

RESEARCH ARTICLE

Artificial canopy gaps accelerate restoration within an exotic *Pinus radiata* plantation

Adam S. Forbes^{1,2}, David A. Norton¹, Fiona E. Carswell³

We created small-scale artificial canopy gaps to accelerate the growth of mature indigenous forest canopy species for restoration of an 18-year-old exotic *Pinus radiata* plantation forest, in the Marlborough Sounds, New Zealand. Small and large circular gaps were formed by felling. Seedlings of two indigenous forest canopy species, *Podocarpus totara* (Podocarpaceae) and *Beilschmiedia tawa* (Lauraceae), were planted within artificial gaps and undisturbed plantation canopy. Seedling height growth, mortality, and occurrence of animal browse were monitored at approximately 6-month intervals over 17 months. Both *P. totara* and *B. tawa* differed significantly in height growth and in animal browse occurrence among artificial gap treatments. Growth of the light-demanding *P. totara* was better under large canopy gaps, whereas growth of the shade-tolerant *B. tawa* increased under gaps of any size but was most consistent under small gaps. For *P. totara*, any significant restoration benefit of gap formation on height growth was lost when browsed seedlings were taken into account. Animal browse significantly limited *B. tawa* height growth in large but not in small gaps. Small-scale canopy gap creation is an effective method of modifying light transmission to the plantation understorey and accelerating seedling growth rates. Canopy gap size can be used to optimize understorey illumination according to species-specific light requirements. The increased occurrence of animal browse in gaps requires consideration. Artificial canopy gaps within planted monocultures create structural heterogeneity that would otherwise take an extended period of time to develop. These results further support the role of plantations as indigenous forest restoration sites.

Key words: canopy intervention, forest restoration, non-harvest forestry, *Pinus radiata*

Implications for Practice

- Artificial canopy gaps can accelerate seedling height growth for indigenous canopy trees, accelerating forest restoration within exotic *Pinus radiata* plantations.
- Seedling growth performance can be maximized by matching canopy gap size with species-specific requirements for light.
- Artificial canopy gaps may increase the occurrence of mammalian animal browse.
- Recommended methods of mitigating animal browse effects on seedling height growth in canopy gaps include browse-resistant species selection, use of optimum gap size, and high planting density.

Introduction

Plantation forests are recognized globally as potential sites for the restoration of indigenous forest communities (Lamb 1998; Lamb et al. 2005; Carnus et al. 2006). Plantation trees are often established on sites with limited opportunities for economic returns, and plantation owners may be more interested in using the plantation stand to facilitate an indigenous secondary forest succession for biodiversity restoration (Lamb et al. 2005). The facilitative role exotic plantation forests can play in the recruitment of indigenous forest species has been widely studied (e.g.

Lugo 1997; Carnus et al. 2006; Brockerhoff et al. 2008). In particular, shelter associated with plantation canopy closure may ameliorate climatic conditions (e.g. frost and desiccation) at open sites that would otherwise prevent indigenous canopy tree seedlings from establishing (Cannell 1999; Brockerhoff et al. 2003; Carnus et al. 2006). However, plantation canopy cover usually increases to a point where excessive shade limits the establishment and growth of indigenous woody species, especially those species that will form the eventual canopy (Yiradaw & Luukkanen 2004). In the absence of intervention, most plantation canopies will persist for many decades before the canopy opens sufficiently (through mortality and gap formation) to result in light transmission characteristics suitable for recruitment of indigenous forest canopy species. Delayed successional development due to shade is particularly the case within *Pinus*

Author contributions: AF, DN conceived research; AF, DN, FC designed research; AF performed the experiment; AF analyzed data and wrote the manuscript; AF, DN, FC edited the manuscript.

¹School of Forestry, University of Canterbury, Private Bag 8400, Christchurch 8140, New Zealand

²Address correspondence to A. S. Forbes, email adam@forbesecology.co.nz

³Landcare Research—Manaaki Whenua, PO Box 69040, Lincoln 7640, New Zealand

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doi: 10.1111/rec.12313

Supporting information at:

<http://onlinelibrary.wiley.com/doi/10.1111/rec.12313/supinfo>

plantations in temperate climates, where an indigenous dominated understorey composition can take 15–20 years to develop, and even then comprises predominantly shade-tolerant understorey species (Allen et al. 1995; Ogden et al. 1997; Brockerhoff et al. 2003). Several more decades may then be required before light conditions are suitable for the establishment of indigenous forest canopy species. Therefore, where exotic plantation managers seek to accelerate a transition toward indigenous forest dominance, methods to optimize understorey light conditions for the early incorporation of indigenous canopy tree species in the forest succession are highly desirable, particularly in relatively young plantations when both the canopy density and the degree of canopy light interception can be high. In addition to limitations imposed by shading, the natural establishment of indigenous canopy species within plantations may not occur due to a lack of either propagule availability or dispersal (Duncan & Chapman 2002). Underplanting plantation stands with mature forest canopy species is a method of overcoming dispersal limitation. However, attainment of specific understorey light conditions is required in order for planted species to thrive in the plantation understorey (Forbes et al. 2015).

Forest canopy gaps serve a critical role in influencing understorey light regimes (Canham et al. 1990). Plantation and restoration managers can stimulate forest succession by creating artificial canopy gaps, mimicking the effect of natural disturbance events on canopy structure and understorey light regimes (Lindh & Muir 2004; Lamb et al. 2005). This approach is underpinned by the gap partitioning hypothesis (see Ricklefs 1977; Denslow 1980), which predicts that species with contrasting life history strategies are able to coexist along resource gradients, such as the resource gradient that exists from intact forest canopy through to the center of a forest canopy gap. Of particular relevance, Ricklefs (1977) suggests that young individuals of tree species will be distributed according to soil and microenvironmental gradients, and when gradients of these two parameters are produced experimentally (e.g. canopy gap creation), distinct responses will be evident, with different species having their own specific gap requirements.

A number of studies have investigated the role of canopy gap creation within *Pinus* (Pinaceae) plantation stands for restoration of indigenous forest communities. Removal of consecutive rows of *Pinus caribaea* in Sri Lanka created different widths of canopy opening strips (4 and 8 m) and resulted in differences in height growth of planted tropical late-successional forest trees (Ashton et al. 1997). Canopy gap creation in boreal *Pinus sylvestris* plantation forest in Finland by scaling experimental canopy gap treatments to canopy tree height (gaps ranged 3–20 m diameter) was found to advance the existing dominant species of the gap understorey, thereby contributing toward restoration goals (Rouvinen & Kouki 2011). In Japan, circular canopy gaps were used to promote forest succession from the understorey of a 40-year-old *Pinus thunbergii* plantation, with gap size the main factor affecting seedling growth and both growth and establishment being greatest in large gaps (Zhu et al. 2003). Results from these studies are consistent with the gap partitioning hypothesis, insofar as the growth performance of forest tree seedlings within artificial canopy gaps is dependent

on both the specific gap light environment (governed principally by gap size) and the respective species life history strategy regarding tolerance of shade.

We suggest that exotic *Pinus* plantations can be used to overcome existing barriers to indigenous forest restoration. In particular, we propose that non-harvest *Pinus* plantations provide shelter to allow canopy trees to regenerate in association with minor canopy manipulations (Norton & Forbes 2013; Forbes et al. 2015). In central New Zealand, we assessed the potential of small-scale canopy gap interventions within relatively young *Pinus radiata* (Pinaceae) plantations to enhance growth of seedlings of two indigenous mature forest canopy tree species, *Beilschmiedia tawa* (Lauraceae) and *Podocarpus totara* (Podocarpaceae). We expect these results to provide insights into the potential use of artificial canopy gaps when restoring non-harvest *P. radiata* plantations, and these results may then be adapted to *P. radiata* plantations in other localities where the restoration of locally relevant indigenous canopy dominants is desired. *Beilschmiedia tawa* and *P. totara* have contrasting shade tolerances. *Beilschmiedia tawa* is a highly shade-tolerant species (Smale & Kimberley 1986; Smale et al. 2008; Lusk et al. 2009) and its seedlings are both shade-tolerant (Burrows 1999) and sensitive to exposure (Knowles & Beveridge 1982). *Beilschmiedia tawa* has the ability to regenerate effectively both in small gaps and under a closed canopy (Smale & Kimberley 1983). These observations suggest that small canopy gaps will be of most benefit to *B. tawa* regeneration. In contrast, *P. totara* is light demanding and has a rapid growth response to canopy opening (Ebbett & Ogden 1998). *Podocarpus totara* is known to regenerate most vigorously in high-light environments such as large windthrow gaps and forest margins, among open scrub (McSweeney 1982), and even in grazed exotic grassland (Bergin & Kimberley 2014).

We hypothesize that the creation of canopy gaps within an 18-year-old *P. radiata* plantation increases light transmission to the forest understorey, which then stimulates height growth of planted seedlings of two indigenous canopy species with contrasting ecologies. We investigated the effect of different sized circular canopy gaps, hypothesizing that larger gaps would provide more favorable conditions for growth of the light-demanding species—*P. totara*, whereas smaller gaps would provide better conditions for growth of the more shade-tolerant species—*B. tawa*.

Methods

Study Area

Located in a coastal position in the Marlborough Sounds, in the northeast of the South Island of New Zealand (41°39'37''S 174°06'15''E), the study area has a mild humid climate (Laffan & Daly 1985) and receives a high number of sunshine hours per year (1948–2014 annual average = 2,289 sunshine hours). The annual average (1941–2014 average) temperature is 13°C, and monthly average temperatures range from 18°C (February) to 7°C (July). Frosts occur rarely and are usually only light (N. Guard 2015, adjacent landowner and resident, personal

communication). The annual average (1968–2000 average) rainfall is 1,411 mm, with monthly rainfall varying from 84 mm (February) to 146 mm (July). Soil moisture deficits can occur during the summer months. Sunshine and temperature statistics were measured at the Blenheim Climate Station, located circa 23 km to the southwest of the site. All other climate data were measured at the Ocean Bay Climate Station, located circa 1 km to the south of the site (National Institute of Water and Atmospheric Research [NIWA] 2013).

The site is located on north-facing, steeply sloping hill country at an elevation range of 40–120 m above sea level (a.s.l.). Soils are well-drained, formed from siliceous parent materials with silty clay to silty clay loam texture, and are of low nutrient status (Walls & Laffan 1986). The underlying geology is weakly metamorphosed Marlborough Schists grading down from Pelorus Group indurated sandstone and siltstone (Beck 1964).

The coastal broad-leaved forest that covered the site prior to European settlement would have been dominated by the angiosperm trees *Beilschmiedia tawa*, *Elaeocarpus dentatus* (Elaeocarpaceae), and *Dysoxylum spectabile* (Meliaceae), with lesser numbers of *Weinmannia racemosa* (Cunoniaceae) and *Fuscospora fusca* (Nothofagaceae) (Walls & Laffan 1986). Podocarpaceae species, including *Podocarpus totara*, would have been present as scattered emergent trees through this forest (Walls & Laffan 1986). However, since the late nineteenth century, much of the wider study area has been cleared of natural forest for pastoral farming (Laffan & Daly 1985). More recently, commercial exotic plantation forestry, principally using *Pinus radiata*, has replaced pastoral agriculture on many of the hill regions within the eastern Marlborough Sounds.

Several introduced mammals are present in the study area, including *Dama dama* (fallow deer) and a small number of *Cervus elaphus scoticus* (red deer) (J. Guard 2013, adjacent landowner and resident, personal communication). *Sus scrofa* (feral pig) were observed within the experimental site over the course of the study, as were fecal pellets of *Trichosurus vulpecula* (brush-tail possum). *Lepus europaeus occidentalis* (brown hare) may also occasionally be present.

Experimental Design

The effect of increased light transmission on indigenous seedling height growth was tested through the creation of two sizes of circular canopy gaps within an 18-year-old (at 2013) *P. radiata* plantation. The 18-year-old stand represented closed-canopy conditions, where successful intervention would allow early incorporation of mature forest tree seedlings within the forest succession. The experimental forest stand was the first rotation of planted *P. radiata* on the site and was thinned to waste at 14 years of age. Prior to the plantation establishment, an exotic shrubland occupied the site, having established itself on abandoned pasture. When the experiment was established, the *Pinus* stand had a mean top height of 24.0 m (± 0.5 , $n = 91$), a mean stem diameter (diameter at breast height, dbh) of 31.7 cm (± 0.5 , $n = 272$), a mean stem density of 831.9 trees/ha

(± 92.1 , $n = 22$), and a mean basal area of 49.5 m²/ha (± 2.5 , $n = 22$).

We selected plot locations at random points using the geographic information system (GIS) ArcMap 10.1 (ESRI 2011), and then we assigned treatments to plots on a random basis. All experimental plots were contained within a circa 22 ha area of plantation forest. To avoid edge influences, plots were not located within a 20 m exclusion buffer around the plantation edge, although the closest plot to this edge was 40 m distant. Interference between plots was avoided by the imposition of a minimum 22 m separation between plot centers, although all plot separation distances were well in excess of this minimum distance. The GIS-derived plot coordinates were located in the field, using a hand held global positioning unit (Garmin GPSmap 62s).

In total, seven small gap treatments, eight large gap treatments, and eight control (unmodified *Pinus* canopy) plots were established. During the course of the experiment, one large treatment plot was heavily browsed by stock entering from an adjacent paddock, and seedling data from that plot were excluded from subsequent analyses. All *P. radiata* trees occurring within either a 2.3 m (small gap) or 5.6 m (large gap) radius of the plots' center points were felled to create circular canopy gaps. The final expanded canopy gap diameter (Runkle 1982) extended to the next nearest tree, resulting in final gap diameters wider than the measurements that were used to initially select trees for canopy gap creation. The two gap sizes aimed to mimic what might be formed naturally from small-scale disturbance resulting from events such as canopy tree mortality or windthrow. The forest canopy was not disturbed in the control plots. Forest canopy structure and understorey light environment were quantified at all plots using 180° hemispherical (fisheye) photography. The effect of canopy opening treatments on the understorey light environment was quantified through measurements undertaken before and after canopy modification. Hemispherical photographs were taken from 1.35 m above-ground level (a.g.l.) at plot centers, using a Pentax K200 DSLR (Tokyo, Japan) fitted with a Sigma 4.5 mm circular fisheye lens. Expanded gap diameter to height ratios (gap ratios) were determined by taking the average of two orthogonal expanded gap diameters divided by the average top height of four gap-edge boarding *P. radiata* trees. Plot exposure was assessed by calculation of mesoscale topographic index, the mean of eight equidistant slopes to horizon measurements measured at the plot center, following McNab (1993). *Pinus* canopy height was measured using a Geosystems Vertex III hypsometer (Langsele, Angermanland). Stand basal area was determined using a basal area prism (factor 4) by multiplying the prism-derived stem count by four (the prism multiplier). Diameter at breast height (dbh) was measured at 1.35 m (a.g.l.).

Within each of the 23 plots, 12 nursery-raised potted seedlings of *B. tawa* and *P. totara* were planted in an alternating grid pattern at 30 cm spacing during August 2013. The planted seedling grid was centered on the gap center point. This coincided with the point from which the hemispherical photograph was taken, and allowed us to relate canopy architecture and gap light transmission results to seedling performance results.

Given the moderate to slow growth rates of these mature canopy species, their relatively sparse foliage cover, and the seedling heights at the start and end of the experiment, we believe that the 30 cm spacing among seedlings was sufficient to avoid above or belowground competition among seedlings. Seedling height, mortality, and occurrence of animal browse were monitored at approximately 6 monthly intervals over the following 17 months. Any shade-induced apical die-back represented part of the intrinsic seedling growth performance among gap treatments, and therefore seedling height measurements were always taken at the highest live apical point. To separate the intrinsic growth rate data collection from growth rate data affected by animal browse, seedlings affected by animal browse were recorded as having been browsed for the remainder of the experiment. The total seedling growth increment and the proportions of both browse occurrence and seedling mortality were calculated once at the conclusion of the experiment. Therefore, these results represent seedling growth performance, the proportional occurrence of animal browse, and seedling mortality over 17 months. Any natural establishment of exotic herbaceous plants within experimental plots was controlled by hand weeding over the duration of the experiment. This eliminated the potential for any competitive effects by exotic herbaceous colonizer species on planted seedling growth.

Statistical Analysis

Differences in slope aspect among experimental plots were assessed using functions of the R (R Development Core Team 2014) circular package, and probability values were calculated using the Wallraff rank-sum test of angular distance, which comprises a usual Kruskal–Wallis rank-sum test. Differences in mean slope and mesoscale topographical index among treatments were assessed using Kruskal–Wallis rank-sum test. Percentage canopy openness data were logit transformed before differences among experimental treatments were tested using Wilcoxon rank-sum test. The experimental effects on proportional changes in light transmission were assessed using a generalized linear model (GLM) applying the binomial family and default logit link function. Post hoc pairwise comparisons of significance were carried out for GLMs using the `glht` function of the R `Multcomp` package.

Over the course of the experiment, some seedlings were browsed by introduced mammalian herbivores, and we expect that this would have a confounding effect on seedling growth rates. In order to exclude the confounding effect of mammal browse on seedling growth rate results, we analyzed the growth rates of “unbrowsed seedlings” for each species separately. The analysis of “unbrowsed seedlings” enabled us to analyze the intrinsic growth rates of the two species and avoid the confounding effect of mammal browse. We then carried out a second, separate, analysis of grouped “browsed” and “unbrowsed” seedling growth rate data for each species (“all seedlings combined”). This analysis of all seedlings combined provided an illustration of the net growth rate for each species when creating canopy gaps for restoration, in the presence of introduced herbivores.

Differences in mean seedling height at the time of experiment establishment were assessed using one-way analysis of variance (ANOVA). The effect of experimental canopy gap treatments on “unbrowsed seedling” height growth was assessed using simple linear regression. The combined effects of canopy gap creation and the occurrence of mammalian animal browse on “all combined” seedling height growth were assessed using multiple linear regression. For inclusion in multiple regressions, the proportional occurrence of animal browse (explanatory variable) was logit transformed.

Differences in the proportional occurrence of mammalian animal browse and mortality among experimental treatments were assessed separately using GLMs applying the binomial family, with default logit link function, or quasibinomial family, with *F*-test when a model was over-dispersed. For *P. totara* mortality, due to unsatisfactory GLM diagnostics, Fisher’s exact test was used to assess differences in the proportion of mortality among experimental treatments. All error estimates given are one standard error of the mean unless otherwise stated.

Seedling relative height growth (RHG) was calculated using the formula:

$$\text{RHG} = T2 - T1/T1 \quad (1)$$

where *T1* and *T2* were absolute seedling heights measured at the time of experiment establishment and 17 months later, respectively. Therefore, the RHG results represent the growth increment over a 17-month period.

The imaging software Gap Light Analyzer (GLA, Version 2, Burnaby, British Columbia; Frazer et al. 1999) was used to extract percentage canopy openness and light transmission data from hemispherical photographs. For GLA modeling, the growing season was defined as 1 September–31 March, the default solar constant used was 1,367 W/m², and the cloudiness index, spectral fraction, and beam fraction were all set at 0.5.

Results

Physical plot characteristics (Table S1, Supporting Information) among experimental treatments were similar. Mean slope values among experimental treatments were not significantly different (Kruskal–Wallis rank-sum [$H(2) = 4.57$, $p = 0.102$]) and ranged from 18 to 29°. Slope aspects were generally to the north, and mean slope aspect values did not differ significantly among treatments (Kruskal–Wallis χ^2 [$H(2) = 3.01$, $p = 0.222$]). Mesoscale topographical index values also showed sites were of similar exposure among treatments (Kruskal–Wallis rank-sum [$H(2) = 0.96$, $p = 0.618$]).

Gap Characteristics and Gap Light Environments

Mean gap ratio scores differed significantly (one-way ANOVA [$F_{[2,20]} = 65.41$, $p < 0.001$]) among intact forest canopy (control) (0.20 ± 0.01), small gap treatments (0.40 ± 0.03), and large gap treatments (0.58 ± 0.03). Differences among all treatments were all $p < 0.001$. Canopy gap creation significantly increased percentage canopy openness (Wilcoxon rank-sum

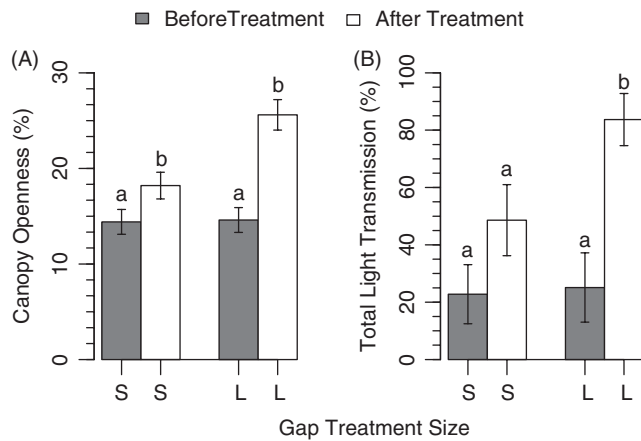


Figure 1. Mean forest canopy openness (%) and total light transmission (%) of two sizes of experimental canopy gap treatments (S, small gap [mean 9.4 ± 0.7 m diameter]; L, large gap [mean 14.6 ± 1.0 m diameter]) before and after gap creation treatment, within an 18-year-old *Pinus radiata* plantation, Marlborough Sounds, New Zealand. Paired columns with coinciding letters indicate no significant difference, whereas column pairs with different letters indicate significant differences at $p < 0.05$. Error bars represent ± 1 SE.

test [$W(n_1 = 7, n_2 = 7) = 8, p = < 0.038$] at both small gap treatments (before = 14.4% (± 1.3), after = 18.2% (± 1.4)) and large gap treatments (before = 14.6% (± 1.3), after = 25.6% (± 1.6), $t(7) = -5.988, p = < 0.001$) (Fig. 1A). Gap creation significantly increased the percentage of total light transmitted to the forest understorey (generalized linear regression [$F_{[3]} = 13.9, p = 0.003$]), with significant ($\beta = 2.729; p = 0.031$) increases in light transmission resulting from creation of large gaps (before = 25.1% (± 12.1); after = 83.7% (± 9.1)) (Fig. 1B). Total light transmission increased as a result of small gap creation (before = 22.8% (± 10.3); after = 48.6% (± 12.4)), although this increase was much less than that of large gap creation and was not statistically significant ($\beta = 1.17; p = 0.427$). Although not statistically significant, small gap creation was sufficient to effect considerable growth response in planted seedlings. Absolute total radiation (direct plus diffuse) over the growing season at 1.35 m (a.g.l.) differed significantly (one-way ANOVA [$F_{[4,33]} = 7.979, p = < 0.001$]) among gap treatments. In small gaps, absolute total radiation increased ($p = 0.086$) from $0.53 \text{ mol m}^{-2} \text{ d}^{-1}$ (± 0.15) to $1.13 \text{ mol m}^{-2} \text{ d}^{-1}$ (± 0.27); and in large gaps, radiation increased ($p = 0.001$) from $0.40 \text{ mol m}^{-2} \text{ d}^{-1}$ (± 0.04) to $1.33 \text{ mol m}^{-2} \text{ d}^{-1}$ (± 0.18). Significant differences occurred in total radiation between unmodified canopy $0.44 \text{ mol m}^{-2} \text{ d}^{-1}$ (± 0.06) and both small ($p = 0.027$) and large gaps ($p = 0.002$), respectively.

Seedling Growth Response and Occurrence of Animal Browse

***Podocarpus totara*.** The initial mean absolute height of *P. totara* seedlings was 294.7 mm (± 7), and absolute seedling heights did not differ significantly among treatments (one-way ANOVA [$F_{[2,19]} = 0.636, p = 0.540$]). Seventeen months after gap creation, *P. totara* seedlings were significantly different

among the gap treatments (one-way ANOVA [$F_{[5,32]} = 5.275, p = 0.001$]) (Fig. 2A). Mean absolute seedling heights by treatment were: “control unbrowsed” = 322.2 mm (± 12); “control all combined” = 322.1 mm (± 12); “small unbrowsed” = 358.8 mm (± 20); “small all combined” = 368.6 mm (± 16); “large unbrowsed” = 424.8 mm (± 27); and “large all combined” = 397.7 mm (± 19). Unbrowsed *P. totara* seedlings under large gaps (0.52 ± 0.11 RHG) grew to approximately four times the height of either unbrowsed (0.13 ± 0.03 RHG; $p = 0.004$) or all combined (0.12 ± 0.04 RHG; $p = 0.004$) *P. totara* seedlings growing under the unmodified forest canopy (Fig. 2A). Unbrowsed seedlings under large gaps grew at 200% the rate of unbrowsed seedlings under small gaps. However, animal browse within large gaps limited mean seedling height (0.38 ± 0.08 RHG) to an extent that there was no significant difference (all $p > 0.05$) in mean height growth performance between large gaps and any other gap treatment (Fig. 2A). Under small gaps, all combined (0.31 ± 0.06 RHG) and unbrowsed (0.24 ± 0.06 RHG) *P. totara* seedlings achieved greater mean height growth compared to those under unmodified forest canopy, although those height growth differences were not statistically different ($p > 0.05$). Nor was *P. totara* growth significantly different (all $p > 0.05$) for any other gap treatment–browse status combination (Fig. 2A).

The proportion of *P. totara* seedlings affected by animal browse differed significantly among the gap treatments (generalized linear regression [$F_{[2,18]} = 8.099, p = 0.003$]) (Fig. 2B). *Podocarpus totara* seedlings growing under either small ($54.8 \pm 5.4\%$; $\beta = 2.199, p = 0.017$) or large ($70.4 \pm 5.4\%$; $\beta = 2.876, p = 0.002$) gaps received a significantly greater occurrence of animal browse compared to those *P. totara* seedlings growing under unmodified canopy ($11.4 \pm 3.3\%$). The difference in occurrence of animal browse of *P. totara* seedlings between small and large gaps was not significant ($\beta = 0.676, p = 0.601$).

Gap size and occurrence of animal browse explained a significant amount of the variance in the height growth of *P. totara* seedlings (multiple linear regression [$F_{[5,15]} = 10.45, p = < 0.001, R^2 = 0.78, R^2_{\text{adjusted}} = 0.70$]) (Table 1). Gap creation and *P. totara* height growth were positively associated, and the occurrence of animal browse was negatively associated, with *P. totara* height growth. Both small and large gap treatments significantly predicted *P. totara* seedlings height growth. The occurrence of animal browse was not a significant predictor of *P. totara* height growth. A significant interaction ($\beta = 23.769, p = 0.028$) occurred for *P. totara* height growth between animal browse in small gap treatments, meaning that height growth in small gaps is likely to be dependent on the extent of animal browse.

Gap size explained a significant amount of the variance in the height growth of unbrowsed *P. totara* seedlings (simple linear regression [$F_{[2,13]} = 12.4, p = < 0.001, R^2 = 0.66$]). A positive association was found between gap creation and *P. totara* height growth. Gap size significantly predicted unbrowsed *P. totara* seedling height growth for large gaps ($\beta = 111.46, p = < 0.001$), but not for small gaps ($\beta = 36.87, p = 0.073$).

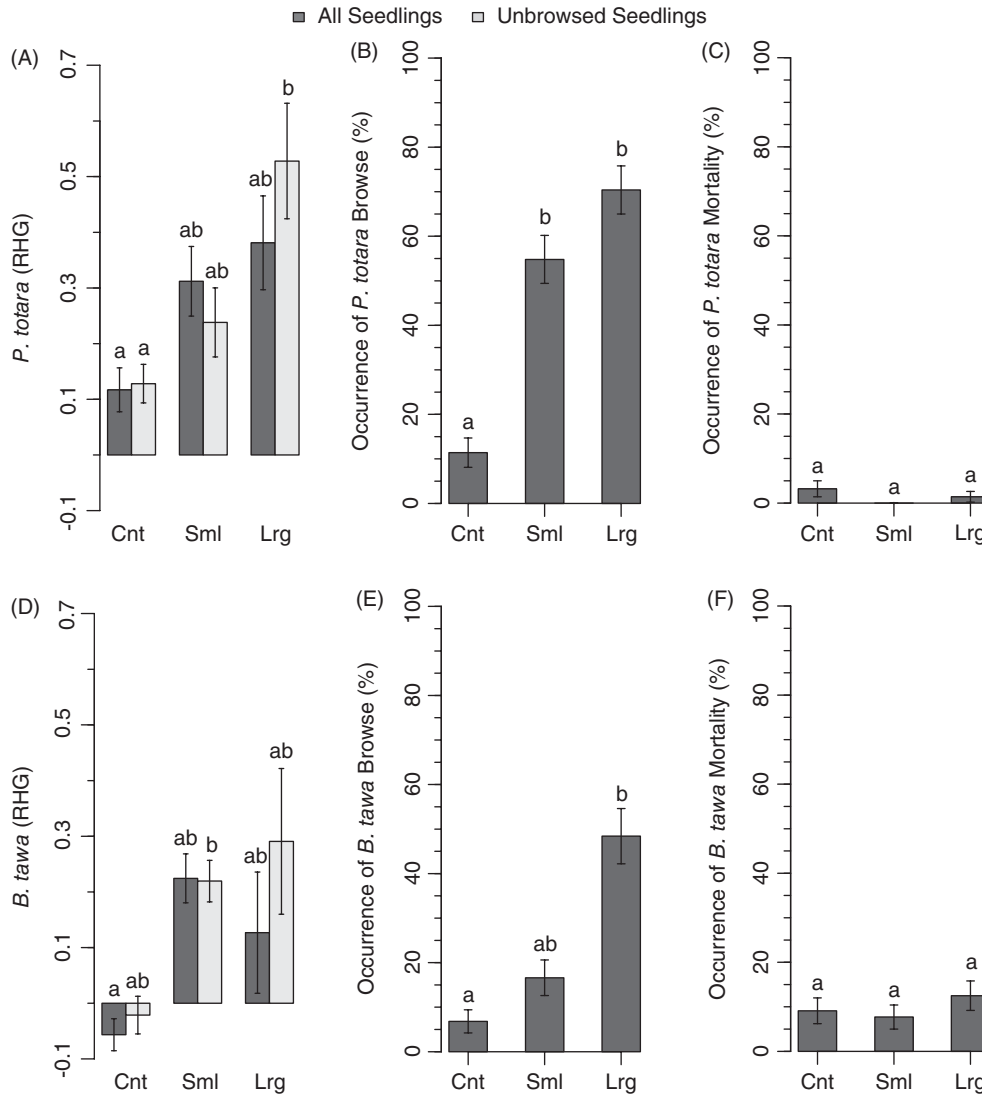


Figure 2. Seedling performance 17 months following experimental canopy gap creation within 18-year-old *Pinus radiata* plantation forest, Marlborough Sounds, South Island, New Zealand. Experimental treatments were intact forest canopy (Cnt), small gap (Sml), and large gap (Lrg). Note that RHG rates (A & D) are given separately for seedlings unaffected by mammalian browse (“unbrowsed seedlings”) and browsed and unbrowsed seedlings combined (“all seedlings”). Columns with coinciding letters indicate no significant difference, whereas columns with different letters indicate significant differences at $p < 0.05$. Error bars represent ± 1 SE.

Podocarpus totara seedling mortality did not differ significantly among gap treatments (all $p > 0.05$) (Fig. 2C), with mortality rates of 3.2% (± 2.0) under unmodified canopy gaps, 0% under small gaps, and 1.4% (± 1.2) under large canopy gaps.

***Beilschmiedia tawa*.** Initial mean absolute *B. tawa* height was 228 mm (± 4), and these seedling heights were not significantly different among experimental plots (one-way ANOVA [$F_{[2,19]} = 2.68$, $p = 0.094$]). Seventeen months after gap creation, mean height growth of *B. tawa* seedlings differed significantly among gap treatments (Kruskal–Wallis rank-sum [$H(5) = 17.782$, $p = 0.003$]) (Fig. 2D). Mean absolute seedling heights by treatment were: “control unbrowsed” = 227.5 mm (± 10); “control all combined” = 220.5 mm (± 10); “small

unbrowsed” = 267.6 mm (± 15); “small all combined” = 268.1 mm (± 16); “large unbrowsed” = 293.5 mm (± 27); and “large all combined” = 217.1 mm (± 43). The significant difference ($p = 0.041$) in *B. tawa* height growth was between all combined seedlings under unmodified canopy (-0.06 ± 0.03 RHG) and unbrowsed *B. tawa* under small gaps (0.23 ± 0.04 RHG). Under large gaps, all combined (0.13 ± 0.11 RHG) and unbrowsed (0.29 ± 0.13 RHG) *B. tawa* seedlings showed considerable variability in height growth. *Beilschmiedia tawa* height growth was most consistent under small gaps and was, on average, negative under unmodified forest canopy.

The proportion of *B. tawa* seedlings affected by animal browse differed significantly among gap treatments (generalized linear regression [$F_{[2,18]} = 4.831$, $p = 0.021$]) (Fig. 2E).

Table 1. Multiple regression model fitted to estimate the effect of canopy gap size and the occurrence of mammalian animal browse on the height growth of indigenous *Podocarpus totara* seedlings planted within two sizes of experimental canopy gaps created with 18-year-old exotic *Pinus radiata* plantation, Marlborough Sounds, New Zealand. Significance levels are symbolized as: † $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

<i>Podocarpus totara</i>	Estimate	SE	t	p
Intercept	2.75	20.87	0.13	0.897
Small gap	71.22	23.52	3.03	0.008**
Large gap	140.35	25.25	5.56	<0.001***
Browse occurrence	-12.51	8.34	-1.52	0.150
Small gap: browse occurrence	23.77	9.75	2.44	0.028*
Large gap: browse occurrence	-9.51	9.86	-0.97	0.350

Beilschmiedia tawa browse was significantly ($\beta = 2.552$, $p = 0.024$) greater under large gaps ($48.4 \pm 6.2\%$) compared to unmodified forest canopy ($6.8 \pm 2.6\%$). Differences in the occurrence of animal browse to *B. tawa* seedlings between small and control ($\beta = 1.006$, $p = 0.591$), and small and large ($\beta = 1.547$, $p = 0.115$) canopy gap treatments were not significant.

Gap size and occurrence of animal browse explained a significant amount of the variance in the height growth of *B. tawa* seedlings (multiple linear regression [$F_{[3,17]} = 11.18$, $p = 0.002$, $R^2 = 0.66$, $R^2_{\text{adjusted}} = 0.60$] (Table 2). All canopy treatments were significant predictors of *B. tawa* height growth, as was the occurrence of animal browse (all $p < 0.001$). Height growth of *B. tawa* was positively associated with canopy gap creation and negatively associated with both intact forest canopy and the occurrence of animal browse. For *B. tawa* height growth, there was no significant interaction ($p > 0.05$) between gap size and the occurrence of animal browse.

Gap size explained a significant amount of the variance in the height growth of unbrowsed *B. tawa* seedlings (simple linear regression [$F_{[2,16]} = 8.96$, $p = 0.002$, $R^2 = 0.53$]). Both small ($\beta = 59.16$, $p = 0.004$) and large ($\beta = 74.75$, $p = 0.002$) gap sizes significantly predicted *B. tawa* height growth.

The occurrence of *B. tawa* seedling mortality did not differ significantly (generalized linear regression [$F_{[2,18]} = 0.226$, $p = 0.799$]) among gap treatments (Fig. 2F), with *B. tawa* mortality rates of 9.1% (± 2.9) under unmodified canopy gaps, 7.7% (± 2.7) under small gaps, and 12.5% (± 3.3) under large canopy gaps.

Discussion

Small-Scale Canopy Gaps Optimize Understorey Light Environment

Canopy interventions within even-aged exotic plantation monocultures provide a means of diversifying forest structure and composition, thereby improving forest habitat and associated biological diversity (Coates & Burton 1997; Lindenmayer et al. 2006), and creating conditions that would otherwise take an extended period of time to develop naturally (Kuuluvainen et al. 2002). As predicted, we found that small-scale canopy gap formation in an 18-year-old exotic *Pinus radiata* plantation significantly increased light transmission to the forest understorey and increased height growth rates of

planted indigenous *Podocarpus totara* and *Beilschmiedia tawa* seedlings. We also found that species with differing requirements for light performed differently according to canopy gap size. Light-demanding *P. totara* showed an increased rate of height growth in large gaps, whereas *B. tawa* height growth increased with gaps of any size, although *B. tawa* growth was less variable under small gaps.

These results are consistent with the existing literature, which shows that artificial canopy gap size plays a significant role in controlling light transmission to the forest understorey, and also that artificial gaps within plantation forests can be sized to provide optimum light conditions for the recruitment of specific forest tree species in restoration. Within a *Pinus thunbergii* plantation, in coastal Japan, more than 1-year-old seedlings increased in density and growth with increasing size of artificial canopy gap, or canopy openness (Zhu et al. 2003). A minimum gap size for the survival of *P. thunbergii* seedlings was determined to be ≥ 1.0 gap ratio, or greater than 30% canopy openness. Gaps of ≥ 1.5 gap ratio, or greater than 40% canopy openness, were required for *P. thunbergii* seedlings to achieve sapling growth stage.

In contrast, our data for New Zealand temperate forest tree seedlings within an 18-year-old *P. radiata* plantation show a lower requirement for light. In our central New Zealand study area, we found that gap ratio and canopy openness values of 0.40 gap ratio/18.2% and 0.58 gap ratio/25.6% were best for growth of *B. tawa* and *P. totara*, respectively. We would expect some variability in seedling growth performance among plantations of different physical attributes or geographical location and these are aspects we have not been able to assess in our experiment as it was carried out in a single plantation.

In Ontario, Canada, thinning treatments within a *Pinus resinosa* plantation created canopy openness and percentage light transmission within the ranges 15–29% and 13.3–33.5%, respectively. Five years after thinning, indigenous seedling diameter, height, and stem volume were positively correlated with both thinning intensity and canopy opening size (Parker et al. 2001). Seedling stem relative growth rates of *Fraxinus*, *Pinus*, and *Quercus* differed significantly among different sized canopy openings (Parker et al. 2001). In Sri Lanka, tropical forest canopy tree species were successfully established under artificial canopy openings within a *Pinus caribaea* plantation forest. In this study, satisfactory seedling establishment required gap sizes that transmitted at least 50% of total available

Table 2. Multiple regression model fitted to estimate the effect of canopy gap size and the occurrence of mammalian animal browse on the height growth of indigenous *Beilschmiedia tawa* seedlings planted within two sizes of experimental canopy gaps created with 18-year-old exotic *Pinus radiata* plantation, Marlborough Sounds, New Zealand. Significance levels are symbolized as: † $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

<i>Beilschmiedia tawa</i>	Estimate	SE	t	p
Intercept	-66.81	16.38	-4.08	<0.001***
Small gap	81.09	16.91	4.79	<0.001***
Large gap	99.31	21.98	4.52	<0.001***
Browse occurrence	-17.34	4.25	-4.07	<0.001***

light, and 4–5 times the amount of light available under intact *P. caribaea* canopy (Ashton et al. 1997), a considerably greater light requirement than created in our *P. radiata* gap treatments.

Our results are consistent with existing knowledge regarding the light requirements of *P. totara* and *B. tawa* (Smale & Kimberley 1986; Ebbett & Ogden 1998; Smale et al. 2008; Lusk et al. 2009). Total solar radiation under the unmodified forest canopy ($0.44 \text{ mol m}^{-2} \text{ d}^{-1}$) was similar to the light compensation point reported by Lusk et al. (2015) for *P. totara* ($0.42 \text{ mol m}^{-2} \text{ d}^{-1}$) and considerably greater than the light compensation points reported for *B. tawa* of $0.08 \text{ mol m}^{-2} \text{ d}^{-1}$ (Lusk & Jorgensen 2013) and $0.09 \text{ mol m}^{-2} \text{ d}^{-1}$ (Lusk et al. 2015). Our mean per-annum scaled growth rate for unbrowsed *P. totara* (22 mm/year) under the intact *Pinus* canopy is intermediate between those growth rates found under approximately equivalent illuminations by Ebbett and Ogden (1998) from a glasshouse trial (572 mm/year (± 146 SD) at 25% of full sunlight) and from mature open *Weinmannia racemosa* forest with *Kunzea ericoides* (Myrtaceae) and *B. tawa* (24 mm/year (± 15 SD) at 20% of full sunlight), within the Whirinaki Forest Sanctuary, central North Island (Ebbett & Ogden 1998). In contrast, *B. tawa* seedling growth rates are intrinsically slow and, in some circumstances, may be negative (West 1995) or variable (Knowles & Beveridge 1982). Under the intact *Pinus* canopy in this study, due to a combination of slow-growth rate and apical die-back, unbrowsed *B. tawa* growth rates were negative (-8 mm/year), and in large gaps growth was highly variable, although the high degree of exposure in large gaps might explain this variability. Unbrowsed *B. tawa* growth rates from small gaps (34 mm/year) and large gaps (45 mm/year) are less than the 50–300 mm/year range found by Knowles and Beveridge (1982) in their releasing trial within indigenous shrub hardwood cover.

Implications of Animal Browse

Gap creation was associated with an increase in the occurrence of animal browse. The foliage of *B. tawa* and *P. totara* are both moderately palatable to *Trichosurus vulpecula* (Sweetapple et al. 2013). Although both *B. tawa* and *P. totara* are recognized as generally being avoided in the diet of introduced ungulates, ungulate browse of these species does occur (Forsyth et al. 2003) and young *P. totara* shoots can be a preferred food for deer at times when foliage nutrient levels are seasonally elevated. Although there is evidence from European temperate forests (Kuijper et al. 2009) that ungulates, and in particular *Cervus elaphus scoticus*, preferentially forage within forest

clearings, we are unable to say from our data whether it was the gap per se, or the additional planted seedling and exotic herbaceous plant growth occurring within the higher light environments of gaps, that caused the increased browse occurrence. *Podocarpus totara* height growth increased in large gaps only for unbrowsed seedlings. When browsed *P. totara* seedlings were taken into account, there were no significant differences in height growth among gap treatments, and the apparent benefit of gap creation was reduced. In large gaps, where *B. tawa* browse was greatest, animal browse significantly limited *B. tawa* seedling height growth.

Exotic *Pinus* Gaps for Forest Restoration

In the New Zealand context, our results suggest that, if *P. totara* seedlings can be protected from animal browse, then large canopy gaps (e.g. gaps typically of 5.6 m radius; 0.58 gap ratio; 84% of total available light transmitted) in mid-rotation *P. radiata* plantation stands would be preferable to smaller gaps, or intact forest canopy, for establishing this species. The benefit of large gaps to unbrowsed *B. tawa* seedling height growth is uncertain. Considering the high variability in *B. tawa* height growth data from large gaps, along with the species' known strong shade-tolerance and sensitivity to exposure (Knowles & Beveridge 1982), small gaps (e.g. gaps typically of 2.3 m radius; 0.40 gap ratio; and 50% of total available light transmitted) are likely to be optimal over either intact forest canopy or large gaps, for *B. tawa* recruitment. Although not assessed in our experiment, we do note that light gradients differ across forest gaps (e.g. shaded gap edge vs. highly illuminated gap center). We suggest that with some further assessment, it may be possible to incorporate a diversity of species with differing shade tolerance into artificial canopy gaps, by locating species in suitable gap microsites according to species-specific shade tolerance and gap light distribution.

Given the increased occurrence of animal browse from gap creation, in circumstances where animal browse cannot be prevented, our results suggest that, for *P. totara*, large canopy gaps are likely to be preferable to small canopy gaps. However, high-density plantings may be required to mitigate against the effects of animal browse. For *B. tawa*, our results provide evidence that animal browse under small gaps had little effect on seedling height growth. These results mean that smaller gaps are likely to be the best for *B. tawa* seedling growth, regardless of the degree of animal browse.

Internationally, plantations are recognized for the role they play in increasing landscape connectivity, buffering existing

forest remnants, providing habitat for both common and threatened species, and conserving soil and water resources (Carnus et al. 2006; Brockerhoff et al. 2008). Global trends of increasing cover by plantation forest (Food and Agriculture Organisation of the United Nations [FAO] 2011) coupled with the role of habitat change on global declining biodiversity trends (Pereira et al. 2012) suggest that opportunities for biodiversity management can be found in improved plantation management. From their outset, plantations may be managed for non-harvest purposes, such as soil or water conservation, or changes in social or cultural values over their lifetime may mean that they are not intended to be harvested. Under these circumstances, non-harvest plantations provide one approach for restoring indigenous forest communities, and provide a means of managing plantations to maximize indigenous species success. As our gap experiment was conducted in only one plantation, we are unable to assess the effects of variables that affect seedling performance in gaps of given dimensions, and that might vary among plantations. Such factors include *Pinus* age class, slope aspect, geographical location, and soil type. Therefore, there is scope for further gap experiments in *P. radiata* plantations of different age classes and on different topographies and soils, and also with different indigenous species—taking into account species-specific shade tolerance and palatability. Nevertheless, our results provide further support to the existing literature that shows canopy gap interventions are a means of promoting indigenous forest recruitment from plantation understories, and this intervention is likely to assist in achieving multiple non-harvest forest restoration management objectives.

Acknowledgments

We thank P. Forrest for allowing the experiment within his plantation forest, and V. Harris (PALMS Ltd) for assistance with early logistical planning. Morgan's Road and Treeline plant nurseries supplied indigenous seedlings. The financial support of the University of Canterbury New Zealand School of Forestry is gratefully acknowledged. Three anonymous reviewers provided very useful comments on an earlier version of this manuscript.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Experimental plot site characteristics.

Coordinating Editor: Fernando Valladares

Received: 30 April, 2015; First decision: 3 July, 2015; Revised: 13 October, 2015; Accepted: 26 October, 2015; First published online: 27 November, 2015