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RESEARCH

Effects of neighbouring vegetation on planted indigenous tree establishment in modified environments: a New Zealand case study

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Abstract

Large-scale tree planting with indigenous trees is one approach to combatting climate change and environmental degradation. However, a significant challenge with establishing planted indigenous forests at scale, particularly in New Zealand, is that our knowledge and capacity to achieve this in highly modified environments, covered by invasive species, is relatively poor. The purpose of our study was to quantify the survival and growth of five indigenous tree species (three gymnosperms, two angiosperms) planted either on their own (weed-free) or in association with an indigenous (*Leptospermum scoparium* J.R. Forst) or exotic (*Cytisus scoparius* (L.) Link) shrub species. We monitored survival and growth following planting for 2.5 years. Results showed that survival for the gymnosperms was >90% for all treatments. In contrast, survival of the two angiosperms was poor, and, in general, not significantly related to the presence or absence of neighbouring vegetation. The response to vegetation management for tree height was similar across all species: weed-free treatment>*L. scoparium* treatment>*C. scoparius* treatment. Diameter growth was also highest for all tree species in the weed-free treatment, compared to the two other vegetation management treatments, but the extent of the increase varied by tree species. We found no direct evidence for neighbouring vegetation facilitating early survival and growth of the five indigenous tree species tested at our study site. However, the outcomes require testing at scale and across environments to underpin future forest restoration efforts.

Keywords Vegetation management · Inter-specific competition · Native afforestation · *Nothofagus* · Podocarpaceae · Survival · Growth

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Introduction

Large-scale tree planting is one approach to combatting climate change and environmental degradation that is being advocated for and implemented globally (Bastin et al. 2019; Besseau et al. 2018; Science Task Force for the UN Decade on Ecosystem Restoration 2021). The purpose of this afforestation drive is to increase carbon sequestration and address a suite of environmental challenges such as habitat and species loss, soil erosion and declining water quality (Lewis et al. 2019; Bloomberg 2023; Case et al. 2023; Climate Change Commisssion 2021; Ministry for the Environment 2024). Massive deforestation has occurred in New Zealand over the last 500 years, first through Māori and then European colonisation, effectively reducing the area of forested land from 82 to 23% of the land surface area (Ewers et al. 2006), a fraction of the original forested state. In parallel with many other countries, the New Zealand government is committed to addressing the impacts of human-induced deforestation on environmental quality and climate change by incentivising afforestation of degraded land with both indigenous and exotic trees (Suryaningrum et al. 2022; Ministry for the Environment 2024). However, there are significant challenges with afforestation with indigenous species, especially at scales exceeding 5 hectares, not least due to the high establishment costs associated with nursery stock production and planting (Forbes 2022). Further, while natural regeneration may be possible (as a low-cost option) in some areas, much of the land suitable for indigenous afforestation is too far from natural seed sources and/or too degraded to support forest regeneration (e.g. Cieraad et al. 2015) leaving active planting as the only viable option to achieve large-scale landscape-level change with trees and forests (Forbes et al. 2020; Kremer and Bauhus 2020).

One significant challenge with establishing planted indigenous forests at scale, particularly in New Zealand, is that our knowledge and capacity to achieve this in highly modified environments is relatively poor (Jalonen et al. 2023, Marshall et al. 2023). For example, in New Zealand, it is several decades since there was any focus on fundamental and applied research to develop establishment practices (including seed sourcing, propagation, seedling quality, site-species matching, planting and tending techniques) for indigenous tree species. Beyond fundamental studies on species regeneration and function within natural ecosystems (Bieleski 1959a, b; Kaplick et al. 2018; Lusk 2004, 2019; Lusk et al. 2009; Stephens et al. 1999; Verkaik and Braakhekke 2007; Warrington et al. 1989) there are few published applied studies on factors affecting planted tree survival and growth (Burrows et al. 2015; Davis et al. 2013; Ebbett and Ogden 1998; Forbes et al. 2016; Hawkins et al. 1991; Laughlin and Clarkson 2018) in unnaturally disturbed and highly modified sites. The general lack of specific knowledge on how to propagate, plant, establish and manage indigenous tree species planted at scale into a range of highly modified environments results frequently in establishment failures and overly expensive planting operations, regardless of planted forest purpose, function and/or species mix used.

While there are a wide range of indigenous tree species which could be used in afforestation programmes in New Zealand, Podocarpaceae species such as *Podocarpus totara* G. Benn ex D. Don, *Dacrydium cupressinum* Lamb., *Dacrycarpus dacrydioides* (A. Rich.) de Laub, Araucariaceae species such as *Agathis australis* (D. Don) Lindl. and Nothofagaceae species are often popular choices for planting for a variety of social, cultural and economic reasons. Known to be tree species with relatively slow-juvenile growth (Beveridge et al. 1987), these species have been reported to both benefit from (facilitation) and be vulnerable

to (competition) the presence of neighbouring vegetation such as grass, ferns, tree-ferns, and shrub species (indigenous or exotic) for several years after planting (Bergin and Kimberley 2003; Beveridge et al. 1985; Burrows et al. 2015). For example, cutting lanes into 'nurse crops' of indigenous shrubs (e.g. *Leptospermum scoparium* J.R. Forst (mānuka) and/or exotic weeds (e.g. *Ulex europaeus* L. (gorse), and planting seedlings of late-successional tree species within these lanes, has been trialled to establish planted indigenous forest, but the method has been reported to have mixed success (Steward and Firm 2020). These somewhat conflicting positions make it difficult to prescribe suitable recommendations for managing neighbouring vegetation, when planting indigenous trees at a forest-scale in regions likely to be inundated with exotic grasses, herbs and/or shrubs.

Globally, numerous studies have shown that (competitive) neighbouring vegetation is one of the most important factors influencing tree growth and survival for economically important planted tree species such as *Pinus radiata* D. Don (Richardson et al. 2006, 2019; Wagner et al. 2006; Rolando and Little 2009). Decades of research in New Zealand have led to a clear understanding of the response of *P. radiata* to resource competition from associated herbaceous and woody vegetation and detailed evidence on the area and duration of competition control needed to optimise early survival and growth (Mason et al. 1997; Richardson 1993; Richardson et al. 2019). Along with research to develop efficient methods of vegetation control, this knowledge has supported the development of cost-effective, site-specific vegetation management regimes for sites occupied by New Zealand's many highly invasive, fast growing and difficult-to-control plant species (Williams and Timmins 2002; Saunders et al. 2017; Hulme 2020). Compared to *P. radiata*, planted indigenous tree species with their slower juvenile growth rates are probably more vulnerable to competition from invasive weeds, yet little effort has been invested in research to quantify their responses to the presence of neighbouring vegetation (native or exotic) during establishment. This fundamental knowledge, coupled with the development of suitable control treatments to manage interspecific plant interactions, is needed to optimise vegetation management in terms of the area and duration needed to achieve establishment goals.

Forest vegetation management often involves removing or suppressing vegetation that otherwise outcompetes planted tree seedlings for site resources (water, light, nutrients) (Walstad and Kuch 1987), however, not all neighbouring vegetation interactions are of a competitive nature. For example, plant facilitation occurs via moderation of biotic stressors, e.g. fungal disease (Simard and Vyse 2006), and abiotic stressors such as high air temperature or frost (Gómez-Aparicio et al. 2004), leading to an increase in survivorship and/or growth of at least one of the interacting plants (Bertness and Callaway 1994; Lin et al. 2013; Gómez-Aparicio 2009). Therefore, understanding the interplay between competition and facilitation has enormous ecological and practical value when establishing new forests. There is already a general perception that many of the New Zealand indigenous tree species, notably those from the Podocarpaceae family, require a facilitating 'nurse crop or canopy' during the establishment phase. Thus, to optimise vegetation management regimes on highly modified and weedy sites it is important to quantify whether invasive weeds, such as *Cytisus scoparius* Link (broom) or *U. europaeus* (gorse), could serve as facilitators rather than being competitors (Atkinson et al. 2022; Burrows et al. 2015). Quantification of both facilitation and competition as well as any trade-offs in terms of tree survival and growth from different vegetation management regimes will be crucial for successful afforestation efforts.

The purpose of our study was to provide some preliminary indications on the factors influencing planted indigenous tree survival and growth on highly modified sites. The knowledge gained can be used to support future trials aimed at providing recommendations for large-scale tree planting programmes across New Zealand. Specifically, our objective was to quantify the survival and growth of five indigenous tree species growing either on their own (weed-free) or in association with an indigenous (*L. scoparium*) or exotic (*C. scoparius*) shrub species. We set out to test the hypothesis that for all five tree species the presence of neighbouring vegetation had no effect on early tree survival and growth. We also predicted that tree species would vary in their survival and growth response to the presence of neighbouring vegetation.

Materials and methods

Study area and experimental design

The trial was established in the Scion research area, Rotorua New Zealand (176.269° E, 38.157° S), in spring (October) of 2020. The region has a mild temperate climate, with an expected mean annual rainfall of 1353 mm, evenly distributed throughout the year and a mean annual temperature of 12.2 °C. Soil at the site is a well-drained, deep, moderately fertile pumice soil (yellow-brown Ngakuru loam) with a high water holding capacity. Previous characterisation of the site (Richardson et al. 1996) indicated that the soil was moderately acidic, and with the possible exception of magnesium, which was rated as "very low", there were no significant nutrient limitations identified. Episodic pest control meant that densities of browsing animals were expected to be low.

Prior to planting the trial, the site was lightly prepared with a tractor blade to remove vegetation, break-up the surface, level the site and improve uniformity. There was no vegetation on the site at the start of the trial. The trial was a factorial design laid out as a randomised complete block with three blocks. Treatments comprised all combinations of five indigenous tree species and three vegetation management treatments (Table 1), i.e. a total of 15 plots per block (plot size: 5 m × 5 m) and a grand total of 45 plots. The tree species included: *P. totara*, *D. cupressinum*, *D. dacrydioides*, *Nothofagus solandri* (Hook.f.) Oerst and *Knightia excelsa* R.Br. The selected tree species were chosen based on proportional use in the NZ Government's One Billion Trees programme, established in 2018 (Te Uru Rākau 2018), and because they are known to be popular for large-scale restoration programmes. The three vegetation management treatments were designed to establish three levels of com-

Table 1 Description of the tree species and vegetation management treatments used in the two-factor randomised complete block design trial with three replication blocks, in which the response of indigenous trees to manipulation of neighbouring vegetation was evaluated

Treatment factors	
Tree species	Vegetation Management
Podocarpus totara G.Benn. ex D.Don (totara)	Weed free
Dacrydium cupressinum Lamb. (rimu)	Mānuka (*L. scoparium* J.R. Frost)
Dacrycarpus dacrydioides (A.Rich.) de Laub (kahikatea)	Broom (*C. scoparius* Link)
Nothofagus solandri (Hook.f.) Oerst. (black beech)	
Knightia excelsa R.Br. (rewarewa)	

petition or facilitation, i.e. ranging from no vegetation (weed-free), an indigenous neighbour (Mānuka) at medium density and highly invasive exotic neighbour (Broom) at high density.

Each plot consisted of 5 × 5 trees of a single tree species, planted at 1 m × 1 m spacing. Measurements were restricted to the inner 3 × 3 trees to minimise edge effects from adjacent plots, as these were established without a buffer zone between them. The *L. scoparium* seedlings were planted at 1 m spacing between the tree rows (6 × 6 plants) whilst the *C. scoparius* seedlings were planted at 0.5 m spacing within and in-between each planted row (11 × 11 plants) (Figure S1). The rationale for planting *L. scoparium* at 1 × 1 m was that this represents the highest planted density likely to be used in practice. The higher density of *C. scoparius* reflects the invasive nature of this species and in many situations, it will emerge from seed at much higher densities (Paynter et al. 2003).

The procedure for establishment and maintenance of each vegetation management treatment follows:

- Weed free: Plots were maintained close to weed free by regular removal of all emerging vegetation, either manually (first 12 months) or using a selective herbicide (Agpro Haloxyfop™ 100, AGPRO NZ Ltd, Auckland, at 0.6% active ingredient per litre) applied with a SOLO® back-pack sprayer (Solo Kleinmotoren GmbH, Sindelfingen, Germany) whilst protecting the trees with an inverted plastic cone (12–24 months). In the third year (> 24 months), vegetation was manually removed from a 0.75 m diameter circular area from around the planted tree and the remaining plot-area was sprayed, as above. No damage to the planted seedlings was noted from the application of herbicide.
- Mānuka (low-density indigenous neighbour): *L. scoparium* seedlings were planted at 1.0 m spacing (Figure S1) at the same time as trees were planted. The only additional vegetation management was continuous removal of natural regeneration of *C. scoparius* that emerged in the plots.
- Broom (high-density exotic neighbour): *C. scoparius* seedlings were planted at 0.5 m spacing (Figure S1) at the same time as trees. No further vegetation management was carried out.

Indigenous trees and shrubs were sourced in-house (Scion nursery) or from regional nurseries where they were grown in plastic polyurethane bags or plastic pots with volume between 0.5 and 1 L. The *C. scoparius* seedlings were grown from seed collected from the Scion experimental forest area and raised in containers at the Scion Nursery; these seedlings were approximately three months old at the time of trial establishment. Initial sizes of the five tested species are shown in supplementary table S1.

The trial was planted in October 2020. Air and soil temperature, rainfall and soil moisture (0, 15 and 30 cm) for the duration of the study were measured with a Campbell Scientific weather station situated approximately 50 m south of the trial area. These data have been summarised for the first two seasons after planting (Figure S2).

Data collection

The different vegetation management treatments act on tree growth through alterations of the micro-environment around each tree, modulating the availability of different resources (light, water, nutrients). However, we did not monitor the microclimate or resource avail-

ability changes within each treatment, so our study focused on comparing tree survival and growth across the three treatments.

Measurements of planted trees were made immediately after planting and were repeated six more times (at 4, 9, 12, 16, 23 and 31 months) after trial establishment. Measurements on the central nine indigenous trees in each plot included: height (cm; with a tape measure or height pole), ground-line diameter (mm; digital caliper), survival (dead/alive), and competition index (CI). Competition indices are useful to assess the intensity of neighbourhood crowding around a focal plant/tree (Richardson et al. 1999). For this trial, the CI for each measurement tree was based on the number of 45° segments of an inverted 90° cone, with its apex at 50% tree height, that were occupied by neighbouring vegetation (Figure S3). Each segment that was occupied was given a score of 1 and the total scores were summed to give the overall CI i.e. if all segments were occupied the maximum score would be 8 representing a high degree of shading or neighbourhood crowding.

Measurements of the height (cm) of the planted *C. scoparius* and *L. scoparium* shrubs were made at the same time as the tree assessments with the last measurement occurring 16 months after trial establishment. At each assessment nine shrubs within the measured plot were assessed.

Data analyses

All analyses were performed in R version 4.3.1 (R Core Team, 2023).

Tree mortality

Final mortality counts at 2.5 years (31 months) after planting were modelled using a logistic regression performed using the *glm* function, with mortality as the response variable and tree species (5 levels) and vegetation treatment (3 levels), and their interaction, as categorical fixed effects. The inclusion of an interaction term between species and treatment was tested using an analysis of deviance with Chi-squared test. We also assessed differences between treatments within species by conducting single-species sequential analyses of deviance with Chi-squared test, with treatment as a categorical fixed effect and initial tree size (height or groundline diameter) as a continuous fixed effect.

Tree growth

Relative growth over the studied period of 2.5 years (or 31 months) was modelled for tree height, tree groundline diameter and plot basal area. Plot basal area was calculated using the sum of stem basal area (based on the groundline diameter measurement) of the 9 internal trees of each plot. We excluded *K. excelsa* from these analyses, as this species experienced high mortality and very few individuals survived past the second summer.

Growth for the three measures was modelled using a mixed model linear regression. Estimates were obtained using the *lmer* function from the *lme4* package in R with the REML algorithm (Bates et al. 2015), and 95% confidence intervals around estimates were obtained by parametric bootstrap using the *bootMer* function from the lme4 package. Relative growth rate (ratio of final value over initial value on a log scale) was used as the response variable, and tree species and treatment with their interactions were included as categorical

fixed effects. Block was included as a random effect for the height and groundline diameter models. As basal area is at the plot level, there is only one replicate per block for this measurement and therefore blocks effects had to be ignored, and the *lm* function was used to obtain estimates.

The significance of species-by-treatment interaction terms were tested using type III Wald F-tests with the Kenward-Roger degrees of freedom for models involving random effects for the groundline diameter and height models, and standard F-test for the basal area fixed effects model. Tukey's Multiple Comparison test was performed using the *glht* function from the *multcomp* package (Hothorn et al. 2008) to determine differences between treatments.

Results

Mortality

Mortality of 26%, 41% and 54% occurred in *N. solandri* plots in the first 4 months after planting in the weed-free, Mānuka and Broom treatments, respectively, after which minimal additional mortality was observed (Fig. 1). In contrast, mortality for *K. excelsa* was negligible for the first year after planting across all treatments, followed by almost all trees dying over the second summer (between November 2021 and March 2022, Fig. 1). Mortality across the other three species and vegetation treatments was low during the 2.5 years of the experiment, with more than 90% of trees surviving for the Podocarpaceae species. We did not detect any significant overall effect of treatment on mortality after accounting for species, but the interaction between species and treatment was significant (Table 2). As most of the effects of treatment were within species, single-species analyses were also conducted, with treatment as the only factor. As power to detect the effect of continuous variables such as initial height on mortality is extremely low for species experiencing very low or very high mortality, initial size variables were only tested as predictors in the *N. solandri* model. None of the single species analyses of deviance detected a significant effect of the vegetation treatments on mortality at month 31. However, the *N. solandri* model indicated a slightly higher mortality in *C. scoparius* plots compared to weed-free plots (Wald test, $z = 1.671$, $p = 0.095$) and a weak negative effect of initial tree height (estimate = -0.005, Wald test, z=-1.704, $p = 0.089$). The latter result suggests that initially taller trees may be more likely to survive during early establishment.

Tree growth

Tree growth varied widely across species over the experimental period (Fig. 2). The response to vegetation management treatment for tree height growth was similar across species: height growth was the greatest in the weed-free treatment, followed by the *L. scoparium* (Mānuka) treatment, and then the *C. scoparius* (Broom) treatment. (Tables 3 and 4; Figs. 2 and 3). The *N. solandri* was by far the fastest growing tree species, with individuals reaching over 3 m in the treatments without competition (weed-free) within 2.5 years after planting (juvenile current annual increment of more than 1 m/yr). This species was followed by *D. dacrydioides*, *D. cupressinum* and *P. totara*, which were on average 45%,

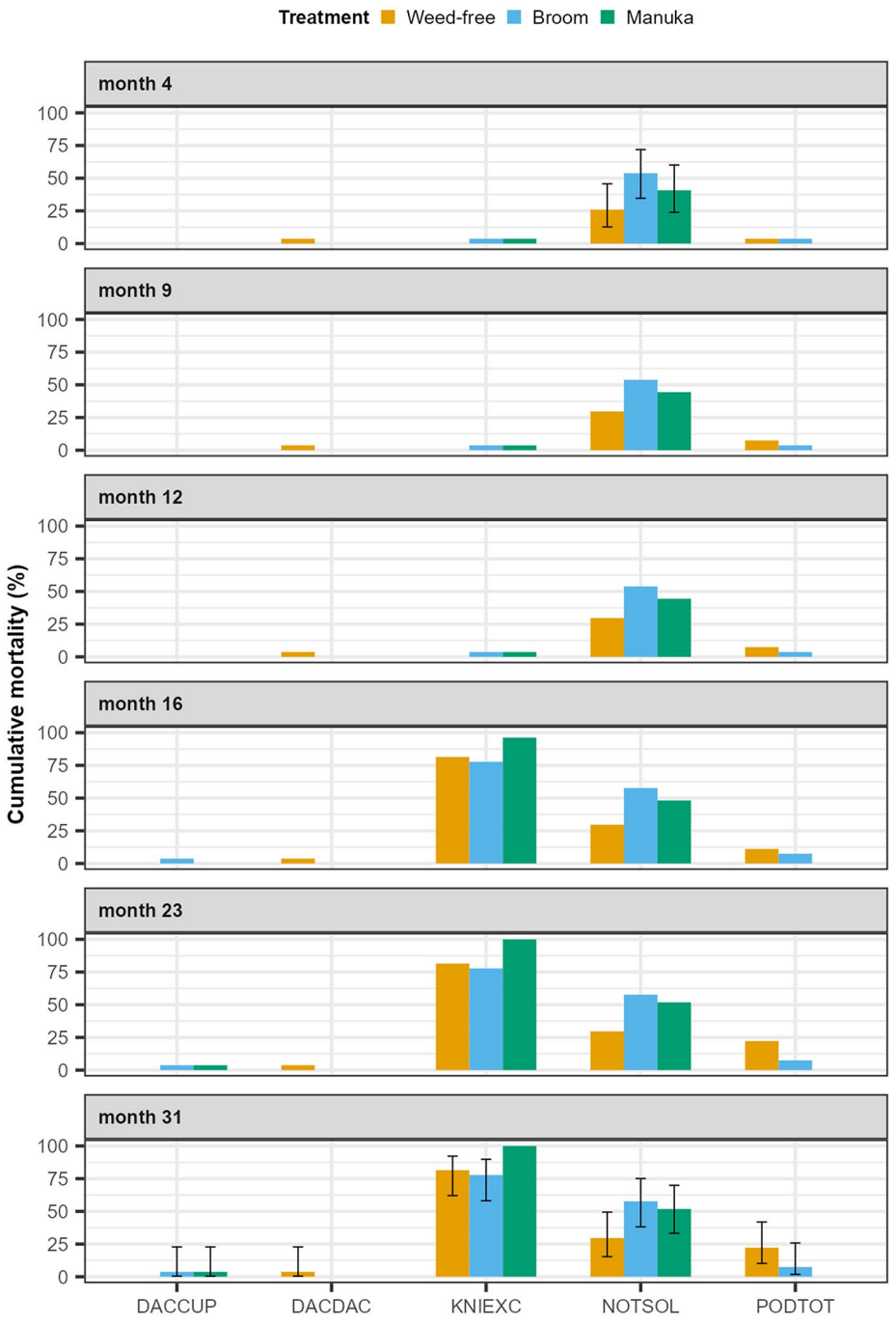

Fig. 1 Cumulative mortality of each indigenous tree species in each treatment over time, with 95% confidence intervals from species-specific generalised linear model results for the last assessment (month 31). Confidence intervals were not calculated or displayed for species-treatment categories where all trees survived or all trees died. Species codes: DACCUP=*Dacrydium cupressinum*, DACDA=*Dacrycarpus dacrydioides*,, KNIEXC=*Knightia excelsa*, NOTSOL=*Nothofagus solandri*, PODTOT=*Podocarpus totara*

Table 2 ANOVA table of results from the sequential analysis of deviance with Chi-squared test for a binomial generalised linear mixed model relating tree mortality to species, treatment, and their interaction

Factor	Df	Deviance	Resid. Df	Resid. Dev	Pr(>Chi)
Intercept			401	483.09	
Species	4	227.11	397	255.97	5.52E-48
Vegetation treatment	2	0.85	395	255.13	0.66
Species: vegetation treatment	8	26.49	387	228.64	8.66E-04

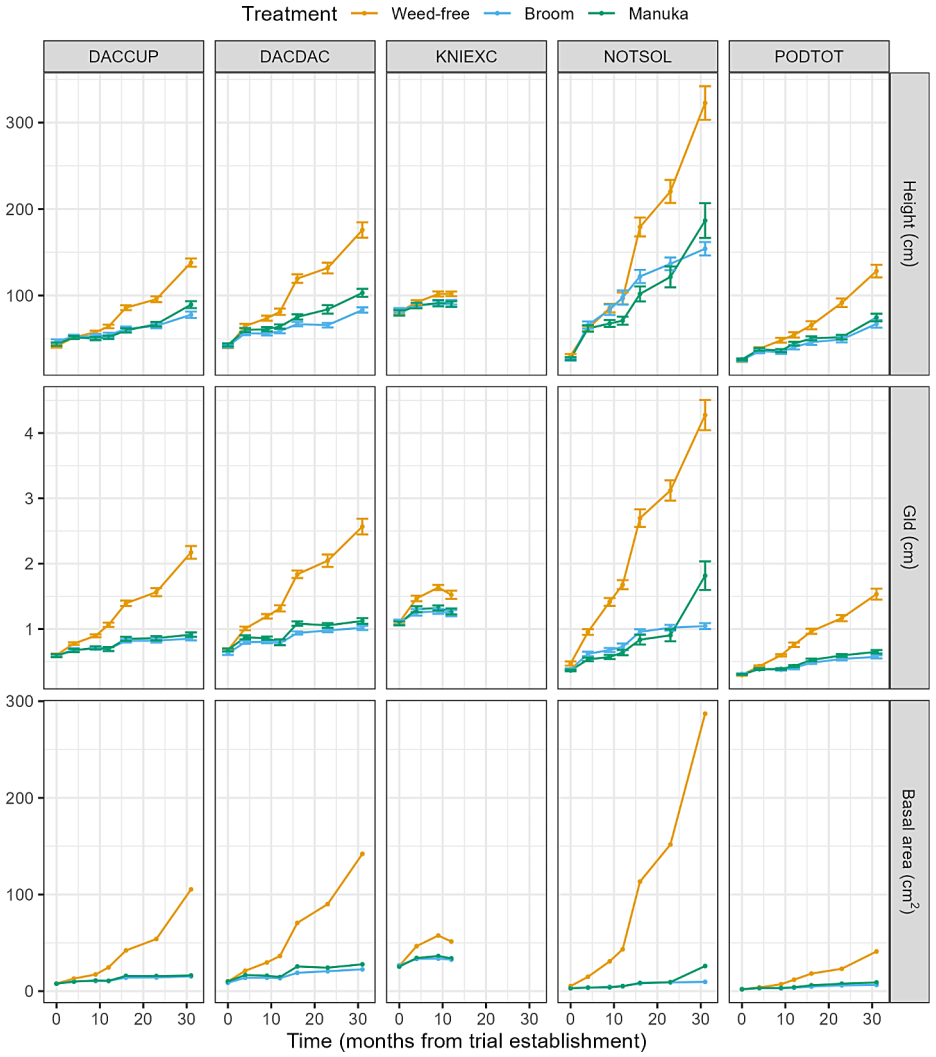

Fig. 2 Growth-curves based on averaged (height and ground-line diameter (Gld)) or summed (basal area) values across blocks and plots for each species and treatment, with standard errors. Formal analyses were conducted on final measurements only. Species codes: DACCUP=*Dacrydium cupressinum*, DACDAC=*Dacrycarpus dacrydioides*, KNIEXC=*Knightia excelsa*, NOTSOL=*Nothofagus solandri*, PODTOT=*Podocarpus totara*

Table 3 ANOVA table of results from final tree size models

Height:

Type III Wald F tests with Kenward-Roger df

	F	Df	Df.res	Pr(>F)
(Intercept)	1052.72	1	2.10	7.18E-04
Species	127.92	3	252.52	2.10E-50
Treatment	125.31	2	253.13	1.49E-38
Species: treatment	1.09	6	252.67	0.37

Groundline diameter:

Type III Wald F tests with Kenward-Roger df

	F	Df	Df.res	Pr(>F)
(Intercept)	1090.71	1	12.96	6.76E-14
Species	66.33	3	254.10	1.04E-31
Treatment	102.22	2	255.07	2.50E-33
Species: treatment	5.44	6	254.38	2.58E-05

Basal area:

Type I F-test

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Species	3	13.71	4.57	26.73	7.97E-08
Treatment	2	28.29	14.14	82.74	1.71E-11
Species: treatment	6	0.57	0.09	0.55	0.76
Residuals	24	4.10	0.17		

57% and 60% shorter than *N. solandri* at the end of the studied period. In comparison to the weed-free treatment, the Broom treatment showed a height growth reduction of 52% in *N. solandri*, 47% in *P. totara*, 52% in *D. dacrydioides* and 44% in *D. cupressinum* (Fig. 2).

Diameter growth was highest for all species in the weed-free treatment, compared to the two other vegetation management treatments, but the extent of the increase varied by tree species (Tables 3 and 4; Figs. 2 and 3). We did not detect any difference in diameter growth between trees in the Mānuka and Broom treatments for all species expect *N. solandri*, which showed greater diameter growth in the Mānuka treatment. It is possible that we did not detect a difference of the same nature in other species because of their slower growth rate and restricted trial duration (Fig. 2). Mean basal area growth across all species was also higher in the weed-free treatment. As for groundline diameter results, we observed a slightly higher growth in the Mānuka plots than in Broom plots, but the difference was not significant. In comparison to the weed-free treatment, the Broom treatment showed a diameter growth reduction of 76% in *N. solandri*, 63% in *P. totara*, 60% in *D. dacrydioides* and 61% in *D. cupressinum* (Fig. 2).

Unfortunately, no assessments of tree physiology (gas exchange, water status) or the micro-environment (light availability, air and/or soil temperature, soil water content) were made in this trial. However, growth assessments of the planted *L. scoparium* and *C. scoparius* shrubs were made for the first 16 months of the trial and the level of competition surrounding each tree was assessed throughout the trial, scored as a competition index. The rapid growth of the *C. scoparius*, in relation to the planted trees, meant that competition indices for the trees in the Broom treatments were high throughout the trial, and similarly

Table 4 Model description and Tukey contrasts between treatments for height, diameter and basal area analyses. None = weed-free treatment

Height					
Final model: log(height_final/height_initial) ~ species + treatment + (1|block)					
All species	Contrast	Estimate	Std. Error	z value	Pr(>|z|)
	Broom - None == 0	-0.71	0.045	-15.84	< 0.01
	Mānuka - None == 0	-0.56	0.046	-12.29	< 0.01
	Mānuka - Broom == 0	0.15	0.046	3.37	< 0.01
Groundline diameter					
Final model: log(gld_final/gld_initial) ~ species + treatment + species: treatment + (1|block)					
	Contrast	Estimate	Std. Error	z value	Pr(>|z|)
N. solandri	Broom - None == 0	-1.25	0.09	14.20	< 0.01
	Mānuka - None == 0	-0.60	0.09	6.33	< 0.01
	Mānuka - Broom == 0	0.65	0.11	6.17	< 0.01
D. dacrydioides	Broom - None == 0	-0.82	0.06	12.96	< 0.01
	Mānuka - None == 0	-0.82	0.06	12.93	< 0.01
	Mānuka - Broom == 0	1.8E-03	6.3E-02	2.9E-02	1
D. cupressinum	Broom - None == 0	-0.94	0.06	14.88	< 0.01
	Mānuka - None == 0	-0.87	0.06	13.40	< 0.01
	Mānuka - Broom == 0	6.7E-02	6.5E-02	1.03	1
P. totara	Broom - None == 0	-1.03	0.07	14.87	< 0.01
	Mānuka - None == 0	-0.88	0.07	13.01	< 0.01
	Mānuka - Broom == 0	0.14	0.07	2.20	0.53
Basal area					
Final model: log(ba_final/ba_initial) ~ species + treatment					
All species	Contrast	Estimate	Std. Error	t value	Pr(>|z|)
	Broom - None == 0	-2.01	0.161	-12.49	< 0.01
	Mānuka - None == 0	-1.71	0.161	-10.65	< 0.01
	Mānuka - Broom == 0	0.30	0.161	1.84	0.17

so for the Mānuka treatment (Fig. 4A & B). Importantly, not captured by the competition score is the density of the competing vegetation and developing crown cover which was much higher for *C. scoparius* in the Broom treatment than for *L. scoparium* in the Mānuka treatment (Fig. 5). The difference in competition levels between the Mānuka and Broom treatments was only slightly reflected in tree growth patterns, with marginally faster growth observed in the Mānuka treatment compared to the Broom treatment (Fig. 3).

We extended the height and ground-line diameter models (summarised in Table 4) by adding competition index score (CI) as an average value across all measurements, as a fixed effect. We found that with the addition of CI as an explanatory variable the improvement in height and diameter models was barely discernible (height: ANOVA $F = 5.18$, $p = 0.02$; diameter: $F = 4.89$, $p = 0.03$); the R^2 increased from 0.736 to 0.741 for height and from 0.848 to 0.851 for ground-line diameter. However, when considered alone, treatment explained growth better than competition index (R^2 of 0.736 vs. 0.731 for height, and 0.848 vs. 0.821 for diameter).

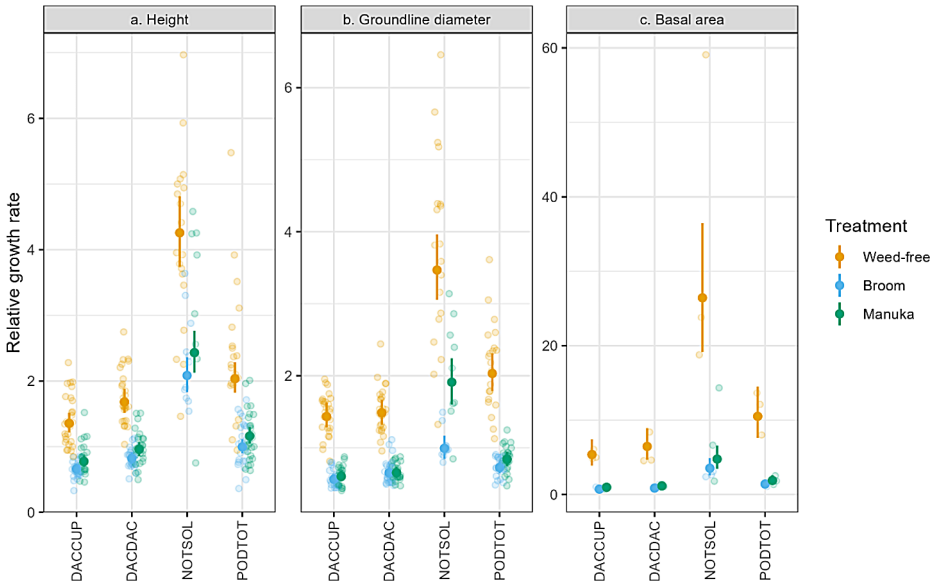

Fig. 3 Data and model predictions of relative growth rate for height (in $cm.cm^{-1}.year^{-1}$), diameter (in $cm.cm^{-1}.year^{-1}$), and plot-level basal area (in $cm^2.cm^{-2}.year^{-1}$). Light-coloured points show original observations with a small jitter to help visualisation, and coloured points and error bars are geometric mean estimates and their 95% confidence intervals from linear models. Species codes: DACCUP=*Dacrydium cupressinum*, DACDAC=*Dacrycarpus dacrydioides*, NOTSOL=*Nothofagus solandri*, PODTOT=*Podocarpus totara*

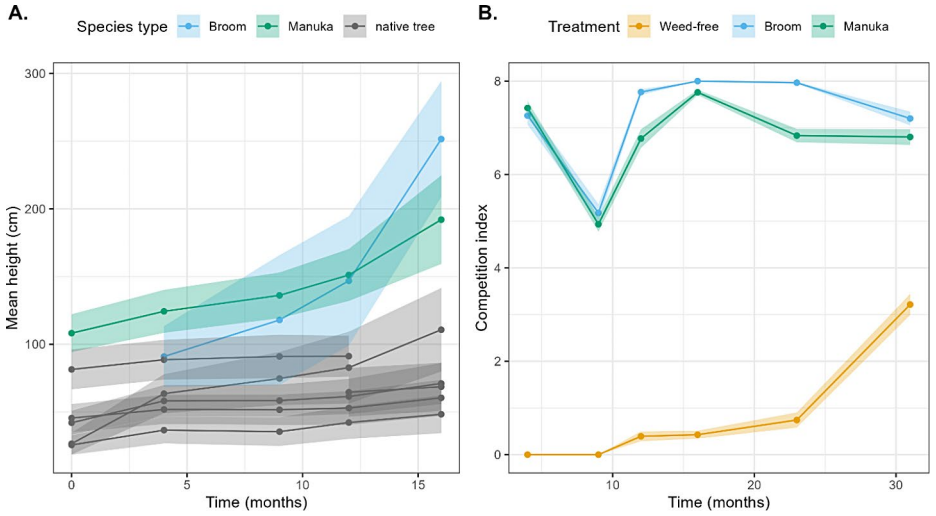

Fig. 4 (**A**) Height growth of the shrub species *L. scoparium* and *C. scoparius* in the Mānuka and Broom treatment plots for the first 16 months of the experiment shown in relation to the indigenous tree height growth averaged by species across treatments. (**B**) Competition index (CI) based on vegetation crowding above 50% tree height for each treatment. Solid lines represent the mean across all blocks, species, and trees (ribbons represent standard error of the mean)

Fig. 5 Weed-free treatment in foreground with (**A**) low density *L. scoparium* (Mānuka) in background and (**B**) high density *C. scoparius* (Broom) in background

Discussion

Except for the high mortality of the *N. solandri* and *K. excelsa* seedlings, survival of the indigenous tree species across the trial was good and largely unaffected by the vegetation management treatments. Good survival of the conifers (*P. totara*, *D. dacrydioides* and *D. cupressinum*) across competition treatments most likely reflects their tolerance of a range of light conditions in the juvenile stage as well as their tolerance of climatic stressors, e.g. frost and drought (Ebbett and Ogden 1998; Lusk et al. 2015; Richardson et al. 2013; Bannister 2007).

Our study area is located at the edge of the natural distribution of *N. solandri* in New Zealand and there is a lack of quantitative data on survival and growth of this species' when planted, which is limiting possibilities for making direct comparisons. However, the available evidence for a closely related species, *Nothofagus cliffortioides* (Hook. f.) Oerst., suggests that poor survival of seedlings planted outside of species' natural boundaries and/or in anthropogenically modified environments is not uncommon (Davis 2004, van Galen et al. 2023). This observation seems in contrast to *N. solandri* being described as more tolerant to extreme conditions, such as low rainfall, and soil fertility, than most New Zealand indigenous tree species (Leathwick 1998; Wardle 1970). Being obligately ectomycorrhizal, a lack of symbiotic fungi outside of forest boundaries is often suggested as a barrier to the establishment of *Nothofagus* spp. or as a cause of early mortality (Dickie et al. 2012). However, a mycorrhizal inoculum is not always essential for seedling establishment (van Galen et al. 2023), raising questions as to the drivers of frequent establishment failure. Davis et al. (2004) noted that survival of planted *N. cliffortioides* was strongly affected by removal of competition and the size of seedlings at planting. They found seedlings with root collar diameters > 5 mm at the time of planting survived better than those with smaller diameters. While we noted no relationship between mortality of the *N. solandri* and initial root collar diameter in this study, initial height was related to mortality, with taller seedlings more likely to survive, indicating seedling size played a role in survival. The *N. solandri* seedlings used in our study were in general small, with 74% of seedlings having an initial diameter of less than 4.5 mm and average height was < 30 cm. The *Nothofagus* species, e.g. *N. cliffortioides*, are known to be sensitive to competition for key resources and easily outcompeted by other

neighbouring vegetation (Davis 2004, van Galen et al. 2023; Wardle 1970). Our results showed a considerably higher mortality (28%) of the *N. solandri* seedlings exposed to competition with *C. scoparius*, and marginally higher mortality (15%) where *L. scoparium* was present, indicating competition may have been a factor driving mortality for *N. solandri*. A similar outcome was recorded by Davis et al. (2004) where removal of competition at a mid-elevation grassland site increased the survival of planted *N. cliffortioides* seedlings by 16%. In a meta-analysis of factors affecting the success of restoration with *Nothofagus* spp., van Galen et al. (2021) found shelter and controlling weeds as factors consistently associated with positive restoration outcomes. This finding was somewhat corroborated by a study conducted by Kremer et al. (2021) on shade-intolerant and semi-tolerant *Nothofagus* species established in a range of canopy 'gap' treatments in south-central Chile. Better seedling performance was recorded in treatments with partial rather than full canopy removal, regardless of the species tolerance for shade. These authors controlled neighbouring vegetation throughout their study and noted that the effects of herbs and shrubs on the performance of planted seedlings remained unclear.

Delayed severe mortality of the *Knightia excelsa* seedlings 18 months after planting was a surprise and unrelated to any effects of the presence or absence of neighbourhood vegetation. The *K. excelsa* seedlings were a poor quality to begin with, being oversized and root-bound (height: mean = 81 cm ± 15 cm; in 1 L pots) at the start of the trial. However, if seedling quality was the primary cause of mortality, we would have expected this to manifest earlier in the trial and perhaps after the first summer. It is possible that the severe mortality recorded over the summer of 2021/22 may be related to freezing injury occurring to these seedlings over winter 2021, when air temperatures dropped to below zero on at least three occasions, followed by a very hot and dry January in summer 2022 (Figure S2). Of the five tree species planted in October 2020, *K. excelsa* has the most restricted temperature range, occurring mainly on the New Zealand North Island or north of 41.20° S (Sakai and Wardle 1978). While the trial location was well within the geographic and climatic limits of this species the poor quality of the seedlings and exposure on the highly modified site may have contributed to their vulnerability to climatic extremes, subsequently resulting in high mortality. Lusk et al. (2015) note that the podocarps, *P. totara*, *D. cupressinum* and *D. dacrydioides* are more resistant to frost and drought than the juveniles of angiosperms, such as *K. excelsa*, a characteristic most likely related to their hydraulic architecture which renders them more resistant to freeze-thaw embolisms (Feild 2001; Russo et al. 2010). Further, Lusk et al. (2015) found all *K. excelsa* seedlings that were transplanted into canopy gaps with higher light intensities (>2 mol m^{-2} day^{-1}) failed to establish, suffering severe frost or solar radiation damage.

In terms of growth, all three conifers, *P. totara*, *D. cupressinum* and *D. dacrydioides*, and the angiosperm, *N. solandri*, responded positively to the removal of neighbouring vegetation. However, the magnitude of this response varied across species with a ranking as follows: *N. solandri* > *P. totara* > *D. dacrydioides* > *D. cupressinum*. In New Zealand, there are few similar studies directly examining the impact of manipulation of neighbouring vegetation on planted indigenous tree seedling growth on highly modified sites, especially over the last decade, making a direct comparison of these results with that of others difficult. However, we can interpret our results through studies of the ecophysiology of these species obtained mainly from assessments made on their regeneration patterns and response to

light levels in the natural habitat (e.g. Lusk et al. 2015) or pot experiments (e.g. Ebbett and Ogden 1998).

Removal of neighbouring vegetation more than doubled the growth of the *N. solandri* seedlings over the first 2.5 years of establishment. Davis et al. (2004) also found that reducing competition from grasses through application of herbicide (one pre-plant spray and one release spray operation two years after planting) more than doubled height of planted *N. cliffortioides* seedlings after five years. While we could find few comparative data directly quantifying planted juvenile *N. solandri*, or related species, growth rates in response to differing levels of light (or competition for other resources), it is widely acknowledged that the *Nothofagus* species are one of the most light demanding among major New Zealand forest canopy tree species (Sun and Sweet 1996; Wardle 1984). Thus, the growth response to management of neighbouring vegetation was not a surprising result overall. However, the magnitude of the response was somewhat unexpected with the surviving individuals where neighbouring vegetation was removed reaching an average height of 3.20 m (±0.85 m) and more than double the basal area of seedlings at 2.5 years compared to the treatments where *L. scoparium* or *C. scoparius* were present.

The three podocarps, *P. totara*, *D. dacrydiodes* and *D. cupressinum* responded similarly to the vegetation management treatments, with *D. dacrydiodes*, attaining the greatest size out of the three species when released from the presence of vegetation. As early as 1966, experiments in a natural forest demonstrated that the New Zealand podocarps increased their height growth when released from competition or neighbouring vegetation (Cameron 1966). Subsequent experiments also demonstrated that out of the podocarps *D. dacrydioides* showed the greatest increase in growth in response to elevated radiation, followed closely by *P. totara* and then *D. cupressinum* (Beveridge 1973; Ebbett and Ogden 1998). The general order of the relative growth response to the vegetation management treatments in the present study therefore largely reflects that found by other studies investigating the response of these Podocarpaceae species to increasing light levels, with growth rates within the upper end of the range previously reported (Bergin and Kimberley 2003; Ebbett and Ogden 1998; Lusk et al. 2015; Warrington et al. 1989; Bergin 2003).

Perhaps one of the most surprising outcomes from the study was the almost consistent and similar non-significant growth response to the level of competition from the indigenous and exotic shrubs, *L. scoparium* ("Mānuka treatment") *and C. scoparius* ("Broom treatment"). Our crude assessments of competition (shrub height and competition index; Fig. 4A, B) indicated very similar environments were created by these two shrub species. However, in-reality the stem density of the *C. scoparius* (two times that of *L. scoparium;* Figure S1), its faster growth rate (Fig. 4A) and its greater canopy cover meant that seedlings in the Broom treatment were most likely subjected to much higher levels of competition for resources than those in the Mānuka treatment, particularly after the first summer (Fig. 5). This result indicates either that both competition treatments induced levels of shading above a response threshold or that, most likely, the plant interaction outcomes were shaped also by competition for other limited resources (water and/or nutrients). Either way, the indications are that these shrub species did not facilitate growth but rather competed for resources with the planted seedlings at this site.

The trial's location within a research forest warrants consideration. A common recommendation for landscape restoration projects in New Zealand involves the management of pest animal populations to mitigate browsing impacts (Forbes et al. 2003). In the absence of

such pest control, dense surrounding vegetation has been shown to reduce browsing of palatable seedlings by either concealing the seedlings from pests (Stutz et al. 2015) or creating physical barriers to browsing (Kuiters and Slim 2003). This trial, however, was conducted in a research area with ongoing pest control, limiting the ability to assess the effects of browsing on weed-free plots compared to the other two vegetation management treatments. Addressing this limitation in future trials is recommended.

As noted previously, there are surprisingly few recent published studies that have been specifically designed to investigate factors, such as soil preparation and management of neighbouring vegetation, that affect early survival and growth of the indigenous New Zealand tree species when planted at scale on highly modified sites. Furthermore, there are few studies (e.g. Tulod et al. 2019) that have specifically investigated the area and duration of competition control required to maximise survival and optimise early growth of planted indigenous trees, for a range of establishment outcomes. We know little about even the herbicides that can safely be used at scale to achieve these goals without compromising seedling health. Good survival of planted trees will always be required for any endeavour to restore ecosystems and/or create a timber resource. High growth rates may not always be important, yet the sooner the trees can occupy the site and reach a stage at which they are 'free to grow' the sooner management intensity can be reduced thereby reducing establishment costs. One approach to estimating the cost-benefit of vegetation management is to quantify the time advancement in growth due to a treatment (Kimberley and Richardson 2004). Many studies have shown that vegetation management generally induces a Type 1 response where the growth trajectory of treated trees eventually becomes parallel to that of untreated trees. Type 1 responses do not alter the carrying capacity of a site but reduce the age at which a stand reaches a target size (e.g. maximum mean annual increment) (Mason et al. 1997; Snowdon and Waring 1984). Type 2 responses occur when a treatment increases the carrying capacity of a site and divergence in growth curves between treated and untreated stands continues throughout the rotation. To confirm that indigenous trees are following a Type 1 response following vegetation management treatments, and to quantify the duration of the time gain, long-term larger-scale experiments are required.

Conclusions

We acknowledge that the size and duration of our study limits the impact of our findings and the potential to extrapolate the outcomes to recommendations that are applicable at scale and over the long-term. Further, this limitation is compounded by the lack of ecophysiological data which unfortunately leave a gap in our understanding of the mechanisms underpinning the observed effects.

Notwithstanding the above, and also putting aside the potential impacts of pest populations and their interaction with neighbouring vegetation, our results indicate neighbouring vegetation (exotic or indigenous) to have little to no significant effect on early survival of the five indigenous species tested under the given environmental conditions. However, our results also indicate that there is the potential for the presence of neighbouring vegetation (exotic or indigenous shrubs) to significantly reduce early growth of all species tested, barring the *K. excelsa* seedlings. We found a consistent response to the presence or absence of neighbouring vegetation, however, the magnitude of that response varied by species,

largely as a function of their shade tolerance (though we acknowledge that we did not measure resource availability across the treatments and trial). As such, indications are that a targeted approach to managing neighbouring vegetation, at least soon after planting, may be required, in terms of area and duration of control, to ensure the optimum microclimate (e.g. lightwell) is created around the newly planted seedlings. If fast growing indigenous or exotic woody-species are used to occupy the site and/or improve tree stem-form or microclimatic conditions during large-scale indigenous tree planting operations, our results would indicate that these neighbouring species would require careful management over the first few years to manipulate site resources and optimise their availability to the target tree.

We recommend that this work is followed by a more comprehensive and mechanistic series of trials to understand and define the establishment and vegetation management requirements to maximise survival and optimise growth of these and other indigenous tree species across a wider range of sites, specifically to define the area and duration of control required to reach the 'free to grow' stage as well as define the tools (e.g. herbicides) that can be used to achieve these goals.

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Declarations

Competing interests The authors declare no competing interests.

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