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low intensity burning to reduce acacias and create more germination niches including for species colonizing from the surrounding native vegetation. An alternative approach suggested by Schneemann and McElhinny (2012) would be to direct seed the shrub and herb species and plant the canopy trees as tubestock at the desired woodland densities.

Acknowledgements

Paul Veivers of Stanwell Corporation provided logistic support in the field. Samantha Nolan assisted with data entry.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Photo S1. Three year-old vegetation development showing dense grass and herb cover between rows, and relatively sparse acacia shrub cover in furrows.

Photo S2. Flowering Blakes Wattle occurring in remnant vegetation of regional ecosystem 12.5.1 on Meandu Mine.

Photo S3. Blakes Wattle dominating a cleared but unmined area of Meandu Mine.

Photo S4. Eleven year-old vegetation development showing moderate density of eucalypts primarily Lemonscented Gum with acacias occurring in the subcanopy.

Photo S5. Eleven year-old vegetation development showing moderate density of eucalypts, primarily Lemonscented Gum with acacias occurring in the subcanopy.

Photo S6. Fourteen year-old vegetation development showing high stem density of Blakes Wattle species with occasional Lemon-scented Gum and Grey Ironbark.

Photo S7. Intense competition between eucalypt and acacia individuals and species in the direct seeded furrows of seven year-old Meandu mine revegetation.

Photo S8. Five year-old vegetation development showing dense canopy of Black Wattle, Blakes Wattle, Zig-zag and Brisbane Golden Wattle.

Table S1. Frequency of occurrence, stem density, basal area and canopy cover of woody plants across the 56 vegetation rehabilitation sites with probable origin of propagules

Canopy manipulations of exotic Bitter Willow (Salix elaeagnos) forest for indigenous seedling recruitment: A pilot study

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Key words: canopy gap, exotic species, forest restoration, nursery crop, podocarp, Salix elaeagnos, seedling recruitment.

Summary

The invasive exotic tree species Bitter Willow (*Salix elaeagnos*; Salicaceae) has colonised areas of rank exotic grassland and has been found to contain indigenous seed, dispersed by frugivorous birds into the monospecific stands. This small pilot study examined whether indigenous seedlings that have germinated in the understorey of exotic Bitter Willow stands could be stimulated to establish through the creation of small-scale canopy gaps. In Bitter Willow forest, four single Bitter Willow trees were poisoned to create canopy gaps. Light transmission and seedling regeneration of tree and shrub species were assessed beneath both the four manipulated and three comparable intact Bitter Willow canopies. Over 3 years,



seedling height and density increased more beneath opened compared to intact Bitter Willow canopies. These results suggest that Bitter Willow can fill the roles of both a facilitative nurse and a perch tree. Larger-scale canopy manipulation experiments of both Bitter Willow and other *Salix* species are needed to determine the full potential of canopy manipulations for forest restoration.

Research Question

Bitter Willow (*Salix elaeagnos*) is exotic to the New Zealand flora, being one of a number of species of the *Salix* genera that have been introduced for use in controlling waterway bank erosion (Wilkinson 1999). However, Bitter Willow exhibits vigorous vegetative reproduction and forms naturalised, often monospecific stands in and around wet areas, such as waterway margins and wetlands (New Zealand Plant Conservation Network [NZPCN] 2016). In the study area, Bitter Willow has established into rank exotic grassland, on a riparian site that was largely cleared of indigenous forest cover many decades earlier.

This study observed indigenous mature forest canopy species naturally establishing in stands of Bitter Willow. Indigenous seeds were dispersed by frugivorous bird species from nearby indigenous forest to the exotic Bitter Willow stands. A pilot study was established to experimentally test whether the existing indigenous forest regeneration could be improved by creating small gaps in the Bitter Willow canopies. It was hypothesised that smallscale (single tree) canopy manipulations would locally increase light transmission to the Bitter Willow understorey and thereby stimulate the regeneration of indigenous canopy tree seedlings. It was expected that species favouring forest canopy gaps for regeneration, such as the relatively light-demanding podocarp species (Lusk & Ogden 1992), would benefit from the small-scale canopy manipulations.

Methods

Study site

The study site was located on a river terrace of the Tukituki River, Central Hawke's Bay (39°54′35″S 176°18′30″E WGS84), at 300 m above mean sea level. The annual average (1921–1998 average) rainfall was 1 108 \pm 24 mm, with monthly rainfall varying from 86 \pm 7 mm (February) to 113 \pm 7 mm (July). Climate data were measured at the Blackburn climate station located approximately 2.5 km to the north-east of the study area (National Institute of Water and Atmospheric Research [NIWA] 2016).

Experimental treatments

Small-scale artificial canopy gaps were created among naturalised stands of 6-m-tall Bitter Willow, during spring 2012. Canopy gaps were created by poisoning individual

Bitter Willow trees among Bitter Willow forest through basal drilling and dosing with undiluted Glyphosate[™] herbicide. The resulting circular canopy gaps were of 5–6 m diameter.

Permanently marked 6×6 m vegetation plots were established, being aligned relative to the poisoned/intact Bitter Willow trunk centre point. Transmitted photosynthetically active radiation (PAR) was surveyed using 180° hemispherical (fisheye) photography, in 2013. Hemispherical photographs were taken using a Pentax K-3 DSLR fitted with a Sigma 4.5-mm-circular fisheye lens, taken at 1.35 m above-ground level (a.g.l.) at the centre of each canopy gap/vegetation plot.

Seven vegetation plots were located subjectively within the study area, to obtain study sites within continuous and even Bitter Willow canopy. Experimental treatments [either: canopy gap (n=4) or canopy intact (n=3)] were randomly allocated to plot locations. All plots were located within a 1 km length of river terrace. The trial was established at one site to ensure that all of the plots were comparable in terms of abiotic environment. Plots were separated by >10 m to ensure independence among plot measurements. Seedlings were monitored within a grid of 12 permanently marked 0.75-m^2 circular subplots in each plot. Seedlings were tallied according to the height classes: 16--45, 46--75, 76--105, 106--135 cm. This partitioning of seedling heights allowed for temporal progression of seedling heights to be identified.

Measurements of seedling regeneration were restricted to species of woody trees and shrubs, as these were the species which might eventually contribute to a future forest canopy. Within the vegetation plots were several exotic vine and shrub weed species (Old Man's Beard, *Clematis vitalba*; Tutsan, *Hypericum androsaemum*; Blackberry, *Rubus fruticosus*; Japanese Wineberry, *Rubus phoenicolasius*). These exotic weed species were controlled on an annual basis so as not to shade the measured seedlings and thus confound the experimental results. As there were no other seedlings of woody exotic tree or shrub species measured, there were no exotic tree or shrub species in the measured seedling composition. Seedling measurements commenced in spring 2012 and concluded in the summer of 2015.

In addition, seedling and forest canopy composition were surveyed (in 2016) in four 6×6 m vegetation plots in a protected old-growth podocarp-broadleaved forest remnant that was located on the same river terrace, 2.5 km to the south-east of the experimental Bitter Willow plots. This provided a comparison of the experimental results with seedling and tree data from representative old-growth forest.

Soils were assessed (in 2016) to determine any significant differences among treatment, control and reference plots. Twelve 15-cm cores were collected from the soil A

horizon in each vegetation plot. Soil samples were bulked per vegetation plot and analysed for carbon-to-nitrogen ratio (C:N). The area of, and distance to, indigenous forest seed sources was measured from the centre of each vegetation plot. Indigenous forest occurred within 50 m of all treatment and control plots. The mean distance to the nearest indigenous seed source was 34 ± 3.5 m for treatment plots and 29.5 ± 2.5 m for control plots.

Statistical analysis

All statistical analyses were undertaken using R (R Development Core Team 2016). Differences in light environment between manipulated and intact Bitter Willow stands were compared using generalised linear modelling (GLM). Absolute transmitted photosynthetically active radiation (PAR) was modelled, using a GLM with the binomial family. The percentage of total available PAR transmitted to 1.35 m a.g.l. was assessed, using a GLM, with the betareg function. The significance of the treatment effect was determined using a likelihood ratio test (LRT).

The seedling survey results were analysed using a repeat-measures design, whereby the initial 2012 survey results were compared with the 2015 results. All seedlings were bulked per vegetation plot for the analysis of height and density. The effect of the experimental canopy-opening treatment on seedling densities was assessed using a general linear mixed-effects model (GLMM), applying the lme4 package. The GLMM addressed issues of temporal autocorrelation associated with the repeat-measures survey design. In the GLMM, canopy status (canopy gap vs. intact canopy) was modelled as the fixed effect and plot as the random effect, assuming a Poisson distribution for the seedling count data. The variance between every experimental unit was included as a random effect in the model. The significance of the treatment effect was determined using a LRT. Differences in podocarp seedling densities between treatment and control (as of 2015), and in the reference site, were assessed with a GLM, using the Poisson family for seedling count data, and the significance of the treatment effect was determined using a LRT.

Differences in the abundance of indigenous seedling species among treatments were assessed using nonmetric dimensional scaling (nMDS) of the Vegan package. Differences in ordination space among treatments were tested, using permutational multivariate analysis of variance with the adnois function. The contribution of within-site variability was assessed using the function betadisper. The nMDS ordination was further examined through similarity percentage analysis (SIMPER) to distinguish which seedling species discriminated most strongly between treatments.

Differences in soil C:N were assessed using the non-parametric Kruskal-Wallis rank sum test.

Results

Canopy structure, light transmission and soil C:N

Small-scale Bitter Willow canopy manipulations significantly ($X^2(2) = 8.59$, P = 0.003) increased absolute transmitted PAR at 1.35 m a.g.l. at the plot centres. Absolute transmitted PAR was significantly greater beneath canopy-opening treatments ($16.4 \pm 2 \, \text{mol/m}^2/\text{day}$) compared to intact Bitter Willow canopies ($6.75 \pm 1 \, \text{mol/m}^2/\text{day}$). The percentage of total available transmitted PAR was significantly ($X^2(2) = 10.77$, P = 0.001) greater beneath canopy-opening treatments ($38.5 \pm 4\%$) compared to intact ($15.9 \pm 3\%$) Bitter Willow canopies.

Soil C:N (H(2) = 0.833, P = 0.66) was not significantly different among treatment, control or reference vegetation plots.

Seedling beight and density

Three years after canopy opening, the pilot study results showed that seedling heights beneath canopy gaps were increased in the 16–45, 46–75 and 76–105 cm height classes (Fig. 1b) compared to the 2012 baseline. The greatest change in seedling height was the recruitment of tree and shrub species into the 16–45 cm height class (2012 = 617 \pm 133 stems ha, 2015 = 2 284 \pm 535 stems ha). Over the same duration, seedling heights beneath intact Bitter Willow canopy showed little change (Fig. 1c).

Canopy opening resulted in significant ($X^2(1) = 9.40$, P = 0.01) increases in the seedling density of indigenous tree and shrub species (Fig. 1b,c). Over 3 years, beneath opened Bitter Willow canopies, mean seedling densities increased from 2 376 \pm 414 to 10 000 \pm 3388 seedlings per ha. Beneath intact Bitter Willow canopies, seedling densities showed little change compared to the 2012 baseline (2012 = 412 \pm 41 seedlings per ha, 2015 = 1 687 \pm 957 seedlings per ha). In the old-growth reference forest, the mean seedling density was 7 593 \pm 2 530 seedlings per ha (see Appendix S1 for reference site seedling and tree data).

Seedling species composition

The full seedling species composition results are reported in Appendix S2.

Discussion

The increase in seedling height and density within the treated areas suggests that Bitter Willow canopy manipulations can increase the structural development of indigenous seedlings already dispersed into the forest floor. The observed progression of seedling heights through the seedling height tiers (Fig. 1b) indicates that the canopy manipulations are leading to the recruitment of a sapling-phase structure of indigenous canopy species. These

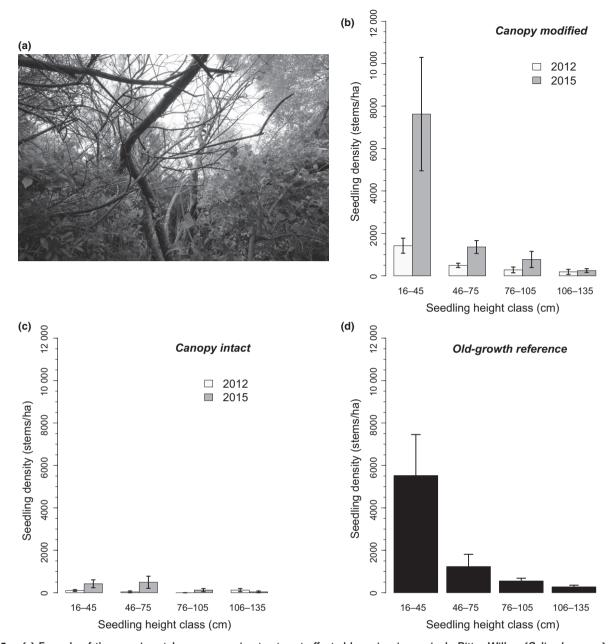


Figure 1. (a) Example of the experimental canopy-opening treatment effected by poisoning a single Bitter Willow (*Salix elaeagnos*) among an otherwise continuous Bitter Willow canopy. Mean indigenous canopy tree seedling abundance (± 1 SEM) according to seedling height class, in (b & c) canopy manipulation treatment (n = 4), and intact control (n = 3) vegetation plots, 3 years after canopy manipulation, and in (d) nearby old-growth forest.

pilot study results provide new insights into the potential role of Bitter Willow as a facilitative nurse species, and the results also provide indirect evidence that Bitter Willow serves as a perch tree for frugivorous (seed dispersing) bird species.

The natural regeneration of indigenous forest tree species has also been noted under intact canopies of riparian (Meurk & Swaffield 2000) and gully (Clarkson & McQueen 2004) *Salix* forests located elsewhere in New Zealand. Based on the pilot study results, it is suggested that further

studies of the potential for canopy manipulations in other species of *Salix* forest are needed.

The facilitative nurse role of Bitter Willow is similar to that observed within naturalised Australian stands of Camphor Laurel (*Cinnamomum camphora*), a species that is exotic to Australian rainforests (Kanowski *et al.* 2008). In a similar vein to Bitter Willow, Camphor Laurel is able to invade retired pastures to subsequently create a nursery environment, fostering the recruitment of indigenous rainforest canopy species. Experimental manipulations of

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Camphor Laurel have involved various approaches to temporal staging and gap size (Kanowski *et al.* 2008), and similar questions should be addressed in New Zealand's naturalised *Salix* stands. For Bitter Willow in particular, there may be potential for use of differently timed and sized canopy manipulations to favour particular canopy species based on their microclimate-related life-history traits (Kanowski *et al.* 2008; Forbes *et al.* 2016).

The results showing changes in species composition also raises the hypothesis of whether canopy manipulations of *Salix* stands might provide an opportunity to restore species that are specifically reliant on gap creation for regeneration. For example, in forest shade, the initiation of the regeneration of New Zealand's long-lived podocarps is disturbance related, and as such, the successful establishment and growth of those podocarp seedlings requires a competitive release (Lusk & Ogden 1992). These results suggest that Bitter Willow canopy manipulations mimicked a natural canopy-opening disturbance and thereby promoted the establishment of the relatively light-demanding podocarp species in the seedling bank.

Implications for Management

The exotic Bitter Willow stands shaded out the exotic grass cover and provided both a structure suitable for use by perching frugivorous birds and a nursery environment where indigenous seedlings dispersed into the forest floor could develop. These canopy manipulation pilot study results suggest that further investigations are needed into the potential for canopy manipulations of both Bitter Willow and other *Salix* species. In particular, larger-scale canopy manipulation experiments investigating the effects of gap size and the timing of gap creation on the recruitment of indigenous forest canopy species are required.

Acknowledgements

I thank the Hawke's Bay Regional Council (HBRC) for funding this research. Keiko Hashiba (HBRC) assisted with field survey and data analysis. Vicki Klein and Penny Andersen assisted with fieldwork. I thank Dr. Daniel Gerhard of the University of Canterbury for statistical advice.

The survey of Inglis Bush Scenic Reserve was undertaken with the permission of the Department of Conservation (Authorisation Number: 50039-RES). Prof. David Norton (University of Canterbury) and Dr. Paul Blaschke and two anonymous reviewers provided useful comments on an earlier version of this manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Seedling densities among Bitter Willow (*Salix elaeagnos*) stands subjected to small-scale canopy manipulation and intact canopies, at the time of experimental manipulation (2012), and 3-years later (2015).

Appendix S2. The seedling composition differed significantly (F3,13 = 1.87, P = 0.019, R² = 0.36) between 2012 and 2015.