WEED RESEARCH An International Journal of Weed Biology, Ecology and Vegetation Management

DOI: 10.1111/wre.12158

Comparison of management strategies for controlling *Nassella trichotoma* in modified tussock grasslands in New Zealand: a spatial and economic analysis

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Received 18 May 2014
Revised version accepted 23 February 2015
Subject Editor: Lammert Bastiaans, WUR, The Netherlands

Summary

The weedy grass *Nassella trichotoma* (nassella tussock), historically an economically damaging invader of modified tussock grasslands in New Zealand, currently causes little if any reduction in farm production. This is a result of successful historical regional management programmes in which plants have been removed manually (by grubbing) each year before they seed. To inform a debate about the need for ongoing regional management, we developed a stage-structured spatially explicit integrodifference equation population model and linked this to a cost analysis. We used the model to compare the weed's future population trajectories and related regional control costs over 50 years under three alternative management scenarios. The total discounted (3% p.a.) costs of *no management*, *three-yearly grubbing* and continued *annual grubbing* were NZ $417 million, $736 million and $131 million respectively. These analyses indicate that annual grubbing of *N. trichotoma* returns a net benefit of $286 million ($417 – $131 million) compared with doing nothing and a net benefit of $605 million ($736 – $131 million) compared with a 3-yearly grubbing programme. These results support the continuation of *annual grubbing* as the long-term economically optimal management strategy for *N. trichotoma* on pastoral farms infested by the weed in New Zealand.

Keywords: weed population model, serrated tussock, nassella tussock, integrodifference, matrix model, cost–benefit analysis.

LAMOUREAUX SL, BASSE B, BOURDÔT GW & SAVILLE DJ (2015). Comparison of management strategies for controlling *Nassella trichotoma* in modified tussock grasslands in New Zealand: a spatial and economic analysis. *Weed Research* **55**, 449–460.

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 *c.* 1860 (Healy, 1945). Following 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), reinvading *N. trichotoma* plants have been removed annually (by manually digging them out; a process known as grubbing) in regionally co-ordinated management programmes (Dingwall, 1962). This effort, sustained until the present day, has resulted in the weed falling to population densities that no longer reduce live-weight gains of sheep and other grazing animals (Bourdôt *et al.*, 1992).

The need for ongoing management by grubbing, and its optimum intensity and frequency remain topics of debate among landholders and regional policymakers.

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In an earlier attempt to inform this debate, Denne (1988) developed a bio-economic model for *N. trichotoma*, based on data and anecdotal information on the demography of the weed available at the time (Healy, 1945; Campbell, 1982) and the costs associated with the weed and its management. While an economic threshold analysis supported management of the weed at its current low population densities, an optimisation analysis suggested that grubbing once every 3 years would maximise the net benefit to New Zealand (Denne, 1988). This reduced grubbing frequency strategy was not adopted due to concerns that the 30–40 years to reach the saturation density of 50 000 plants ha^{-1} from a starting density of 0.55 seedlings ha^{-1} assumed by Denne (1988) underestimated the weed's potential population growth rate in the absence of grubbing. Thus, the species would increase in population density and geographic extent, rather than be controlled, under such a strategy.

Recent experiments in North Canterbury modified tussock grasslands indicated that estimates of the time to reach saturation are highly variable [35–482 years from a starting density of 17 plants ha^{-1} (Lamoureaux *et al.*, 2011)]. The distribution of population growth rates is also highly variable and right-skewed with a few very high rates (James *et al.*, 2011). Nevertheless, it is possible that the population growth rate of *N. trichotoma* is on average slower today than historically due to less disturbed and hence more competitive grassland vegetation on farms today (Lamoureaux *et al.*, 2011). These experiments also revealed that some demographic processes in *N. trichotoma* (flowering, seed production, plant mortality) were strongly plant-size-dependent. Another study showed that the plant death rate due to grubbing was size-dependent and, on average, much lower than that assumed by Denne (Verkaaik *et al.*, 2006). These revelations supported the need for a plant-size-structured model for population growth in this weed, parameterised using data on the weed's demographic processes under current pastoral farm management conditions (Verkaaik *et al.*, 2006; Lamoureaux *et al.*, 2011). Only then might realistic simulations of alternative grubbing management strategies, and their economic consequences, be possible (Lamoureaux *et al.*, 2011). A new model would also ideally need to be spatially explicit, because in both the Marlborough and Canterbury regions, *N. trichotoma* exists as a metapopulation made up of many spatially separate populations varying greatly in size and distributed across many hundreds of pastoral farms (James *et al.*, 2011). Such a model would be able to account for spread of the weed between properties and the effect on the metapopulation of grubbing rates that are either population size- and/or population density-dependent.

The model that we present here (NASSIM) is a spatially explicit plant-size-structured simulation version of an implicitly spatial metapopulation model for *N. trichotoma* developed earlier (James *et al.*, 2011). It is parameterised using demographic data on *N. trichotoma* from field experiments (Lamoureaux *et al.*, 2011). Coupled with the lost revenue and control costs associated with *N. trichotoma*, it enables analysis of the behaviour of the metapopulation and the economics of its control under alternative management strategies, including spatially variable strategies. We apply the model here to compare the economics of three alternative management strategies.

Materials and methods

The model

The population density distribution of *N. trichotoma* in the Hurunui district, North Canterbury, New Zealand, was simulated using a plant life history stage-structured, integrodifference spatial model (NASSIM). The model's extent is a 200 × 200 km (4 million ha) area in North Canterbury encompassing approximately 900 *N. trichotoma*-infested pastoral properties in the Hurunui district (Fig. 1). Within this area, at continuous spatial co-ordi-

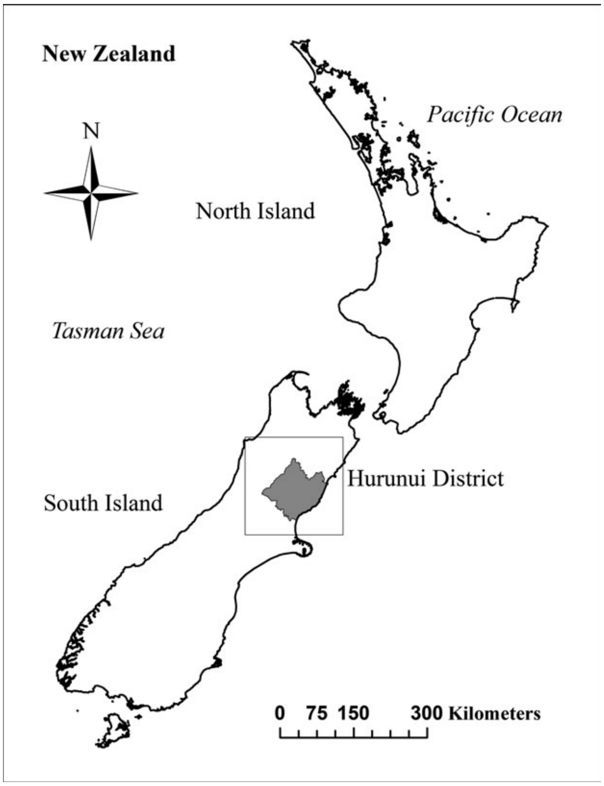

Fig. 1 Map of New Zealand showing the Hurunui district (grey area) of North Canterbury and the model's extent (200 km x 200 km box surrounding the Hurunui district). The average size of a property in the Hurunui district is about 360 ha (approximately 23 15 ha cells in the model).

nates (x, y), the model counts the number of *N. trichotoma* plants twice a year for 50 years with $t = 0, 1, 2, 3, \ldots, 50$ being spring censuses and $t = 0.5, 1.5, 2.5, \ldots, 49.5$ autumn censuses. The model begins in spring 2010 ($t = 0$) making the first season (the interval from $t = 0$ to $t = 0.5$) a summer. It follows seven *N. trichotoma* life stages (Fig. 2) comprising two seedbank stages denoted as *SB1* and *SB2* for seeds that have been in the seedbank for less than or greater than one year respectively. In addition, there are five plant stages denoted as *Imm*, *VS*, *S*, *M* and *L* for plants that have an average basal diameter (mm) classified respectively as immature [0, 10 mm), very small [10, 20 mm), small [20, 60 mm), medium [60, 140) and large (≥140 mm) (Lamoureaux *et al.*, 2011). Most model parameters were derived from data from field experiments in North Canterbury (Verkaaik *et al.*, 2006; Bourdôt & Saville, 2011; Lamoureaux *et al.*, 2011) (Table 1). The

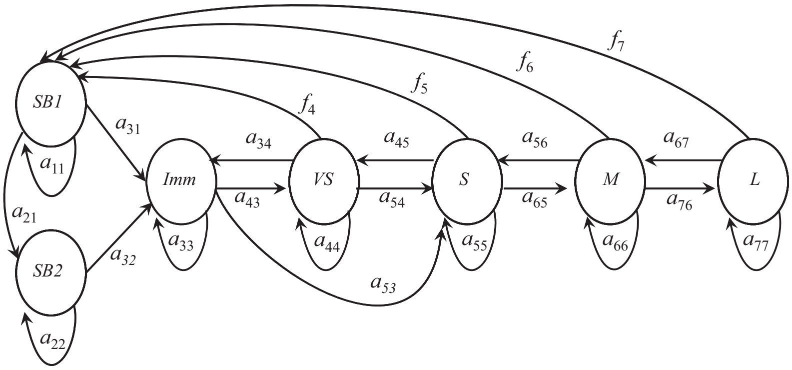

Fig. 2 A 6-monthly life cycle graph for *Nassella trichotoma* (autumn–spring or spring–autumn) depicting different plant size and seed-age life stages with possible transitions. The stages are seeds in the soil less than and more than 1 year old (*SB1* and *SB2* respectively); immature non-reproductive plants (*Imm*); very small (*VS*), small (*S*), medium (M) and large (*L*) plants able to reproduce.

Table 1 Definitions of NASSIM model input parameters

Parameter	Description
t	Time 0–50 years
x, y	Continuous spatial co-ordinates (km) covering an extent 200 × 200 km
dx, dy	Grid square length 0.3906 km
SB1, *SB2*, *Imm*, *VS*, *S*, *M*, *L*	Life stage acronyms: Seedbank seeds (*SB1* and *SB2*) in the soil less than and more than 1 year respectively; immature non-reproductive plants (*Imm* [0, 10 mm)); very small (*VS* [10, 20 mm)); small (*S* [20, 60 mm)); medium (*M* [60, 140)) and large (*L* ≥ 140 mm)) plants
$p, q = 1, 2, \ldots, 7$	Life stage indices
$n_p(x, y, t)$	Number of individuals in life stage p, plants or seeds ha^{-1} at location (x, y) and time t
n_{p0}	Initial ($t = 0$) average number of individuals in life stage p, plants or seeds ha^{-1} (average over initial infested area)
a_{pq}	Transition rate: Probability of transferring from life stage q to stage p per 6-month period: where $p > q$ (growth); $p < q$ (shrinkage); $p = q$ (stasis)
α_p, $p \geq 4$	Probability of a plant in life stage p producing seed
s_p, $p \geq 4$	The number of seeds produced per reproducing plant in stage p per 6-month period
ν	The proportion of seeds produced that are viable
β	Probability of a seed entering the seedbank
$f_{1q} = \alpha_p s_p \nu \beta$, $p \geq 4$	Number of viable seeds that join the seedbank
g_p	Proportion removed (grubbed) per 6-month period
σ^2	Variance of dispersal kernel
$k(d)$	Dispersal kernel which gives the probability of seeds dispersing distance $d = \sqrt{(x-u)^2 + (y-v)^2}$ kilometres from (u,v) to (x,y)
$\mathbf{K}$	Dispersal kernel matrix
$\mathbf{n}_t^{xy}$	Column vector of life stages at location (x, y) and time t
$\mathbf{A}_S = [a_{pq}]$ $\mathbf{A}_W = [a_{pq}]$	Summer (S) and winter (W) transition matrices
$\mathbf{F}_S$	Fecundity matrix (summer only)
$\mathbf{G}_S = [g_p]$ $\mathbf{G}_W = [g_p]$	Summer (S) and winter (W) grubbing matrix (diagonal) where g_p is the grubbing rate in life stage $p = [1–7]$

density of *N. trichotoma* in each life stage at each location (x, y) at time t is represented by the vector $\mathbf{n}(x, y, t) = \mathbf{n}_t^{xy}$ where:

$$\mathbf{n}_t^{xy} = \begin{bmatrix} n_{SB1} \\ n_{SB2} \\ n_{Imm} \\ n_{VS} \\ n_S \\ n_M \\ n_L \end{bmatrix}_t^{xy}$$

The model conforms to the stage-structured integro-difference equation derived from conservation equations for plant demographics and dispersal, as presented in Neubert and Caswell (2000), and uplifted from one to two spatial dimensions and to two seasons (summer, S and winter, W):

$$\mathbf{n}_{t+1}^{xy} = (\mathbf{I} - \mathbf{G}_W)\mathbf{A}_W(\mathbf{I} - \mathbf{G}_S) \iint_R (\mathbf{K}(x-u, y-v) \circ (\mathbf{F}_S + \mathbf{A}_S))\mathbf{n}_t^{uv} du dv. \qquad (1)$$

Reading from right to left, Eqn (1) represents the ecology of *N. trichotoma* during a typical year (t to $t + 1$): summer life stage transitions ($\mathbf{A}_S$) and fecundity ($\mathbf{F}_S$) followed by dispersal ($\mathbf{K}$) over the region R, summer grubbing ($\mathbf{G}_S$), winter transitions ($\mathbf{A}_W$) and winter grubbing ($\mathbf{G}_W$). Here, $\mathbf{I}$ is the identity matrix, and the symbol $\bigcirc$ denotes element by element multiplication. All matrices $\mathbf{A}$, $\mathbf{F}$, $\mathbf{K}$, $\mathbf{G}$ and $\mathbf{I}$ have dimension 7 × 7 due to the seven life stages.

Although the model is continuous in space, the integral in Eqn (1) was evaluated numerically. All computer code was written using the free software package GNU Octave (version 3.6.4). The spatial region was discretised as a grid comprising $2^9 \times 2^9 = 512 \times 512 = 262\,144$ cells. Spatial co-ordinates (km) were indexed as (x_i, y_j), the bottom left-hand corner of each cell, where $i = 1,\ldots,512$ and $j = 1,\ldots,512$. The respective width and length of each cell were $dx = dy = 0.3906$ km (an area of approximately 15 ha).

Transitions between life stages

The life stage transition matrix $\mathbf{A}$ has the (p, q)th element a_{pq} being the probability of transitioning from life stage q to p in a 6-month interval where life stages are numbered 1–7 in their natural order *SB1*, *SB2*, *Imm*, *VS*, *S*, *M* and *L* respectively (Fig. 2). Summer and winter transition matrices were as follows:

$$A_S = \begin{array}{ccccccc} SB1 & SB2 & Imm & VS & S & M & L \\ \left[\begin{array}{c} 0 \\ 0.79 \\ 0.21 \\ 0 \\ 0 \\ 0 \\ 0 \end{array}\right. & \begin{array}{c} 0 \\ 0.92 \\ 0.006 \\ 0 \\ 0 \\ 0 \\ 0 \end{array} & \begin{array}{c} 0 \\ 0 \\ 0.67 \\ 0.15 \\ 0.02 \\ 0 \\ 0 \end{array} & \begin{array}{c} 0 \\ 0 \\ 0.029 \\ 0.63 \\ 0.32 \\ 0 \\ 0 \end{array} & \begin{array}{c} 0 \\ 0 \\ 0 \\ 0.036 \\ 0.86 \\ 0.09 \\ 0 \end{array} & \begin{array}{c} 0 \\ 0 \\ 0 \\ 0.005 \\ 0.033 \\ 0.91 \\ 0.04 \end{array} & \left.\begin{array}{c} 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 1 \end{array}\right] \end{array}$$

$$A_W = \begin{array}{ccccccc} SB1 & SB2 & Imm & VS & S & M & L \\ \left[\begin{array}{c} 0.18 \\ 0 \\ 0.026 \\ 0 \\ 0 \\ 0 \\ 0 \end{array}\right. & \begin{array}{c} 0 \\ 0.92 \\ 0.006 \\ 0 \\ 0 \\ 0 \\ 0 \end{array} & \begin{array}{c} 0 \\ 0 \\ 0.67 \\ 0.20 \\ 0.036 \\ 0 \\ 0 \end{array} & \begin{array}{c} 0 \\ 0 \\ 0.018 \\ 0.46 \\ 0.48 \\ 0.009 \\ 0 \end{array} & \begin{array}{c} 0 \\ 0 \\ 0.0035 \\ 0.011 \\ 0.80 \\ 0.16 \\ 0 \end{array} & \begin{array}{c} 0 \\ 0 \\ 0 \\ 0 \\ 0.011 \\ 0.94 \\ 0.045 \end{array} & \left.\begin{array}{c} 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \\ 1 \end{array}\right] \end{array}$$

Elements with $p \leq 2$ and $q \leq 2$ correspond to 6-monthly transitions to, from or within soil seedbank stages, as determined from seed survival functions (Lamoureaux *et al.*, 2011). Recruitment probabilities a_{31} and a_{32} (i.e. soil seedbank to immature plant stage transitions) were derived from the seed burial Experiment 2 described in (Lamoureaux *et al.*, 2011) combined with the seed survival functions. All matrix elements a_{pq} with $p > 2$ and $q > 2$ correspond to 6-monthly transition rates for plant growth ($p > q$), shrinkage ($p < q$) or stasis ($p = q$) and were estimated from experimental data collected for this purpose (Lamoureaux *et al.*, 2011).

As population densities increase, it is likely that there are corresponding decreases in recruitment and plant growth transition rates. In the absence of data at these high densities, we chose to decrease those transition rates linearly as the percentage coverage of plants increased; that is, each a_{pq} value in the above matrices ($\mathbf{A}_S$ and $\mathbf{A}_W$) was replaced by itself multiplied by (100 – percentage coverage)/100. The percentage coverage of plants in cell (x_i, y_j) was estimated from the number of plants m^{-2} in each plant life stage and the experimentally measured coverage (m^2) of a plant in each life stage: $Imm = 0.000043$ m^2; $VS = 0.000179$ m^2; $S = 0.003302$ m^2; $M = 0.034\,636$ m^2 (Lamoureaux SL, unpubl. obs.). The coverage of large plants was estimated by assuming that all land is covered by large plants at carrying capacity [35 000 plants ha^{-1} (James *et al.*, 2010)], so a large plant should cover 1/3.5 = 0.2857 m^2.

Fecundity

The nonzero elements f_{pq} ($p = 1$, $q = 4,\ldots,7$) of fecundity matrix $\mathbf{F}_S$ give the number of viable *N. trichotoma* seeds to be dispersed from reproducing life stage q to the seedbank *SB1* in a 6-month summer interval. More specifically, $f_{1q} = s_q v \alpha_q \beta$, where s_q is the number of seeds produced per plant in life stage q, v is the proportion of seeds produced that are viable, α_q is the probability of a plant in life stage q producing seed, and β is the probability of a viable seed joining the seedbank *SB1* life stage. Values for α_q, where $q \in \{4,5,6,7\}$, were derived from Lamoureaux *et al.* (2011) and are $\alpha_4 = 0.21$ (95% CI [0.14, 0.28]); $\alpha_5 = 0.67$ (95% CI [0.62, 0.72]); $\alpha_6 = \alpha_7 = 0.98$ (95% CI [0.97, 0.99]), where CI = confidence interval.

The number of seeds (viable and non-viable) produced per plant each summer in reproducing life stage *VS*, *S*, *M* and *L* were respectively $s_4 = 313$ (95% CI [0, 791]); $s_5 = 1691$ (95% CI [1236, 2145]); $s_6 = 11\,251$ (95% CI [9633, 12 868]); and $s_7 = 64\,455$ (possible range [23 360, 117 594]) (Lamoureaux *et al.*, 2011). The proportion of seeds produced that are viable is $v = 0.46$ (95% CI [0.31, 0.61]) (Lamoureaux & Bourdôt, 2002).

The probability β of a seed entering the seedbank cannot easily be measured. Instead, we estimated it by running the underlying no dispersal stage-structured matrix model under the current management strategy (annual spring grubbing). Monitoring data suggested that *N. trichotoma* population levels in the Hurunui district have been more or less static for the past 16 years under this management strategy (Bourdôt and Saville (2011) and Saville DJ, unpubl. obs.), and a value of $\beta = 0.006$ was required in the model to achieve this stability.

Dispersal

The (p, q)th element of the 7 × 7 dispersal kernel matrix $\mathbf{K}(x - u, y - v)$ is the dispersal kernel from stage q to stage p, that is the probability of propagules produced by life stage p at location u, v appearing in life stage q at location x, y. For *N. trichotoma*, seeds disperse from reproducing plants only to the soil seedbank (*SB1*). We assumed the dispersal kernel from reproducing plant life stages (q = 4, 5, 6 and 7) to the soil seedbank ($p = 1$) is (two-dimensional) Gaussian; that is $\mathbf{K}_{pq}(x - u, y - v) = k(d)$ was the dispersal kernel that gave the probability of seeds dispersing distance $d = \sqrt{(x-u)^2 + (y-v)^2}$ kilometres from (u,v) to (x,y) as:

$$k(d) = \frac{1}{2\pi\sigma^2}\exp\left(-\frac{d^2}{2\sigma^2}\right). \tag{2}$$

With Gaussian dispersion and $\sigma = 0.2$ km, approximately 95% of seeds were dispersed 0.4 km from the parent plant.

Where there is no dispersal ($p \neq 1$, $q \notin [4,5,6]$), the dispersal kernel is the Dirac delta function, $\delta(x, y)$, a generalised function which is zero everywhere apart from at the point (x, y) where it is infinite. This function integrates to one and in this context leaves seeds at the location of the parent plant (Neubert & Caswell, 2000).

Dispersal kernels from stage q to stage p were assumed to be symmetric, so the integral in Eqn (1) became a convolution that (because the spatial discretisation was a power of 2) was evaluated using a fast Fourier transform (Nussbaumer, 1982). With Gaussian dispersal, our grid resolution gave approximately 95% of seeds staying within the immediate neighbourhood of the parent cell. This value corresponded with field observations (L. Smith pers. comm.).

Only seeds that land in ‘nassella-habitable’ sites can join the soil seedbank. We defined habitable areas as those classified as 2–6 in the New Zealand Land Use Capability assessment (Fig. 3): land with slight to moderate limitations to sustain one or more productive uses (Lynn *et al.*, 2009). Seeds that are dispersed to any of the other land use classes (1, 7 and 8) were assumed lost and did not contribute to population growth in the model.

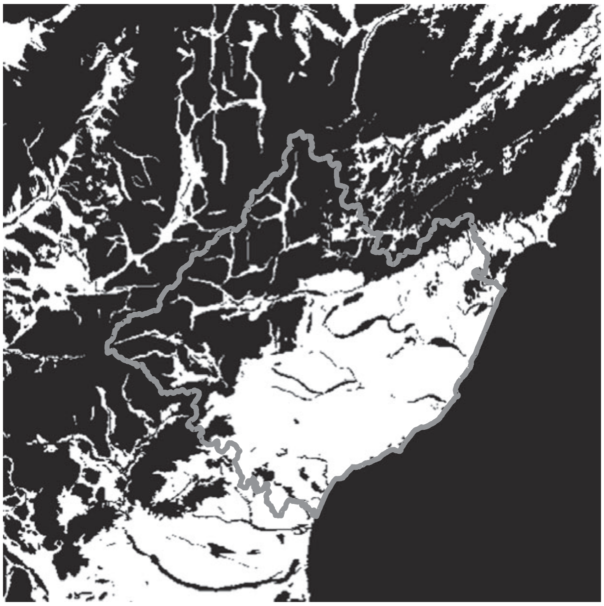

Fig. 3 Map of North Canterbury showing the extent of *Nassella trichotoma*-habitable land [in white – Land Use Capability (LUC) classes 2–6 (Lynn *et al.*, 2009)]. Also shown is the boundary of the Hurunui district (grey) for which the model is parameterised.

Grubbing

The end of season diagonal grubbing matrix is **G** where the (p, p) $(p \geq 3)$ element is g_p, the proportion of plants removed via grubbing of plants at stage p at the end of the season. There is no grubbing of seeds and so $g_p = 0$ when $p = 1$ or 2. October 31 (i.e. end of winter or spring) grubbing rate estimates in life stage *Imm*, *VS*, *S*, *M* and *L* are respectively $g_3 = 0.16$ (95% CI [0.10, 0.22]); $g_4 = 0.24$ (95% CI [0.19, 0.29]); $g_5 = 0.38$ (95% CI [0.34, 0.42]); $g_6 = 0.60$ (95% CI [0.51, 0.68]); and $g_7 = 0.11$ (95% CI [0, 0.35]) (Verkaaik *et al.*, 2006). We did not consider management strategies with end of summer (autumn) grubbing, as this is currently not a common management practice.

Because grubbing efficacy would likely decline at low plant densities, density-dependent grubbing was incorporated into the model by decreasing g_p as the population density of the *N. trichotoma* plants in that life stage (n_p) declined, using the function:

$$g_p(n_p) = \begin{cases} g_{p0}\frac{n_p}{n_{p0}} & ; \quad 0 \leq n_p < n_{p0} \\ g_{p0} & ; \quad n_p > n_{p0} \end{cases} \tag{3}$$

where n_{p0} is the initial ($t = 0$) plant population density in life stage p averaged across the initially infested region (i.e. 4.4, 7.8, 15.0, 3.77, and 0.25 plants ha^{-1} in life stages *Imm*, *VS*, *S*, *M*, and *L* respectively) and g_{p0} is the grubbing rate as defined above, based upon the experimental data of Verkaaik *et al.* (2006).

Initial spatial distribution of plants in each life stage

The initial ($t = 0$) spatial distribution of plants in each life stage was found using the following steps:

Step 1. The local regional authority, Environment Canterbury, supplied property-based grubbing 'compliance' data comprising a property identity number, the number of plants grubbed in the spring of 2010 and the property area (ha). We assumed that all of these data and estimates derived from them apply only to 'visible' plants of size classes *S* or greater; *Imm* and *VS* are too small to be visible.

Step 2. Property boundary data (source: Land Information New Zealand (LINZ) and licensed by LINZ for reuse under the Creative Commons Attribution 3.0 New Zealand license) was combined with the compliance data in a shapefile using ArcMap$^{\text{TM}}$ software by Esri (2012 version 10.1) to give a grubbed-plant density distribution (visible plants grubbed per hectare). This was exported as a raster and then text file table (i.e. grid) giving the density of *N. trichotoma* grubbed (visible plants ha^{-1}) in each 15 ha cell. Any cell without data was assumed to have a grubbed-plant density of 0 plants ha^{-1}.

Step 3. The total number of visible plants estimated in the Hurunui district from monitoring data [a five-year average (2008–2012) from a stratified random survey of about 50 properties conducted each autumn (Bourdôt & Saville, 2011)] was 4.31 times the total number of visible plants grubbed according to the 2010 compliance data. We applied this scaling factor to convert the number of visible plants grubbed per hectare to the number of visible plants per hectare.

Step 4. The final step involved estimating the number of plants in each life stage *Imm*, *VS*, *S*, *M* and *L* from the number of visible plants (*S*, *M* and *L* life stages). This was carried out using data collected by Verkaaik *et al.* (2006) who estimated that the proportion of plants in each plant life stage is *Imm* = 0.14 [0.12, 0.16]; *VS* = 0.25 [0.23, 0.28]; *S* = 0.48 [0.45, 0.51]; *M* = 0.12 [0.10, 0.14]; and *L* = 0.01 [0.003, 0.013] (95% CI in square brackets). These same data were used to calculate multipliers to convert the number of visible plants to the number of plants in any individual plant life stage.

Initial (t = 0) number of seeds in the soil seedbanks

The plant population density distribution of *N. trichotoma* in the Hurunui district has remained relatively unchanged for the past 16 years (Bourdôt and Saville (2011) and Saville, DJ, unpubl. obs.), so it was assumed that the number of seeds joining the soil seedbank life stage *SB1* has been relatively constant over this time. The number of *N. trichotoma* seeds in the soil seedbank life stage *SB1* at location (x, y) was estimated by ignoring dispersal and summing, over the reproducing life stages (q = 4,5,6,7), the number of viable seeds produced (f_{1q} × number of *N. trichotoma* plants in life stage q). The initial number of seeds in *SB2* was estimated as $n_{SB2} = 1.16 \times n_{SB1}$ using the seed survival functions from Lamoureaux *et al.* (2011).

Cost analysis

The combined cost of *N. trichotoma* (\$ ha^{-1}) for each grid square was calculated as:

$$\begin{aligned} &\text{Combined cost}(\$\ \text{ha}^{-1}) \\ &\quad = \text{Lost Revenue} + \text{Variable Cost} + \text{Fixed Cost}, \end{aligned}$$

where

$$\begin{aligned} \text{Lost Revenue}(\$\ \text{ha}^{-1}) &= \text{Net Revenue} \\ &\quad + (\text{Percent coverage of} \\ &\quad N.tricotoma)/100. \end{aligned}$$

Net revenue (\$ ha^{-1}) was estimated at \$400 ha^{-1}. This was based on an average of 3.9 stock units ha^{-1}

and a gross margin of \$101.75 stock unit^{-1}, the latter equal to a gross margin of \$37 stock unit^{-1} (Ministry of Agriculture & Fisheries, 2009) scaled up (using before tax farm profits from 2008/2009 (\$87 ha^{-1}) to 2011/2012 (\$239 ha^{-1}) (Ministry of Primary Industries, 2011) to reflect increases in profits since 2009.

The variable cost (\$) of grubbing a *N. trichotoma* plant (VC_{pp}) is dependent on the number of visible plants (n_{VP}) ha^{-1} according to the function:

$$VC_{pp} = \begin{cases} 1.71 & 0 \le n_{VP} < 1177 \\ 1.71 - \frac{(1.71-0.083)}{(10\,000-1177)}(n_{VP} - 1177) & 1177 \le n_{VP} < 10\,000 \\ 0.083 & n_{VP} \ge 10\,000. \end{cases} \quad (4)$$

where the \$1.71 is the cost when the population density is between 0 and 1177 visible plants per ha (L. Smith pers. comm.). For densities above 1177 visible plants ha^{-1}, we assumed the cost decreased (less searching time) linearly until 10 000 visible plants ha^{-1}. At densities ≥10 000 visible plants ha^{-1}, we assumed a cost of \$0.083 per plant based on a grubbing rate of 36% (the overall grubbing rate for visible plants), 10 s to grub each plant and \$30 h^{-1} labour cost. The fixed costs of controlling *N. trichotoma* in the Hurunui district (864 640 ha) during 2010–2011 were estimated to be \$0.38 ha^{-1} year^{-1} and attributed to compliance inspections, searching, monitoring and education (L. Smith pers. comm.).

The present value of combined costs PV_{cc} (\$ ha^{-1}) is the sum over a time frame of 50 years of all the combined costs discounted back to the present-day value (t = 0), using the social discount rate i = 0.03 [used in various developed countries (Parker, 2011)]:

$$PV_{cc} = \sum_{t=0}^{50} \text{Combined Costs} \times \frac{1}{(1+i)^t} \quad (5)$$

From this, a total cost (TC) across the Hurunui district was calculated by summing the present values of combined costs, over all the spatial co-ordinates (x, y) in the Hurunui district:

$$TC = \sum_{x,y} PV_{CC}. \quad (6)$$

Three alternative management scenarios

The following management scenarios were considered:

1 *Annual grubbing*: This is the current management strategy (status quo) where plants are grubbed annually before seeding with a compliance date in spring (September/October). Data show that under this scenario, approximately 36% of visible plants are grubbed in spring every year (Verkaaik *et al.*, 2006) and populations have remained stable for the past 16 years (Bourdôt and Saville (2011) and Saville, DJ, unpubl. obs.).

2 *No management*: Under this hypothetical scenario, *N. trichotoma* would be declassified as a pest and land occupiers would be free to make control decisions independent of regulation. In reality, some land occupiers would still do some control, but the basic assumption would be that *N. trichotoma* would increase in population density due to a reduction in the control effort. For the model, we set the grubbing rate (for each *N. trichotoma* size class in the model) and fixed costs (of control) to zero.

3 *Three-yearly grubbing*: Under this scenario, grubbing takes place in the spring every third year. This was considered the optimal scenario under a cost–benefit analysis by Denne (1988).

The total cost values (TC) for the specific scenarios *annual grubbing*, *no management* and *three-yearly grubbing* were denoted as TC_{AG}, TC_{NM} and TC_{3Y} respectively.

Sensitivity analysis

A sensitivity analysis was conducted to see whether the comparisons of the three management scenarios were robust to changes in model inputs. The percentage change in the total cost value ratios TC_{NM}:TC_{AG} and TC_{3Y}:TC_{AG} was calculated as parameters were varied ±10% their default value. Some parameters were varied individually, while other nonzero parameters were combined into natural groups, for example seed production per plant across all the life stages. Probabilities were kept within the unit interval.

Results

Comparison of the population trajectories of *N. trichotoma* under three contrasting management scenarios

For the *annual grubbing* scenario over a 50-year time frame, the model gave an approximately constant average (over the initial infested area) *N. trichotoma* density of ~15 visible plants ha^{-1} (Fig. 4). In comparison, average densities for the *no management* scenario increased over time, reaching a plateau of ~56 000 plants ha^{-1} from around year 35. Average densities under the *three-yearly grubbing* scenario showed an increasing trend over time, similar to that of the *no management* scenario but with densities less than those of the *no management* scenario.

The spatial extent of *N. trichotoma* under all three scenarios at year 50 remained confined to the Hurunui

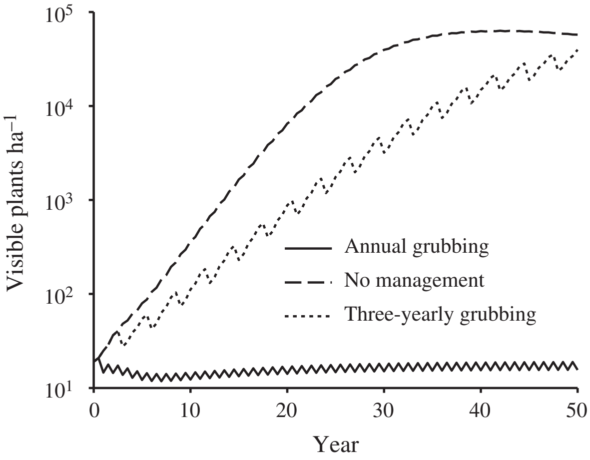

Fig. 4 Trajectories of the population density of *Nassella trichotoma* (averaged over the land area infested in the Hurunui district at the start of the simulation in 2010) over 50 years for the three management scenarios from a starting density of 19 plants ha^{-1}.

district (Fig. 5). Under *annual grubbing*, densities remained between 10 and 70 plants ha^{-1} (Fig. 5A), while under *no management*, densities reached over 35 000 plants ha^{-1} in most places (Fig. 5B). Under *three-yearly grubbing*, the densities of *N. trichotoma* became high along the coast, but decreased inland (Fig. 5C).

Comparison of the costs of three contrasting management scenarios

The trajectories over time of the discounted combined costs per year (Fig. 6A) increased to a plateau in the *no management* scenario, decreased slightly over time under *annual grubbing* and oscillated with an increasing trend over time in *three-yearly grubbing* scenario. After *c.* year 22, the combined costs per year under the *annual grubbing* regime were (on average) less than those of the other two scenarios. Under the *three-yearly grubbing* scenario, the contribution of lost revenue to the combined costs oscillated and increased markedly in the 'grubbing years' over time (Fig. 6B).

The total cost [Eqn (6)] of the *no management* scenario (TC_{NM} = \$417 million) and the *three-yearly grubbing* scenario (TC_{3Y} = \$736 million) were respectively 3.2 and 5.6 times the total cost of the *annual grubbing* scenario (TC_{AG} = \$131 million). These total costs indicated that annual grubbing of *N. trichotoma* returns a net benefit of \$286 million (\$417 – \$131 million) compared with doing nothing and a net benefit of \$605 million (\$736 – \$131 million) compared with a 3-yearly grubbing programme.

Sensitivity of total costs (TC) to 10% variations in model parameters

Over all 10% parameter variations in the sensitivity analysis, the *three-yearly grubbing* scenario was the most expensive (i.e. the greatest value of *TC*) and the *annual grubbing* was the least expensive. This comparison was robust if the time frame chosen for the cost analysis is >30 years (Fig. 7) with a discount rate <9% (Fig. 8).

When considering the grubbing rates in all the plant life stages, the total costs were most sensitive to grubbing rate changes in medium-sized plants (Table 2). A 10% reduction in the grubbing rate of the medium plants life stage resulted in a 17% and 8% reduction in costs for the TC_{AG} and TC_{NM} values respectively. A 10% increase in the grubbing rate of the medium plants life stage resulted in a 12% and 4% decrease in total costs for the $TC_{AG}$and TC_{NM} values respectively.

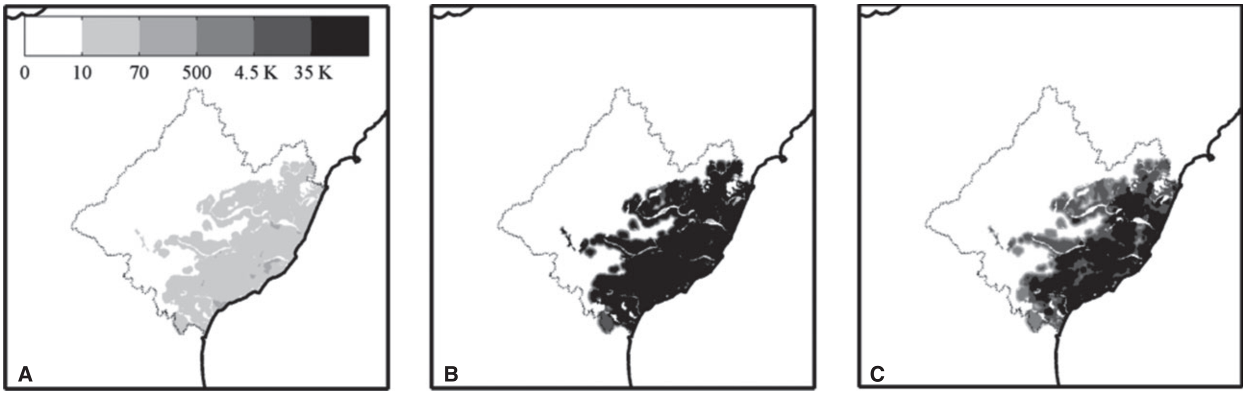

Fig. 5 The spatial extent and population density (plants ha^{-1}) of *Nassella trichotoma* within the Hurunui district (boundary is the dotted line) of North Canterbury, New Zealand, 50 years in the future (2060) as simulated for three alternative management strategies: *annual grubbing* (A), *no management* (B) and *three-yearly grubbing* (C). 'K' represents multiplication by 1000.

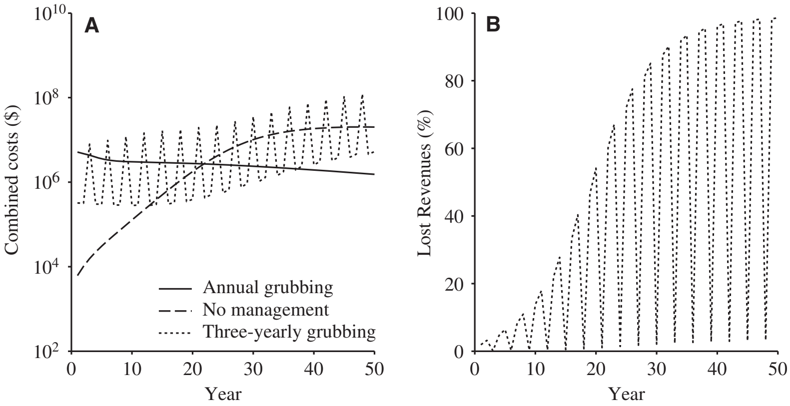

Fig. 6 Trajectories (A) of the discounted (3%) combined costs (NZ$) of *Nassella trichotoma* per year across the Hurunui district. In the case of *three-yearly grubbing*, lost revenues as a percentage of combined costs are shown in (B). Lost revenues are less than 1% of the combined costs in the *annual grubbing* case, and 100% when there is *no management*.

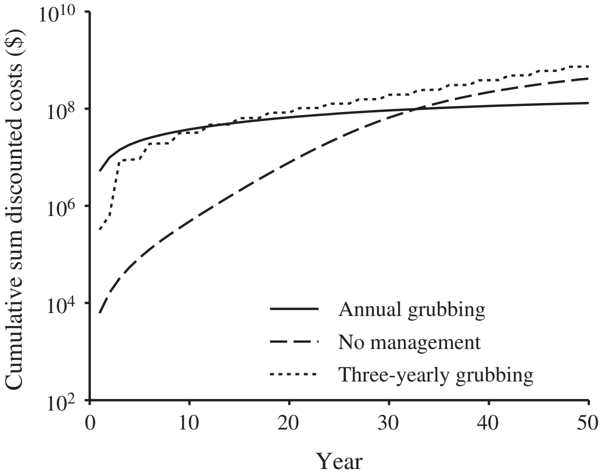

Fig. 7 Trajectories of the cumulative sum of discounted combined costs (NZ$) over 50 years. The cumulative sum at year 50 is the same as the total cost (*TC*).

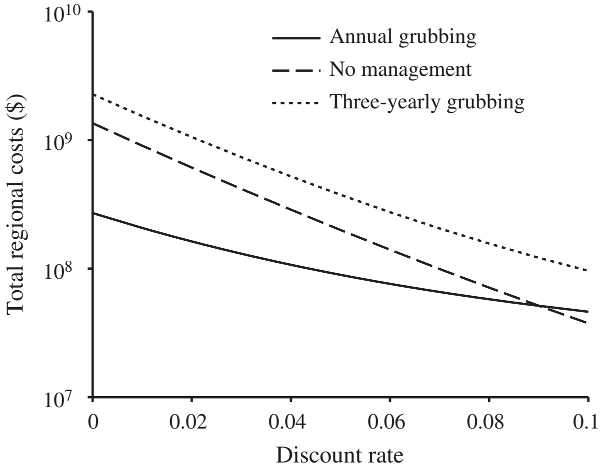

Fig. 8 Trajectories of the cumulative sum of discounted combined costs (NZ$) at year 50 versus discount rate.

Sensitivity of total cost ratios to 10% variations in model parameters

A sensitivity analysis of the ratios TC_{NM}:TC_{AG} and TC_{3Y}:TC_{AG} showed that most parameter variations of ±10% of their default values (3.2 and 5.6 respectively) resulted in a total cost ratio variation less than or equal to ±10% (Table 3). The exceptions to this were some of the local population dynamics parameters as follows:

1. A simultaneous 10% reduction in all seedbank transition and survival parameters (a_{pq}, p, $q \le 2$) resulted in a 11.4% increase in the total cost ratio TC_{NM}:TC_{AG}.
2. A 10% decrease in plant survival (stasis) rates caused a 41% and 45% decrease in the total cost ratios TC_{NM}:TC_{AG} and TC_{3Y}:TC_{AG} respectively.
3. A 10% decrease in plant growth transition rates resulted in a 11.5% decrease in the total cost ratio TC_{3Y}:TC_{AG}.
4. A 10% increase or decrease in the grubbing rate for medium plants resulted in a total cost ratio TC_{NM}:TC_{AG} changing by −15% or 13% respectively.

Discussion

Model validation

The model can be validated by comparing its outputs under the current management strategy (*annual grubbing*) with monitoring data collected over 16 years (Bourdôt and Saville (2011) and Saville DJ, unpubl. obs.). The model predicted a more or less stable population over time (Figs 4 and 5 A) with a constant average density ~15 visible *N. trichotoma* plants ha^{-1} over the 50-year time frame, averaged over the infested area. This is consistent with the monitoring data where an approximately stable average density of 16 visible plants ha^{-1} was observed over the 16 years up until autumn 2013.

Further model validation is achieved by considering the *no management* scenario in which average densities

Table 2 Sensitivity of total costs (TC) to 10% variations in NASSIM model parameters

% change in parameter	−10%	+10%	−10%	+10%
Grubbing parameter (life stage)	% change in TC_{AG} (default value NZ$131 million)		% change in TC_{3Y} (default value NZ$736 million)	
g_3 (*Imm*)	3.11	−2.96	1.44	−1.42
g_4 (*VS*)	3.49	−3.32	1.58	−1.57
g_5 (*S*)	4.83	−4.01	0.37	−0.61
g_6 (*M*)	16.99	−11.75	7.58	−7.88
g_7 (*L*)	6.93	−5.93	1.53	−1.53

Table 3 Sensitivity of total cost ratios TC_{NM}:TC_{AG} and TC_{3Y}:TC_{AG} to 10% variations in NASSIM model parameters

% change in parameter	−10%	+10%	−10%	+10%
Parameter	% change in ratio TC_{NM}:TC_{AG} (default value 3.2)		% change in ratio TC_{3Y}:TC_{AG} (default value 5.6)	
a_{pq} seedbank reduction ($p, q \leq 2$)	11.45	–	−0.75	–
a_{pq} recruitment, $q \leq 2$, $p = 3$)	4.02	−4.97	−7.49	6.05
a_{pq} plant survival (stasis) reduction ($p = q \geq 3$)	−40.64	–	−44.91	–
a_{pq} plant growth rates ($p > q \geq 3$) (with an opposite change in stasis)	2.97	−8.39	−11.51	4.18
α_p, $p \geq 4$	4.30	−1.74	−7.47	1.57
s_p, $p \geq 4$	4.30	−5.29	−7.47	5.94
v	4.30	−5.29	−7.47	5.94
β	4.30	−5.29	−7.47	5.94
$f_{1q} = \alpha_p\ s_p\ v\ \beta$, $p \geq 4$	4.30	−5.29	−7.47	5.94
g_3	−3.01	3.05	−1.62	1.59
g_4	−3.37	3.43	−1.85	1.81
g_5	−4.61	4.17	−4.25	3.54
g_6	−14.52	13.31	−8.04	4.38
g_7	−6.48	6.31	−5.05	4.68
σ^2	−1.21	0.91	−0.86	0.64
Scale factor	6.62	−5.59	4.24	−3.67
SB2 as a per cent of SB1 ($t = 0$)	0.29	−0.29	0.22	−0.22
Land cover per plant (m^2) (all plant stages)	−2.53	2.32	−3.18	−2.77
i	5.12	−4.97	4.39	−4.25
VC_{pp} Variable costs per plant	10.28	−8.52	8.32	6.90
Revenue (NZ$ per ha)	−9.99	9.98	−0.8	0.8
Fixed costs per plant	0.64	−0.64	0.53	−0.52

(visible plants ha^{-1} averaged over the infested area) approached carrying capacity at year 35 from a starting density of 19 plants ha^{-1}. This is consistent with estimates of times to saturation of 35–482 years from a starting density of 17 plants ha^{-1} (all life stages) in Lamoureaux *et al.* (2011) and 30–50 years from a starting density of 0.55 seedlings ha^{-1} in Denne (1988).

The current strategy is the most cost effective

Denne (1988) suggested that the optimal economic management scenario was *three-yearly grubbing* and that this result was robust for discount rates from 2 to 10%. Our model simulations showed that the trajectories of average densities of visible plants over time under the *three-yearly grubbing* strategy have a similar (albeit slower) increasing trend to those of the *no management* strategy (Fig. 4) and that the current management strategy *annual grubbing* is more cost effective than *three-yearly grubbing* for discount rates from 0 to 10% (Fig. 8). However, above about 9% discount rate the costs of *annual grubbing* exceed those of *no management*. This is most likely because the costs of high densities in the future are discounted to almost zero at these higher discount rates. In New Zealand, a discount rate of 10% was recommended for cost–benefit analyses by Treasury until 2010, when the rate was revised to 8% [New Zealand Treasury, 2008 (Revised 2010)]. Worldwide, high discount rates in economic analyses have caused controversy and there has been a movement to reduce them – especially for social economic analysis (e.g. climate change issues) (Parker, 2011). Thus, our use of a 3% discount rate in comparing alternative management strategies of *N. trichotoma* fits with current thinking.

Our model suggested the highest costs are incurred under the *three-yearly grubbing* scenario, a result of the cumulative effect of ongoing population increase (Fig. 4) and its associated grubbing costs and production revenue losses. Denne's conclusion that three-yearly grubbing is optimal holds only in simulations with relatively high grubbing efficacies (>95% of plants grubbed) and slow population growth rates, both of which were considered realistic at the time. It is apparent from Fig. 8 in Denne (1988) that when a grubbing rate closer to the average 36% determined from recent field measurements is used (Verkaaik *et al.*, 2006), annual grubbing is favoured over reduced-frequently grubbing programmes and the apparent conflict between the two models disappears.

Infestations are spatially contained over time

NASSIM predicted that the extent of the infestation over time remains more or less contained within the Hurunui district boundary under all three scenarios

(Fig. 5). In part, this is because the model allows *N. trichotoma* seed to become established only in areas that are habitable by the weed (defined by land use). Uninhabitable areas form a natural boundary preventing spread to the east and west (Fig. 3). There are potential corridors to the north and south through which *N. trichotoma* may spread. However, with the scenarios chosen here, the 50-year time frame and the small variance of the Gaussian dispersal ($\sigma^2 = 0.04$), we did not see much spread in these directions. This result supports the observations by Denne (1988) that '…in the 40 years of management in northern South Island the distribution of nassella tussock has changed little,…' and that the 'Nassella tussock may have reached the limit of its range in North Canterbury……'. The latter observation is supported by a climate niche model that revealed occurrences of the weed at the western, northern and eastern limits of the species' climatically suitable range in North Canterbury (Kriticos *et al.*, 2004).

Local population dynamics are important

The sensitivity analysis showed that the total cost ratios TC_{NM}:TC_{AG} and TC_{3Y}:TC_{AG} were sensitive to 10% changes in some of the local parameters, in particular reduction in local plant survival without grubbing (stasis) (Table 2). This illustrates the importance of the 'within-property' dynamics of *N. trichotoma* compared with the 'between-property' (i.e. dispersal) dynamics as emphasised by James *et al.* (2011). Reduction of local plant survival is predominantly via grubbing which incurs its own costs. The total costs for *annual grubbing* (TC_{AG}) decreased as grubbing rate increased (Table 2) due to more land being freed up and a consequent reduction in lost revenues. The total costs for the *no management* scenario (TC_{NM}) remained constant, as there are no grubbing costs involved under this scenario.

Concentrate on grubbing medium and large plants

Increasing grubbing effort by 10% in medium plant life stages caused the largest reduction (12% for *annual grubbing* and 8% for *3-yearly grubbing*) in the total costs [Eqn (6)] compared with the other plant life stages (Table 2). Spending time on the manual removal of smaller plants, a life stage that contributes little to the soil seedbank as compared with medium and large plants, may not be an economically effective strategy.

Conclusions

According to the model NASSIM, run with default parameters over a 50-year time frame, the current management strategy of annual spring grubbing (termed *annual grubbing*) is the most cost effective of the three scenarios *annual grubbing*, *no management* and *3-yearly grubbing*. This conclusion is robust for variations of parameters ±10% their default values, which were derived from the entire body of *N. trichotoma* data collected in New Zealand over the last 16 years.

Acknowledgements

This work was funded in part by Environment Canterbury, the Ministry of Business, Innovation and Employment under the Undermining Weeds Project (C10X0811) and AgResearch Core Funding. The authors would like to thank James Powell, Department of Mathematics and Statistics, Utah State University, for advice on some of the details of programming the integrodifference model and in particular for making his web course (Spatio-Temporal Models in Ecology: an Introduction to Integro-difference Equations) notes available online (http://www.math.usu.edu/powell/wauclass/labs.html). These notes were used as the basis for the coding of the model presented in this study. The authors would also like to thank Simon Harris (Harris Consulting) for advice on the implementation of the cost–benefit analysis and Laurence Smith (Environment Canterbury) for information on costs associated with managing *N. trichotoma* in North Canterbury.

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