



Does habitat manipulation enhance native woody seedling recruitment in a dryland river floodplain?

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Abstract: Recruitment failure of native plants is common in dryland ecosystems in New Zealand. We investigated whether herbicide control of invasive grasses or restoration of either shrub cover or the natural disturbance regime (river gravel deposition after flooding) can promote seedling establishment of the critically endangered shrub *Olearia adenocarpa* and two common species also found in river floodplain ecosystems (*Carmichaelia australis* and *Sophora microphylla*). *Olearia adenocarpa* seedlings have been observed only after invasive grasses were controlled with herbicide and when browsing mammals were also excluded. We used a field experiment to compare seedling establishment in four treatments: (1) shade cloth shelters, a proxy for native shrub cover; (2) river gravel addition, to simulate gravel deposition during flooding; (3) herbicide application, to kill invasive grasses; (4) untreated controls. For *C. australis*, provision of shade and shelter (hereafter referred to as shade) and herbicide application both promoted seedling emergence compared to controls, but few seedlings survived after two years. For *O. adenocarpa*, we found weak evidence that shade, herbicide and gravel increased seedling emergence, but the effects were small and few seeds germinated. Establishment of *S. microphylla* seedlings was unaffected by shade, but gravel and herbicide treatments reduced seedling emergence compared to controls. Seed germination was also low for *S. microphylla*. During a drought in the second spring, soil moisture was higher in all treatments than in untreated controls. Soil moisture was lower in gravel plots than in untreated controls at all other times. Shade also increased soil moisture in the first spring. The effects of herbicide on soil moisture were variable. Our findings indicate that the loss of native shrublands and invasion by non-native grasses limits the establishment of *C. australis* seedlings in dryland river floodplains, and that the effects of these changes are not easily overcome. While *O. adenocarpa* seedlings cannot compete with invasive grasses, other factors also limited recruitment of this species, and *S. microphylla*, in this study.

Keywords: *Carmichaelia australis*, disturbance, facilitation, invasive grasses, *Olearia adenocarpa*, recruitment limitation, shade, *Sophora microphylla*

Introduction

Many ecosystems in the eastern South Island of New Zealand are highly modified from their pre-human state, including altered vegetation composition, vegetation structure, and disturbance regimes. Human fires transformed forests and shrublands into grasslands soon after humans arrived c. 700 years ago (McWethy et al. 2010). These semi-arid, dryland ecosystems were further modified after European settlement in the 19th century by fires, agriculture and the introduction of non-native plants and herbivores (Walker et al. 2009). While some sites still retain significant components of their original flora, many native plants are failing to recruit (Widyatmoko & Norton 1997; Dawson et al. 2005; Wotton 2018). Without recruitment, remaining individuals are effectively 'the living dead' (Janzen 1986) and species may be doomed to extinction unless management intervention occurs.

Across ecosystems, the requirements for recruitment vary among species, and form a species' regeneration niche (Grubb 1977). For most plant species, early recruitment is limited by a combination of seed supply (seed limitation) and safe sites for seedling establishment (establishment limitation), but the effects of establishment limitation are usually stronger (Clark et al. 2007). Disturbance can promote the regeneration of early successional or ephemeral species (Hiero et al. 2006; Rogers et al. 2005). For example, in riparian floodplains, seedlings of some species establish following flood events (White 1979). However, disturbance is thought to have been less important than environmental stress in constraining the historic distribution of currently threatened plants in eastern dryland sites of New Zealand (Rogers et al. 2005).

The loss of woody vegetation may be a key factor limiting the availability of safe sites, and thus plant recruitment, in eastern South Island drylands. Trees and shrubs can act as

nurse plants by ameliorating harsh conditions, which increases seedling recruitment beneath their canopy, particularly in dry environments (Valiente-Banuet & Ezcurra 1991; Gomez-Aparicio et al. 2004; Burrows et al. 2015). Woody cover provides both shade and shelter, which may directly facilitate native plant recruitment by reducing temperature and evaporation, and increasing moisture availability (Flores & Jurado 2003). Woody vegetation may also indirectly facilitate native plant recruitment, by suppressing competition from light-demanding non-native grasses (Walker et al. 2014). In arid and semi-arid ecosystems, grasses are strong competitors and can prevent the establishment of native woody species by monopolising soil moisture and nutrients, and reducing light at ground level (Williams & Hobbs 1989; D'Antonio & Vitousek 1992; Combs et al. 2011). Other biotic factors including seed predation, herbivory and host-specific pathogens may also limit seedling establishment, but are not the focus of this study.

Olearia adenocarpa (dry plains shrub daisy, Asteraceae) is a critically endangered shrub confined to the Waimakariri and Rakaia River floodplains in the Canterbury region of the eastern South Island and is failing to recruit in the wild. There are fewer than 700 adults remaining and it is one of the 50 most threatened New Zealand plants (Heenan & Molloy 2004). *Olearia adenocarpa* occupies stony, sandy sediments in abandoned river channels, and is thought to colonise these sites after floods deposit fresh sediments (Heenan & Molloy 2004). However, this habitat has been modified in several respects. Natural disturbance regimes have been altered, with flood protection works now preventing the Waimakariri and Rakaia Rivers from flooding to their full natural extent. Burning and grazing have largely replaced these native shrublands with grasslands dominated by invasive species. *Olearia adenocarpa* is also browsed by rabbits and hares, which are being managed by fencing. Other remnant native woody species are also experiencing recruitment failure in these ecosystems.

During maintenance of fenced *Olearia adenocarpa* restoration planting sites, *O. adenocarpa* seedlings were sometimes observed when the ground beneath and between plantings was kept largely bare through regular herbicide application (P Grove & S Brailsford, unpubl. data). The aim of this study was to determine the efficacy of herbicide application compared to alternative management techniques to promote seedling establishment of native woody species *O. adenocarpa*, *Carmichaelia australis* and *Sophora microphylla* (both Fabaceae). We conducted a field experiment to test whether obstacles to shrub regeneration can be overcome by restoring the natural disturbance regime (river gravel deposition during floods) or native shrub cover.

Methods

Study site and species

We conducted field experiments inside a hare-exclusion fence enclosing c. 1 ha at Rakaia Island, Canterbury (43.77430° S 172.09305° E). Rakaia Island is a large island in the Rakaia River, c. 19 km long by 4 km at its widest point (Patrick & Grove 2014). Most of the island is River Protection Reserve managed by the Canterbury Regional Council (Environment Canterbury). This reserve includes a c. 15 ha area of shrubland and grassland at the island's northern end, which was retired from grazing in 1985 and is managed as part of a larger conservation area (Patrick & Grove 2014). The vegetation in this area consists of scattered native shrubs dominated by

Discaria toumatou (matagouri), with occasional *O. adenocarpa* and *Ulex europaeus* (gorse) and one *Carmichaelia australis* shrub. Native mosses and lichens are prominent in the ground cover, together with (mostly non-native) grasses and herbs. Occasional *S. microphylla* grow nearby. The soil at the site is recent and stony (Patrick & Grove 2014). In late 2017, very low rainfall led to a drought in Canterbury (NIWA 2018).

Olearia adenocarpa is a small-leaved shrub up to 1.5 m tall (Heenan & Molloy 2004). Its seeds are 2–2.5 mm long achenes topped by a 2.9–4.2 mm pappus (Heenan & Molloy 2004). *Carmichaelia australis* is a variable shrub widespread throughout mainland New Zealand except for the southern South Island (Heenan 1996). In Canterbury river floodplains it reaches a height of up to c. 2m. Its dehiscent pods contain 1–5 hard-coated seeds 2.2–4 × 1.7–2.8 mm (Heenan 1996). *Sophora microphylla* is a tree up to 25 m tall, found throughout the main islands of New Zealand (Heenan et al. 2001). *Sophora microphylla* has indehiscent pods with up to 12 hard-coated seeds 5.5–8.5 × 4.0–5.5 mm (Heenan et al. 2001).

Experimental design

We compared the effects of four treatments on seedling recruitment over two years: (1) shade cloth shelters; (2) river gravel addition; (3) grass removal with herbicide; (4) untreated controls. Fifteen replicates were placed at random locations, with one 1 × 1 m plot of each of the four treatments allocated randomly within each location (Fig. 1). Shade cloth shelters had a wooden frame 0.3 m high covered in green 70% shade cloth, but unattached near the ground to allow access by rodents and invertebrates. Shade cloth shelters and gravel were placed in the field in late January 2016. River gravel was collected from the Rakaia riverbed and a c. 10 cm deep layer was applied to gravel plots. The gravel at the surface of plots (where seeds germinate) included sand and closely resembled the composition and size of gravel deposited in nearby dry riverbeds. Herbicide plots were sprayed in October and December 2015 with the broad-spectrum herbicide glyphosate. Follow-up control using a grass-specific herbicide (haloxyfop-P-methyl) was carried out monthly or as required (depending on grass growth) during spring and summer for both years of the experiment. All herbicide and gravel plots were sprayed with glyphosate in April 2017 to kill weeds that established over the summer (only one seedling of the focal species was alive in plots at this time).

In January 2016 we collected *C. australis* seeds from 29 plants on the Waimakariri River floodplain at Macleans Island, Canterbury (43.494215° S 172.45883° E), and *S. microphylla* seeds from 10 plants at Rakaia Island. We collected *O. adenocarpa* seeds in February at Rakaia Island from 30 plants in both 2016 and 2017. Seeds of *C. australis* (100 seeds per subplot), *O. adenocarpa* (200 seeds) and *S. microphylla* (40 seeds) were sown on the surface into one separate 20 × 20 cm subplot for each species per treatment plot in April 2016 (Fig. 1). Species were allocated randomly to subplots and subplots were separated by at least 10 cm. Virtually all *O. adenocarpa* seedlings died by the end of the first year, so a second batch of *O. adenocarpa* seeds was sown in May 2017 into the same subplots as used previously (c. 382 seeds per subplot, mean number of seeds in 0.13 g batches weighed using a Kern balance accurate to 0.1 mg). Two corners of each seed sowing subplot were marked with galvanised nails, with species indicated by fine coloured wire. Nails were soaked in tap water and rinsed prior to use to reduce zinc leaching into subplots, which may occur with factory-fresh



Figure 1. Experimental replicate with four treatment plots, clockwise from top left: herbicide, untreated control, shade and gravel. Black squares (shown here only in the gravel plot) illustrate the three seed sowing subplots (one per species) within each treatment plot.

galvanised metal. Any residual leaching was expected to be minimal and localised in the corners. *Carmichaelia australis* and *S. microphylla* seeds were scarified with sandpaper (120 and 80 grit, respectively) to break dormancy prior to sowing. The pappus was removed from *O. adenocarpa* seeds before weighing and sowing to prevent seeds from being blown out of plots.

We counted the number of seedlings in subplots in May 2016, November 2016, March 2017, November 2017 and April 2018. We measured soil moisture at the soil surface in plots at the same time (except for May 2016) using an HH2 soil moisture meter with a ThetaProbe ML2 sensor, which has an accuracy of $\pm 3\%$ (Delta-T Devices Ltd, Cambridge, UK). For each plot, we took three soil moisture measurements and calculated the mean.

To estimate the number of *O. adenocarpa* seeds to sow in field plots, in October 2015 we sowed seeds collected from Rakaia Island in March 2014 in the nursery at Otari-Wilton's Bush, Wellington. We sowed twenty-five seeds in each of ten 1 litre plastic pots (13 cm diameter) containing seed-raising mix. *Olearia adenocarpa* seeds were sown on the surface of the seed raising mix and covered with a fine (c. 1 mm) layer of perlite. We counted seedlings emerged every 2–3 weeks for 7 weeks and removed emerged seedlings.

We measured seedling emergence under benign conditions for all three species by sowing seeds into 1 litre pots. Seeds in the nursery were from the same batches with the same treatments as those sown in the field and sown within one week of sowing seeds in the field. For each species, we sowed twenty-five seeds into each of ten pots. *Olearia adenocarpa*

seeds were sown as described above. *Carmichaelia australis* seeds were placed on the surface and then covered with a fine layer (c. 1 mm) of seed raising mix then a fine layer of perlite. *Sophora microphylla* seeds were pressed into the surface and covered with c. 5 mm of seed raising mix then a fine layer of perlite. In 2016 and 2017 we monitored *O. adenocarpa* seeds fortnightly for 6.5 months, then every 2–4 weeks for another 6 months. We monitored *C. australis* and *S. microphylla* seeds fortnightly for 6 months then every 2–4 weeks for another 18.5 months, four to six months after germination had virtually ceased. Seedlings were removed from pots post-emergence.

Statistical analysis

We analysed seedling data for *C. australis* in November 2016 and November 2017, and these were treated as independent of each other rather than repeated measures (as all seedlings were dead in between), and for *O. adenocarpa* and *S. microphylla* only in November 2016. Too few seedlings of both *O. adenocarpa* and *S. microphylla* emerged in 2017 to analyse the data. Likewise, there were too few seedlings of any species to analyse data in May 2016, March 2017, and April 2018.

For each species, we modelled seedling abundance using a binomial generalised linear mixed-effects model (GLMM) with successes and failures (number of seedlings and total number of seeds – number of seedlings) as the response variable using the lme4 (Bates et al. 2015) package in R (R Core Team 2018). For *C. australis* in November 2017, we subtracted the number of seedlings established in November 2016 from the number of seeds sown to estimate the number of seeds remaining in subplots. Models included treatment as

a fixed effect and replicate as a random effect, and we tested these models for overdispersion using the R package sjstats (Lüdtke 2018). If overdispersion was present, we compared the Binomial model with an observation-level random effect Binomial model (Harrison 2015) and used Akaike information criterion adjusted for small sample size (AICc) to select the best model (Akaike 1974; Hurvich & Tsai 1989; Burnham & Anderson 2002). Binomial models for *C. australis* and *O. adenocarpa* were overdispersed and observation-level random effect binomial models provided a better fit to seedling abundance data in these cases. For *C. australis* and *O. adenocarpa* models, replicate was removed as a random effect as its variance was near zero, and when it was included the models failed to converge. A binomial model was used for *S. microphylla* and no overdispersion was detected. We calculated theoretical R^2 (Nakagawa & Schielzeth 2013), AIC and AICc weights using MuMIn (Barton 2018).

Soil moisture was modelled separately for each time using a Beta GLMM in the R package glmmTMB (Brooks et al. 2017), with treatment as a fixed effect and replicate as a random effect (Ferrari & Cribari-Neto 2004). To assess the usefulness of all models, we compared each model to a null model for the same data containing random effects only, using AICc and the likelihood of each model, given the data (the ratio of AICc weights for the two models; Burnham & Anderson 2002).

Results

Carmichaelia australis seedlings were present in 67% of subplots in November 2016 (the first spring following seed sowing) but no seedlings remained alive by March 2017 (Fig. 2). A second flush of *Carmichaelia australis* seed germination was observed in 2017, probably from germination in the preceding autumn as seedlings were much larger than those seen in November 2016. *Carmichaelia australis* seedlings

were present in 47% of subplots for this species in November 2017 but only two seedlings were still alive in April 2018 (Fig. 2). *Olearia adenocarpa* and *S. microphylla* seedlings were present in 27% of subplots in November 2016, but only one *O. adenocarpa* and no *S. microphylla* seedlings were present in March 2017. The only surviving *O. adenocarpa* seedling was in gravel and was c. 12 cm tall, with an equally long tap root (this seedling was dug up after gravel and herbicide plots were sprayed with glyphosate in April 2017). Only seven *O. adenocarpa* and three *S. microphylla* seedlings emerged in subplots in November 2017, though the *O. adenocarpa* had died by April 2018.

We found strong evidence that treatment affected the number of *C. australis* seedlings compared to untreated controls (Table 1). In November 2016 there were more *C. australis* seedlings in shade plots than in untreated control plots, and fewer seedlings in gravel plots (Fig. 2). The negative effect of gravel was stronger than the positive effect of shade (Fig. 3). In November 2017 there were more *C. australis* seedlings in herbicide plots than in control plots, but no effect of shade or gravel (Figs. 2, 3). Treatment explained 43.7% and 27.9% of the variance in *C. australis* seedling abundance in November 2016 and 2017, respectively (Table 1).

We found little evidence for an effect of treatment on the number of *O. adenocarpa* seedlings compared to untreated controls (Table 1). There was a trend towards more seedlings in the shade, herbicide and gravel treatments, but the coefficient estimates overlapped zero (Fig. 3), and the model that included treatment had less support than the null model containing only random effects (Table 1).

Treatment affected the number of *S. microphylla* seedlings (Table 1). In November 2016 there were fewer *S. microphylla* seedlings in both gravel and herbicide plots than in control plots, but shade had no effect (Figs. 2, 3).

Treatment affected percentage soil moisture compared to untreated controls (Table 2). During the drought in November 2017, shade, gravel, and herbicide plots all had higher soil

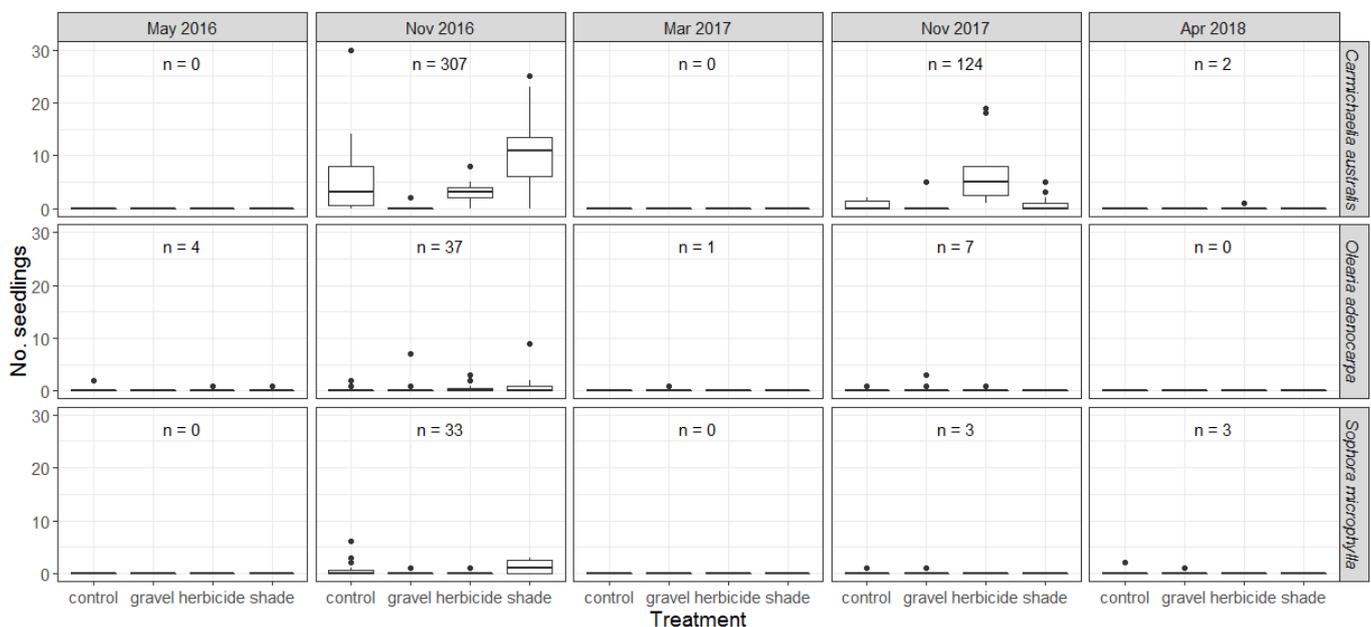


Figure 2. Seedling abundance in 20 x 20 cm seed sowing subplots at Rakaia Island, Canterbury. Boxplot displays median (solid horizontal bar), 25th and 75th percentiles (upper and lower horizontal bars), 1.5 x inter-quartile range (whiskers) and outliers (points). n = total number of seedlings.

Table 1. Generalised linear mixed-effects model results for predictors of the number of seedlings. K = total number of model parameters; $\log(L)$ = log-likelihood; AICc = Akaike Information Criterion with second order bias correction; AICc weight = probability of model being the best in this set of candidate models; $Marginal R^2$ = variance explained by fixed effects; $Conditional R^2$ = variance explained by fixed and random effects.

Species	Time	Model	K	$\log(L)$	AICc	AICc weight	$Marginal R^2$	$Conditional R^2$
<i>Carmichaelia australis</i>	November 2016	Treatment + random effect	5	-136.278	283.7	1	0.437	0.556
		Random effect only	2	-162.298	328.8	0		
	November 2017	Treatment + random effect	5	-89.163	189.4	1	0.279	0.46
		Random effect only	2	-108.144	220.5	0		
<i>Olearia adenocarpa</i>	November 2016	Treatment + random effect	5	-56.185	123.5	0.131	0.059	0.517
		Random effect only	2	-57.746	119.7	0.869		
<i>Sophora microphylla</i>	November 2016	Treatment + random effect	5	-53.175	117.5	1	0.273	0.411
		Random effect only	2	-67.05	138.3	0		

Table 2. Generalised linear mixed-effects model results for predictors of percentage soil moisture. See Table 1 for explanation of terms.

Time	Model	K	$\log(L)$	AICc	AICc weight
November 2016	Treatment + random effect	6	153.46	-293.3	1
	Random effect only	3	75.46	-144.5	0
March 2017	Treatment + random effect	6	157.87	-302.1	1
	Random effect only	3	72.72	-139.0	0
November 2017	Treatment + random effect	6	194.5	-375.4	1
	Random effect only	3	174.13	-341.8	0
April 2018	Treatment + random effect	6	166.69	-319.8	1
	Random effect only	3	72.421	-138.4	0

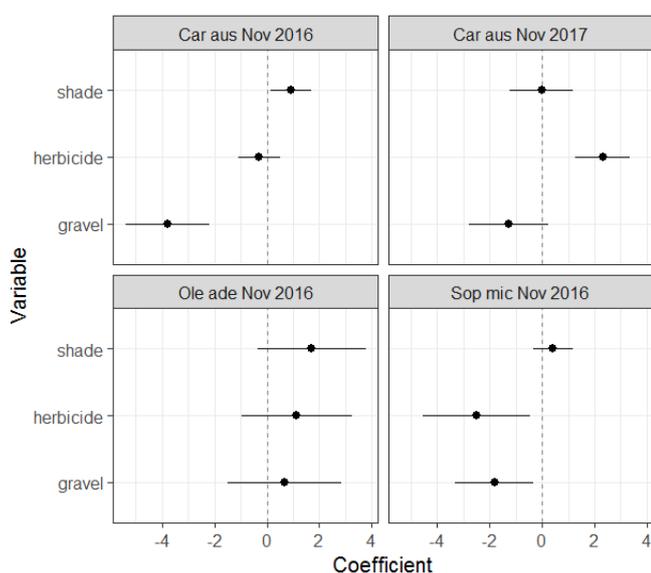


Figure 3. Model coefficients and 95% confidence intervals for the effect of treatments on the number of seedlings compared to untreated control plots (dashed line). Car aus = *Carmichaelia australis*, Ole ade = *Olearia adenocarpa* and Sop mic = *Sophora microphylla*.

moisture than untreated controls (Figs. 4, 5). Gravel plots had much lower soil moisture than untreated controls at all other times (Figs. 4, 5). Soil moisture was higher in shade plots than untreated controls in November of both years, although the effect was larger during the drought (Figs. 4, 5). Soil moisture in herbicide plots was variable, with no effect

in November 2016 or March 2017, a considerable increase in November 2017 and a slight decrease in April 2018 compared to untreated controls (Figs. 4, 5).

Carmichaelia australis seeds in the nursery continued germinating for 24 months after sowing (although only one seed germinated between 18 and 24 months), with 65.2% (± 14.1 , mean \pm SD) germinating overall. *Olearia adenocarpa* germination in the nursery was variable, with 37.2% (± 14.4) of seeds sown in 2015 germinating, 17.6% (± 15.1) in 2016 and 30% (± 7.8) in 2017. Most *O. adenocarpa* seeds germinated within 4–5 weeks of sowing. *Sophora microphylla* germination in the nursery was high ($74.8 \pm 11.3\%$) and continued for 20 months after sowing.

Discussion

We found effects of various treatments on seedling emergence and survival over short periods in two of our three species, but still had very low levels of survival to the end of our experiment. That suggests that our treatments sometimes enhanced the first stages of regeneration, but were insufficient to allow recruitment, at least during the time period when our experiment took place, which had very low soil moisture in late 2017 due to a drought (NIWA 2018). The fact that our treatments did sometimes enhance seedling emergence is consistent with previous work.

Too few *O. adenocarpa* seeds may have been added to experimental plots, thus limiting seedling establishment. In a good year, adult plants each produce thousands of seeds but the population at Rakaia Island is small (c. 16 wild plants and 150 restoration plantings), limiting the amount of seed that could be collected.

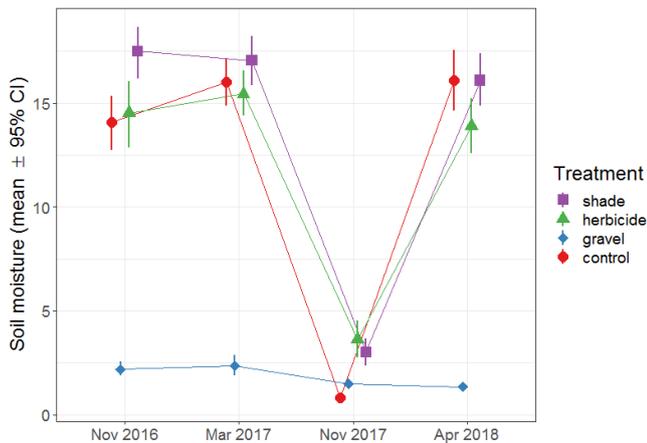


Figure 4. Percentage soil moisture in 1×1 m experimental plots at Rakaia Island, Canterbury.

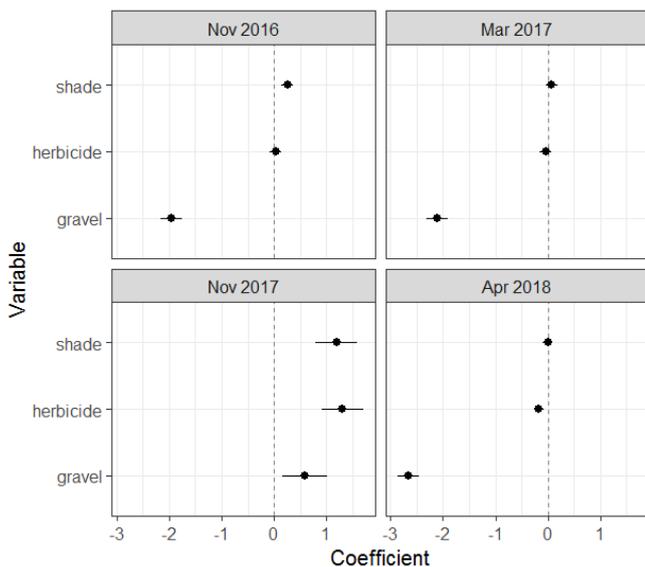


Figure 5. Model coefficients and 95% confidence intervals for the effect of treatments on soil moisture compared to untreated controls (dashed line).

It is unclear why treatment effects for *C. australis* differed between the two years of our study. Possible causes include differences in the timing of glyphosate application and germination between years and the drought in late 2017. Shade and herbicide may have had different effects on seedling mortality during the drought, via some mechanism other than soil moisture (which was similar in these two treatments during the drought).

Short-term effects of competition

Invasive grasses appeared to limit seedling emergence of *C. australis* at Rakaia Island. Competitive exclusion of native seedlings by non-native grasses is widespread, both in New Zealand and globally (D'Antonio & Vitousek 1992; Lloyd et al. 2002; Combs et al. 2011; Lambert 2015). For example, competition from the non-native grass *Agrostis capillaris* suppressed germination and seedling growth of dryland natives *Olearia lineata* and *O. bullata* (Lambert 2015), and also strongly reduced the growth of several native

Acaena and *Chionochloa* species in New Zealand (Lloyd et al. 2002). The rare Australian herb *Astragalus sinuatus* doubled its recruitment and survival when the invasive grass *Bromus tectorum* was removed (Combs et al. 2011). Removal of non-native grasses increased shrub growth in Hawaii, most likely due partly to increased nitrogen availability rather than increased soil moisture (D'Antonio et al. 1998). At Rakaia Island, competition for soil moisture may be one of the mechanisms by which non-native grasses limited *C. australis* seedling emergence. During the drought, removal of grasses with herbicide increased both soil moisture and the number of *C. australis* seedlings. However, soil moisture was similarly high in shade, which had no effect on seedling abundance at that time.

While there was only weak evidence that control of non-native grasses promoted *O. adenocarpa* seedling establishment in this study, previously *O. adenocarpa* seedlings have been observed only following herbicide control of invasive grasses (P Grove & S Brailsford, unpubl. data). In contrast, we found that herbicide control of grasses reduced *S. microphylla* seedling emergence and had no detectable effect on *O. adenocarpa*.

Short-term effects of shade

A lack of shade also appeared to limit the recruitment of *C. australis* at Rakaia Island. This is consistent with other studies in eastern South Island dryland ecosystems that report greater survival of native seedlings and higher native vegetation abundance and diversity where shade is present (Walker et al. 2014; Norton & Young 2016; Rodrigues et al. 2017).

Facilitation by nurse plants may provide seedlings and understorey plants with a range of benefits, including enhanced plant water relations, higher soil nutrient levels, protection from herbivores and nutrient transfer via shared mycorrhizal networks (Callaway 1995; 1998). Nurse plants may ameliorate the effects of drought and high temperatures by increasing air humidity and reducing solar radiation, soil and air temperatures, wind speed, evaporation and transpiration beneath their canopy (Holmgren et al. 1997; Flores & Jurado 2003).

Ecological theory predicts that facilitation should increase along an abiotic gradient of increasing stress (the stress-gradient hypothesis; Bertness & Callaway 1994). The stress-gradient hypothesis has been debated (Holmgren & Scheffer 2010), but is supported by a global meta-analysis showing a shift towards facilitation with increasing stress (He et al. 2013). Empirical evidence also shows that shade promotes plant growth and survival to the greatest extent in species characteristic of less fertile and drier habitats (Semchenko et al. 2012). Facilitation by nurse plants is therefore likely to be a strong driver in dryland river floodplains of the eastern South Island. Shade can increase soil moisture (Payne & Norton 2011; this study), and may enhance growing conditions even for those species that are tolerant of dry environments (Semchenko et al. 2012), as found in our study for *C. australis*. Recent work suggests that facilitation may collapse when conditions are so extreme that nurse plants are no longer effective at ameliorating stress (Michalet et al. 2014). This may have occurred in our study during drought conditions in late 2017 when soil moisture was low even with shade. The collapse of facilitation has so far been demonstrated in response to extreme grazing, disturbance and nutrient stress, but not in response to extreme drought (Michalet et al. 2014).

Shade may also have an indirect effect on plant recruitment by reducing the effects of competition from non-native grasses (Walker et al. 2014). Shade can reduce the growth of non-

native grasses by 20–80% in New Zealand (Dodd et al. 2005), and in dryland ecosystems appears to ameliorate the effects of non-native grass competition on individual native species (Lambert 2015) and community diversity (Walker et al. 2014).

Longer term effects

Soil moisture in our field experiment at Rakaia Island was lower during drought conditions in spring 2017 (NIWA 2018) than in 2016 and may have limited seedling recruitment. *Olearia adenocarpa* total percentage seedling emergence in spring 2017 was also one-tenth of that in spring 2016, despite higher seed viability in 2017. The drought in November 2017 reduced soil moisture to a much greater extent than shade increased soil moisture at any time, suggesting that random climatic variations may have an important influence.

Seedling establishment in our study was low in a year with typical rainfall (NIWA 2017), suggesting that recruitment in this ecosystem is challenging even in normal years. A lack of seedling recruitment is common in dry and stressful environments (e.g. Andersen 1989; Williams & Hobbs 1989; James et al. 2011). Canterbury river gravels are stressful sites for seedling establishment, with hot, dry summers and shallow, free-draining soils. Long-lived shrubs need to recruit only occasionally, and suitable conditions for germination and seedling establishment may occur infrequently. *Olearia adenocarpa* adults can live for several decades, with some individuals surviving for almost a century (Heenan & Molloy 2004). During nine years (2010 to 2018) of managing *O. adenocarpa* at three Rakaia Island planting sites, recruitment was sporadic and inconsistent among sites, years and seasons (P Grove & S Brailsford, unpubl. data). One of these sites had germination in spring 2012, autumn and spring 2013 and spring 2014. A second nearby site had no germination. A third, more distant site had germination in spring 2013 and autumn and spring 2014. While many of the seedlings that germinated between 2012 and 2014 have survived and grown and adults are producing seeds, no new seedling establishment has occurred at any of these planting sites since spring 2014 (P Grove & S Brailsford, unpubl. data).

Sporadic establishment has been documented for shrub species in stressful ecosystems elsewhere. In California, USA, *Baccharis pilularis* ssp. *consanguinea* seedlings usually fail to establish in grassland as their roots cannot reach permanently moist soil below the depth of grass roots before soils dry out in spring (Williams & Hobbs 1989). Establishment occurs only when rains extend into the warmer spring months, combining favourable temperatures with sufficient soil moisture (Williams & Hobbs 1989). Similarly, sporadic seedling establishment was observed in a Canadian river island, but once established, mortality rates were low because of the species' ability to resprout following damage (Barnes 1985). *Carmichaelia australis* and *S. microphylla* both have long-lived seeds (Grüner & Heenan 2001; Norton et al. 2002), and *S. microphylla* has been found in soil seed banks (Partridge 1989). Species with seed banks may be able to take advantage of sporadic favourable conditions by augmenting the current year's seed crop.

Heenan and Molloy (2004) suggested that *O. adenocarpa* recruitment was largely dependent on colonisation of fresh river gravels deposited during flood events. The gravel treatment in our study reduced soil moisture considerably, but interestingly, the only seedling in our experiment to survive a summer was growing on gravel. While we are unable to confirm Heenan and Molloy's (2004) hypothesis, we suggest that *Olearia adenocarpa* may also be adapted to surviving

in river floodplains due to its ability to resprout (P Grove, pers. comm.). River floodplain species may have a range of adaptations to flooding, including light seeds dispersed by wind and water, large annual seed crops, fast growth rates, low shade tolerance and the ability to resprout following damage (White 1979). *Carmichaelia australis* and *S. microphylla* seedlings were both less successful on gravel, suggesting they are not adapted to establish following flood events.

Inbreeding depression may also be limiting woody plant recruitment in dryland river floodplains. In *S. microphylla*, inbreeding depression is widespread and few selfed offspring survive (Robertson et al. 2011). In *O. adenocarpa*, there is some evidence suggesting that inbreeding depression occurs in self-compatible individuals, with reduced growth and higher mortality of selfed offspring than outcrossed seedlings (Heenan et al. 2005).

Conclusion

The loss of native shrub cover and invasion by non-native grasses both appear to be limiting *C. australis* seedling recruitment to some extent. Nevertheless, *S. microphylla* largely responded negatively to habitat manipulation and the response of *O. adenocarpa* was unclear, suggesting that other factors may also be involved. It is possible that successful establishment from seed may occur for only a small percentage of seeds and in only some years, so that experiments with large quantities of *O. adenocarpa* seeds spanning years with good spring and summer rainfall, or with a watering treatment, may be necessary to promote recruitment of this critically endangered species in lowland Canterbury river floodplain ecosystems.

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