Scotch broom facilitates indigenous tree and shrub germination and establishment in dryland New Zealand

Larry Burrows[1*], Ellen Cieraad[1] and Nicholas Head[2]

[1]Landcare Research, PO Box 69040, Lincoln 7640, New Zealand
[2]Department of Conservation, Private Bag 4715, Christchurch 8140, New Zealand
*Author for correspondence (Email: burrowsl@landcareresearch.co.nz)

Published online: 4 December 2014

Abstract: It is common practice in New Zealand dryland areas to chemically or mechanically control invasive woody weeds, including Scotch broom (*Cytisus scoparius*). Such weed control is not always effective in achieving the often implicit aim of advancing the restoration of indigenous woody vegetation. We used a field experiment on a braided river terrace on the Canterbury Plains to test how five different management treatments of broom cover affected the germination, survival and growth of six indigenous tree and shrub species in a dryland setting. Mulched, root-raked and crushed treatments resulted in low seed germination and high mortality of planted seedlings, which was apparently due to the associated soil disturbance and microsite conditions. Significantly higher germination and survival rates of indigenous woody species under the living broom canopy indicated that the facilitative effects of the living canopy outweighed any negative effects. With no evidence of unassisted regeneration of indigenous plants from local sources during our experiment, our results suggest that retaining a live broom canopy was most beneficial for the germination and establishment of planted indigenous woody seedlings at this site. Compared with sowing and planting after mechanical or chemical broom control, sowing seeds and planting seedlings under the living broom canopy was also the cheapest management strategy to advance the succession of indigenous woody species in these dryland weed communities.

Keywords: competition; *Cytisus scoparius*; facilitation; gorse; nurse crop; rehabilitation; restoration; *Ulex europaeus*; weed control; weed management

Introduction

Establishment of indigenous trees and shrubs under invasive woody weeds is of interest to conservation practitioners as a low-cost means of controlling weeds and advancing restoration. Exotic woody communities can be managed as successional systems with 'minimal interference' (Wilson 1994) to support indigenous species and to eventually restore indigenous forest. For example, stands of invasive nitrogen-fixing gorse (*Ulex europaeus* L.) provide effective nurse environments for indigenous species around New Zealand (Lee et al. 1986; Williams & Karl 2002; Sullivan et al. 2007). Such indigenous regeneration appears particularly successful in areas with high rainfall, fertile soils and available indigenous seed sources (Wilson 1994). It remains unclear whether widespread woody weeds can aid indigenous restoration in dry environments where soils may be poor or degraded and indigenous seed sources are frequently absent, such as in dryland areas of New Zealand's South Island (Walker et al. 2009a).

The net balance between positive (facilitation) and negative (competition) interactions between a nurse shrub cover and understorey plants determines whether the understorey plants are aided by the nurse cover (Holmgren et al. 1997; Maestre et al. 2003; Armas & Pugnaire 2005). Studies in other semi-arid or arid locations have shown that nurse shrubs can have a facilitative effect in drier locations and in drier years compared with wet ones (Tielborger & Kadmon 2000; Maestre et al. 2001; Flores & Jurado 2003; Padilla & Pugnaire 2007). The benefit of nurse plants has been demonstrated to aid restoration elsewhere, particularly in semi-arid or arid conditions (Castro et al. 2004; Gómez-Aparicio et al. 2004; Padilla & Pugnaire 2007; Rey et al. 2009; Pugnaire et al. 2011), as they may increase soil nutrient availability and decrease evapotranspiration (Abdallah & Chaieb 2012).

Scotch broom (*Cytisus scoparius* (L.) Link) is a widespread nitrogen-fixing woody weed in New Zealand (Bascand & Jowett 1982; Department of Conservation Weeds database, C. Howell, 2012). It is particularly common in semi-arid dryland zones (Walker et al. 2009a) and dominates in areas colder and drier than gorse-dominated sites (Carswell et al. 2012). It is common practice in New Zealand to chemically or mechanically control invasive woody weeds, including broom, prior to planting. Mechanical disturbance of the standing cover (such as mulching or crushing) may create initial opportunities for the indigenous seed-stock or planted seedlings. However, such control may do little to assist recovery of indigenous vegetation if the conditions that are created are too harsh for establishment of indigenous species, if competitive woody weeds recover quickly through resprouting or re-establishment from long-lived seed banks, or if the disturbance created by the treatment, or the mere effect of weakening or removing one weed, results in unexpected invasion by another weed (Allen et al. 1995; Rees & Paynter 1997; Williams 1998; Downey & Smith 2000; Buckley et al. 2007; Harris et al. 2013). Spraying the broom cover with herbicide eliminates the resource competition, retains (at least initially) the dead-standing cover, and results in little mechanical disturbance, but it also eliminates any indigenous woody species that are present. Therefore, an Australian study suggested that a 'wiser management option, at least in the short term, may be avoidance of all disturbance, especially for stands of mature broom' (Downey & Smith 2000).

Unlike gorse, broom is not generally regarded as a useful nurse crop for recovery of indigenous woody vegetation in New Zealand. It has been suggested that broom stands may be self-perpetuating (Walker et al. 2009b), develop into blackberry (*Rubus fruticosus* L.) stands, or give way to exotic forests (Williams 2011). Nonetheless some establishment of indigenous seedlings has been observed under broom cover, and it has been suggested that establishment of trees and shrubs in broom stands may in time result in saplings overtopping the broom and shading it, leading to succession to forest trees (McCracken 1993 unpubl. report for Canterbury Regional Council; Wilson 1994; Carswell et al. 2012). However, in more arid conditions in New Zealand, broom is also known to compete strongly with planted conifers for light and water (Watt et al. 2003), which suggests that in dryland settings a broom canopy could have an overall negative effect on any indigenous woody species establishing beneath its cover. Quantitative studies on the use of broom as a nurse cover for indigenous restoration are lacking (Williams 2011), and are particularly needed for dry sites where restoration or advancement of the succession to indigenous woody vegetation is challenging (Walker et al. 2009b).

We used a field experiment to test how different management treatments of broom cover affect the germination, survival and growth of six indigenous tree and shrub species in a South Island dryland setting. We discuss environmental factors that may affect the outcomes, and management implications for establishing indigenous trees and shrubs into broom-dominated areas in the drylands.

Methods

Site

The study was carried out near Ealing on an alluvial terrace of the Rangitata River, Canterbury Plains (44°01'56" S, 171°23'00" E), in the New Zealand dryland zone (Walker et al. 2009a). The site has sandy loam soil and receives c. 700 mm annual rainfall. Most of the site is covered by exotic woody weed species such as Scotch broom, gorse and blackberry, while open areas are dominated by the exotic grass browntop (*Agrostis capillaris* L.).

Fifteen plots (10 × 12 m) in homogeneous broom stands were marked out on the basis of broom dominance and height: mean percent (±SE) broom cover across plots was 19% (±0.51) > 2.0 m, 59% (±0.63) 2.0–0.3 m, and 12% (±0.22) < 0.3 m. Woody species other than broom occupied c. 10% of total cover on plots. Mean broom canopy height across all plots was 1.9 m (±0.06) although some individual plants attained c. 4.0 m. Dimensions of broom plants measured from other sites in Canterbury suggest mean age at Ealing to be c. 6–8 years old (LB unpubl. data) and the oldest individual bushes across the experimental site were between 8 and 12 years old. The few other exotic woody invasive species present included gorse, blackberry and sweet briar (*Rosa rubiginosa* L.), but mean richness of woody species was very low overall (4.1 ± 0.28 species per plot).

Plots were fenced to exclude occasional sheep and cattle, leaving a buffer of at least 3 m between the fence and the plot margin. Traps were set inside the fences to capture invasive brushtail possums (*Trichosurus vulpecula*).

Treatments

Management treatments included mechanical and chemical methods used for broom control in agricultural, forestry or restoration settings (Balneaves & McCord 1990; Williams 1998; Talbot 2000; Oneto et al. 2010). Three repetitions of five treatments were randomly assigned to selected broom plots, and the treatments were applied by commercial land-preparation contractors. The following treatments were applied to the assigned plot areas plus buffer zone:

1. Root-rake – A root-rake mounted on a tracked excavator ripped off the broom cover, along with roots and most of the topsoil, and the debris was taken away.
2. Mulch – A tractor-mounted brush-mulcher turned all standing broom into a layer of mulch c. 10 cm deep.
3. Roller-crush – A tracked bulldozer or excavator drove over the standing vegetation in more than one pass leaving a crushed layer of broken plant material c. 0.5 m deep. Some broom shrubs died but others survived this treatment.
4. Spray – Herbicide (picloram/triclopyr (Tordon™ Brushkiller) at 300 ml 100 L^{-1}) with penetrant (Boost™ at 100 ml 100 L^{-1}) (Dow AgroSciences) was applied with a spray gun from a ground-based vehicle 6 weeks before planting.
5. Control – Live standing broom canopy retained; this is the ‘experimental control’, i.e. no management treatment of the broom stand was carried out.

Plants and seeds

We planted 10 seedlings, and sowed 10 sets of 100 seeds, of each of six indigenous tree or shrub species, on a 1 × 1 m grid within each 10 × 12 m plot. The seeds and seedlings of the six species were randomly assigned to the 120 grid points within each plot. The species were *Kunzea ericioides* (kānuka), *Cordyline australis* (cabbage tree), *Coprosma robusta* (karamū), *Sophora microphylla* (kōwhai), *Pittosporum tenuifolium* (kōhūhū) and *Plagianthus regius* (lowland ribbonwood). These were selected as they represent early-successional species that naturally occur on these alluvial terraces (Meurk 2008). For simplicity, species are referred to hereafter by their generic name. Plants and seeds were sourced locally (Opuha Nurseries, Geraldine), except for c. 50% of *Plagianthus* seeds, which came from a national seed supplier (www.proseed.co.nz).

The roots of the nursery-grown seedlings were washed free of soil prior to planting to remove any effect of residual nursery soil and to replicate forestry planting techniques. Planted seedlings had a mean height of c. 30 cm and their quality (as indicated by root-collar diameter; Wilson & Jacobs 2006) was consistent within a species but varied between species, and for this reason we have not compared seedling responses between species.

Subsamples of the same seed-lots were tested for viability by cutting and staining using tetrazolium (Peters 1970). Seeds of most species had high viability (>95%), *Coprosma* had moderate viability (43%) and *Kunzea* had low (<5%) viability. We sprinkled the seeds onto the mineral soil after brushing aside litter or mulch off an area of 0.1 × 0.1 m, and then placed a 0.2 × 0.2 m wire mesh cage over the area to exclude disturbance by granivorous birds (mainly California quail *Callipepla californica* and Eurasian blackbird *Turdus merula*).

The seeds were sown and seedlings planted in September 2008; rain the day before and the two days after planting watered the seeds and seedlings. No additional water, fertiliser or weed control was applied to any of the treatments.

Measurements

We measured every planted seedling and checked each set of sown seeds for germinants in four censuses (January 2009, October 2009, August 2010 and April 2012). In each census, we measured the total extended height to shoot tip and orthogonal crown widths (to determine crown volume) of each seedling. As the seedlings were randomly assigned to treatments at the start of the experiment, we assumed that there were no initial treatment differences in seedling dimensions. The first census, in January 2009, was carried out after a 5-month settling period to allow the planted seedlings to stabilise from the shock of planting and was used in the calculation of relative height growth rate. Seed germinants were counted at each census. As the germinated seedlings were not marked, their individual persistence could not be tracked through time, but the maximum count of germinants for each subplot across all four census times provides an estimate of the minimum number of germinated seeds during the experiment.

In April 2012, we excavated and harvested all surviving planted seedlings. Each plant was divided into above- and below-ground parts, roots were hand-washed free of soil, and both parts were dried at 60°C to constant mass, and weighed to determine root, shoot and total biomass.

Environmental conditions

At two times in April 2012, once in a dry spell (12 April, after 12 days without rain) and 3 days after a significant rain event (27 April), topsoil moisture (% volume) was estimated at 15 points within each plot using a HH2 Moisture Meter (Delta T Devices, Cambridge, England). Weather data from the nearest weather station with publicly available data for the duration of the experiment (Orari Estate, 11.8 km south-west of the study site) were downloaded from www.cliflo.niwa.org.nz. We used these data (monthly rainfall, minimum, mean, and maximum temperature) to compare weather conditions during the experiment with the 30-year (1981–2010) means.

Analyses

Statistical analyses were conducted in R version 2.15.2 (R Development Core Team 2012). Linear mixed-effects models were fitted to seed germination, seedling survival and growth data, with block and species as random intercepts, using the *lmer* function in the package *lme4* (Bates et al. 2014). A model with only an intercept ('null' model) was compared, using analysis of variance, with a model that included treatment as a fixed effect. Germination and establishment success were modelled using three responses: (1) the proportion of seeds that germinated; (2) the proportion of planted seedlings that survived the first summer, and (3) the proportion of planted seedlings that survived to the end of the experiment. Since overall germination rates were very low, we also calculated and modelled the proportion of subplots in which *any* germination was recorded at any of the four censuses during the experiment. All proportions were modelled assuming binomial error distributions, and overdispersion was accounted for by including an individual-level random effect, if required.

The effect of treatment on seedling growth was also modelled using linear mixed-effects models, with a Gaussian error distribution and species and plot-within-block as random effects. Response variables included seedling height after the first summer and at the end of the experiment, relative height and volumetric growth rates, and above- and below-ground biomass at harvest. Data deviating from a normal distribution were transformed prior to statistical analyses (seedling height and relative height growth rates were square-root-transformed, while biomass, root:shoot ratio and relative volumetric growth rates were log-transformed). Soil moisture differences between treatments were also investigated using a linear mixed-effects model, with plot within block as the random effect. Adjusted treatment means were calculated using the *effect* function in the R package *effects* (Fox 2003), which calculates the mean for each level of interest while averaging over all random effects, and presents back-transformed means and standard errors. A posteriori treatment contrasts were calculated using Tukey's honest significant difference with the *glht* function in the *multcomp* R package (Hothorn et al. 2008).

Costs for the different treatments are provided first as the actual establishment costs for the experimental setup, and second as contractors' estimates for treating large areas. Costs were provided by the invoices from contractors for the establishment of the three 10 × 12 m plots (+ buffer area) per treatment. The same contractors provided estimates for treating a hectare as if it was part of a larger scale (> 100 ha) operation. For comparison both were converted to dollars per hectare, and costs associated with fencing, predator control, sowing and planting (which were common across treatments) were excluded. Costs are reported excluding GST, and represent values and estimates from 2008. Relative indices of regeneration success per unit ($1) treatment costs were calculated by dividing the overall mean germination and survival probability (see Fig. 1a and 1c, multiplied by 1 000 000 and 100, respectively, for visualisation purposes) by the estimated cost per hectare of a large-scale operation. The included cost of the Control treatment was $0 per hectare, but was set to $1 per hectare in order to calculate the regeneration success indices.

Results

Seed germination

Rates of seed germination were very low. At the final harvest (April 2012, after four summers and 3.5 years), 310 seedlings out of a total of 90 000 sown seeds (0.3% germination and survival rate) were counted across all plots and treatments. During previous measurements more germinants had been counted, indicating that most were ephemeral. During the course of the experiment at least 1541 seeds germinated (including 613 *Plagianthus*, 539 *Pittosporum*, 305 *Sophora*, 66 *Coprosma*, 10 *Kunzea* and 8 *Cordyline* seeds; an overall minimum germination rate of 1.7%). At final harvest, surviving germinated seedlings were 285 *Sophora*, 14 *Pittosporum* and 11 *Plagianthus*; germinants from the other species did not survive (Table 1).

Significantly more seeds (192) had germinated and survived until the end of the experiment under the intact broom canopy ('Control') compared with other treatments ($P < 0.02$, Fig. 1a, Table 2), and only *Sophora* had substantial germination in treatments other than Control (Table 1). The proportion of subplots where any germination occurred at any of the four census times was significantly higher in the Control than in the Mulch and Root-rake treatments ($P < 0.03$), but did not differ between the Control, Roller-crush and Spray treatments (Fig. 1b).

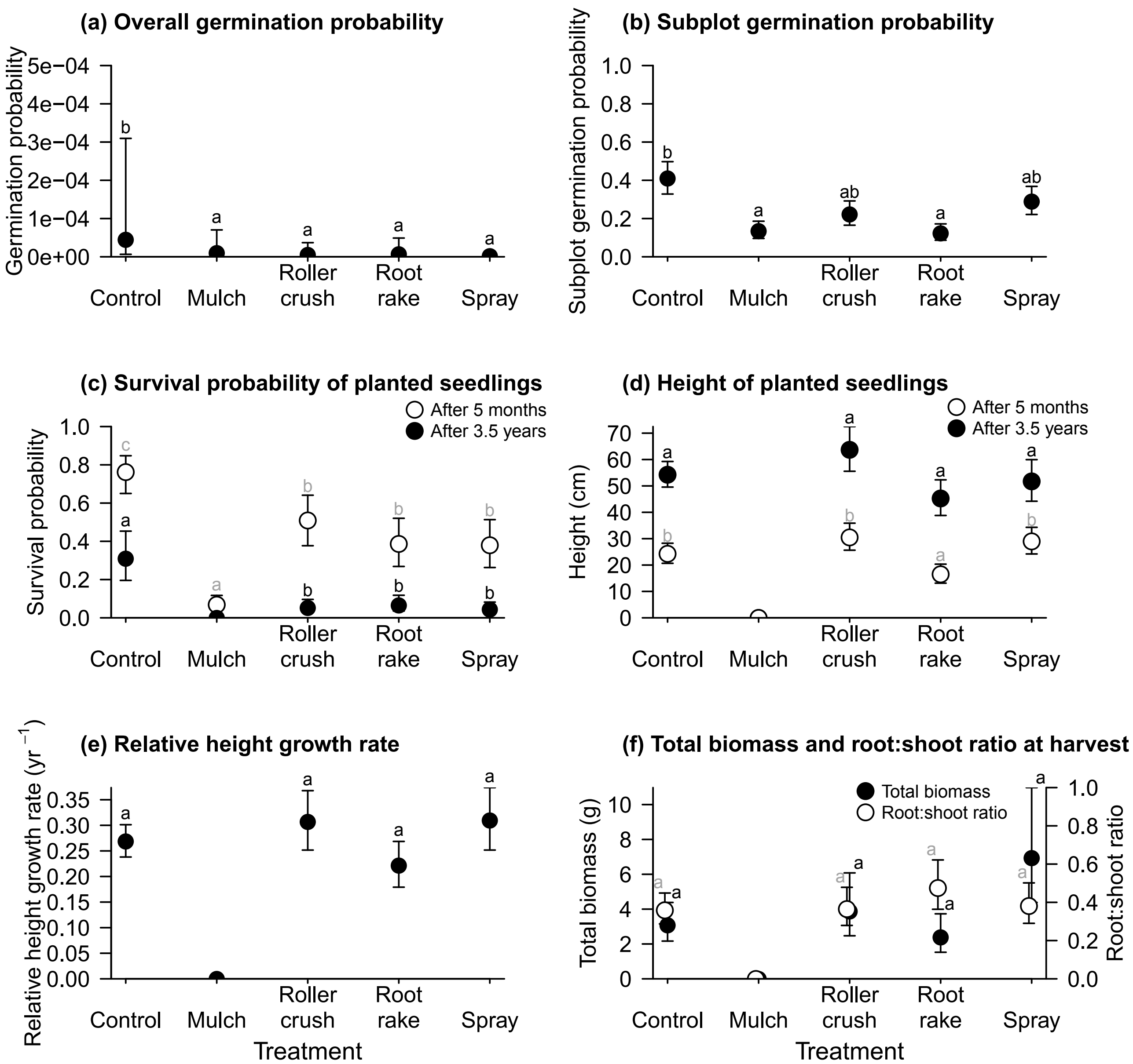

Figure 1. Germination, seedling survival and growth of indigenous plant species sown and planted across five broom management treatments at Ealing, Canterbury Plains. (a) Overall probability of germination; (b) Probability of subplots containing at least one germinated seed for each treatment; (c) Survival probability of planted seedlings after 5 months and after the whole experiment (3.5 years); (d) Height of surviving planted seedlings in different treatments after 5 months and 3.5 years; (e) Relative height growth rate, and (f) total biomass (above- plus below-ground) of surviving seedlings at the end of the experiment. Data are means of treatments across all species with average random effects ± one standard error. No seedlings survived in the Mulch treatment. Different letters indicate significantly different means across treatments (Tukey post hoc test); in (d) (height of plants after 3.5 years) the post hoc test was carried out after accounting for plant height after 5 months.

Seedling survival

More than 55% of planted seedlings died during the first five months of the experiment (September 2008–January 2009). Seedling survival during this time differed significantly between treatments ($P < 0.0001$, Fig. 1c, Table 2). By the end of the study, all seedlings of all species had died in the Mulch plots. There were no differences in survival between the Spray, Roller-crush or Root-rake treatments, but survival in the Control was significantly higher than in the other treatments ($P < 0.001$; Fig. 1c).

Of the 900 planted seedlings, 115 (<13%) survived until the end of the experiment. Of these, more than half (66) were in Control plots, which was significantly more ($P < 0.0001$) than in the Root-rake, Roller crush and Spray treatments (19, 16 and 14 seedlings, respectively). Seedling survival was highest for *Plagianthus*, *Kunzea* and *Cordyline* (41, 27 and 26 seedlings, respectively). Survival of *Coprosma* and *Sophora* seedlings was very poor (2 and 6 seedlings, respectively), and *Pittosporum* seedlings had intermediate survival (13).

Table 1. Minimum number of germinants from each early-successional species and broom (*Cytisus scoparius*) treatment recorded on 10 × 12 m dryland plots at Ealing, Canterbury Plains, during the course of the experiment ('Min', equal to the sum of the maximum count of germinants for each 1 × 1 m subplot across all four census times), and the final number of germinants that were alive at the end of the experiment ('Final'); 3000 seeds of each species were sown per treatment (1000 seeds per species per plot × 3 plots per treatment).

	Control		Mulch		Roller crush		Root rake		Spray		All treatments	
	Min	Final	Min	Final	Min	Final	Min	Final	Min	Final	Min	Final
Coprosma robusta	21	0	0	0	21	0	0	0	24	0	66	0
Cordyline australis	0	0	0	0	8	0	0	0	0	0	8	0
Kunzea ericoides	0	0	0	0	0	0	0	0	10	0	10	0
Pittosporum tenuifolium	262	11	34	0	109	0	40	3	94	0	539	14
Plagianthus regius	164	11	11	0	113	0	32	0	293	0	613	11
Sophora microphylla	182	170	48	47	32	27	31	31	12	10	305	285
All species	629	192	93	47	283	27	103	34	433	10	1541	310

Table 2. Linear mixed-effects model results for the different response variables. P-values are presented for the effect of broom management treatment (fixed effect) on the response variables (NS = $P > 0.05$). Species and plot within block (or plot within block only, in the case of the soil moisture model) were included as random effects; in case of overdispersion, an individual-level random effect was also included. Germination probability was assessed as the proportion of seeds within each subplot that germinated ('Overall') and the proportion of subplots in which *any* germination was recorded ('Subplot'). Seedling survival probability and height were tested both at 5 months after experimental set-up, and at harvest (after 3.5 years).

Response variable		*N*	*P* (Treatment)
Germination probability	Overall	900	0.018
	Subplot	15	<0.001
Seedling survival probability	5 months	900	<0.0001
	3.5 years	900	<0.0001
Seedling height	5 months	110	0.0004
	3.5 years	110	NS$^+$
Relative height growth rate		110	NS
Relative volumetric growth rate		107	NS
Root:shoot ratio		110	NS
Total biomass		110	NS
Soil moisture		225	NS

$^+$ After accounting for seedling height at 5 months

Seedling growth

Seedling height after the first five months was variable, but seedlings were significantly smaller in the Root-rake treatment than in the other treatments ($P < 0.001$, Fig. 1d). At the end of the experiment a similar pattern could be seen ($P = 0.002$), but this was driven by the height at 5 months (when accounting for height at this time, the differences after 3.5 years were not significant; $P = 0.24$, Fig. 1d, Table 2). The relative growth rate of the surviving seedlings (growth rate per year relative to the plant dimensions 5 months after planting) did not differ significantly between treatments, either when expressed as height growth ($P = 0.53$; Fig. 1e) or volumetric growth ($P = 0.15$;Table 2). Treatment did not significantly affect total biomass (above- plus below-ground dry matter) or the root:shoot ratio of the surviving seedlings ($P = 0.07$ and $P = 0.46$, respectively; Fig. 1f, Table 2).

Environmental conditions

There was no significant treatment difference in the soil moisture across the plots before or after rain ($P = 0.17$ and $P = 0.53$, respectively; Fig. 2). While the site received rain the day before planting and the two days directly after planting, the following three months (spring of the year from 1 July 2008 to 30 June 2009) were dry, with an average monthly rainfall of 34 mm, compared with the long-term (1981–2010) mean of 52 mm. During this time, mean daily maximum temperature was 1.8°C warmer than the long-term mean. The whole 2008–2009 year was 0.2°C warmer than the long-term mean, and received 91% of the long-term average rainfall. The 2009–2010 year had temperatures similar to the long-term mean (+0.03°C), but it was wetter than normal (+17% more rain). Overall, the year 2010–2011 was warmer (+0.5°C) and drier (81%) than the long-term mean. Spring and summer of the 2011–2012 year were colder (−0.6°C) and wetter (37%) than the long-term average.

Costs of treatments

Excluding the costs of fencing and planting (which were common across treatments), costs of the site preparation ranged from $500 to $1000 per hectare when executed on a large scale, except for the Control treatment, which cost nothing (Fig. 3a). Indices of regeneration success per unit cost showed much higher cost-benefit ratio for the Control treatment, compared with other treatments (Fig. 3b).

Discussion

This study provides the first quantitative results of the effect of different mechanical and chemical control methods of broom cover on the germination and establishment of indigenous woody species in New Zealand. We undertook our study in a semi-arid dryland environment, where broom has limited value as a 'nurse' for indigenous woody vegetation recovery (Carswell et al. 2013). We found that the best rates of seed germination and seedling survival resulted from the least disturbance of the broom canopy and cover, which also was the cheapest management option.

Natural re-establishment of indigenous woody species into broom stands relies on the size and age of the broom, local environmental conditions, and the availability of indigenous seed sources in the area (Carswell et al. 2013). Indigenous seed sources are rare in the vicinity of our study site and we observed no natural re-establishment within our experimental plots over the course of the experiment. There can be a lack of regeneration, even when seed sources are available: for example, in a restoration project near Taupo, no seedlings of indigenous potential canopy species were found in 12 plots in broom shrubland despite nearby seed sources (Smale et al. 2001). Similarly, in an area surrounded by a seed source of

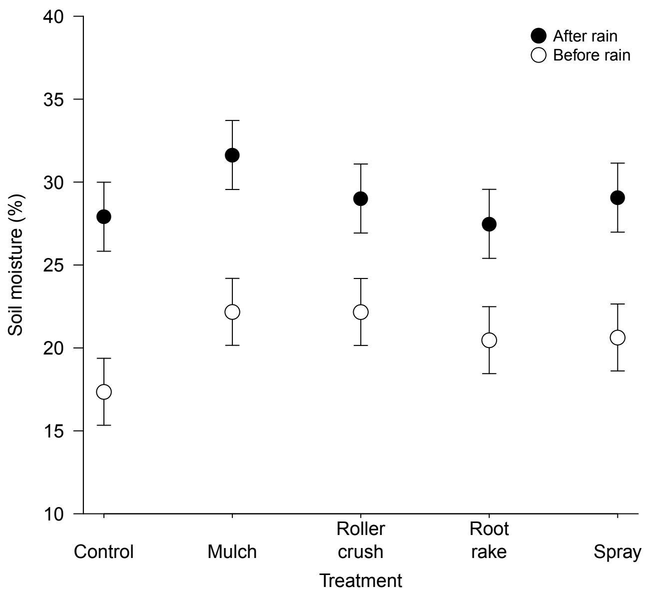

Figure 2. Soil moisture levels across broom management treatments at Ealing, Canterbury Plains, before and after a big rain event in April 2012. Treatments did not significantly affect soil moisture (see Table 2).

mānuka (*Leptospermum scoparium*) on the Hanmer Range, North Canterbury, the indigenous shrub failed to regenerate into neighbouring broom plots that had been sprayed 4 years prior and monitored annually (Williams 1998). Carswell et al. (2013) modelled the key predictors for natural reversion of gorse and broom to indigenous forest and shrubland and indicated that the probability of natural regeneration in the dryland zone is inherently low. Our results show that, even with ample supplied seeds, very few seeds germinated (3%), and of those at least 80% died (Fig. 1), with strong differences between species (Table 1). Poor resulting establishment is a common finding in seed-sowing trials (Stevenson & Smale 2005). Overall, most germinants were of *Plagianthus* but the majority of these were ephemeral. The hard-coated long-lived *Sophora* seeds (Norton et al. 2002) did not start germinating until after the first year, and by the end of the experiment the surviving germinants were dominated by *Sophora.*

Seedling germination and establishment rates are known to vary significantly with local above- and below-ground micro-environmental conditions, and vegetation that ameliorates abiotic stress can have a beneficial (nurse) effect on newly establishing seedlings. Nurse effects may be particularly important in dry environments, where shrubs may have strong facilitative effects on survival and initial growth of seedlings because their canopy provides protection from temperature extremes and improves the water balance of the regenerating indigenous seedlings (Maestre et al. 2003; Gómez-Aparicio et al. 2005; Pugnaire et al. 2011). For example, in a Mediterranean savannah, seedling survival under living shrubs was more than double that in open microsites after 1 year (Gómez-Aparicio et al. 2004). Nurse effects can be disrupted by management treatments that alter existing vegetation cover and seedling establishment, whether directly (by changing temperature, light, humidity, soil moisture and disturbance regimes), indirectly (through altering plant competition and herbivory), or a combination of direct and indirect effects (Holmgren et al. 1997).

Seed had the highest germination probability in the two treatments with the least amount of disturbance to the canopy (Control and Spray), and the living canopy (Control) also enhanced the survival of planted seedlings relative to the mechanically-disturbed treatments (Fig. 1). After the first five months, survival of planted seedlings under living broom canopy was at least two times higher, and after four summers more than six times higher, than in other treatments. The pattern of greater seedling survival under the intact canopy of the Control treatment was evident early in our study (Fig. 1c), perhaps because the first three months of our experiment were more harsh than normal. Mean daily maxima were 1.8°C warmer than the long-term (1981–2010) mean, and only two-thirds of the normal rainfall was received in this period. After the initial five months, the height and volume growth rates of surviving seedlings were similar among the treatments in which planted seedlings survived (Fig. 1e, f). This suggests that the vastly different canopy (and therefore light- and temperature-buffered) environments affected survival but not subsequent growth, or that any positive effects of the canopy on subsequent growth were offset by other factors. Detailed measurements of environmental conditions for the different treatments (e.g. light, temperature, and foliage moisture content) were not carried out as part of this study, but these would be required to infer more about the processes that drive the results.

Our three mechanical-disturbance treatments (Mulch, Roller-crush and Root-rake) caused a burst of broom

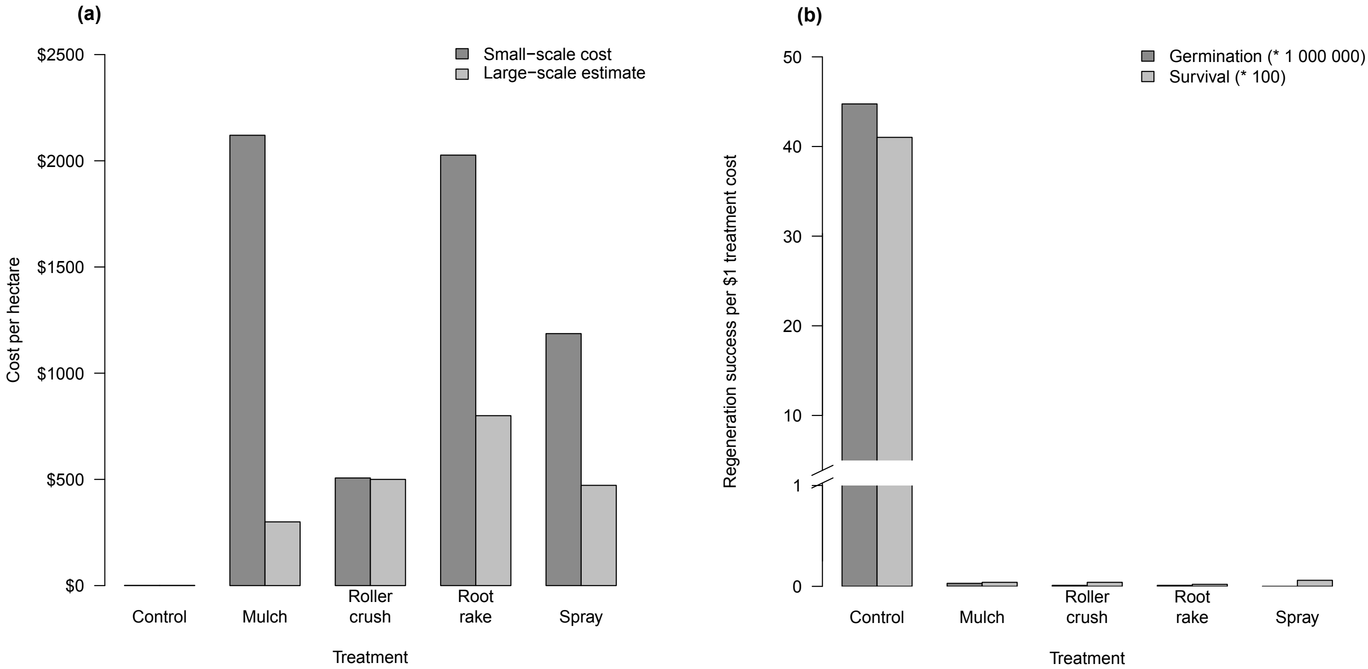

Figure 3. Costs (per hectare) of applying the different broom management treatments as estimated in 2008 (a), and the relative regeneration success per $1 treatment costs (b; based on the large-scale estimate). The costs of fencing, predator control, sowing and planting were not included, as they were equal across treatments. Small-scale costs (a) were created by converting *actual* costs for treatment site preparation of the three 10 × 12 m plots (+ buffer area) to costs per hectare, while large-scale estimates were provided by contractors based on large-scale treatment (> 100 ha). The indices of regeneration success per unit treatment cost (b) were calculated by dividing the overall mean germination and survival probability (see Fig. 1a and 1c, multiplied by 1 000 000 and 100, respectively) by the large-scale cost estimate for each treatment. Note the break in the *y*-axis.

regeneration from its large long-lived seed bank (Lee et al. 1986; Ussery & Krannitz 1998; Williams 1998; Sheppard et al. 2002). Any ground cover, including mulch or litter, can reduce the level of broom regeneration (Sheppard et al. 2002) and allow competing species to establish, but too much mulch or litter can also reduce germination and establishment of indigenous seedlings (Monk & Gabrielson 1985; Moro et al. 1997). Our Mulch treatment had moderate levels of seed germination, but many seedlings succumbed soon after planting and all had died by 3.5 years. We did not test the factors contributing to this mortality, but suggest the mulch layer may have created a different moisture environment. Mulch is often used to retain soil moisture in landscape plantings; however, a thick layer of mulch can also absorb and then evaporate rainfall, without it ever reaching the soil, in effect acting as a barrier to increasing soil moisture (Gilman & Grabosky 2004). In the two other mechanical-disturbance treatments (Roller-crush and Root-rake), broom regenerated from seed, and rerooted or resprouted from the battered broom debris. The Roller-crush treatment resulted in a thick layer of broom debris (approximately 0.5 m) among which the seedlings were planted (into mineral soil), and after the first five months the surviving seedlings were slightly taller than in the Root-rake treatment, where almost all broom debris and most topsoil had been raked aside. This may be explained by the differential survival of taller seedlings that were able to quickly overtop the debris ahead of the regenerating broom in the Roller-crush treatment. In the period following the initial five months, seedling growth rates were approximately equal in both treatments, maintaining the initial height differences (Fig. 1d).

Weed control treatments that alter ground cover and associated microhabitat conditions can also indirectly affect recruitment of indigenous trees through their effects on predator densities and hence seed and seedling predation (e.g. Reader 1991; Manson & Stiles 1998). To guard against such effects and consequent biases in our results, we fenced plots, trapped possums and sowed our seeds under cages in all treatments of our experiment. However, we noted signs of browsing by hares or rabbits on planted seedlings across all of our treatments, suggesting that little (if any) differential seed and seedling predation resulted. It is important to note that the germination results reported here likely represent a more positive scenario than would be applicable in most restoration projects (where sowing in cages would be unrealistic), unless there was associated intensive pest control. In this study, seeds and small germinants were protected from granivores and small herbivores, respectively; although small rodents and invertebrate seed predators retained access.

Management implications

The benefit of nurse plants, particularly nitrogen-fixers in semi-arid or arid conditions, has been advocated to aid the restoration of indigenous vegetation elsewhere (Pugnaire et al. 1996, 2011; Gómez-Aparicio et al. 2004; Padilla & Pugnaire 2007). In cool dry environments N-fixers have an advantage over non-fixers (Monks et al. 2012), and initial establishment of exotic N-fixers may confer an advantage to succeeding woody species by increasing soil N and decreasing evapotranspiration (Vetaas 1992; Abdallah & Chaieb 2012; Magesan et al. 2012). Such factors play an important role not only in the regeneration and establishment of indigenous species, as shown here, but are also likely to affect the succession trajectory and the ultimate community composition (Dungan et al. 2001; McQueen et al. 2006; Sullivan et al. 2007; Walker et al. 2009b; Williams 2011). Our study concurs with the above studies, and suggests that the planting (and to a lesser extent sowing) of woody species under primary successional shrubs may be an effective way of accelerating succession in degraded dryland landscapes, where the direct recovery of tree cover may be very difficult, if not impossible.

Our experimental results show that retaining living broom cover was beneficial to the seed germination and survival of planted seedlings of indigenous woody species, compared with other treatments. It is also the cheapest management option of those tested in this study. Common broom management techniques (spraying, mulching, root-raking and crushing) negatively affected the establishment and survival of planted indigenous woody seedlings at our dryland study site. Although planting is more labour intensive and costly than sowing seeds, for most species it is more likely to be successful in dryland zones, as indicated by the low seed germination overall (with sowing rates equivalent to 500 000 seeds ha^{-1}). However, it is important to note that for species with higher seed germination and survival rates (particularly *Sophora microphylla*), sowing seeds may be a viable option in restoration projects in these dryland zones.

For any mechanical-disturbance treatments to be effective in removing broom cover, follow-up control of regenerating broom would be required over many years (Downey & Smith 2000). While this might be effective in slowing broom regeneration, it inevitably causes additional disturbance, which in turn can result in other opportunistic introduced species colonising the disturbed areas, providing increased competition for the indigenous species (Buckley et al. 2007). Moreover, chemical or mechanical broom control removes other woody seedlings and saplings from a site, including indigenous species, eliminating the potential of these self-established seedlings to contribute to the succession towards an indigenous-dominated woody cover, and resets the broom invasion. This provides an additional incentive for retaining the standing broom cover in areas where natural seed sources are available and regeneration is occurring.

Planting costs will vary between treatments, which will have some bearing on costs of establishment. While we did not assess the differences in planting effort, it is likely that physically-cleared sites (Mulch, Root-Rake) are the cheapest to plant. However, ultimately this would result in an expensive restoration strategy, since planted seedlings in these treatments showed the poorest survival rates. Given the highly unequal cost–benefit ratios between the Control and other treatments (Fig. 3b), we suggest that higher costs of sowing and/or planting under a live broom canopy are more than offset by the higher survival rates.

Acknowledgements

We thank the Peter Keller – Opuha Nurseries, Geraldine, for supplying seeds and seedlings; the Department of Conservation (Geraldine and Christchurch), for supporting the study by providing the site, the materials and the many volunteers who helped sow, plant and measure the seedlings, in particular Dave Anderson who managed setting up the study treatments and pest control; Adrian Monks and Guy Forrester for statistical advice; and Quentin Paynter, Susan Walker and two anonymous reviewers for helpful discussions and comments that greatly improved the manuscript. This research was funded by the New Zealand Foundation for Research, Science and Technology (Restoring Dryland Biodiversity Intermediate Outcome) and core funding from the Ministry of Business, Innovation and Employment to Landcare Research (Biodiversity in Production Landscapes).

References

Abdallah F, Chaieb M 2012. The influence of trees on nutrients, water, light availability and understorey vegetation in an arid environment. Applied Vegetation Science 15: 501–512.

Allen RB, Williams PA, Lee WG 1995. Seed bank accumulation of broom (*Cytisus scoparius*) in South Island. Proceedings of the NZ Plant Protection Conference 48: 276–280.

Armas C, Pugnaire FI 2005. Plant interactions govern population dynamics in a semi-arid plant community. Journal of Ecology 93: 978–989.

Balneaves JM, McCord AR 1990. Gorse control: a trying experience at Ashley forest. In: Bassett C, Whitehouse LJ, Zabkiewicz JA eds Alternatives to the chemical control of weeds. FRI Bulletin 155. Pp. 150–156.

Bascand LD, Jowett GH 1982. Scrubweed cover of South Island agricultural and pastoral land 2. Plant distribution and managerial problem status. New Zealand Journal of Experimental Agriculture 10: 455–492.

Bates D, Maechler M, Bolker B, Walker S 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7. http://www.CRAN.R-project.org/package=1me4.

Buckley YM, Bolker BM, Rees M 2007. Disturbance, invasion and re-invasion: managing the weed-shaped hole in disturbed ecosystems. Ecology Letters 10: 809–817.

Carswell FE, Burrows LE, Hall GMJ, Mason NWH, Allen RB 2012. Carbon and plant diversity gain during 200 years of woody succession in lowland New Zealand. New Zealand Journal of Ecology 36: 191–202.

Carswell FE, Mason NWH, Holdaway RJ, Burrows LE, Payton IJ, Sutherland MA, Price R, Pearce HG, Corich-Hermans O, Williams P 2013. Indirect estimation of gorse and broom 'non-forest land' to 'forest land' transition. MPI Technical Paper No. 2013/. Wellington, Ministry for Primary Industries. 61p.

Castro J, Zamora R, Hódar JA, Gómez JM, Gómez-Aparicio L 2004. Benefits of using shrubs as nurse plants for reforestation in Mediterranean mountains: a 4-year study. Restoration Ecology 12: 352–358.

Downey PO, Smith JMB 2000. Demography of the invasive shrub Scotch broom (*Cytisus scoparius*) at Barrington Tops, New South Wales: insights for management. Austral Ecology 25: 477–485.

Dungan RJ, Norton DA, Duncan RP 2001. Seed rain in successional vegetation, Port Hills Ecological District, New Zealand. New Zealand Journal of Botany 39: 115–124.

Flores J, Jurado E 2003. Are nurse-protégé interactions more common among plants from arid environments? Journal of Vegetation Science 14: 911–916.

Fox J 2003. Effect displays in R for generalised linear models. Journal of Statistical Software 8(15): 1–27.

Gilman EF, Grabosky J 2004. Mulch and planting depth affect

live oak (*Quercus virginiana* Mill.) establishment. Journal of Arboriculture 30: 311–317.
Gómez-Aparicio L, Zamora R, Gómez JM, Hódar JA, Castro J, Baraza E 2004. Applying plant facilitation to forest restoration: A meta-analysis of the use of shrubs as nurse plants. Ecological Applications 14: 1128–1138.
Gómez-Aparicio L, Gómez JM, Zamora R, Boettinger JL 2005. Canopy vs. soil effects of shrubs facilitating tree seedlings in Mediterranean montane ecosystems. Journal of Vegetation Science 16: 191–198.
Harris PT, Cannon GH, Smith NE, Muth NZ 2013. Assessment of plant community restoration following Tree-of-Heaven (*Ailanthus altissima*) control by *Verticillium albo-atrum*. Biological Invasions 15: 1887–1893.
Holmgren M, Scheffer M, Huston MA 1997. The interplay of facilitation and competition in plant communities. Ecology 78: 1966–1975.
Hothorn T, Bretz F, Westfall P 2008. Simultaneous inference in general parametric models. Biometrical Journal 50: 346–363.
Lee WG, Allen RB, Johnson PN 1986. Succession and dynamics of gorse (*Ulex europaeus* L.) communities in the Dunedin Ecological District South Island, New Zealand. New Zealand Journal of Botany 24: 279–292.
Maestre FT, Bautista S, Cortina J, Bellot J 2001. Potential for using facilitation by grasses to establish shrubs on a semiarid degraded steppe. Ecological Applications 11: 1641–1655.
Maestre FT, Bautista S, Cortina J 2003. Positive, negative, and net effects in grass–shrub interactions in Mediterranean semiarid grasslands. Ecology 84: 3186–3197.
Magesan GN, Wang H, Clinton PW 2012. Nitrogen cycling in gorse-dominated ecosystems in New Zealand. New Zealand Journal of Ecology 36: 21–28.
Manson RH, Stiles EW 1998. Links between microhabitat preferences and seed predation by small mammals in old fields. Oikos 82: 37–50.
McQueen JC, Tozer WC, Clarkson BD 2006. Consequences of alien N_2 on vegetation succession in New Zealand. In: Allen RB, Lee WG eds Biological invasions in New Zealand. Ecological Studies 186. Heidelberg, Springer. Pp. 295–306.
Meurk CD 2008. Vegetation of the Canterbury plains and downlands. In: Winterbourn M, Knox G, Burrows C, Marsden I eds Natural history of Canterbury, 3rd edn. Christchurch, Canterbury University Press. Pp. 195–250.
Monk CD, Gabrielson FC Jr 1985. Effects of shade, litter and root competition on old-field vegetation in South Carolina. Bulletin of the Torrey Botanical Club 112: 383–392.
Monks A, Cieraad E, Burrows L, Walker S 2012. Higher relative performance at low soil nitrogen and moisture predicts field distribution of nitrogen-fixing plants. Plant and Soil 359: 363–374.
Moro MJ, Pugnaire FI, Haase P, Puigdefábregas J 1997. Mechanisms of interaction between a leguminous shrub and its understorey in a semi-arid environment. Ecography 20: 175–184.
Norton DA, Godley EJ, Heenan PB, Ladley JJ 2002. Germination of *Sophora* seeds after prolonged storage. New Zealand Journal of Botany 40: 389–396.
Oneto SR, Kyser GB, DiTomaso JM. 2010. Efficacy of mechanical and herbicide control methods for Scotch broom (*Cytisus scoparius*) and cost analysis of chemical control options. Invasive Plant Science and Management 3: 421–428.
Padilla FM, Pugnaire FI 2007. Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. Functional Ecology 21: 489–495.
Peters J ed. 2000. Tetrazolium Testing Handbook. Contribution No. 29 to the Handbook on Seed Testing. First revision. Association of Official Seed Analysts. 62 p.
Pugnaire FI, Haase P, Puigdefábregas J, Cueto M, Clark SC, Incoll LD 1996. Facilitation and succession under the canopy of a leguminous shrub, *Retama sphaerocarpa*, in a semi-arid environment in south-east Spain. Oikos 76: 455–464.
Pugnaire FI, Armas C, Maestre FT 2011. Positive plant interactions in the Iberian Southeast: Mechanisms, environmental gradients, and ecosystem function. Journal of Arid Environments 75: 1310–1320.
R Development Core Team 2012. R: a language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing. ISBN 3-900051-07-0. www.r-project.org/
Reader RJ 1991. Control of seedling emergence by ground cover: a potential mechanism involving seed predation. Canadian Journal of Botany 69: 2084–2087.
Rees M, Paynter Q 1997. Biological control of Scotch broom: modelling the determinants of abundance and the potential impact of introduced insect herbivores. Journal of Applied Ecology 34: 1203–1221.
Rey PJ, Siles G, Alcántara JM 2009. Community-level restoration profiles in Mediterranean vegetation: nurse-based vs. traditional reforestation. Journal of Applied Ecology 46: 937–945.
Sheppard AW, Hodge P, Paynter Q, Rees M 2002. Factors affecting invasion and persistence of broom *Cytisus scoparius* in Australia. Journal of Applied Ecology 39: 721–734.
Smale MC, Whaley PT, Smale PN 2001. Ecological restoration of native forest at Aratiatia, North Island, New Zealand. Restoration Ecology 9: 28–37.
Stevenson BA, Smale MC 2005. Seed bed treatment effects on vegetation and seedling establishment in a New Zealand pasture one year after seeding with native woody species. Ecological Management & Restoration 6: 124–131.
Sullivan JJ, Williams PA, Timmins SM 2007. Secondary forest succession differs through naturalised gorse and native kānuka near Wellington and Nelson. New Zealand Journal of Ecology 31: 22–38.
Talbot E 2000. Cutting and mulching broom (*Cytisus scoparius* (L.) Link): a Tasmanian perspective. Plant Protection Quarterly 15: 183–185.
Tielborger K, Kadmon R 2000. Temporal environmental variation tips the balance between facilitation and interference in desert plants. Ecology 81: 1544–1553.
Ussery JG, Krannitz PG 1998. Control of Scot's broom (*Cytisus scoparius* (L.) Link.): the relative conservation merits of pulling versus cutting. Northwest Science 72: 268–273.
Vetaas OR 1992. Micro-site effects of trees and shrubs in dry season savanna. Journal of Vegetation Science 3: 337–344.
Walker S, Cieraad E, Monks A, Burrows L, Wood J, Price R, Rogers G, Lee B 2009a. Long-term dynamics and rehabilitation of woody ecosystems in dryland South Island, New Zealand. In: Hobbs RJ, Suding KN eds New models for ecosystem dynamics and restoration. The

science and practice of ecological restoration. Washington, DC, Island Press. Pp. 99–111.

Walker S, King N, Monks A, Williams S, Burrows L, Cieraad E, Meurk C, Overton JMcC, Price R, Smale M. 2009b. Secondary woody vegetation patterns in New Zealand's South Island dryland zone. New Zealand Journal of Botany 47: 367–393.

Watt MS, Whitehead D, Mason EG, Richardson B, Kimberley MO 2003. The influence of weed competition for light and water on growth and dry matter partitioning of young *Pinus radiata*, at a dryland site. Forest Ecology and Management 183: 363–376.

Williams PA 1998. Response of broom (*Cytisus scoparius*) to control measures. Science for Conservation 97. Wellington, Department of Conservation. 10 p.

Williams PA 2011 Secondary succession through non-indigenous dicotyledonous woody plants in New Zealand. New Zealand Natural Sciences 36: 73–91.

Williams PA, Karl BJ 2002. Birds and small mammals in kanuka (*Kunzea ericoides*) and gorse (*Ulex europaeus*) scrub and the resulting seed rain and seedling dynamics. New Zealand Journal of Ecology 26: 31–41.

Wilson BC, Jacobs DF 2006. Quality assessment of temperate zone deciduous hardwood seedlings. New Forests 31: 417–433.

Wilson HD 1994. Regeneration of indigenous forest on Hinewai Reserve, Banks Peninsula. New Zealand Journal of Botany 32: 373–383.

Editorial Board member: David Wardle
Received 23 April 2014; accepted 31 August 2014