

## Establishment of *Pseudotsuga menziesii* and *Pinus nigra* seedlings in *Kunzea ericoides* and *Leptospermum scoparium* shrubland communities

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**Abstract:** We compared establishment of Douglas fir (*Pseudotsuga menziesii*) and Corsican pine (*Pinus nigra*) seedlings in kānuka (*Kunzea ericoides*) and mānuka (*Leptospermum scoparium*) shrubland to test the hypothesis that Douglas fir, because of its greater shade tolerance, is better able to establish in woody communities than pine species. Seed of the conifer species was sown under a range of canopy covers at six sites, the cover being low-statured vegetation in openings between stands, stand edges, and moderate and dense canopies. After three growing seasons, survival of Corsican pine seedlings was greatest in the open and declined progressively as canopy cover increased. This contrasted with Douglas fir, where survival was greatest at the canopy edge. Survival of Douglas fir seedlings significantly exceeded that of Corsican pine seedlings under dense canopy positions. Seedling numbers of both species declined significantly with increasing leaf area index of mānuka, but not kānuka stands, where seedling numbers were lower. Leaf area index of mānuka stands accounted for substantially greater variation in number and survival of Corsican pine than Douglas fir seedlings. It is concluded that Douglas fir is better able to establish in shaded environments in woody communities than Corsican pine; however, further monitoring is required to confirm the long-term survival of both species under the moderate and dense canopy positions in this trial.

**Keywords:** canopy cover; leaf area index; seedling establishment

### Introduction

Exotic conifers have been planted widely in New Zealand for timber production, erosion control, provision of livestock shelter on farms, as well as for amenity values. Many species grow well in New Zealand, and a number have shown a propensity to spread as wildings from original plantings into neighbouring vegetation communities. The most common species to spread are European larch (*Larix decidua*)<sup>1</sup>, lodgepole pine (*Pinus contorta*), Corsican pine (*P. nigra*), maritime pine (*P. pinaster*), radiata pine (*P. radiata*), and Douglas fir (*Pseudotsuga menziesii*) (Hunter & Douglas 1984; Ledgard 1988, 2001; Allen & Lee 1989). Hunter and Douglas (1984) observed that establishment of wilding conifer seedlings was more prolific in short, open grassland and open scrubland than in tall closed-canopy grassland, scrubland or forest. Forest and shrubland communities, if disturbed by natural or anthropogenic events, may, however, become vulnerable to invasion by exotic tree species (Richardson et al. 1994).

Kānuka (*Kunzea ericoides*) and mānuka (*Leptospermum scoparium*) are important shrubland species in New Zealand, often dominating communities by themselves or as a mixture (Wardle 1991). They commonly invade grasslands after fire, or where agricultural inputs such as fertiliser or livestock grazing have been reduced. Kānuka and mānuka shrublands normally succeed to tall forest communities, but can also maintain themselves as more or less stable communities if they are in harsh environments, are frequently burnt, are some distance

from forest seed sources, or if seedlings of other establishing species are browsed (Wardle 1991).

The potential exists for kānuka and mānuka shrublands to be invaded by exotic conifer species if there is a seed source in the vicinity. Because they are seral species and are often disturbed by fire, kānuka and mānuka shrublands commonly consist of a mosaic of environments including intact shrub canopies, intervening open grassland or other low-stature communities, and the edges between these communities. These different microsites will differ in light transmission, moisture and perhaps nutrient availability, and so will provide differing opportunities for establishment of exotic conifer seedlings arising from seed dispersed into the shrubland. Conifer species may differ in their preference or tolerance of such different microsites. For example, Allan and Lee (1989) studied establishment of European larch, lodgepole pine and Corsican pine in different microsites within tall tussock (*Chionochloa rigida*) grassland. They found that microsites between tussock canopies were the most favourable for establishment of larch and Corsican pine, while establishment of lodgepole pine was similar in the under-canopy and between-canopies classes. It was suggested that lodgepole pine may be more shade tolerant than the other conifer species, although other factors may have contributed to the difference.

Douglas fir is generally considered to be more shade tolerant than pine species (Hermann & Lavender 1990; Carter & Klinka 1992; Richardson & Rundel 1998; Bond et al. 1999), and because of this is the most likely exotic conifer

<sup>1</sup> Plant names follow the New Zealand Plant Names Database (Allan Herbarium 2002–2011), although Douglas fir is often hyphenated elsewhere to indicate it is not a true fir (*Abies* spp.).

to spread into indigenous forest (Ledgard 2002). However, Szaniawski and Wierzbicki (1978) categorised Douglas fir as shade intolerant, along with Scots pine (*Pinus sylvestris*) and European larch, on the basis of photosynthetic response to irradiance. In New Zealand there are examples of Douglas fir establishing in disturbed mountain beech forest (Ledgard 2002), but similar examples have not been reported for pines, supporting the assertion that Douglas fir more readily establishes in indigenous forest than pines. If Douglas fir is more shade tolerant than pines it should establish more readily in shaded environments in shrubland communities.

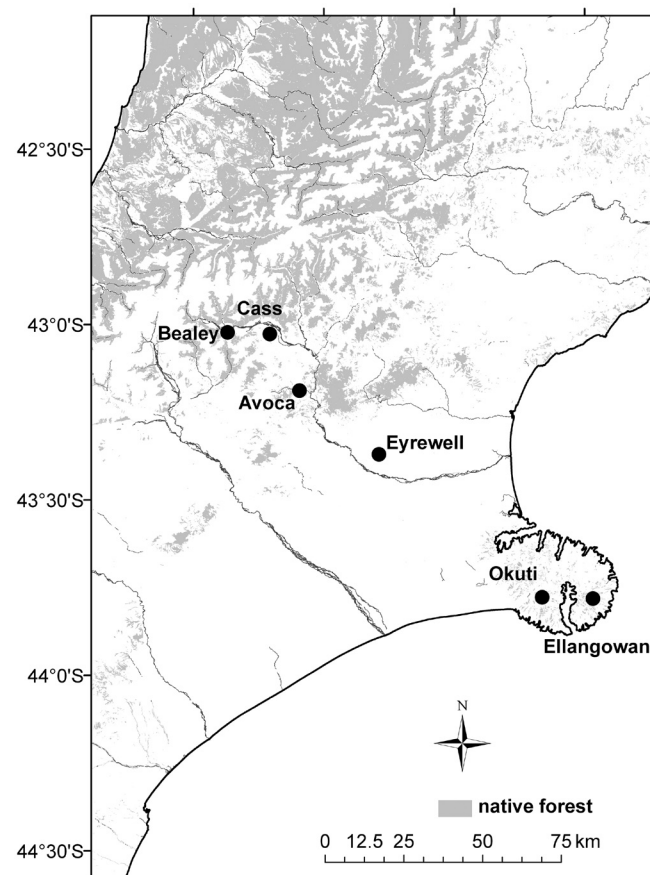
The aim of the present study was to determine if shrubland communities dominated by kānuka and mānuka are more vulnerable to invasion by Douglas fir than by pines by comparing establishment of Douglas fir and Corsican pine, introduced by sowing seed, across a range of environments found in those communities. Corsican pine was chosen for comparison as it is one of the important species to spread in New Zealand and has a similar seed size and seedling growth rate (unpubl. data). Information from the study might be used to assess the risk of Douglas fir invasion of shrubland near plantations and assist in decision-making of priority species to control, and thereby assist in management to reduce the risk of covenanted shrubland communities to invasion by exotic conifer species.

## Methods

### Site characteristics

Three kānuka and three mānuka sites were selected for the study. The sites are aligned along an east–west transect in Canterbury from Banks Peninsula to the upper Waimakiriri catchment (Fig. 1). Each site has dense but discontinuous stands of kānuka or mānuka present, interspersed with open grassland or, at Bealey, moss vegetation. All sites except Eyrewell are on north-west-facing slopes ranging from 4° to 30° (Table 1). The kānuka stands at Ellangowan and Okuti are sites on Banks Peninsula while the kānuka stand at Eyrewell is located in a

lower rainfall environment on the central Canterbury Plains. The three mānuka sites are located in the upper Waimakiriri catchment and increase in elevation and precipitation from east (Avoca) to west (Bealey) (Table 1).



**Figure 1.** Location of study sites. Ellangowan, Okuti and Eyrewell are kānuka sites, Avoca, Cass and Bealey are mānuka sites.

**Table 1.** Stand site and structural characteristics. Standard errors of structural characteristics are shown.

	Elevation (m)	Aspect (°)	Slope (°)	Precipitation (mm)	Mean January max. (°C)	Mean July min. (°C)	Stem density (stems m <sup>-2</sup> )	Stem dbh (mm)	Stem height (m)
<i>Kānuka sites</i>									
Ellangowan	600	346	30	1800	18.7	2.4	0.35 ±0.04	101 ±11.3	7.4 ±0.25
Okuti	230	297	20	1300	20.8	2.9	0.20 ±0.02	99 ±8.2	8.2 ±0.15
Eyrewell	210	-	0	790	23.2	0.3	1.65 ±0.15	43 ±15.5	5.4 ±0.45
<i>Mānuka sites</i>									
Avoca	550	336	4	900	21.8	-0.8	2.10 ±0.40	32 ±3.0	3.6 ±0.12
Cass	760	275	19	1280	19.0	-1.5	3.25 ±0.25	21 ±0.3	3.6 ±0.03
Bealey	820	335	4	1670	18.8	-1.5	5.05 ±1.05	26 ±1.6	3.4 ±0.10

Two plots were used to characterise the stand structure at each site and were subjectively located within dense kānuka or mānuka canopies. The plots were  $10 \times 4$  m in the kānuka stands at Ellangowan and Okuti, and  $5 \times 2$  m at the remaining sites. The total number of stems was recorded for each plot, and heights and breast height diameters were recorded of all trees at Ellangowan and Okuti, and from a sample of 10 trees at the remaining sites.

Measurements of leaf area index (LAI) were made at the time of establishment of seedling plots (see below) and on three further occasions at 0.2 m height above each plot, using a Li-Cor 2000 Plant Canopy Analyser. Seedling plot ground cover was assessed in September 2007 by estimating cover in six categories, namely – grasses, dicotyledonous species, bryophytes and lichens, litter, soil, and rock.

### Seedling plot installation and seedling assessment

Seed of Douglas fir and Corsican pine was sown in September 2006 in  $0.25\text{-m}^2$  plots at four positions with respect to kānuka and mānuka canopy cover at each site, the cover being stand openings, stand edges, and moderate and dense canopies. Plots in stand openings were located 1–5 m from stand edges, and had a mean LAI of 1.1 (range 0.4–1.7). At stand edges, plots were located outside of stands, but within 0.5 m of the kānuka or mānuka stem bases, and had a mean LAI of 2.2 (range 1.5–3.0). Plots at moderate and dense canopy positions were located within stands and had mean LAI values of 3.8 (range 2.7–4.6) and 4.4 (range 3.1–5.3) respectively. There were five replicates of each canopy cover at each site. Seed sowing and subsequent plot assessment was facilitated by placing a  $0.5 \times 0.5$  m grid divided into  $0.1 \times 0.1$  m squares on the ground. The grid was located using a permanent peg in each corner. One hundred seeds of Douglas fir were sown into 10 grouped squares (randomly chosen) on one side of the grid, while Corsican pine was sown on the opposite side, leaving a central row of unsown squares separating the two species. Seeding rates were therefore  $1000\text{ seeds m}^{-2}$ . Seed weights were 11.0 and 10.0 mg seed<sup>-1</sup> and laboratory germination percentages were 96% and 77% for Douglas fir and Corsican pine respectively (information provided by seed-supplying company). To ensure seedling establishment was not limited by lack of mycorrhizal development, 0.5 g of dried, finely ground sporophore material of *Rhizopogon rubescens* ( $1.06 \times 10^{10}$  spores g<sup>-1</sup>) and *R. parksii* ( $1.15 \times 10^{10}$  spores g<sup>-1</sup>) was applied in water solution to the Corsican pine and Douglas fir plot squares respectively. *Rhizopogon rubescens* and *R. parksii* are known mycorrhizal symbionts of pine species and Douglas fir respectively. Germinating seedlings were protected from browsing animals using 0.2-m-high cages of wire netting (18-mm mesh) pinned to the ground.

Seedlings were counted in December 2006 to assess initial establishment, and then autumn and spring in the following years until April 2009, three growing seasons after sowing. Seedling heights were measured periodically. Seedling survival was defined as the number of live seedlings present at the final assessment as a percentage of total seedlings observed during the first growing season. Analysis of variance (ANOVA) was used to determine if there were significant differences between the main treatments of site, cover, and species, and their interactions. Prior to analysis, seedling numbers and seedling survival data were transformed as required to better satisfy the underlying assumptions of the ANOVA. Where significant differences occurred at  $P = 0.05$ , a Student–Newman–Keuls test was used to distinguish between treatments. Correlation

analysis was used to determine if there were relationships between the number of seedlings per plot and LAI, and seedling survival and LAI, and if so, to determine if the relationships differed between Douglas fir and Corsican pine. These analyses were undertaken using the means of the five replicates for each site, and for kānuka and mānuka stands considered both together ( $n = 24$ ) and separately ( $n = 12$ ).

## Results

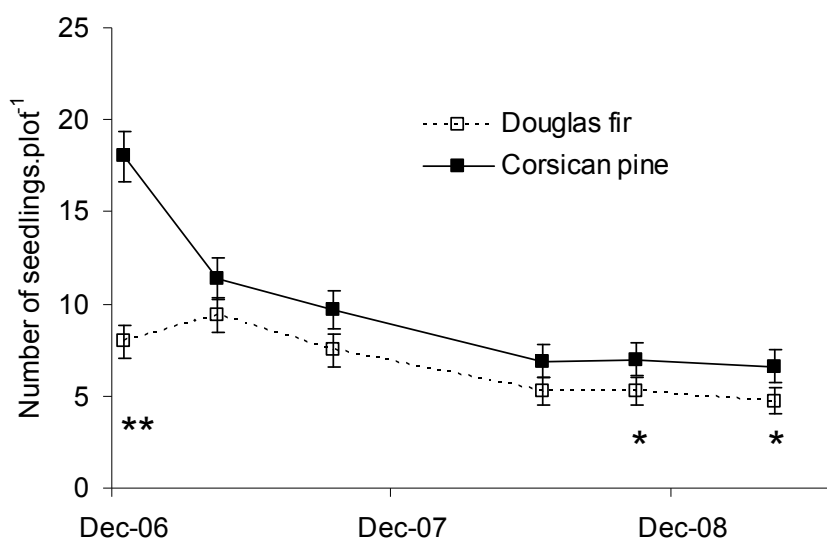
### Stand characteristics

The kānuka stands at Ellangowan and Okuti on Banks Peninsula were characterised by large-diameter, tall, mature stems of relatively low density. The kānuka stand at Eyrewell had lower height and stem diameters, but higher stem density than the Banks Peninsula stands. The mānuka stands were all of lower stature, stem diameter and higher stem density than the kānuka stands (Table 1).

Across all sites litter was a dominant form of ground cover, ranging from 11–52% in open positions to 47–94% under dense canopies. In open positions litter was composed mostly of grass or other herbaceous species; this changed to predominantly leaf and small twig litter of kānuka or mānuka in the moderate- and dense-canopy positions. Grasses and dicotyledonous species formed the dominant living ground cover in open positions at all sites except Bealey, where bryophyte and lichen species were the most important. Bryophytes were also moderately important at Eyrewell under all canopy covers. Bare soil formed a large component under the dense canopy at Ellangowan, and at edge, moderate- and dense-canopy positions at Okuti (data not presented).

### Seedling establishment

Mean Corsican pine seedling numbers exceeded those of Douglas fir at all assessments, the difference being significant at the first and final two assessment dates (Table 2, Fig. 2). Corsican pine seedling numbers were greatest at the first assessment, 3 months after sowing, and declined progressively through to the end of the second growing season. Seedling numbers of Douglas fir increased from the first to the second assessment, indicating that mean germination occurred later in the season than in Corsican pine, before declining toward the end of the second growing season (Fig. 2). Little mortality of either species occurred in the third year (Fig. 2). Across all species and sites, the mean ( $\pm$  standard error) number of seedlings per plot declined in the order: open ( $8.4 \pm 1.25$ ) = edge ( $7.9 \pm 1.41$ ) > moderate canopy ( $4.5 \pm 1.02$ ) > dense canopy ( $2.0 \pm 0.42$ ) at the final assessment. This order had developed by the end of the second growing season (data not presented). Mean seedling numbers were greater at the mānuka sites than the kānuka sites at all but the first assessment date. At the final assessment the mean ( $\pm$  standard error) seedling number per plot declined in the order: Cass ( $11.2 \pm 1.91$ ) = Avoca ( $10.9 \pm 1.74$ ) > Bealey ( $7.8 \pm 1.12$ ) > Okuti ( $2.0 \pm 0.75$ ) = Eyrewell ( $1.4 \pm 0.52$ ) = Ellangowan ( $0.6 \pm 0.26$ ). Again, this order had developed by the end of the second growing season. The first two assessments showed that, although seedling abundance was greater in Corsican pine than Douglas fir, there were significant three-way interactions between species, sites and vegetation cover (Table 2). However, beyond the first growing season there were no interactions between species and vegetation cover.



**Figure 2.** Change with time in Douglas fir and Corsican pine seedling numbers. Values are means of six sites and four vegetation cover types at each site. Asterisks indicate significance of differences at  $P = 0.05$  (\*) and  $P = 0.01$  (\*\*). Bars show standard errors of means.

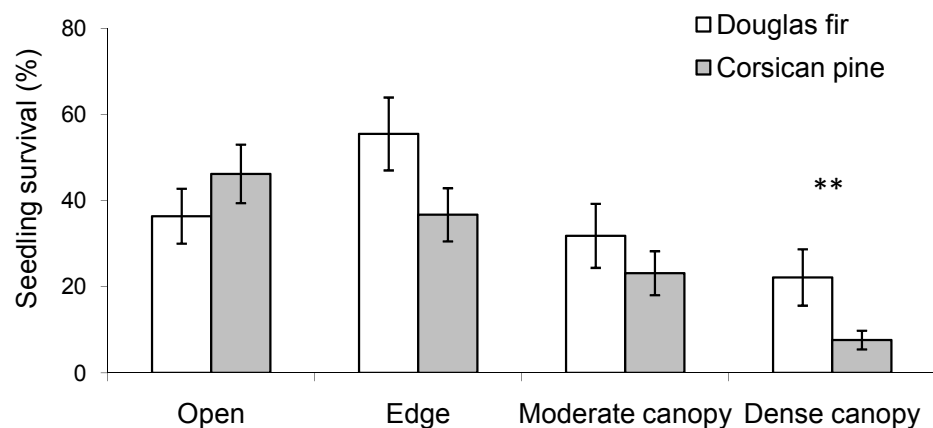
**Table 2.** *F*-values from analysis of variance of treatment effects on seedling numbers at six assessment dates and of height at the final assessment. Analysis of variance of seedling numbers was performed after square-root transformation of data.

	Seedling number	3 months Dec. 2006	7 months Apr. 2007	12 months Sep. 2007	21 months June 2008	25 months Oct. 2008	31 months Apr. 2009	Seedling height	31 months Apr. 2009
Species (Sp)	$F_{1,188}$	79.98***	0.73	3.24	3.14	4.02*	5.38*	$F_{1,102}$	0.01
Site	$F_{5,188}$	32.09***	43.14***	43.30***	38.85***	38.99***	37.07***	$F_{5,102}$	0.14
Cover	$F_{3,188}$	2.28	9.02***	11.30***	15.77**	16.76***	17.16***	$F_{3,102}$	< 0.01
Replicate	$F_{4,188}$	0.34	0.96	0.94	0.65	0.91	1.07	$F_{4,102}$	0.02
Species*Site	$F_{5,188}$	6.94***	6.09***	3.95**	2.66*	2.94*	2.17	$F_{5,102}$	0.71
Species*Cover	$F_{3,188}$	6.53***	0.19	0.07	0.37	0.47	0.94	$F_{3,102}$	0.44
Site*Cover	$F_{15,188}$	2.64**	4.56***	4.44***	5.15***	5.27***	5.00***	$F_{12,102}$	0.11
Site*Sp*Cover	$F_{15,188}$	2.03*	1.76*	1.40	1.02	1.31	1.05	$F_{7,102}$	0.45

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$

Mean seedling survival at the final assessment did not differ significantly between the two species (Douglas fir  $36 \pm 3.8\%$ , Corsican pine  $28 \pm 3.0\%$ ), but there were highly significant ( $P < 0.01$ ) interactions between species and site, and species and vegetation cover. Survival of Douglas fir seedlings was greater than for Corsican pine at Bealey, Cass and Okuti sites while survival of Corsican pine was greater at Eyrewell. Survival of the two species was similar at Ellangowan and Avoca (data not presented). Survival of Corsican pine seedlings was

greatest in the open and declined progressively as canopy cover increased. This contrasted with Douglas fir where seedling survival was greatest at the edge position (Fig. 3). Seedling survival of Corsican pine was greater than for Douglas fir at the open position, whereas survival of Douglas fir seedlings was greater at the edge, moderate- and dense-canopy positions, though the difference was significant only at the dense-canopy position (Fig. 3).



**Figure 3.** Survival of Douglas fir and Corsican pine seedlings at the end of the third growing season, as a percentage of seedlings observed in the first growing season. Values are means of six sites; bars show standard errors. Asterisks indicate significance of differences at  $P = 0.01$  (\*\*).

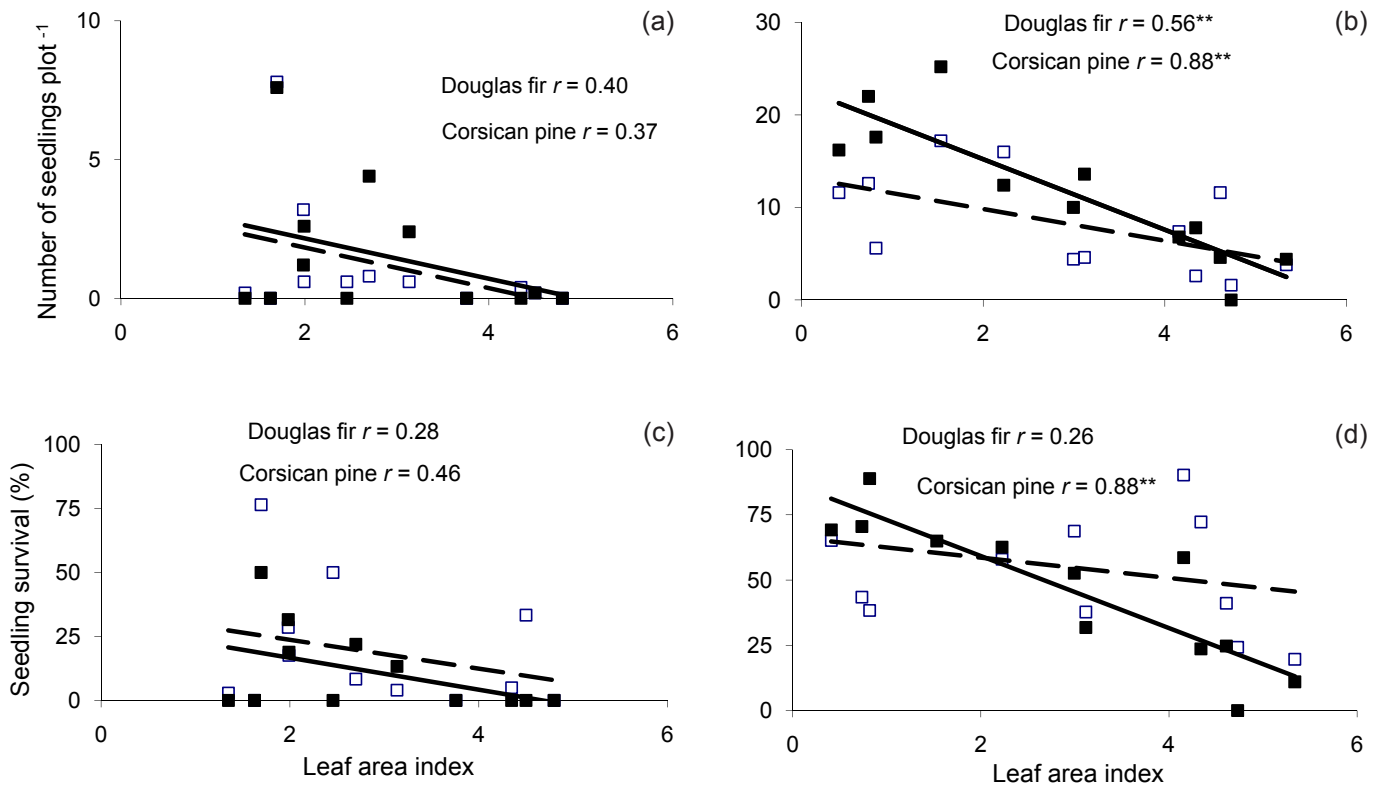
After three growing seasons, significant negative correlations were observed between LAI and both seedling number and seedling survival for Corsican pine ( $r = -0.53$  and  $r = -0.57$  respectively,  $P < 0.01$  in both cases), but not for Douglas fir. When kānuka and mānuka stands were considered separately, no significant relationships were observed for kānuka stands, but for mānuka stands significant, negative relationships were observed between seedling number and LAI for both Douglas fir and Corsican pine (Fig. 4b). For mānuka stands, LAI accounted for 77% and 31% of the variation in Corsican pine and Douglas fir seedling numbers respectively. For seedling survival, there was a significant, negative correlation with LAI for Corsican pine, but not Douglas fir (Fig. 4d), with LAI accounting for 77% and 7% of variation in seedling survival respectively. Regression analysis showed that, for both seedling number and survival, the slopes of the two species' regression lines differed at  $P = 0.10$ .

Analysis of variance showed that, at the last assessment (31 months), mean seedling heights differed between species and cover type, but there was no interaction between these factors (Table 2). On average, Douglas fir seedlings (74 mm) were significantly ( $P < 0.05$ ) taller than Corsican pine seedlings (69 mm) and seedlings were significantly ( $P < 0.05$ ) taller in the open (80 mm) than under shaded (edge, 60 mm; moderate, 52 mm; and dense, 48 mm) canopy positions, but there was no significant difference in heights between the shaded positions.

### Discussion

The hypothesis tested in this study was that Douglas fir, because of its greater shade tolerance, should establish more successfully than Corsican pine under shaded conditions among kānuka and mānuka communities. The highly significant interaction between seedling survival and canopy cover, with greater survival of Douglas fir in shaded positions, and contrasting greater survival of Corsican pine in the open, provides strong support for the hypothesis. The stronger negative relationships between both seedling number and seedling survival and LAI in Corsican pine than Douglas fir further supports the hypothesis. In contrast to Douglas fir, most of the variation in survival of Corsican pine seedlings was explained by overstorey LAI. These relationships confirm that Douglas fir seedlings are less dependent on a high light environment for establishment than Corsican pine seedlings, and may establish more readily under shaded conditions present in shrubland.

The present findings are consistent with results of two recent studies that have compared establishment of Douglas fir with pine seedlings in indigenous shrub and tree communities in the Waimakariri Valley. Cattaneo (2002) found that Douglas fir seedlings established close to plants in subcanopy and canopy tiers in shrubland dominated by *Dracophyllum* sp., while lodgepole pine showed no preference for establishing close to plants in the canopy tier of shrubland dominated by *Chionochloa macra* and *Ozothamnus leptophylla*. Cattaneo



**Figure 4.** Relationships between conifer seedling number and survival, and leaf area index of Douglas fir (open markers and dashed lines) and Corsican pine (closed markers and full lines) in kānuka (a, c) and mānuka (b, d) communities at the end of the third growing season. Asterisks indicate significance of correlation coefficients at  $P = 0.05$  (\*) and  $P = 0.01$  (\*\*). Note vertical-axis-scale differences in panels a and b.

(2002) considered the improved establishment of Douglas fir seedlings close to shrubs may have been due to the light shade and protection from frosts and desiccation provided by shrub vegetation. Few Douglas fir seedlings established in the open inter-shrub vegetation; in contrast a third of the lodgepole pine seedlings were found in the open. This differed from our study where, although the difference in survival between the two species in favour of Corsican pine was greatest at open sites, Douglas fir seedlings were still present in reasonable numbers in open sites three growing seasons after sowing.

More recently, from a study of seedling growth under different forest species, Dehlin et al. (2008) suggested Douglas fir was more shade tolerant than lodgepole pine. They transplanted seedlings of lodgepole pine, Douglas fir and mountain beech (*Nothofagus solandri* var. *cliffortioides*) into stands of each of these species that differed in light transmission and soil properties. Seedlings of all species had low survival and lost biomass under Douglas fir canopies because of low light transmission, and grew best under mountain beech canopies. Lodgepole pine showed the strongest growth response to stand type while Douglas fir showed the weakest response, the weaker response being attributed to the greater shade tolerance of Douglas fir.

Seedlings of both conifers in our study persisted under the moderate- and dense-canopy positions 3 years after sowing, but many appeared weak and unlikely to survive. Shade tolerance has been found to decline with increase in seedling size, especially in less shade tolerant species (Lusk 2004; Kneeshaw et al. 2006; Lusk et al. 2008) so the vigour of seedlings in under-canopy positions may further decline as seedlings age. In contrast, seedlings in the open positions generally appeared robust and likely to survive, although there was substantial variation in colour (from pale yellow to deep green) and development of height growth, suggesting variation in mycorrhizal development. Thus, the relationships between seedling number and LAI will almost certainly change with time. Further assessments will confirm survival patterns of the two species in relation to LAI.

Establishment of both conifers was substantially greater under mānuka than kānuka stands. Poor establishment at the Eyrewell site was almost certainly caused by low moisture availability as it is located on a shallow free-draining Lismore soil with low water storage capacity. There is no obvious climatic explanation for the poor establishment at Ellangowan and Okuti sites. Rainfall was favourable at both sites (data not presented), while summer temperatures are similar and winter temperatures more benign than at any of the mānuka sites. Browsing of seed by invertebrates or mice (*Mus musculus*) may have contributed to the low seedling numbers at both sites as, although the plots were caged, the wire mesh covering would not have precluded their entry. Pine seeds are subject to intense predation by vertebrates, including rodents, in North America (Vander Wall 1994). In New Zealand, seeds of *Nothofagus solandri* var. *cliffortioides* trees may be heavily predated by mice (Ruscoe et al. 2005). Vander Wall (1994) found that *Pinus jeffreyi* seeds placed under litter were removed by vertebrates much more slowly than seeds placed on the surface of bare mineral soil or buried in bare mineral soil with the wing exposed. In the present study the Okuti and Ellangowan sites differed from the remaining sites in that they had high amounts of bare soil in the dense-canopy and, at Okuti, moderate-canopy and edge positions. It is possible that seed removal by mice may have been enhanced by the greater amount of bare soil, contributing to low seedling numbers at these sites.

Our results indicate that Douglas fir is better able to establish in shaded environments in native woody communities than Corsican pine. Although seedlings of both species persist under canopies of both kānuka and mānuka stands in the present study, it appears unlikely that either conifer will ultimately survive under dense intact canopies. However, in disturbed or regenerating communities, both Douglas fir and Corsican pine are likely to find microsites that are suitable for establishment, with Douglas fir establishing most readily along stand edges and under moderately dense canopies and Corsican pine (and other pine species) establishing more readily in open environments between stands. Because of the taller stature of shrubland, conifer seedlings and young plants are much more difficult to detect there than in grassland or other low-stature communities and, therefore, more difficult to remove. Detection will be aided by concentration of search effort in stand openings and along stand boundaries. However, the most effective means of preventing invasion of kānuka and mānuka and other woody shrubland communities by conifer species will be to remove conifer stands that have potential to disperse seed into those communities.

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## References

- Allan Herbarium 2002–2011. Ngā tipu o Aotearoa – New Zealand plants. New Zealand Plant Names Database: <http://nzflora.landcareresearch.co.nz>.
- Allen RB, Lee WG 1989. Seedling establishment microsites of exotic conifers in *Chionochloa rigida* tussock grassland, Otago, New Zealand. *New Zealand Journal of Botany* 27: 491–498.
- Bond BJ, Farnsworth BT, Coulombe RA, Winner WE 1999. Foliage physiology and biochemistry in response to light gradients in conifers with varying shade tolerance. *Oecologia* 120: 183–192.
- Carter RE, Klinka K 1992. Variation in shade tolerance of Douglas fir, western hemlock, and western red cedar in coastal British Columbia. *Forest Ecology and Management* 55: 87–105.
- Cattaneo M 2002. Effects of microsite characteristics, competition and grazing on *Pinus contorta* Dougl. and *Pseudotsuga menziesii* (Mirb.) Franco seedling establishment. Unpublished MForSc thesis, University of Canterbury, Christchurch, New Zealand. 153 p.
- Dehlin H, Peltzer DA, Allison VJ, Yeates GW, Nilsson M-C, Wardle DA 2008. Tree seedling performance and below-ground properties in stands of invasive and native tree species. *New Zealand Journal of Ecology* 32: 67–79.
- Hermann RK, Lavender DP 1990. *Pseudotsuga menziesii* (Mirb.) Franco Douglas fir. In: Burns RM, Honkala BH eds *Silvics of North America. Volume 1. Conifers. Agriculture Handbook 654*. USDA Forest Service, Washington, DC. Pp. 527–540.

- Hunter GG, Douglas MH 1984. Spread of exotic conifers on South Island rangelands. *New Zealand Journal of Forestry* 29: 78–96.
- Kneeshaw DD, Kobe RK, Coates KD, Messier C 2006. Sapling size influences shade tolerance ranking among southern boreal tree species. *Journal of Ecology* 94: 471–480.
- Ledgard NJ 1988. The spread of introduced trees in New Zealand's rangelands — South Island high country experience. Review – Tussock Grasslands and Mountain Lands Institute 44: 1–7.
- Ledgard N 2001. The spread of lodgepole pine (*Pinus contorta*, Dougl.) in New Zealand. *Forest Ecology and Management* 141: 43–57.
- Ledgard N 2002. The spread of Douglas-fir into native forests. *New Zealand Journal of Forestry* 47(2): 36–38.
- Lusk CH 2004. Leaf area and growth of juvenile temperate evergreens in low light: species of contrasting shade tolerance change rank during ontogeny. *Functional Ecology* 18: 820–828.
- Lusk CH, Falster DS, Jara-Vergara CK, Jimenez-Castillo M, Saldaña-Mendoza A 2008. Ontogenetic variation in light requirements of juvenile rainforest evergreens. *Functional Ecology* 22: 454–459.
- Richardson DM, Rundel PW 1998. Ecology and biogeography of *Pinus*: an introduction. In: Richardson D Med. Ecology and biogeography of *Pinus*. Cambridge University Press. Pp. 3–46.
- Richardson DM, Williams PA, Hobbs RJ 1994. Pine invasions in the Southern Hemisphere: determinants of spread and invadability. *Journal of Biogeography* 21: 511–527.
- Ruscoe WA, Elkinton JS, Choquenot D, Allen RB 2005. Predation of beech seed by mice: effects of numerical and functional responses. *Journal of Animal Ecology* 74: 1005–1019.
- Szaniawski RK, Wierzbicki B 1978. Net photosynthetic rate of some coniferous species at diffuse high irradiance. *Photosynthetica* 12: 412–417.
- Vander Wall SB 1994. Removal of wind-dispersed pine seeds by ground-foraging vertebrates. *Oikos* 69: 125–132.
- Wardle P 1991. *Vegetation of New Zealand*. Cambridge University Press. 672 p.

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