The impact of exotic weed competition on a rare New Zealand outcrop herb, *Pachycladon cheesemanii* (Brassicaceae)

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Abstract: Nearly one quarter of New Zealand's unique vascular plant flora is threatened, and weed invasion is implicated in the decline of more than half of these threatened species. However, there is little experimental evidence showing that invasive weeds have a direct impact on threatened native plants. This study experimentally tested the hypothesis that competition with invasive weeds threatens the rare outcrop plant *Pachycladon cheesemanii* (Brassicaceae). *Pachycladon cheesemanii* is a threatened South Island, New Zealand endemic with a distribution nearly confined to rock outcrops. It has disappeared from historical record sites throughout its range. The effects of weed competition and habitat on *P. cheesemanii* establishment, growth and survival were investigated by sowing seed into replicated plots subject to three treatments: weed removal, soil disturbed and unweeded control, in three habitat types: forested and open rock outcrops and open tussock grassland. The experiments were carried out at three locations: Mt Somers (Canterbury), Wye Creek and Diamond Lake (Otago). Within weedy rock outcrop habitat, weed removal significantly increased the rate of *P. cheesemanii* germination, and appeared to increase seedling growth rates, implying that weeds can negatively impact populations. Relative to rock outcrop habitat, *P. cheesemanii* germination was very low in adjacent open grassland habitat regardless of weeding treatment. Demographic monitoring of four natural populations of *P. cheesemanii* revealed that seed production is highly variable among populations and may be limited by browse and mechanical damage to inflorescences. *Pachycladon cheesemanii* does produce a persistent seed bank but most seed is found close to parent populations. Our results suggest that competition with invading weeds threatens current *P. cheesemanii* populations, that plant establishment can be enhanced by weed removal, and that considerable potential exists for artificially expanding populations by sowing seed into appropriate weed-free habitat.

Keywords: establishment; field experiment; *Pachycladon cheesemanii*; recruitment; rock outcrop; seed bank; weed competition; threatened plant.

Introduction

The long-term survival of nearly one quarter of New Zealand's native vascular plant flora is threatened (de Lange *et al.*, 1999), and exotic weed invasion is implicated in the decline of 59% of New Zealand's threatened plant species (Dopson *et al.*, 1999). We surveyed studies that assessed threats facing rare New Zealand plant species published between 1990 and 2002 in *New Zealand Journal of Botany*, *New Zealand Journal of Ecology* and *Biological Conservation*, and found that 17 of the 25 published studies claimed that competition with invasive weeds had been a significant cause of species decline, was a current threat, or both. These claims were based on observations of species distribution, habitat, associated vegetation, population structure and trends, and germination behaviour. However, none of these studies included experimental evidence of a weed competition effect, a situation that generally applies to studies on the impacts of invasive weeds on threatened plants overseas (Huenneke *et al.*, 1990; Walck *et al.*, 1999).

Descriptive research is essential for providing background information on species ecology, distribution and conservation status, and for indicating likely threats facing threatened species (Schemske *et al.*, 1994; Veltman, 1996). But manipulative experiments are necessary to rigorously evaluate these threats, a step that is critical for appropriate species recovery planning (Schemske *et al.*, 1994; Veltman, 1996).

This paper describes a series of experiments designed to test the hypothesis that competition with invasive weeds threatens the rare plant *Pachycladon cheesemanii* (Brassicaceae). *Pachycladon cheesemanii* is a New Zealand endemic perennial herb found in drier parts of the eastern South Island from Marlborough to Southland with a stronghold in central Otago. It is mostly confined to rock outcrops in montane to alpine tussock grassland, mountain beech forest, mixed-broadleaf forest and scrub. Field surveys show that *P. cheesemanii* has declined throughout its range (Wardle, 1999; Anonymous, 2000; Wardle, 2000). Field reconnaissance showed that weed invasion, especially by *Hieracium* sp., appears to threaten virtually all of the current populations, and the decision to investigate weed impacts was based on the consensus of experts that competitive displacement by invading weeds is likely to be the most important factor in the decline of *P. cheesemanii*, and the greatest threat to the future status of the species. *Pachycladon cheesemanii* is rarely observed to suffer herbivory, even when plants are readily accessible to feral and domestic animals (Wardle, 2000, P. Heenan, Landcare Research, Lincoln, N.Z., *pers. comm.*), suggesting that herbivory is unlikely to be a significant threat to the species. Field observations also reveal that flowering and fruit production are high but seedling establishment is variable. This suggests reproductive output is unlikely to limit population growth, but lack of recruitment at some sites may be important.

We tested whether weed invasion threatens *P. cheesemanii* populations by sowing seed in control and weed removal plots in each of three habitat types in which populations of *P. cheesemanii* are currently or historically known (forested rock outcrops, open rock outcrops and montane tussock grassland). Because the basic demography of this species has not been recorded, we also monitored plant growth, reproduction, mortality and seed bank dynamics within naturally-occurring populations in these habitats.

Materials and methods

Study species

Pachycladon cheesemanii [previously *Ischnocarpus novae-zelandiae* (Heenan *et al.*, 2002)] is a small, rosette-forming, taprooted, perennial herb with small white flowers borne on slender terminal racemes. Fruits are passively dehiscent long cylindrical siliques that contain numerous light brown seeds. These seeds have no obvious dispersal mechanism and are probably gravity and wind-dispersed over short distances. Flowering occurs from October to February, and fruiting from November to March. *Pachycladon cheesemanii* has a threat ranking of Gradual Decline (Hitchmough, 2002).

Study sites

We selected three locations with current populations of *P. cheesemanii* for this study (Table 1). These locations were chosen, first, to encompass different habitat types, second, to encompass a sizeable portion of the species' natural range, with two sites in Otago which is the species' stronghold, and third, for logistical reasons (access by 4-wheel drive or less than 1.5 hour walking time), as each location had to be visited repeatedly. All study locations were south-facing with numerous rock outcrops, which is typical habitat for *P. cheesemanii*. Each location is described in more detail below.

Mt Somers

This location is northwest of the summit of Mt Somers

Table 1. Summary of the characteristics of the experimental field sites. Where a location had two sites per habitat type, each site is assigned a number but the plot characteristics are the average from both sites.

					Ground Cover							
Location	Habitat	Site #	Altitude (m)	Aspect (°)	% Exotic	% Native	% Litter	% Rock	% Moss	% Bare	Soil depth (cm)	Notes
Mt Somers	Forested rock outcrop	-	860	120	16.7	8.44	41.4	7.22	0.33	25.89	5.81	
	Open rock outcrop	1	900	140	21.1	12.89	22.06	35.39	2.3	4.17	3.03	
		2	925	240								
	Open tussock grassland	1	900	140	80.7	1.83	15	2.78	0	0	4.78	
		2	925	240								
Wye Creek	Forested rock outcrop	-	575	180	2.06	10.43	24.81	15.31	10.31	37.38	5.23	Destroyed[1]
	Open rock outcrop	-	515	200	23.75	11.25	48.17	5.58	8.33	4.58	3.92	
Diamond Lake	Forested rock outcrop	1	495	168	65	0.83	18.75	12.5	1.67	0.83	2.59	Grazed by sheep[2]
		2	495	170								

[1]. Plot markers were removed so no data obtained from this site.

[2]. This site was trampled and grazed by sheep that were let into the area to graze during the drought of summer 2000/01.

(43°36'S, 117°19'E) in mid-Canterbury. The geology is Upper Cretaceous rhyolite rock, which forms dry, thin and infertile soils. Rock habitats such as bluffs, rock outcrops, boulder fields, and screes are abundant at this location. Mean annual rainfall in the area is 1063mm (1988 – 2000, Environment Canterbury weather station data). The vegetation is modified tussock grassland dominated by weeds such as *Hieracium pilosella* and exotic pasture grasses. It also includes pockets of mountain beech (*Nothofagus solandri* var. *cliffortiodes*) and scrub. There are two natural populations of *P. cheesemanii* at Mt Somers, one of *c.* 65 plants growing under *Hebe rakaiaensis* shrubs under a rock overhang, and the other of seven plants growing in skeletal soils under another rock overhang. Other *P. cheesemanii* plants have been found in the area, but never more than a few plants.

Wye Creek

The Wye Creek Conservation area is beside Lake Wakatipu near Queenstown (45°09'S, 168°46'E). Soils are mainly stony steepland schists which are strongly leached and droughty in the summer. The topography is steep and rugged. The mean annual rainfall is 837mm and the mean annual temperature is 10.4° [Record 130 yrs, National Institute of Water and Atmospheric Research (NIWA)]. The vegetation is a mixture of tussock grassland, mountain beech remnants and scrub. There are two populations of *P. cheesemanii* at this location, one of *c.* 200 plants located along a ledge under an overhanging bluff in mountain beech forest, and a small population of *c.* 20 plants on an open rocky ledge. Weed presence is relatively low, although the invasive weed *Hieracium lepidulum* (tussock hawkweed) is present and appears to be increasing. *Pachycladon cheesemanii* plants are scattered in other bluffs in the area, but not in any abundance.

Diamond Lake

'Diamond Lake' is part of a 3144-ha pastoral lease property located near Wanaka, Central Otago (44°38'S, 168°57'E). The soils are Haast schists with Paradise yellow-brown earths. This locality has a glaciated landscape with lakes, tarns, boulderfields, and steep bluffs. The mean annual rainfall is 689mm and the mean annual temperature is 10.2° (Record 9 years, NIWA). The vegetation consists of remnant mixed-broadleaf forest pockets located along the bluffs and on steeper slopes. *Hieracium lepidulum* is extensive within these forest remnants. Surrounding the remnants is exotic pasture dominated by introduced grasses including browntop (*Agrostis capillaris*), sweet vernal (*Anthoxanthum odoratum*) and cocksfoot (*Dactylis glomerata*). Sheep and cattle currently graze the pasture and have access to the bush remnants. There are ten known populations of *P. cheesemanii* on bluffs in the Diamond Lake area (400 – 675 m a.s.l.), ranging in size from 5–60 plants.

Bob's Cove

Bob's Cove was not an experimental location, but it harbours a *P. cheesemanii* population that was monitored in this study. The population is located on a 2-m tall bank beside a Department of Conservation walking track along Lake Wakatipu (45º02'S, 168º30'E). The climate is similar to Wye Creek. The vegetation is mixed beech-broadleaf forest with few exotic species present. *P. cheesemanii* is found in several locations scattered along the bank, ranging from 1–40 plants.

Field experiments

Mt Somers

The field experiment at Mt Somers was established on 11 November 2000. We identified three habitat types that differed in extent of exotic weed invasion. We then selected five sites in areas where *P. cheesemanii* plants currently do not occur but that appeared similar to current or historical population sites (Table 1):

1. Forested rock outcrop habitat; one site, a moderately weed-free rock outcrop site in mountain beech forest.
2. Open rock outcrop habitat; two sites, both moderately weed-free rock outcrop sites in open tussock grassland.
3. Open tussock grassland habitat; two sites, both very weedy open tussock grassland sites each within 5 m of one or the other of the rock outcrop sites.

The primary aim of this experiment was to test the hypothesis that competition with weeds prevents *P. cheesemanii* from establishing in grassland habitat, from which it is historically recorded, and restricts it to more open rock outcrop habitat.

At each of the five sites we laid out twelve 30 x 30 cm plots in areas judged to be suitable for *P. cheesemanii* establishment (i.e. avoiding areas with solid rock). In each plot, we recorded groundcover characteristics (a visual estimate of percent cover by exotic and native vegetation, litter, moss, rock, and bare ground), measured soil depth by pushing a metal stake into the ground at the plot centre, and recorded the species present in each plot. At each site, we randomly assigned three plots to each of four treatments:

1. Weed removal treatment, where all exotic species were removed by hand weeding and seeds of *P. cheesemanii* were sown into the plot. Reinvading weeds were subsequently removed when the plots

were monitored for germination (see below).

2. Soil disturbed treatment, where plots were raked to a depth of *c.* 1 cm with a hand rake, but weeds were not removed, and seeds of *P. cheesemanii* were sown. Because the weed removal treatment resulted in soil disturbance, this separate soil disturbance treatment was done to isolate the effect of weed removal.
3. Control treatment, where the plot was left intact and seeds of *P. cheesemanii* were sown.
4. Unsown control treatment, where the plot was left intact and no seeds were sown. This treatment was used to estimate germination rates from seed naturally present in the soil. Because there was no natural germination in these plots, they were not used in subsequent analysis.

We sowed approximately 500 *P. cheesemanii* seeds per plot into all but the unsown control plots by scattering the seeds evenly from a height of *c.* 15 cm. The number of seeds per plot is approximate because we calculated quantities of seed by weighing lots equivalent to 500 seeds based on a mean of the weights of 5 lots of exactly 50 seeds. Seeds were obtained from plants cultivated at Lincoln University that had been sourced from central Otago populations. Since these seeds were not sourced from Mt Somers, we removed any sown seedlings surviving to the end of the experiment, and will monitor plots for three years to ensure that any additional seedlings are removed. After sowing, the soil surface of the plot was gently compressed and the plot was watered (*c.* 0.5 l). Plots received supplementary water to increase the likelihood of germination and thus results, and since all plots received the same amount of supplementary water, our treatments were not confounded.

We monitored plots for germination and watered them again on 23 November and 12 December 2000. We monitored for additional germination and seedling survival at monthly intervals after this. Nearly all seedlings that germinated during the summer had died by the end of autumn (April 2000). A second pulse of germination was observed early the following spring (August 2001). These seedlings were tagged with coloured paperclips, and the width of the basal rosette and number of leaves was recorded. Seedling growth (change in width of basal rosette and number of leaves) and survival was recorded again eight weeks after tagging.

Wye Creek and Diamond Lake

The experiment at Wye Creek was established on 25 January 2001 and at Diamond Lake on 26 January 2001. At Wye Creek we selected one site in each of two habitat types, but only one survived (Table 1):

1. Forested rock outcrop habitat; one site, a weed-free rock outcrop site in mountain beech forest. This site was destroyed through the removal of plot markers.
2. Open rock outcrop habitat; one site, a moderately weedy open rock outcrop site.

And at Diamond Lake we selected two sites within one habitat (Table 1):

1. Forested rock outcrop habitat; two sites, both rock outcrop sites in mixed-broadleaf forest with high weed presence (*Hieracium lepidulum* and *Dactylis glomerata*). One of these sites was altered by sheep grazing during a drought.

Although these were rock outcrop habitats, weeds extensively invaded two of the sites. The primary aim of these experiments was to test the hypothesis that competition with invading weeds could affect the establishment, growth and survival of *P. cheesemanii* plants in their current habitat.

At each of the four sites we laid out sixteen 30 x 30 cm plots and recorded plot characteristics as before. We then randomly assigned four plots to each of the four treatments (weed removal, soil-disturbed, control, and unsown control). After treatments had been applied we sowed approximately 800 seeds per plot (number of seeds based on weight measurements as for Mt Somers). These seeds were all sourced from Wye Creek and Bob's Cove, so seedlings were also removed at the end of the experiment and monitored as for Mt Somers. None of these plots received supplementary watering.

We monitored the Wye Creek and Diamond Lake plots for germination on 28 February 2001, one month after establishment because this was the time to first germination we observed at Mt Somers. We monitored the plots again on 18 and 19 April 2001, but since no germination had occurred, monitoring ceased until early spring (4 September 2001) when seedlings were observed. On 9 October 2001, ten randomly chosen seedlings (or all seedlings if there were fewer than 10) at each site were tagged with coloured paper clips, and the number of leaves and maximum width of the basal rosette of each tagged seedling was recorded. Seedling growth (change in width of basal rosette and number of leaves) and survival was recorded again 9 weeks after tagging.

Natural populations

The growth and fecundity of plants in natural populations were recorded at four locations: Mt Somers, Wye Creek, Diamond Lake and Bob's Cove. The habitat characteristics of the four populations are summarised in Table 2. Plants were tagged by placing a metal fencing staple with a numbered label in the soil near the plant. Maximum width of the basal rosette was measured, number of basal leaves was counted, and

Table 2. Characteristics of the four populations of *P. cheesemanii* monitored in this study.

Population	Aspect	Altitude (m)	Habitat	Vegetation
Diamond Lake	SE	680	Open rock outcrop	Exotic grassland/weeds
Bob's Cove	SE	195	Forested bank	Mixed broadleaf forest
Wye Creek	S	575	Forest rock outcrop	Mountain beech
Mt Somers	SE	850	Open rock outcrop	Scrub

the number of flower stalks and fruits or flowers was recorded. Damage to the plant, e.g. from browsing, disease, or insect infestation was noted. At Mt Somers every third adult plant was tagged and five seedlings were tagged. At Diamond Lake every second adult plant and every seedling was tagged. At Wye Creek every fifth adult and every third seedling was tagged. At Bob's Cove every adult in a small section of bluff was tagged. All populations were monitored at approximately monthly intervals for nine months, beginning in December 2000.

Seed bank

We conducted a seed bank study of three natural populations (Mt Somers, Wye Creek, and Diamond Lake) to test whether *P. cheesemanii* produces a persistent seed bank, and to examine whether seed disperses any distance from parent plants. We sampled the seed bank in spring 2000 (23 November at Mt Somers, 5 December at Diamond Lake and 7 December at Wye Creek) to test for the existence of an overwintering seed bank. We then sampled the seed bank in autumn 2001 after most seed produced that year would have dispersed (6 April at Mt Somers, 18 April at Diamond Lake and 19 April at Wye Creek).

To sample the seed bank, we collected ten soil surface samples with a hand spade from within each population, and then from distances of 1m and 3m from the edge of each population. Each sample comprised the soil from an area of about 200 cm^2 to a depth of a few centimetres. The samples were air dried in open plastic bags in a glasshouse for two weeks, then spread out on sand-filled trays and watered as required. All emerging seedlings were counted and identified. If identification was not immediately possible, seedlings were removed and potted for later identification. The experiment was terminated three months after no new *P. cheesemanii* seedlings were observed.

Analysis

Habitat differences

At Mt Somers, differences among habitat types (forested rock outcrop, open rock outcrop and open tussock grassland) in plot characteristics such as ground cover and soil depth, were compared using one-way ANOVA. At Wye Creek and Diamond Lake, plot characteristics were summarised for each habitat, and differences between Wye Creek and Diamond Lake were compared with one-way ANOVA.

Germination

Mt Somers. No germination occurred in many of the plots, so we used logistic regression to model the presence or absence of germination in a plot as function of treatment, habitat type and plot characteristics. Backward selection models were built by removing variables one at a time from a full model of all variables, dropping the least significant variable from the model, and repeating the process until only significant variables remained ($P < 0.05$). Since percent exotic cover and percent bare ground were correlated with treatment (weeding removed exotic cover and increased the amount of bare ground) these variables were excluded from the analysis.

Wye Creek and Diamond Lake. One site at each location was ruined or altered (Table 1). No data were obtained from the Wye Creek forested rock outcrop habitat, and all future references to Wye Creek refer to the open rock outcrop habitat only. Diamond Lake Site #1 however was still used despite being grazed and trampled by sheep. The remaining two sites (Wye Creek open rock outcrop habitat and Diamond Lake Site #2) were similar in that both were sheltered, weedy outcrop habitat, so we combined these sites for analysis. The effects of treatment, site, site by treatment interaction, and plot characteristics on the number of seeds germinating in each plot were analysed with a General Linear Model (GLM). Germination data were first normalised with a square root transformation.

The additional 'treatment' imposed by sheep grazing at Diamond Lake Site #1 provided a new testable prediction: at this site there should be less effect of the weed removal treatment since weed cover had been reduced by grazing in all plots. We tested for a treatment effect at this site using a GLM with square root normalised germination data. We also tested for a site, treatment, and site by treatment interaction by combining the Wye Creek open rock outcrop site and Diamond Lake Site #2 as one site, and the sheep-grazed Diamond Lake Site #1 as a second site. We predicted a significant site by treatment interaction if weed cover affects germination, because there should be a strong effect of the weed removal treatment at Wye Creek and Diamond Lake Site #2, but less of an effect at Diamond Lake Site #1.

Seedling growth and survival

Seedling survival in experimental treatments was calculated as the mean percent of tagged seedlings alive per plot after nine weeks at Wye Creek and Diamond Lake, and eight weeks at Mt Somers. The growth rate of tagged seedlings was calculated as the percent change per week between the initial and final measurements, using both leaf number and width of the basal rosette.

We present descriptive data for Mt Somers because so few seedlings survived in the weedy grassland habitat where we expected to see the strongest effects of weed removal on plant performance. For Wye Creek and Diamond Lake, we used GLMs to model the effects of site and treatment on survival and growth in terms of leaf number and rosette width. By December 2001, much of the grazed and trampled vegetation in the control and soil-disturbed plots at Diamond Lake Site #1 had recovered, while the weeded plots remained weed-free. We could therefore examine treatment effects on growth and survival at this site, which we did by combining this data with that for the remaining Diamond Lake and Wye Creek sites. Here, we used Kruskal-Wallis non-parametric ANOVA to examine the effects of treatment on survival, and GLMs to examine the effects of site and treatment on both survival and growth rates.

Results

Field experiment

Mt Somers

Habitat differences. The major difference between habitat types at Mt Somers was that exotic cover was much higher in the open tussock grassland than in either of the rock outcrop habitats (One-way ANOVA $F_{2,42} = 77.286$, $P < 0.0001$; Table 1).

Germination. There were two pulses of germination at Mt Somers, the first beginning one month after sowing (December 2000), and the second early the following spring (August 2001). The first germination pulse in early summer occurred during a period of mild conditions following seed sowing. The remainder of summer 2001, however, was the driest on record in Canterbury for 140 years (NIWA, 2001), and germination ceased until early spring when the drought was broken.

Half of the plots that had germination in early summer also had germination in spring. The habitat-related pattern of seed germination was similar in both pulses. Very little germination occurred in the open tussock grassland habitat in either pulse, with the forested rock outcrop habitat having highest germination in the first pulse, and the open rock outcrop habitat highest in the second (Table 3). Because we were interested in the effects of habitat and treatment on germination, regardless of the timing of germination, we combined data from the two pulses for analysis.

Habitat type, native cover, litter cover and moss cover all explained significant variation in germination probability when all variables were included in a full model (Table 4a). Backward selection left habitat type, litter cover and moss cover as significant explanatory variables. Germination was more likely to have occurred in plots in the forested rock outcrop habitat, followed by the open rock outcrop habitat, and was least likely in the open tussock grassland habitat (Table 4b). High litter cover had a negative effect on germination, whereas high moss cover favoured germination (Table 4b).

Seedling survival and growth. Mortality of tagged seedlings was high during the eight weeks of spring in which they were monitored, with only 22/42 seedlings in the open rock outcrop habitat and 11/19 seedlings in the forested rock outcrop habitat surviving. Seedling leaf number increased by a mean of 14% per week from initial measurements in the open outcrop habitat and 25% per week in the forested outcrop habitat. Width of the basal rosette increased on average by 1.8% per week in the open outcrop habitat and 2.9% per week in the forested outcrop habitat.

Table 3. The number of *P. cheesemanii* seedlings present in the summer (December 2000) and spring (August 2001) germination pulses in experimentally sown plots (of *c.* 500 seeds sown per plot) at Mt Somers, by habitat type. *n* = number of plots.

Pulse	Total seedlings	Habitat type		
		Forested rock outcrop (*n* = 9)	Open rock outcrop (*n* = 18)	Open tussock grassland (*n* = 18)
December 2000	133	64	55	14
August 2001	242	24	141	0

Table 4. Results of logistic regression modelling with the presence or absence of germination in a plot as the response variable, and habitat type, treatment, and plot characteristics as explanatory variables, at Mt Somers. a. The significance of each explanatory variable measured as the change in deviance from a full model that included all variables. b. The final model obtained using backwards selection. More positive parameter estimates indicate that the variable has a more favourable effect on germination.

a.

Variable	Change in deviance	d.f.	*P*
Habitat	19.444	2	0.001
Treatment	0.949	2	0.975
Native cover	4.418	1	0.05
Litter cover	11.643	1	0.001
Moss cover	7.588	1	0.01
Rock cover	2.917	1	0.1
Soil depth (cm)	2.515	1	0.5
Model deviance = 37.912, with 9 d.f. $P < 0.0001$			

b.

Variable	Parameter estimate	S.E.
Intercept	3.444	1.404
Forested rock outcrop	4.279	2.458
Open rock outcrop	4.274	1.309
Open tussock grassland	0	
Litter cover	-0.122	0.057
Moss cover	0.824	0.57
Model deviance = 32.398, with 4 d.f. $P < 0.0001$		

Wye Creek and Diamond Lake

Site characteristics. Plots at Wye Creek had less exotic cover than plots in the two sites at Diamond Lake (Table 1), although Wye Creek had higher litter cover which mostly comprised dead cocksfoot, the dominant exotic species at this site. The combined litter and exotic cover at Wye Creek was similar to the exotic cover at Diamond Lake and probably more representative of the 'weediness' of the site. Nevertheless, litter was not removed in the weed removal treatment. The cover of native plants ($F_{1,46}$ = 10.6, $P < 0.0001$) and moss ($F_{1,46}$ = 4.28, $P < 0.002$) was higher at Wye Creek than Diamond Lake (Table 1).

Germination. In these sheltered, weedy habitats, treatment had a weak effect on the number of seeds germinating across all plots (GLM $F_{2,21}$ = 2.979, P = 0.073). However, one control plot had abnormally high germination (201 seedlings compared with an average of 25 seedlings in the remaining control plots) and removal of this clear outlier increased the strength of the treatment effect (GLM $F_{2,20}$ = 3.973, P = 0.035). We suspect that this is a biologically significant result, with the relatively weak statistical support stemming from a lack of power due to low replication following the loss or damage of two of our experimental sites. No other variables had a significant effect on germination.

As predicted, germination was highest in the weed removal treatments, followed by the soil disturbed treatments, and lowest in the control treatments at both Wye Creek and Diamond Lake (but not in the grazed Diamond Lake Site #1) (Table 5). There was no indication of site or site by treatment interaction effects on germination, implying that treatment had a similar effect on germination at both sites, which justifies combining the two sites for analysis.

The prediction that the additional treatment imposed by sheep grazing at Diamond Lake Site #1 would mask the effects of the weed treatments was confirmed. When site, treatment, and site by treatment effects were modelled with the grazed Diamond Lake Site #1 plots included as one site, and the combined

Table 5. The number of *P. cheesemanii* seeds germinating in experimentally sown plots at Wye Creek and Diamond Lake (September 2001), by location, site and treatment. Each treatment at each site comprised four plots.

Location	Site	Total germination	Treatment: Weed removal	Treatment: Soil disturbed	Treatment: Control
Wye Creek	Open rock outcrop	391	270	74	47
Diamond Lake	Forested rock outcrop #1	1825	560	195	1070
	Forested rock outcrop #2	251	113	77	61

Wye Creek and Diamond Lake Site #2 as a second site (and with the outlier plot excluded), there was a significant site by treatment interaction (GLM, P = 0.029), indicating that the treatment effects differed in the grazed and ungrazed plots. There was no significant treatment effect on germination at the grazed site alone.

Seedling survival and growth. Seedling survival and growth were significantly related to site, but there was no significant treatment or site by treatment interaction when data for Wye Creek and the two Diamond Lake sites were combined (Table 6). At the Diamond Lake sites, treatment had a weak effect on survival rates, with survival highest in the weed removal treatments and lowest in the control (Kruskal-Wallis ANOVA χ^2 = 5.255, P = 0.072). Although not statistically significant, mean growth rate, both in terms of leaf number and rosette width, was consistently higher in the weed removal treatments at all sites (Table 6).

Natural population dynamics

For the nine-month period when population demography was monitored, less than 1% of tagged adult plants died, but tagged-seedling mortality ranged from 25 to 45%. The percentage of flowering plants ranged from 15% at Diamond Lake to 90% at Mt Somers (Table 7). Browse and mechanical damage to inflorescences were observed in each population. Damage was highest at Diamond Lake with 30% of tagged plants affected. Individuals in all populations tended to decrease in size during the dry summer months with recovery over winter. Leaf senescence was common during summer, and perhaps more severe during this especially dry season, but most plants had begun to form new leaves at the rosette crown by late winter. Many new seedlings were observed at Wye Creek and Diamond Lake in the spring, but virtually all of these had died, apparently due to water stress, by the end of summer.

Table 6. Seedling survival and growth rates of *P. cheesemanii* in experimentally sown plots at Wye Creek and Diamond Lake. Also shown are the results of General Linear Models with mean percent increase in leaf number, rosette width (cm), and mean percent survival over 9 weeks as the response variables, and site and treatment as the explanatory variables.

Location	Site	Mean increase in leaf number (%)	Mean increase in width (%)	Mean survival (%)
Diamond Lake	Forested rock outcrop #1	20.3	7.5	81.1
	Forested rock outcrop #2	14.5	6.4	68.8
Wye Creek	Open rock outcrop	6.5	-0.8	45.6
	$F_{3,24}$	3.931	6.684	3.411
	P	0.037	0.006	0.051
	Treatment			
Diamond Lake (Sites #1 and #2)	Control	11.5	2.7	57.6
	Soil disturbed	11	3.6	66.7
	Weeded	18.8	6.9	71.1
	$F_{2,15}$	1.685	2.06	0.477
	P	0.212	0.156	0.627

Table 7. Characteristics of the four natural populations of *P. cheesemanii* that were monitored in this study. The population sizes are estimates from November 2000. Width of the basal rosette and number of basal leaves are mean values taken over a nine-month period. Flowering data are from January 2001, when flowering was at its maximum for all populations. Number of flower stalks and fruit or flowers is the mean value of all tagged flowering plants. n = the number of tagged plants.

Population	Size of population	n	Width of basal rosette (cm)	# basal leaves	% of tagged plants flowering	# flower stalks	# fruit or flowers
Diamond Lake	40	20	4.6	9.3	15	2.3	10.8
Bob’s Cove	35	20	6.3	6.4	47	1.7	7
Wye Creek	200	32	8.6	6.2	41	2.6	11.4
Mt Somers	65	30	6.0	4.8	90	1.9	8.3

Table 8. Seed bank data from three natural populations of *P. cheesemanii*. The mean number of emerging *P. cheesemanii* seedlings per m^2, and the frequency of occurrence (percentage of soil samples in which seedlings emerged) for 10 soil samples taken from each of three distances: zero metres (within the population), one, and three metres from the population.

Date	Population	Distance (m)					
		0		1		3	
		Mean	Frequency (%)	Mean	Frequency (%)	Mean	Frequency (%)
Nov 2000	Mt Somers	74.5	80	0.5	10	0	0
Dec 2000	Wye Creek	18	50	12	50	0	0
	Diamond Lake	12	50	19	20	0	0
April 2001							
	Mt Somers	249	100	20.5	90	1.65	22
	Wye Creek	136.5	90	20	50	0.55	10
	Diamond Lake	36.5	66.7	16.5	20	0	0

Seed bank

Pachycladon cheesemanii does produce a persistent viable seed bank. Although seed appears to be present in the soil throughout the year, soil seed reserves in spring were much lower than in autumn, suggesting that seed is lost from the soil seed bank following seed production in autumn (Table 8). The Diamond Lake site showed much less of a difference between spring and autumn, possibly due the low seed output for this population in 2001 (Table 7). The amount of seed in the soil decreased with increasing distance away from the populations, with very little seed found three metres away (Table 8). Exotic weeds dominated the soil seed bank in spring and autumn, with the exception of spring at Wye Creek, when native species comprised 60% of the species that germinated in our trial (Miller, 2002).

Discussion

Field experiments

Our results support the hypothesis that invasive weeds threaten *P. cheesemanii* populations in rock outcrop habitats. Removal of exotic vegetation resulted in an increase in germination rates of sown seed in both forested and open rock outcrop habitats in Central Otago, relative to control treatments. There was also a tendency for seedling survival to be higher in plots with exotic vegetation removed, relative to control plots.

Weed removal experiments in natural populations of rare plants elsewhere have also shown that weeds can threaten populations by inhibiting seedling establishment (Gurevitch, 1986; Foster, 1999; Walck *et al.*, 1999). Pavlik *et al.* (1993b) found no effect of weed competition on the germination of experimentally sown *Amsinckia grandiflora* seeds (a rare herb), but weed competition did reduce survival, reproductive output and plant size. Although our experimentally sown seedlings were not followed for long enough to obtain data on reproductive output, it is likely that exotic weeds would also have reduced reproductive output given that plant growth was reduced and plant size and reproductive output are correlated (Pavlik *et al.*, 1993b; Dyer and Rice, 1999; Hamilton *et al.*, 1999). The ingression of weeds such as *Hieracium lepidulum* and *H. pilosella* into the rock outcrop habitat of *P. cheesemanii* is thus a critical threat to the long-term survival of the species, and is a likely mechanism of past population decline and habitat restriction. Management of exotic weeds in current *P. cheesemanii* populations appears critical to prevent further declines in this species.

Our results also suggest that different factors may be important in regulating populations in different habitats and across the range of *P. cheesemanii* (see also Kluse and Doak, 1999). At Mt Somers, there was no treatment effect on germination. Here, we expected to find a strong treatment effect in the open tussock grassland habitat, which was dominated by *Hieracium pilosella* and in which weed removal created extensive patches of bare ground. Instead, there was almost no germination in this habitat, with establishment restricted to the more sheltered rock outcrop habitats. It appears that, at least in very dry years, open habitat is generally unsuitable for *P. cheesemanii* establishment regardless of the presence of weeds, and restriction to rock outcrops may in part reflect a requirement for sheltered establishment conditions. In the north of its range, *P. cheesemanii* is often observed growing under the canopy of native shrubs, such as snow totara (*Podocarpus nivalis*), and tussocks, which again suggests a requirement for shelter. It is plausible that the loss of shelter following the removal of taller native vegetation cover from large areas of the South Island during the last 150 years has contributed to the disappearance of *P. cheesemanii* from grasslands, although records indicate it was probably never widespread in this habitat. It would be informative to repeat the weed removal experiment in a wetter year to see whether germination rates in grassland habitat improve and whether weed removal effects then become apparent; or to repeat the experiment with an additional watering or shelter treatment.

Establishment rates were higher in the forested rock outcrop habitat than the open rock outcrop habitats at Mt Somers. However, there were no significant differences between patterns of establishment at the forested Diamond Lake sites and the open Wye Creek site. Forested rock outcrops were probably typical habitat for *P. cheesemanii* prior to the large-scale deforestation that accompanied human settlement in New Zealand, but the results of this study are not general enough to conclude whether forested or open habitats appear more suitable for *P. cheesemanii* today. A comparison of *P. cheesemanii* performance in many open and forested sites would better answer this question, and would be useful for restoration efforts.

Natural populations

Seed production in glasshouse populations of *P. cheesemanii* is generally high (P. Heenan, *pers. comm.*). In the four natural populations monitored in this study, the proportion of plants flowering showed a wide range from 15 to 90%. This is similar to the range of plants flowering (33 – 100%) reported in twelve previously-surveyed populations (of 10 or more individuals; Wardle, 1999). The low proportion of plants flowering during the study season in the Diamond Lake population (15%) appeared to have an impact on the seed bank, with few seeds recorded from soil samples at this site. Seed production may also be limited by inflorescence damage by insect and animal browse and/or mechanical damage. At low levels this damage may affect overall productivity only slightly, but when populations are small with a low proportion of flowering plants, as at Diamond Lake, the impacts are more significant. Although browsing has not previously been considered a threat to *P. cheesemanii* populations, our observations suggest it should be considered further.

Soil seed banks are important for the conservation of threatened plant species in that they provide a reserve of material that can buffer populations from stochastic events (Harper, 1977; van der Valk and Pederson, 1989; Pavlik *et al.*, 1993a; Rowland and Maun, 2001). *Pachycladon cheesemanii* does produce a persistent viable seed bank with germinable seed detected in the soil year round. However, the residual seed bank, from which seedling recruitment in spring occurs, was much smaller than the seed bank detected in the autumn just after seed had dispersed. The maximum mean seed density was 249 seeds/m^2, while the maximum local seed density was 750 seeds/m^2 (both at Mt Somers). Given that individual plants are capable of producing thousands of seeds each (P. Heenan, *pers. comm.*), these levels are quite low, indicating that much seed is lost altogether.

Many other plant species germinated in the soil samples, but these were mostly exotic weeds found at the sites. At Diamond Lake, especially, the soil seed bank was dominated by exotic weeds, with weed invasion possibly contributing to the poor performance of this population. The soil seed bank at Wye Creek had the greatest species richness and the greatest proportion of native species in the spring. This may be a reflection of the less-degraded condition of this site, which in turn may be reflected in the large *P. cheesemanii* population at Wye Creek.

Seedling survival was low in the monitored populations and may be an important factor limiting *P. cheesemanii* population growth. However, this could be an aberration given the extremely dry conditions during the study period. Longer-term monitoring of seedling survival in natural populations is required to determine the importance of this factor.

Conclusions

Our experiments show that exotic weeds can inhibit *P. cheesemanii* establishment in rock outcrop habitat, and that, at least in very dry years, *P. cheesemanii* has low success establishing in open grassland habitat regardless of whether weeds are present or not. Both weed invasion and loss of shelter may have contributed to population declines. Within the current rock outcrop habitat, weed invasion poses a significant threat to *P. cheesemanii* populations by lowering establishment, and most likely reducing growth and survival of plants. Weeds are probably having a negative impact on *P. cheesemanii* populations in currently weedy habitats such as at Diamond Lake. Browse and mechanical damage to inflorescences were also widely observed in natural populations, and warrant further study as possible factors limiting seed production in *P. cheesemanii.*

Pachycladon cheesemanii, while still relatively widespread, occurs in small, scattered populations that are nearly all threatened by invasive weeds. Our results suggest that weed control would benefit *P. cheesemanii* populations, and there is considerable potential for expanding existing populations, or establishing new populations in appropriate habitat, by weed removal and seed sowing.

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