoma* seeds were not added, very few seedlings of *N. trichotoma* arose irrespective of site, aspect or disturbance, and all of these died, resulting in net population sizes in year 7 of zero in all cases (Table 4). In contrast, in all but one case, many seedlings arose when seeds were added (from 0 to 51% of the sown seed). More arose on the southwest-slope plots than on the northeast plots at two of the three sites and more arose on disturbed plots in all but one case, although this was significant only on the southwest slope at Sealrock 1. Death rates were high in all cases, resulting in low net population sizes representing 0–9% of the sown seed at 7 years from sowing. Most of the recruitment occurred in the first year, implying low levels of dormancy in the sown seeds, whilst most deaths occurred within the first two years (Fig. 5).

Of the plants arising during the first year on the “+seed + disturbance” treatment, only 12 survived beyond 5 years. All mortalities were “natural”. The basal diameters of these first-year survivors reveal that their growth continued on the northeast slopes, whilst on the southwest slopes, growth was initially slower and ceased after three years (Fig. 6). Flowering occurred only on the northeast slopes in plants 3 or more years old.

3.3. Experiment 3 – buried seed longevity

There was no significant effect of either site or aspect on the decay rates of viable seeds in either the 0–1 or the 1–5 year periods in Experiment 3a, and no effect of site, aspect or seed provenance on the decay rates in these two periods in Experiment 3b (Fig. 7).

In Experiment 3a (as an average over all sites), the decay in viable seeds in the first year (or 1.0219 years to be exact) was 76%; thereafter it was slower, at $(1 - e^{-0.301}) \times 100 = 26\%$ year⁻¹ (of the viable seeds present at the beginning of each successive year) (Fig. 7a). In Experiment 3b, for which samplings were done at three-monthly intervals during the first year, the decay in viable seeds occurred primarily during the first three months (or 0.2548 years to be exact) and was 89%; thereafter it was estimated to be zero (Fig. 7b). In Experiment 3b, the year 3 and 4 data points appear unexpectedly high, but we have been unable to find a plausible explanation (e.g., involving between year differences in TTC technique and interpretation, TTC batch and TTC solution age).

3.4. Experiment 4 – plant size and seed yield

The (square root transformed) number of panicles plant⁻¹, spikelets (potential seeds) panicle⁻¹ and their product, spikelets plant⁻¹, for each of the three sites in each of 2001 and 2002 are plotted against plant basal diameter in Fig. 8 along with the linear regressions fitted across sites and years. Slopes for all variables for individual sites

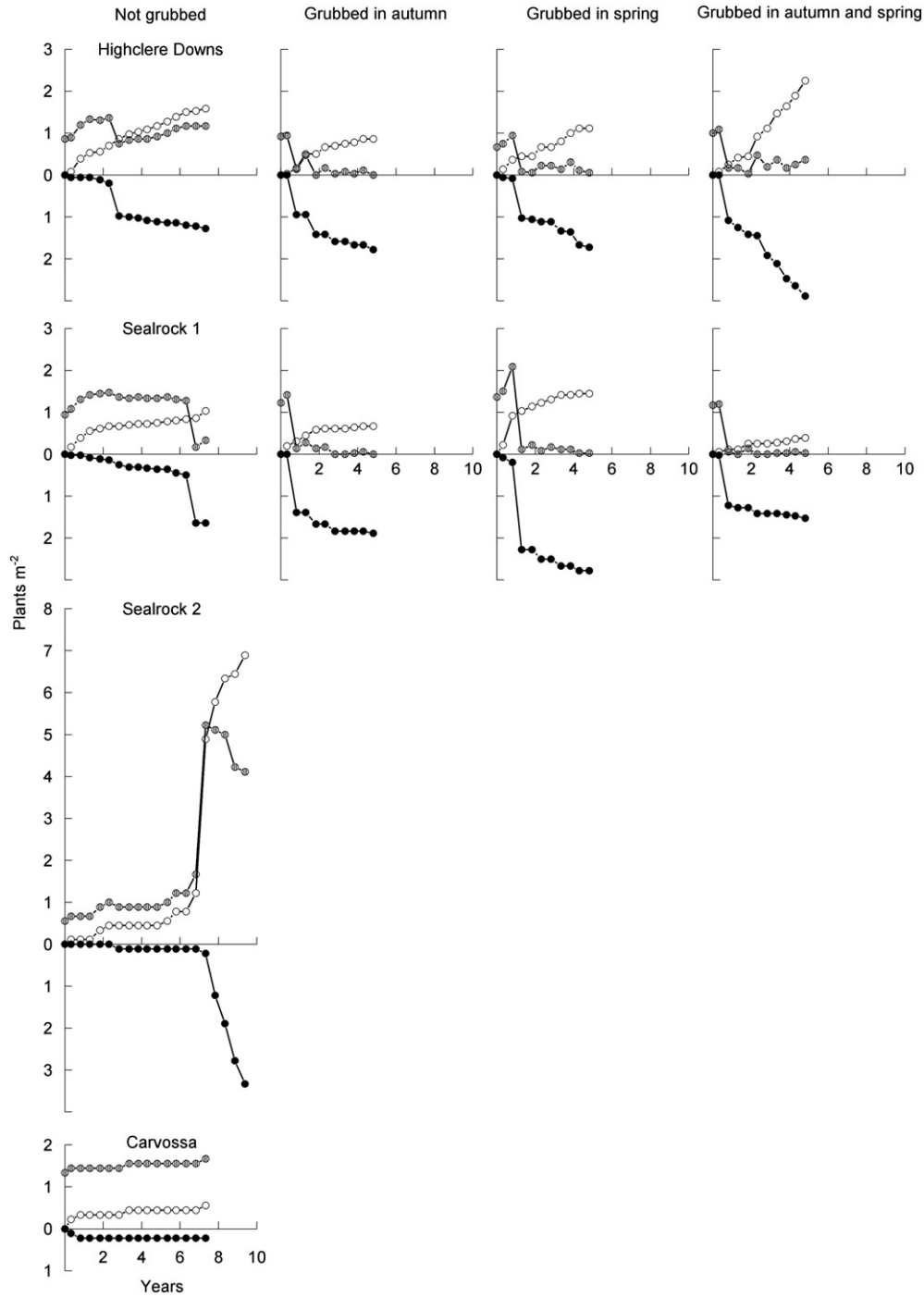


Fig. 1. Population flux in *Nassella trichotoma* in pastures on northeast slopes at four sites in North Canterbury in the absence of grubbing and under three different annual grubbing treatments (grubbed in autumn, grubbed in spring, grubbed in autumn and spring) at two of the sites in Experiment 1. Plotted against years from the beginning of the experiment (mean of 23 Dec 1998) are: cumulative gains (○—○); cumulative losses (●—●) and net population size (○—●). NB: the abrupt increase in losses on the not-grubbed plots at Highclere Downs in October 2001 (at 2.8 years) and at Sealrock 1 in October 2005 (at 7.8 years) resulted from accidental grubbing operations.

Table 2
Population growth rate estimates for *Nassella trichotoma* in Experiment 1 for the “not grubbed” northeast facing plots. Assuming exponential growth between the first N_0 and last N_t , using April measurements (Fig. 1), the intrinsic rate of population increase r , is $r = \ln[(N/N_0)^{1/t}]$ where t is years and $N_t = N_0 e^{rt}$. The doubling time is $t = \ln(2)/r$ and the net reproductive rate, in units of plants plant⁻¹year⁻¹, is e^r .

	Highclere Downs		Sealrock 1	Sealrock 2	Carvossa	Means (weighted by years)
	Before accidental grubbing	After accidental grubbing				
Intrinsic rate of increase, r	0.2130	0.0841	0.0275	0.2021	0.0204	0.107
Doubling time (years)	3.25	8.24	25.19	3.43	33.91	6.49
Net reproductive rate, e^r	1.237	1.088	1.028	1.224	1.021	1.113

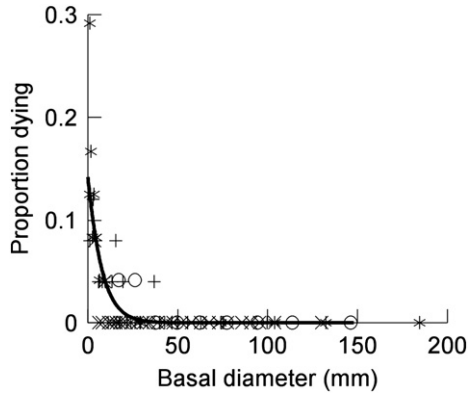


Fig. 2. Relationship between the probability of a *Nassella trichotoma* plant dying within a six-month period and its basal diameter at the beginning of this period on the “not grubbed” plots in Experiment 1, based on data pooled over four sites and seven years. The fitted logit equation is $p = e^{\text{lin}} / (1 + e^{\text{lin}})$, where $\text{lin} = -1.802 - 0.1408 \times d$, where p = proportion dying and d = basal diameter (mm). Symbols give the proportion of plants dying in successive groups of either 24 or 25 plants, where the data were pooled across the 7 years, sorted according to increasing basal diameter, then grouped; Highclere Downs (+), Sealrock 1 (x), Sealrock 2 (*) and Carvossa (o).

within each year, except for spikelets panicle⁻¹ at Sealrock 2, were significant ($P < 0.001$). In 2001 the slopes of the regressions of panicles plant⁻¹ and spikelets plant⁻¹ for Sealrock 2 were significantly lower from those for Greta Valley and Waipara River. Also, the slope of the regression for spikelets panicle⁻¹ was significantly lower for Sealrock 2 than Waipara River. There were no other differences between sites in the slopes of these relationships. The data values ranged from 0 to 1160 for panicles plant⁻¹, 8 to 86 for spikelets panicle⁻¹ and 0 to 51,388 for spikelets (potential seeds) plant⁻¹.

4. Discussion

The rates of population increase in the absence of grubbing in Experiment 1 (Fig. 1 and Table 2) enable estimation of the time needed for a founder population of *N. trichotoma* to fully occupy its niche on a farm. This is the “growth rate” parameter in Denne’s (1988) population model for which a realistic value, based on anecdote, was considered to be 40 years starting from an initial population of 500 seedlings on a typical 900 ha farm (0.55 plants ha⁻¹). Economic analyses using this model were highly sensitive to time-to-saturation across the range 10–100 years considered, highlighting the need for a robust estimate. To that end we assume that population growth in *N. trichotoma* slows as density approaches an upper limit (Cousens and Mortimer, 1995) and so can be described by the logistic model,

$$N_t = N_0 \cdot K / [N_0 + (K - N_0) \cdot \exp(-r_0 t)], \tag{2}$$

where N_t is the density (plants ha⁻¹) at time t (years), N_0 is the density at time $t = 0$, K is the carrying capacity (saturation density) (plants ha⁻¹) and r_0 is the intrinsic rate of population growth. From eq. (2), the time required for a population of initial size N_0 to attain (for example) 90% of the carrying capacity K is

$$t = 1/r_0 \cdot \ln\{(K - N_0) / [(1/0.90 - 1) \cdot N_0]\}. \tag{3}$$

Estimates of K for *N. trichotoma* (eq. (3)) in modified tussock-grasslands in New Zealand vary from 20,000 and 50,000 (Taylor, 1987) to 34,000 plants ha⁻¹ (Healy, 1945). Taking the average of these estimates gives $K = 35,000$, a value similar to the maximum of 40,000 used by Denne. Assuming that the five estimates of r in Table 2, derived from measurements in *N. trichotoma* at starting densities of approximately 10,000 plants ha⁻¹ (Fig. 1) approximate

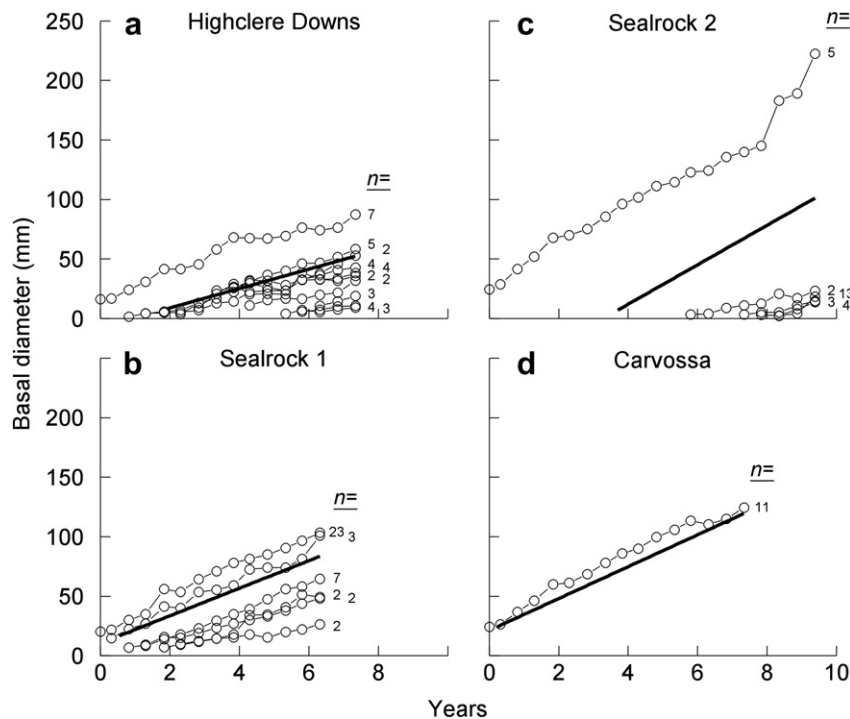


Fig. 3. Growth in basal diameter (mm) of *Nassella trichotoma* plants from each cohort that survived until the end of the experiment, for “not grubbed” plots on the northeast slopes in Experiment 1 for (a) Highclere Downs, (b) Sealrock 1, (c) Sealrock 2 and (d) Carvossa. Mean values are shown (o) for all cohorts consisting of two or more surviving plants; the number of surviving plants in each cohort (n) is shown on the graphs. The numbers of cohorts with a single surviving plant (not shown on graph) were (a) 3, (b) 5, (c) 5 and (d) 3. The equations for the average lines, fitted by analysis of covariance, are (a) $y = 30.7 + 8.1(t - 4.7)$, (b) $y = 49.3 + 11.6(t - 3.5)$, (c) $y = 53.7 + 16.6(t - 6.5)$ and (d) $y = 71.1 + 13.4(t - 3.7)$, where y is basal diameter in mm and t is time in years after the beginning of the experiment. For (b) Sealrock 1, the time period for these data was shortened due to an accidental grubbing and for (c) Sealrock 2 the data collection period was extended.

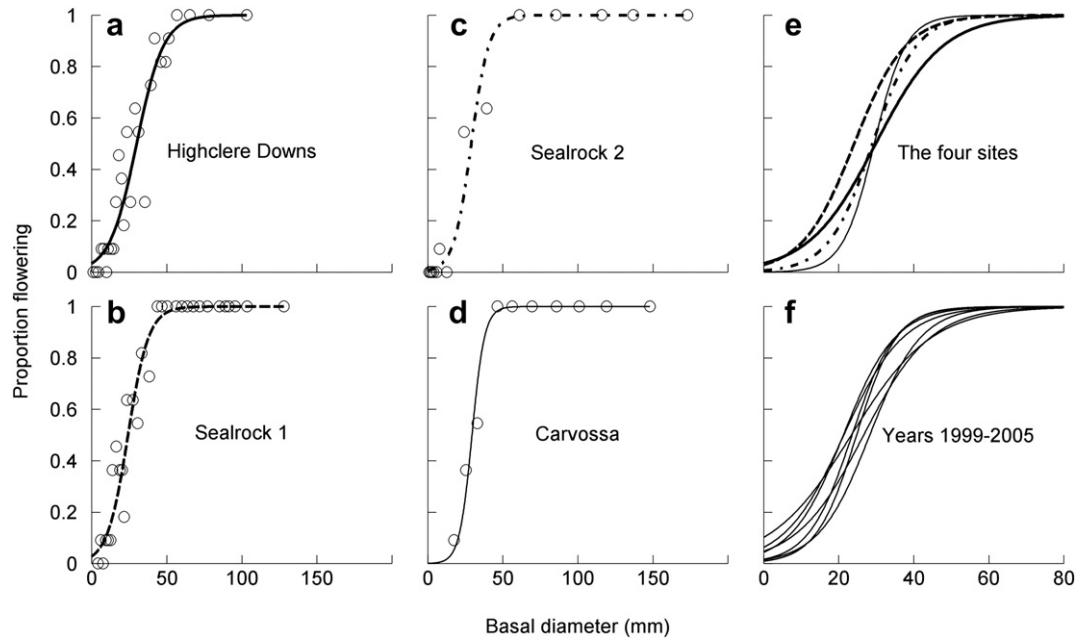


Fig. 4. Relationships between the probability of a *Nassella trichotoma* plant flowering and its basal diameter on the “not grubbed” plots at the four sites over seven years in Experiment 1. The fitted logit equations are $p = e^{\text{lin}} / (1 + e^{\text{lin}})$, where (a) $\text{lin} = -3.324 + 0.1114 \times d$ for Highclere Downs, (b) $\text{lin} = -3.504 + 0.1454 \times d$ for Sealrock 1, (c) $\text{lin} = -4.959 + 0.1712 \times d$ for Sealrock 2 and (d) $\text{lin} = -7.04 + 0.2391 \times d$ for Carvossa, where p = proportion flowering and d = basal diameter (mm). Symbols give the proportion of plants flowering in successive groups of either 10 or 11 plants, where the data are pooled across the 7 years, sorted according to increasing basal diameter then grouped. In (e) the above fitted curves are given without the data and in (f) the logit curves are shown for each of the 7 years fitted to the data pooled across the four sites (equations are not given). Over all sites and years, the fitted logit equation is $\text{lin} = -3.646 + 0.1325 \times d$.

r_0 (eq. (3)), then r_0 varies between 0.213 and 0.02; this assumption is reasonable since it is unlikely that plants at this density would interfere with their neighbours. For comparison, the value of r_0 from the exponential model of population growth used by Denne, $r_0 = \ln(40,000/0.55)/40 = 0.2799$, is considerably higher than our empirical estimates.

Using the five estimates of r_0 from Table 2 with $K = 35,000$ and $N_0 = 17$ (the current mean density in the Hurunui District (Bourdôt and Saville, 2007)) in eq. (3), t ranges from 46 to 482 years with a mean $t_{0.90} = 210 \pm 198$ (one standard deviation) years. By comparison, using the value $r_0 = 0.2799$ derived from Denne's exponential model, $t_{0.90} = 35$ years. These estimates of time from initial introduction to saturation (210 and 35 years) differ by

a factor of six. This difference in time-to-saturation estimated from our experiments and from anecdote in the mid 1980s implies that modified tussock-grasslands in North Canterbury are less susceptible now to invasion by *N. trichotoma* than they were historically. This could be explained by the reduced use of fire as a vegetation management tool, less overgrazing, an increase in fertiliser use, the introduction of exotic pasture species and a dramatic decline in rabbit populations enabled by the 1948 Land Act and the wool boom of 1951 (Bell and Douglas, 1992; Douglas and Allan, 1992) leading to grasslands that are less disturbed and less prone to invasion (Healy, 1945).

The management-decision implications of this result are two-fold. Firstly, in the national cost-benefit analysis of annual

Table 3
The effect of grubbing treatments on the rates of gain (recruitment) and loss (death + coalescence) of *Nassella trichotoma* plants from late December 1998 until mid October 2003 in Experiment 1. Values are means over four replicates. – indicates valid statistical analysis not possible due to too many zero values.

Treatment	Gains (plants $\text{m}^{-2} \text{y}^{-1}$)	Seasonal gains (plants m^{-2} (6 months) $^{-1}$)		Losses (plants $\text{m}^{-2} \text{y}^{-1}$)	Seasonal losses (plants m^{-2} (6 months) $^{-1}$)	
		Spring–Summer (October–April)	Autumn–Winter (April–October)		Spring–Summer (October–April)	Autumn–Winter (April–October)
<i>Highclere Downs</i>						
Control	0.24	0.11	0.13	0.07	0.05	0.03
Grubbed in autumn	0.18	0.14	0.04	0.00	0	0
Grubbed in spring	0.23	0.15	0.09	0.04	0.01	0.03
Grubbed in autumn & spring	0.47	0.29	0.18	0.00	0	0
Least significant diff. (5%)	0.51	0.36	0.19	–	–	–
<i>Sealrock 1</i>						
Control	0.16	0.09	0.07	0.08	0.04	0.03
Grubbed in autumn	0.14	0.08	0.06	0.00	0	0
Grubbed in spring	0.30	0.12	0.18	0.04	0.02	0.02
Grubbed in autumn & spring	0.08	0.03	0.05	0.01	0.01	0
Least significant diff. (5%)	0.22	0.15	0.11	–	–	–

Table 4

The effects of disturbance and addition of *Nassella trichotoma* seeds (1600 m^{-2}) on recruitment, deaths and net population size of *N. trichotoma* (plants m^{-2}) in grazed pastures at three sites on two aspects, and overall, in North Canterbury, accumulated over the 7-year duration of Experiment 2 (in the case of “seeds added”, data correspond to the year 7 data points in Fig. 5). Recruits and net population size are also given as a percentage of seeds added, and deaths as a percentage of recruits (in italics). SW = southwest; NE = northeast; LSD = Least Significant Difference; Signif. of diff. = Significance of difference between “Not disturbed” and Disturbed when *N. trichotoma* seeds added; ns = not significant; * = significant at 5% level of probability; ** = significant at 1% level of probability.

	Aspect	<i>N. trichotoma</i> seeds not added		<i>N. trichotoma</i> seeds added				LSD (5%) (no. m^{-2})	Signif. of diff. (no. m^{-2})
		Not disturbed	Disturbed	Not disturbed		Disturbed			
		(no. m^{-2})	(no. m^{-2})	(no. m^{-2})	(%)	(no. m^{-2})	(%)		
Recruits									
Highclere Downs	SW	0	0	44	2.8	84	5.3	254	ns
	NE	4	0	228	14.3	180	11.3	343	ns
Sealrock 1	SW	0	4	80	5.0	716	44.8	261	**
	NE	0	0	0	0	248	15.5	276	ns
Carvossa	SW	4	0	216	13.5	820	51.3	809	ns
	NE	0	4	68	4.3	80	5.0	76	ns
Overall		1	1	106	6.6	355	22.2	320	ns
Deaths									
Highclere Downs	SW	0	0	44	100	84	100	254	ns
	NE	4	0	224	98.2	172	95.6	339	ns
Sealrock 1	SW	0	4	80	100	568	79.3	307	*
	NE	0	0	0	–	224	90.3	264	ns
Carvossa	SW	4	0	204	94.4	796	97.1	742	ns
	NE	0	4	68	100	60	75.0	61	ns
Overall		1	1	103	97.5	317	89.5	285	ns
Net population size									
Highclere Downs	SW	0	0	0	0	0	0	–	–
	NE	0	0	4	0.25	8	0.50	32	ns
Sealrock 1	SW	0	0	0	0	148	9.25	177	ns
	NE	0	0	0	0	24	1.50	49	ns
Carvossa	SW	0	0	12	0.75	24	1.50	76	ns
	NE	0	0	0	0	20	1.25	24	ns
Overall		0	0	3	0.17	37	2.33	59	ns

grubbing, a time-to-saturation density of less than 35–65 years was necessary (depending on assumed stock prices and rate of spread) to achieve a Net Present Value of 0.0 and hence profitable management (Fig. 3 in Denne, 1988). Slower rates of population growth as in our experiments, would have led to the opposite conclusion; the management programme being non-profitable at a national scale.

Secondly, as illustrated by Denne, the slower the population growth rate, the stronger is the economic case at the individual farm scale for grubbing less frequently than annually (Fig. 8 in Denne, 1988). Counteracting this effect is that as the efficiency of grubbing falls the economic case for more frequent grubbing increases (Fig. 8 in Denne, 1988). Recent experiments showed that on average, only 34% of *N. trichotoma* plants are grubbed during commercial grubbing operations (Verkaaik et al., 2006), an efficiency far lower than the 50–100% previously assumed. Also, the percentage grubbed is not, as previously assumed, constant across all plant-size classes, but rather, increases with plant diameter to a maximum of 60% grubbed at 95 mm, declining thereafter (Verkaaik et al., 2006). This supports the need for a size-structured population model for *N. trichotoma* to enable a realistic analysis of population growth under alternative management strategies.

The need for a size-structured population model is also supported by the size dependencies of plant mortality (Fig. 2), flowering (Fig. 4) and seed production (Fig. 8). In Denne's (1988) population model, only adult plants die, and do so due to crowding, although Healy (1945) had shown that mortality among seedlings can be as high as 100%. In our field experiments, where there was little or no crowding, only plants less than 50 mm in basal diameter died, and the probability of doing so increased sharply

below 50 mm diameter (Fig. 2). The effect of restricting mortality to adults probably results in overestimation of population growth during the early phase of the invasion (r_0) and thus a quicker approach to saturation (K). By contrast, the assumption that time to reproductive maturity is 1–3 years from germination (Table 1 in Denne, 1988) is supported by Experiments 1 and 2. In Experiment 1, averaged over all plants and sites, the models fitted to the probability of flowering show that a plant must attain a basal diameter of 28 mm to have a 50% chance of flowering (Fig. 4). Since these naturally-occurring plants were growing at an average rate of 12 mm year^{-1} , the mean age of a plant with a 50% chance of flowering is $28/12 = 2.3$ years. Similarly, plants sown in Experiment 2 flowered only after reaching three years of age.

Seed yield in Denne's population model was taken to be 100 seeds plant^{-1} in the plant's first seeding year (at age 1–3 years), and 100,000 year^{-1} in a “mature” plant (Healy, 1945). The results from Experiment 4 suggest that 100 seeds plant^{-1} may be an underestimate; here the number of spikelets (each with potentially one seed) plant^{-1} is $(13.48 + 1.188 \times \text{basal diameter})^2$ (Fig. 8). Thus the average 3-year-old reproductive plant of 30 mm diameter on a northeast slope (Fig. 6) will produce 2413 spikelets, many more than 100 seeds plant^{-1} assumed by Denne. By contrast, Denne's assumption, of 100,000 seeds (mature plant) $^{-1}$ may be realistic providing that the historical average “mature” plant diameter was about 255 mm, since by the above equation a plant of this size will produce 100,122 spikelets.

The number of seeds entering the soil, surviving in the soil seed bank, and their rates of germination and recruitment as plants to a *N. trichotoma* population can also be expected to have substantial effects on population growth in the absence of management, and hence also on the economics of grubbing. Denne's population

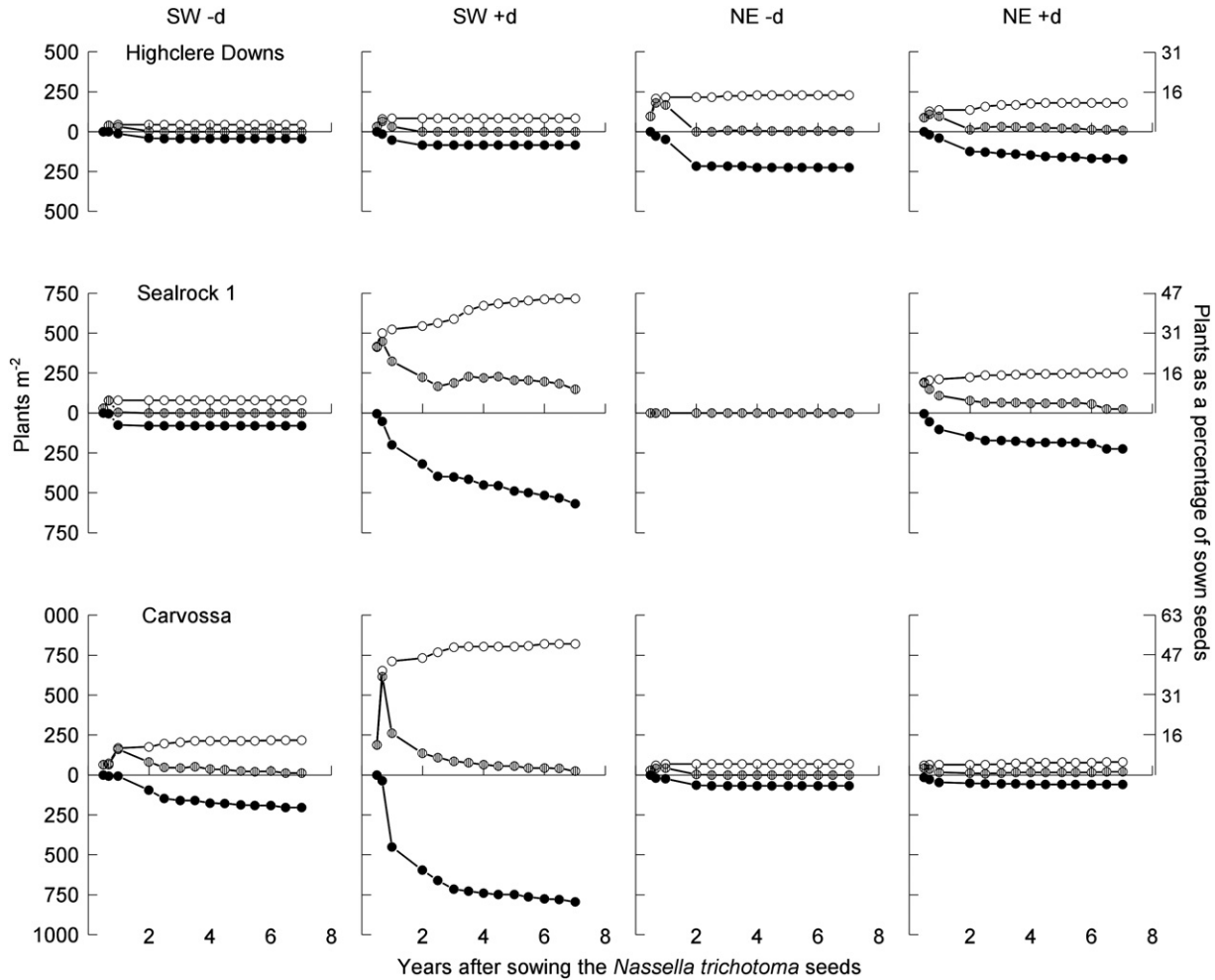


Fig. 5. Population flux in *Nassella trichotoma* in grazed pastures at three sites in North Canterbury, New Zealand, in which seeds of *N. trichotoma* were added to either disturbed (+d) or intact (–d) pasture on either northeast (NE) or southwest (SW) slopes in Experiment 2. Plotted against years from the beginning of the experiment (21 April 1999) are: cumulative recruits (○—○); cumulative deaths (●—●) and net population size (○●—○●) averaged over four replicate plots. Data from the “–seed” plots are not shown.

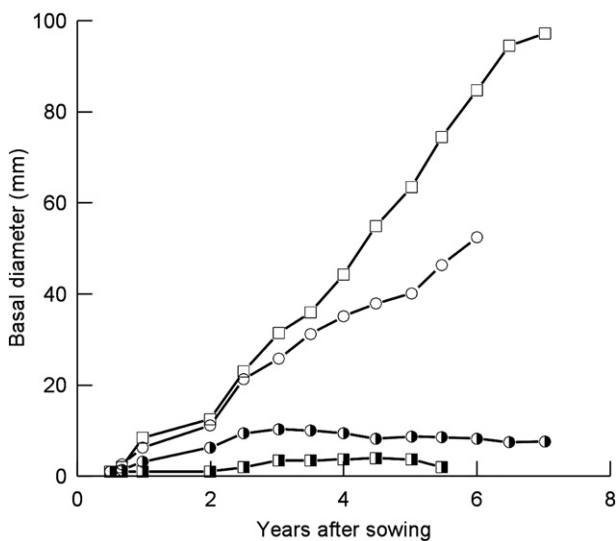


Fig. 6. Increase over time in the basal diameter of the *Nassella trichotoma* plants that recruited in the first year, and that survived beyond 5 years, on the “+seed + disturbance” treatment on northeast and southwest slopes at Sealrock 1 (○ and ●; 6 and 2 plants respectively) and Carvossa (□ and ■; 2 plants each) in Experiment 2. The six plants surviving on the northeast slope at Sealrock 1 were accidentally grubbed in year 6, and the two plants on the southwest slope at Carvossa died from natural causes in year 5.

model apparently assumed all seeds produced enter the soil. However, a recent experiment in Canterbury, NZ, suggests that only 2.6% do so (Lusk et al., 2008) implying that Denne’s model would overestimate population growth. Also, the annual seed survival rate of 0.1–0.2% year⁻¹ in Denne’s model may be one or two orders of magnitude lower than actual rates according to Experiment 3 in which 26 and 11% of viable seeds added to the soil in pasture survived for the first year, and 74 and 100% (of those surviving) survived annually thereafter (Fig. 7), leading to underestimation of population growth in Denne’s model. The extent to which these model assumptions cancel with respect to predicted population growth is unknown.

Denne also assumed that seeds produced new plant recruits from the seed bank (“germinated”) at a rate of 0.1–0.2% annually based on observations in Australia (Campbell, 1982) and New Zealand (Healy, 1945). By contrast, in Experiment 2, in which seeds were added to the undisturbed soil surface in pasture on NE slopes, the measured recruitment rates of between 0 and 0.25% over seven years (Table 4) reveal that the actual annual recruitment rate may be much lower ($\leq 0.25/7 = 0.04$). The higher recruitment in Denne’s model would tend to overestimate population growth.

A significant simplification in Denne’s population model is that all land is uniformly susceptible to invasion. The effect of this assumption is probably nil since the benefits and costs of

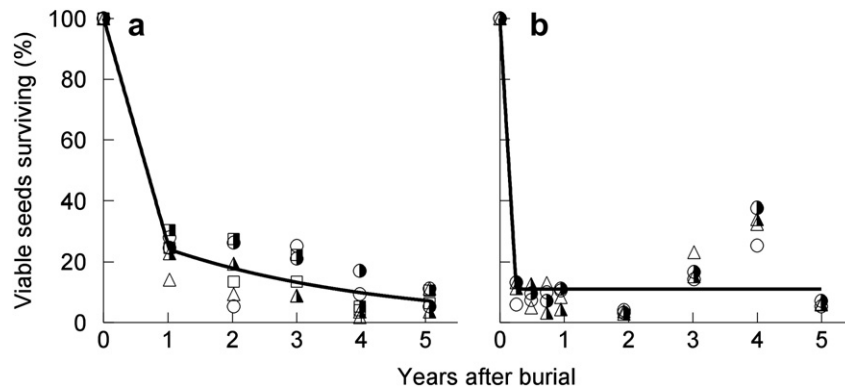


Fig. 7. The decay of seeds of *Nassella trichotoma* following burial 25 mm deep in pasture at (a) three sites in April 1999 (Experiment 3a) and (b) two sites in April 2001 (Experiment 3b). Symbols give the means for northeast and southwest slopes (open and half-filled respectively) for Sealrock 1 (\circ , \bullet), Highclere Downs (\triangle , \blacktriangle) and Carvossa (\square , \blacksquare). In (a) the decay in the first year is given by $y = 100 - (75.93/1.0219)t$ (based on the initial sampling and that closest to year one, at $t = 1.0219$ years), and thereafter by $y = 24.07e^{-0.301(t - 1.0219)}$, where y is the number of viable seeds remaining as a percentage of the number of viable seeds buried and t is time (years after burial). In (b) the decay in the first three months is given by $y = 100 - (88.93/0.2548)t$ (based on the initial sampling and that closest to three months, at $t = 0.2548$ years), and thereafter by $y = 11.07$ (that is, no decay, corresponding to a fitted parameter of $b = 0$).

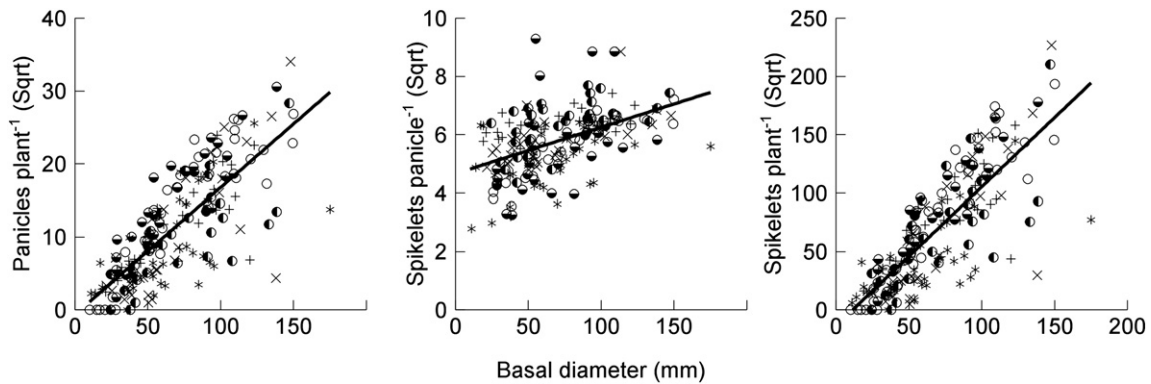


Fig. 8. Relationships between square root of the number of panicles plant⁻¹ (y_1), spikelets panicle⁻¹ (y_2), and spikelets plant⁻¹ (y_3), and plant basal diameter (d) (mm) in *Nassella trichotoma* at three sites in each of 2001 and 2002 in Experiment 4. The sites for 2001 are Sealrock 2 (*), Greta Valley (\bullet) and Waipara River (\circ) and those for 2002 are Highclere Downs (+), Sealrock 1 (\times) and Waipara River (\bullet). The lines are the regressions fitted to the data from all sites and years for each variable: $y_1 = -0.634 + 0.174d$, $y_2 = 4.66 + 0.016d$ and $y_3 = -13.48 + 1.188d$.

management would have been equally inflated, cancelling each other. In reality the ability of *N. trichotoma* to invade pasture depends upon aspect ($N > W > E > S >$ flat land) and vegetation class (tussock-grassland and scrubland $>$ forest $>$ improved pasture) (Bourdôt and Saville, 2005). Our inability to find sites on southerly/easterly-facing slopes for Experiment 1 and that the *N. trichotoma* plants in Experiment 2 establishing from sown seed grew continually on the northeast slopes whilst not on the southwest slopes (Fig. 6), are consistent with the observation that southwest slopes are at low risk of invasion (Healy, 1945). An explanation for this is that the more persistent vegetation cover on these “shady” slopes prevents *N. trichotoma* plants that establish there from growing large enough to reproduce. These considerations justify restricting a population model for *N. trichotoma* to the northerly-facing land.

5. Conclusions

From experimental data using a logistic model, we have derived an estimate of 210 years for *N. trichotoma* to increase to 90% of carrying capacity supporting the hypothesis that population growth is slower than may have occurred historically in the modified tussock-grasslands in North Canterbury, New Zealand. As a possible explanation, we have also shown that the rates of some demographic processes, in particular seedling recruitment and seeds entering the

soil, may be much lower than in the past. This may be due to a less disturbed vegetation cover as a result of reduced use of fire, lowered grazing pressure from rabbits and livestock, and generally improved pasture management through subdivision, fertiliser use and the over-sowing of exotic clovers and grasses. Finally, the size-dependence of many processes supports the need for a size-structured model to explain population growth in this weed.

Acknowledgements

We thank the Foundation for Research, Science and Technology, New Zealand, for funding this research under the programmes Outsmarting Weeds (C10X0318) and Undermining Weeds (C10X0811), Gerald Herbert, Trevor Carson and Peter Lamb for providing the sites for the experiments, Environment Canterbury for logistical and financial support and Stan van Uden and Michelle Verkaaik for technical support.

References

- Beggs, J.P., 1958. Control of *Nassella* tussock. In: Matthews, L.J. (Ed.), 11th New Zealand Weed and Pest Control Conference. The New Zealand Weed Control Conference Inc., Triple Links Hall, Blenheim, pp. 14–19.
- Bell, J., Douglas, M., 1992. Control and management of rabbits. In: Floate, M. (Ed.), Guide to Tussock Grassland Farming. New Zealand Pastoral Agriculture Research Institute Ltd, Mosgiel, pp. 93–98.

- Bourdôt, G., Saville, D., 2005. Monitoring Nassella Tussock (*Nassella trichotoma*) Under Environment Canterbury's Regional Pest Management Strategy – Year 8 (2004–2005). AgResearch, Lincoln, 31 pp.
- Bourdôt, G., Saville, D., 2007. Monitoring Nassella Tussock (*Nassella trichotoma*) Under Environment Canterbury's Regional Pest Management Strategy – Year 10 (2006–2007). AgResearch, Lincoln, 27 pp.
- Bourdôt, G.W., Hurrell, G.A., Saville, D.J., 1992. Eradication of nassella tussock (*Nassella trichotoma*), an unlikely outcome of grubbing. *New Zealand Journal of Agricultural Research* 35, 245–252.
- Campbell, M.H., 1982. The biology of Australian weeds. 9. *Nassella trichotoma* (Nees) Arech. *Journal of the Australian Institute of Agricultural Science* 48, 76–84.
- Cousens, R., Mortimer, M., 1995. *Dynamics of Weed Populations*. Cambridge University Press, Cambridge.
- Denne, T., 1988. Economics of nassella tussock (*Nassella trichotoma*) control in New Zealand. *Agriculture, Ecosystems and Environment* 20, 259–278.
- Dingwall, A.R., 1962. The weeds of Canterbury. In: Matthews, L.J. (Ed.), 15th New Zealand Weed and Pest Control Conference. The New Zealand Weed Control Conference Inc., Caledonian Hall, Christchurch, pp. 15–22.
- Douglas, M., Allan, B., 1992. The tussock grassland. In: Floate, M. (Ed.), *Guide to Tussock Grassland Farming*. New Zealand Pastoral and Agriculture Research Institute Ltd, Mosgiel, pp. 9–22.
- ECan, 2005. *Canterbury Regional Pest Management Strategy 2005–2015*. Environment Canterbury.
- Gibbs, H.S., 1980. *New Zealand Soils – An Introduction*. Oxford University Press, Wellington.
- Healy, A.J., 1945. *Nassella Tussock (Nassella trichotoma (Nees.) Hack.)*. Field Studies and Their Agricultural Significance. Department of Scientific and Industrial Research New Zealand.
- Lamoureux, S., Bourdôt, G., 1999. Nassella tussock management in New Zealand. In: Bishop, A.C., Boersma, M., Barnes, C.D. (Eds.), *Twelfth Australian Weeds Conference*. Tasmanian Weed Society Inc., Hobart, Australia, pp. 16–19.
- Leonard, W.F., 1956. Nassella Tussock. In: Matthews, L.J. (Ed.), 9th New Zealand Weed Control Conference. The New Zealand Weed Control Conference Inc., Caroline Bay Hall, Timaru, pp. 29–35.
- Leonard, W.F., 1962. Nassella tussock control – research and field practice. In: Matthews, L.J. (Ed.), 15th New Zealand Weed and Pest Control Conference. New Zealand Weed and Pest Control Conference Inc., Caledonian Hall, Christchurch, pp. 39–46.
- Lough, R.S., 2009. *The Current State of Rabbit Management in New Zealand – Issues, Options and Recommendations for the Future*. MAF Biosecurity New Zealand, 100 pp.
- Lusk, C.S., Lamoureux, S.L., Hurrell, G.A., Bourdôt, G.W., 2008. Estimating the fate of seeds in a *Nassella trichotoma* population. *New Zealand Plant Protection* 61, 111–115.
- Milne, R.A., 1954. Nassella tussock control. In: Matthews, L.J. (Ed.), 7th New Zealand Weed Control Conference. The New Zealand Weed Control Conference Inc., Red Lecture Theatre, Medical School, Dunedin, pp. 75–81.
- Peters, J., 2000. *Tetrazolium Testing Handbook*. Contribution 29. Association of Official Seed Analysts, Lincoln, p. Loose Leaf.
- Smith, L.P., Lamoureux, S.L., 2006. When science meets policy – Nassella tussock in New Zealand as a case study. In: Preston, C., Watts, J.H., Crossman, N.D. (Eds.), 15th Australian Weeds Conference. Weed Management Society of South Australia, Adelaide, pp. 450–453.
- Taylor, N.J., 1987. *Ecological Aspects of Nassella Tussock (Stipa trichotoma)*. Botany Division, Department of Science and Industrial Research, Lincoln, New Zealand, 76 pp.
- Verkaaik, M.L., Lamoureux, S.L., Bourdôt, G.W., 2006. Efficacy of grubbing is plant size dependent in Nassella tussock. In: Preston, C., Watts, J.H., Crossman, N.D. (Eds.), 15th Australian Weed Conference – Managing Weeds in a Changing Climate. Weed Management Society of South Australia, Adelaide, pp. 880–882.