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Radiata Management Theme

Task No: F50011
Milestone Number: 1

Report No. FFR- R030

Modelling the influence of site and weed competition on juvenile modulus of elasticity in *Pinus radiata* across broad environmental gradients

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**Research Provider:
Scion**

Date: 2008

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EXECUTIVE SUMMARY

Data from a nationwide set of *Pinus radiata* plots established at a range of conventional stand densities were analysed at age six to (i) determine how environment and competition from weeds influence dynamic modulus of elasticity (E) of the stem base, (ii) develop a predictive multiple regression model of E for basal stemwood, and (iii) identify significant direct and indirect environmental influences (through stem slenderness) on E using path analysis.

Site had a highly significant ($P < 0.001$) influence on E , which exhibited a three-fold range from 1.6 to 5.3 GPa, across the 30 sites. When compared to the weed-free controls, weed competition had a significant ($P < 0.0001$) and substantial effect on E , increasing values by on average 16% (2.76 vs. 2.38 GPa).

The positive linear relationship between stem slenderness (determined as tree height/ground-line tree diameter) and E was by far the strongest relationship ($R^2 = 0.71$; $P < 0.001$) among the 20 variables that were significantly related to E . A multiple regression model that included stem slenderness, minimum air temperature in mid-autumn as positive linear relationships and net N mineralisation in a negative linear form accounted for 86% of the variance in E . A one-at-a-time validation indicated that this model was stable and unbiased, with the validation accounting for 82% of the variance in E . The final path analysis model included minimum air temperature in mid-autumn, net N mineralisation, below-canopy solar radiation, and slenderness as significant ($P < 0.05$) positive direct influences on E . Below-canopy radiation, maximum air temperature during mid-summer, soil total phosphorus, and C:N ratio were indirectly associated with E through their significant ($P < 0.05$) direct relationship with stem slenderness.

INTRODUCTION

Advances in tree breeding and changes in silvicultural practice over the last few decades have greatly enhanced growth rates of plantation-grown conifers. These growth gains have led to shorter rotation lengths and an increased proportion of juvenile wood (Downes *et al.*, 2000). Juvenile wood is generally characterised by low density, thin cell walls, short tracheids with small lumens, high grain angle, and high microfibril angle, with the result that it has low strength and stiffness, and poor dimensional stability compared to mature wood (MacDonald and Hubert, 2002). The growing recognition that this juvenile wood is of low value has resulted in a recent shift in the way plantations are managed. Rather than focusing solely on maximisation of merchantable volume, management strategies are now starting to use genetic stock and implement practices that balance growth rate with optimisation of wood properties in the cambium (Evans, 1997; Downes *et al.*, 2000).

In the widely grown plantation softwood *Pinus radiata*, a useful indicator of corewood quality is modulus of elasticity (E), which measures the resistance of wood to deformation under an applied load. Although E is not an important property for pulp, it is used as a threshold criterion in machine stress grading of structural timber (Walker and Nakada, 1999), and is also a key property for determining quality of laminated veneer lumber. Modulus of elasticity is often considered more important than strength (modulus of rupture) for predicting wood quality, because *P. radiata* boards rarely break in normal use; much more frequently a load results in excessive deflection (Walford, 1985). When compared with other internationally traded structural lumber species, plantation-grown *P. radiata* has relatively poor E and dimensional stability. As stemwood E of *P. radiata* increases with cambial age up to five-fold over the first 30 years (Cave, 1968), the low values of E found within the corewood are most limiting for its utilisation in timber-based products.

Recent research shows that *P. radiata* corewood E can be manipulated by management. At single sites, significant and substantial gains in E have been shown through increasing initial stand density (Lasserre *et al.*, 2005; Waghorn *et al.*, 2007a, b) and use of clones with improved wood properties (Lindström *et al.*, 2004). The influence of weed competition on corewood E of *P. radiata* is not so clear. While substantial gains in E have been found with high levels of woody weed competition (Watt *et al.*, 2005) other research has found competition from herbaceous species to have no significant effect on E (Mason, 2006). Further research is therefore required to resolve this disparity.

Modulus of elasticity is also known to range widely across environmental gradients. For *P. radiata*, the most comprehensive published study examined the determinants of E using a nationwide series of plots where trees were grown at extremely high stand densities (40 000 stems/ha⁻¹) for a short period of time (four years) to compress the rotation length (Watt *et al.*, 2006). The threefold range in E found in this study was largely attributable to positive relationships with stem slenderness and minimum air temperature during early autumn which collectively in a multiple regression model accounted for 75% of the variance in E . Although these findings provide useful insight into the key determinants of E , further research is required to validate confirm??? that findings apply to stands grown under operational stand densities over longer periods.

Linking the environment with wood properties at a broad scale requires high quality information on the climatic and edaphic conditions over a range of sites at the time new wood was laid down. This type of data is available from a nationwide series of site quality

plots established at sites encompassing the range of climatic and edaphic conditions found throughout plantations of *P. radiata* within New Zealand (Watt *et al.*, 2008). Through utilising data from *P. radiata* plots at these sites where trees were grown both with and without competition from weeds, the aims of this study were to (i) determine the influence of site and weed competition on E at the stem base, (ii) develop a predictive model of E sensitive to the effects of environment and weed competition, and (iii) identify significant direct and indirect environmental influences (through stem slenderness) on E using path analysis.

METHODS

Location of Site Quality Plots

Sites were selected to represent the range in soil properties on which planted forests are currently established in New Zealand. Plots used within the trial series were established within the seven major soil orders on which 97.6% of the *P. radiata* resource occurs (R. Simcock, pers. comm.). The number of sites established on each soil order was weighted to be representative of the corresponding plantation area on which the soil order is found (Fig. 1).

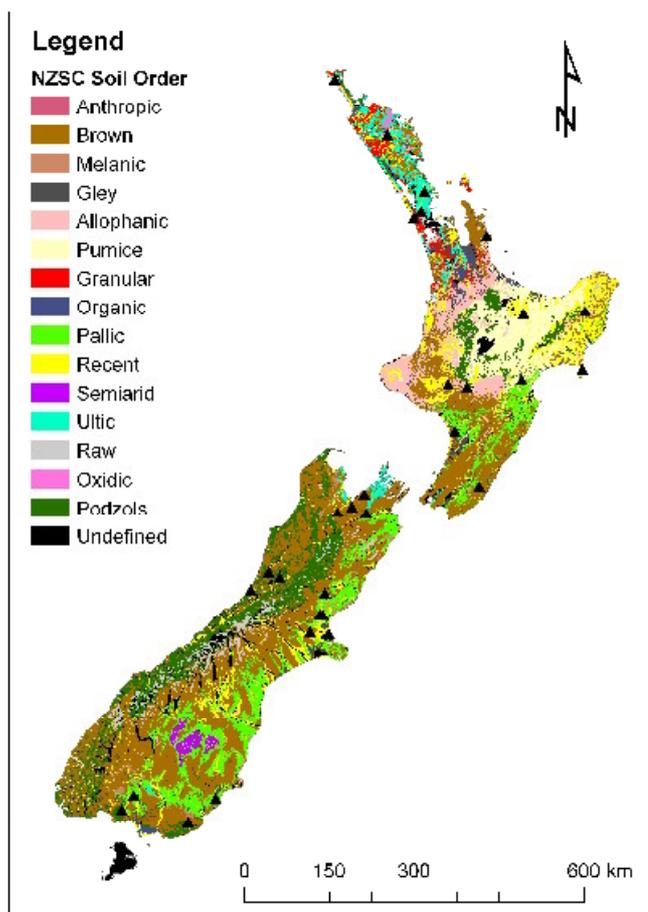


Figure 1. Distribution map of soil orders in New Zealand, showing location of site quality plots used in this study.

Sites were further screened using climatic surfaces (Leathwick and Stephens, 1998) to ensure that selected areas represented the considerable range in meteorological conditions found throughout New Zealand's planted forests. When compared to long-term average values for all plantation forests (long run meteorological data obtained from Anon., 1983), meteorology at the 30 selected sites almost completely encompasses the range in total annual rainfall (NZ plantations 609-3 718mm vs. our sites 636-3 276mm), and is broadly equivalent to the lower extreme and exceeds the upper extreme of mean annual air temperature (NZ plantations 8.0-15.6 °C vs. our sites 8.2-15.8 °C).

Experimental Design

At each of the 30 selected locations, permanent 40m x 40m sample plots were established at conventional initial stockings, ranging from 425 to 1,250 stems/hectare⁻¹, using *P. radiata* seedlings with a growth and form factor of 19¹ (Vincent and Dunstan, 1989). A 0.04ha circular plot was installed at the centre of the permanent sample plot and divided into two areas of equal size, with one side receiving complete weed control and the other no weed control. Weed control was achieved by annual spray application in spring and again in late summer, if required, throughout the six-year duration of the trial.

Climatic Measurements, below canopy radiation and water balance

Meteorological data were obtained from thin-plate spline surfaces (Hutchinson and Gessler, 1994) fitted to meteorological station data (Leathwick and Stephens, 1998), at a spatial resolution of 100m². Average monthly, seasonal, and annual values were extracted from these climate raster surfaces for windspeed, solar radiation, rainfall, vapour pressure deficit, mean, maximum and minimum temperature.

The radiation transmitted beneath the canopy at age three was estimated at all sites, in plots with and without weeds, using Beers Law as,

$$Q_t = G_a (\exp^{-k(L_t+L_w)}) \quad (1)$$

where G_a is average daily solar radiation above the canopy, k is the light extinction coefficient (assumed to be 0.5 for a spherical leaf angle distribution), and L_t and L_w are, respectively, projected leaf area indices of the trees and weeds. Following Watt *et al.* (2007), projected needle area, A_f , (m² tree⁻¹) was determined from ground-line basal area, A_b , (m² tree⁻¹) for trees growing both with and without weeds as $A_f = 2969 A_b$; $P < 0.0001$; $R^2 = 0.98$. Using annual measurements of tree diameter, this equation was used to determine site-specific temporal changes in projected leaf area index, L_t , as the quotient of A_f , and the area allocated to each tree determined as (10 000m²/stand density). Measurements of projected L_w taken in plots with weeds, using a leaf area meter (LAI-2000, Li-Cor, Lincoln, NE, USA) at stand ages of 1 to 3 were used to develop the following relationship between L_w and the mean height of the tallest four weeds surrounding each tree, h_w , as $L_w = 0.339h_w$; $P < 0.0001$; $R^2 = 0.76$. Using measurements of h_w taken in all plots with weeds at age three, this equation was used to estimate L_w .

Daily root-zone water storage, W_t for both treatments, was determined at all sites, using a water balance model (see Watt *et al.*, 2007 for full description) implemented through the modelling system Vegetation Manager (fully described in Watt *et al.*, in prep.). Daily meteorological data required for the water balance model includes total rainfall, solar radiation, and maximum, minimum and mean air temperature. The model also requires estimates of maximum available root-zone water storage, W_{max} . These inputs were determined from the underlying interpolated surfaces (Mitchell, 1991; Newsome *et al.*, 2000; Leathwick *et al.*, 2002) used by VMAN, by specifying the plot co-ordinate. The determination of daily rainfall within this database follows the method described by Palmer (2008).

¹ The growth and form rating is an index which ranks improvements in growth and form of a particular seedlot relative to unimproved seed (Vincent, 1987).

The water balance model also requires seven other parameters (see Watt *et al.*, in prep for values), for which the default values have been determined in a previous detailed study (see Watt *et al.*, 2007), and tree leaf area index. Tree leaf area index was estimated using the method described above. For each of the 30 sites, the water balance model was used to determine average W_i and average fractional W_i as $W_f = W_i/W_{\max}$. Average daily values over the six years since plot establishment were used for both W_i and W_f in analyses.

Measurements of Soil Properties

Soil physical properties were measured on samples of mineral soil taken from the edges of undisturbed plots, located at the site, immediately prior to planting. Air capacity (at 10 kPa), macroporosity (at 5 kPa), total porosity, bulk density, particle density and void ratio were determined to 100mm following the procedures described by Gradwell (1972). To ensure that results between sites were not affected by *in situ* site variation in volumetric water content, cone penetration resistance was measured in the laboratory at -10 kPa on soil samples extracted from 0 to 100mm.

A soil pit was excavated down to impermeable layers prior to plot establishment in an undisturbed area adjacent to the plots at each location to determine soil texture. From this pit, particle size was measured by dispersing the field-moist soil in water with an ultrasonic probe and separating the <2 μ m, 2-63 μ m and 63 μ m -2mm fractions by sedimentation (Claydon 1989). Final values of particle size were determined by weighting estimates by soil layer over the depth of the roots at each site, determined by destructive sampling of adjacent plots of four-year-old *P. radiata* at each site (see Watt *et al.*, 2008 for details).

A comprehensive set of soil chemical measurements was taken from each 0.02ha area at the centre of the permanent sample plots at age four years. Soil samples were taken between trees from 0 - 100mm depth of mineral soil with a 25mm diameter corer at 16 points and bulked to give 16 cores per plot. As soon as the samples arrived at the lab, the field moist samples were sieved through a 6mm sieve, mixed thoroughly, and half of the sample was air dried at 30°C. They were analysed for soil moisture, pH in water, total carbon (C), total nitrogen (N), total phosphorus (P), organic P, inorganic P, Bray P, Olsen P, exchangeable bases, and CEC, following the methods described by Blakemore *et al.* (1987). Results are expressed on an oven dry basis (105°C).

Net N mineralisation was measured on field moist samples by incubating 5.0g (oven-dry equivalent) of mineral soil at 60% of water-holding capacity in 125-mL polypropylene cups covered with polyethylene (30 μ m) for 56 days at 25°C (Scott *et al.* 1998). Mineral-N (ammonium-N and nitrate-N) was measured at 0 and 56 days by extracting the soil with 50ml of 2 M KCl, shaking for 1 hour, and then filtering. Extractable ammonium-N and nitrate-N were measured colorimetrically with a Lachat Quickchem FIA8000 analyser. Net N mineralisation was calculated as the difference in ammonium-N and nitrate-N values at 0 and 56 days. The % nitrate-N within the extractable N was calculated after 56 days incubation.

Tree Dimensions and Modulus of Elasticity

At age six, measurements of root-collar diameter (D), tree height (H) and green crown height (C) were taken on all trees that were not malformed within the permanent sample

plot. Stem slenderness was determined from these measurements as H/D , and relative green crown height was determined as C/H . Immediately after these measurements were made, acoustic green velocity, V_A , was determined from path length (S) and transit time (Δt), as,

$$V_A = S/\Delta t \quad (2)$$

The IML electronic hammer (Instrumenta Mechanik Labor GmbH, Wiesloch, Germany) was used to determine V_A on the standing trees using a path length of 1.0m, centred at 20% of the total tree height. For each tree, measurements of V_A were taken on a single side of the tree, using multiple hammer hits, until 3 readings that were in close agreement were obtained. Assuming a green density of $1,000\text{kg/m}^3$, green dynamic modulus of elasticity was determined from these measurements as,

$$E = \rho V_A \quad (3)$$

Data Analysis

All analyses were undertaken using SAS (SAS Institute, 2000). A two-way analysis of variance (ANOVA) was used to test for the main effects of weed control and site on E , stand structural characteristics, soil water balance, radiation transmitted beneath the canopy and soil chemical properties within the top 100mm of the mineral horizon.

Multiple regression models for modulus of elasticity and stem slenderness were developed. Variables were introduced sequentially into the model starting with the variable that exhibited the strongest correlation, until further additions were not significant or did not improve the overall model R^2 by more than 3%. Variable significance was determined manually using an F -test, with the significance tested for each variable addition against the residual sum of squares for the previous model. Variable selection was undertaken manually one variable at a time, and plots of residuals were examined prior to variable addition to ensure that the variable was included in the model using the least biased functional form.

For the final models the degree of multicollinearity between variables was assessed using the variance inflation factor, with values of less than 10 indicating that multicollinearity is within acceptable bounds (Der and Everitt, 2001). Residuals were plotted against independent variables and predicted values to determine model bias.

A one-at-a-time cross validation was undertaken to check the bias and accuracy of the final model for modulus of elasticity. This was accomplished by excluding the first site as a single-element test set, and fitting the model over all other sites. Using this fitted model, E was then predicted at the first site. This process was repeated for all remaining plots, to generate data for the validation. Predicted values for E were then plotted against respective actual values to determine bias, while model accuracy was examined using the coefficient of determination between predicted and actual E .

To determine the influence of structural variables on E , independent of climatic and edaphic variation between sites, a mixed effects model was constructed. In this model structural variables were treated as fixed effects, while site was added as a random effect.

The effect of each structural variable on E was assessed through examination of both the F and P value.

The site level multiple regression modelling approach was supplemented with path analysis to control for the effect of common cause. Path analysis is a multivariate statistical technique that bridges the gap between empirical observation and theoretical research. This technique requires development of a preconceived causal model in which directional flow and the inter-relationships among independent (exogenous) and dependent (endogenous) variables are specified. In this study the causal model can be used to quantify the influence of environmental variables directly on E and indirectly on E via stem slenderness (see Fig. 2). A more complete description of path analysis is given in Wright (1921, 1934), Li (1975) and Rao and Morton (1980).

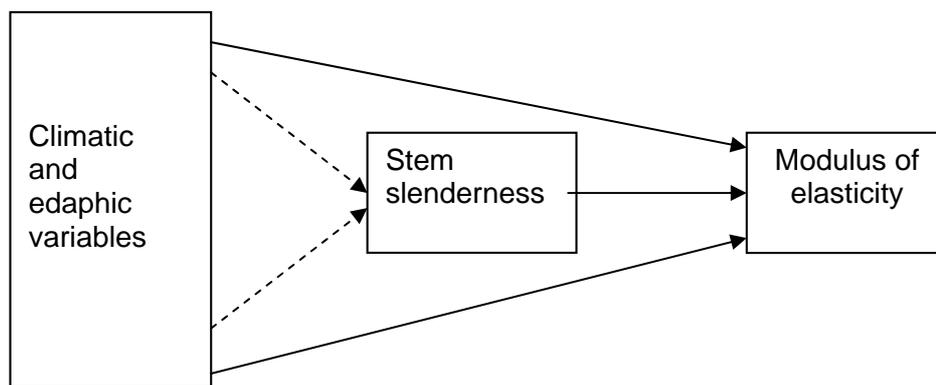


Figure 2. Proposed causal pathways linking environment with modulus of elasticity (E). Solid lines represent direct pathways of influence, while dashed lines represent indirect pathways of influence on E , via stem slenderness.

Using the CALIS procedure (SAS Institute, 2000), path analysis was used to determine the significance of pathways illustrated in Figure 2, using environmental variables identified in multiple regression models of stem slenderness and modulus of elasticity. Non-significant pathways, denoted by t -values of less than 1.96 were removed from the model. After all non-significant pathways were removed, model statistics were examined. For the overall model, values of the chi-square ratio greater than 0.05 indicate an acceptable fit between model and data. However as the chi-square statistic has some limitations as an inferential test (see Kaplan 1990, for review), the goodness of fit index, normed fit index and comparative fit index were also used to determine the adequacy of the model fit to the data. All of these indices range from 0 to 1, with values over 0.9 indicating an acceptable fit between model and data. A model exhibiting acceptable fit between the model and the data also has normalised residuals that are less than 2.

RESULTS

Influence of Site on Climate and Soil Physical Properties

There was considerable variation in climate between sites (Table 1). Across sites, mean annual rainfall ranged five-fold from 636 to 3 276 mm, between sites located respectively on the east and west side of the main axial ranges in the South Island. Annual average temperature exhibited a two-fold variation from 8.2 °C at a high elevation South Island site, to 15.8 °C at a coastal site in the northern North Island (Table 1). There was a four-fold range in average annual windspeed (6.7 to 24.4 km hr⁻¹).

Table 1. Site level variation in climatic variables and soil physical properties. Values shown are the mean followed by the range in brackets for the 30 sites.

Variable	Mean and Range
Climatic variables	
Mean average annual temp. (°C)	11.5 (8.2-15.8)
Mean min. annual temp (°C)	6.9 (3.8-12.0)
Mean min. April temp. (°C)	7.7 (4.7-13.0)
Solar radiation (MJ m ⁻² day ⁻¹)	14.2 (12.1-15.4)
Rainfall (mm yr ⁻¹)	1 457 (636-3,276)
Average windspeed (km hour ⁻¹)	13.1 (6.7-24.4)
Soil physical properties	
Coarse sand (%)	7 (0-66)
Medium sand (%)	10 (1-42)
Fine sand (%)	22 (3-69)
Sand (%)	39 (8-99)
Silt (%)	38 (1-71)
Clay (%)	23 (1-54)
Bulk density (g cm ⁻³)	0.97 (0.43-1.44)
Particle density (g cm ⁻³)	2.5 (2.2-3.0)
Penetration resistance (MPa)	0.76 (0.29-2.37)
Total porosity (% v/v)	62.0 (43.7-81.7)
Macroporosity (%)	21.2 (3.8-49.5)
Air capacity (%)	24.1 (4.4-53.0)
Void ratio	1.9 (0.8-4.8)

The selected sites included extremes in soil texture ranging from single-grained scoria and sandy soils to clay loam soils. Variation in soil texture was considerable for all texture classes, and exhibited the greatest range for the sand (8 to 99%) and silt (1 to 71%) fractions (Table 1). Soil physical properties also exhibited considerable variation between sites. This variation was most pronounced for the closely related variables macroporosity and air capacity, which ranged from 4-50% and 4-53% respectively across sites (Table 1).

Impact of Site and Weed Competition on E, Structural and Edaphic Variables

Modulus of elasticity exhibited a significant ($P<0.001$) three-fold variation across sites (1.58 – 5.26 GPa). Compared to the weed-free control, weed competition significantly ($P<0.001$) increased E by on average 16% across all sites (2.76 vs. 2.38 GPa). Gains

attributable to weed competition were noted at 25 out of the 30 sites, and ranged in magnitude from 3% to 71% (Fig. 3). At the remaining five sites, reductions in E from weed competition were less marked, ranging from 3% to 32% (Fig. 3).

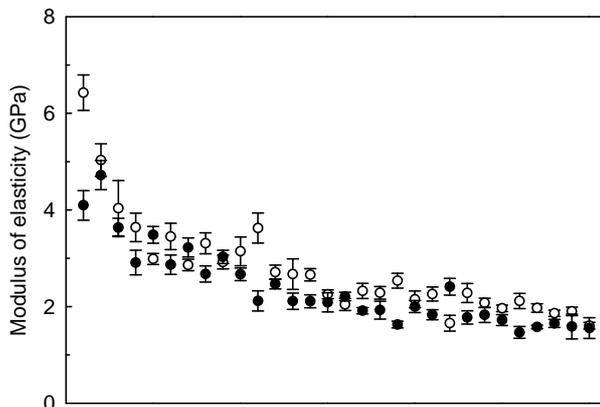


Figure 3. Site variation in modulus of elasticity for plots with (closed circles) and without (open circles) weed control. Values are sorted in descending order, after averaging at the site level. Each value shown is the mean with associated standard error.

All stand structural characteristics significantly varied between sites (Table 2). The treatment averaged range in height, and diameter at age six was considerable across sites, varying three-fold for diameter (133-350mm) and two-fold (4.6-11.3m) for height. Site level variation was also marked for stem slenderness (tree height/ground-line diameter) ranging two-fold from 30 to 62m m⁻¹, and green crown height and relative green crown height (crown height/tree height), which respectively ranged from 0 to 2.8m and 0 to 0.43m m⁻¹. Competition from weeds had a significant detrimental influence on tree ground-line diameter and height, inducing average reductions of 29, and 14% respectively for these characteristics (Table 2). Weed competition also significantly increased stem slenderness and relative green crown height, by 24 and 50% respectively, but no significant treatment differences were noted for actual green crown height.

Table 2. Stand structural characteristics, average fractional available volumetric water content (θ_a), average root-zone water storage, and soil chemical properties in the top 100mm of the mineral soil for plots with and without weed control at 30 sites. The influence of weed control (WC) and site on each soil property is shown by partial R^2 values followed by significance levels. Asterisks *, **, *** represent significance at $P = 0.05, 0.01$ and 0.001 , respectively. Values with no asterisks are not significant at $P=0.05$.

	With weed control		No weed control		Analysis of variance	
	Mean	Range	Mean	Range	Site	WC
Structural variables, and θ_a						
Root collar diameter (mm)	235	167-340	168	76-360	0.64***	0.28***
Height (m)	7.96	4.7-11.3	6.83	2.8-11.3	0.85***	0.08***
Stem slenderness ($m\ m^{-1}$)	34.6	24.7-51.2	42.8	31.6-79.5	0.61***	0.24***
Crown height (m)	0.67	0-3.17	0.83	0-2.46	0.89***	0.01
Relative crown ht ($m\ m^{-1}$)	0.08	0-0.43	0.12	0-0.39	0.86***	0.04***
Average Q_t ($MJ\ m^{-2}\ day^{-1}$)	7.50	1.92-12.39	2.98	0.33-10.02	0.37*	0.48***
Av. root-zone water storage (mm)	60.1	19.0-158.2	54.6	15.3-145.0	0.98***	0.01***
Average θ_a	0.71	0.56-0.94	0.65	0.44-0.94	0.85***	0.10***
Chemical properties						
Carbon (%)	4.97	1.2-13.9	5.35	1.3-14.8	0.935***	0.004
Total N (%)	0.26	0.03-0.61	0.28	0.02-0.65	0.935***	0.005
C:N ratio	21.0	11.2-39.9	21.8	11.4-55.7	0.935***	0.003
pH	5.23	3.98-6.73	5.21	4.2-6.5	0.969***	0.0003
CEC ($cmol\ g^{-1}$)	17.4	4.0-39.0	18.4	5.2-48.5	0.963***	0.003
Exch. Na ($cmol\ g^{-1}$)	0.18	0.03-0.43	0.22	0.03-0.78	0.761**	0.021
Exch. K ($cmol\ g^{-1}$)	0.33	0.02-0.84	0.41	0.03-1.05	0.928***	0.027**
Exch. Mg ($cmol\ g^{-1}$)	2.40	0.1-37.0	2.52	0.3-36.2	0.999***	0.0001
Exch. Ca ($cmol\ g^{-1}$)	3.27	0.3-9.8	3.57	0.4-9.9	0.957***	0.003
Sum bases ($cmol\ g^{-1}$)	6.18	0.4-42.6	6.72	0.7-42.8	0.991***	0.001
Base saturation (%)	34.2	9.4-109.2	34.5	10.4-88.3	0.970***	6×10^{-5}
Olsen P ($mg\ g^{-1}$)	9.70	1.7-35.2	8.30	1.3-35.6	0.893***	0.009
Bray P ($mg\ g^{-1}$)	22.3	1.8-63.0	17.8	1.6-99.1	0.864***	0.014
Inorganic P ($mg\ g^{-1}$)	127	21.2-349.6	111	9.5-306.9	0.926***	0.009
Organic P ($mg\ g^{-1}$)	288	5.2-755	287	10.3-715.1	0.957***	5×10^{-6}
Total P ($mg\ g^{-1}$)	415	50.6-889.9	398	45.0-850.5	0.946***	0.001
Nitrate-N at end of incubation (%)	86	0-104	63	0-99	0.594***	0.138**
Ammonium-N at day 0 ($mg\ kg^{-1}$)	3.51	0.03-12.3	4.91	0-19.7	0.857***	0.026*
Net N mineralisation ($mg\ kg^{-1}$)	48.1	5.6-140.8	56.1	0-162	0.883***	0.01

Radiation below the tree and weed canopy significantly varied across sites by five-fold (1.83 vs. $9.84\ MJ\ m^{-2}\ day^{-1}$). Between sites, average fractional available volumetric water content significantly ranged from 0.52 on a dryland site with low annual rainfall (636mm) to 0.94 on a wet site with annual average rainfall of $3\ 276\text{mm}$. Average root-zone water storage exhibited a significant nine-fold range across sites from 17mm to 150mm . Competition from weeds significantly reduced radiation below the tree and weed canopy, fractional available volumetric water content, and root-zone water storage (Table 2).

All chemical properties exhibited significant variation between sites (Table 2). When averaged at the site level, variation was most marked for ammonium-N at day 0, exchangeable Mg, and organic P, which respectively ranged 556-fold, 197-fold and 95-fold across sites. In contrast, the only soil chemical properties significantly influenced by weed competition were ammonium-N at day 0 and exchangeable K, which increased, relative to the weed free control, by respectively 40% and 24% (Table 2).

Modelling Site Effects on E and Stem Slenderness

In total 20 variables were significantly related to E (Fig. 4). The positive linear relationship between stem slenderness and E was by far the strongest relationship ($R^2 = 0.71$) among those that were significant (Fig. 4). For the other tree dimensions examined, neither height, green crown height or relative green crown height were significantly related to E . Although the negative linear correlation between E and tree diameter was significant ($P=0.018$), this relationship was weak ($R^2 = 0.09$). Neither stand density, windspeed or either of the two variables associated with water balance were significantly related to E .

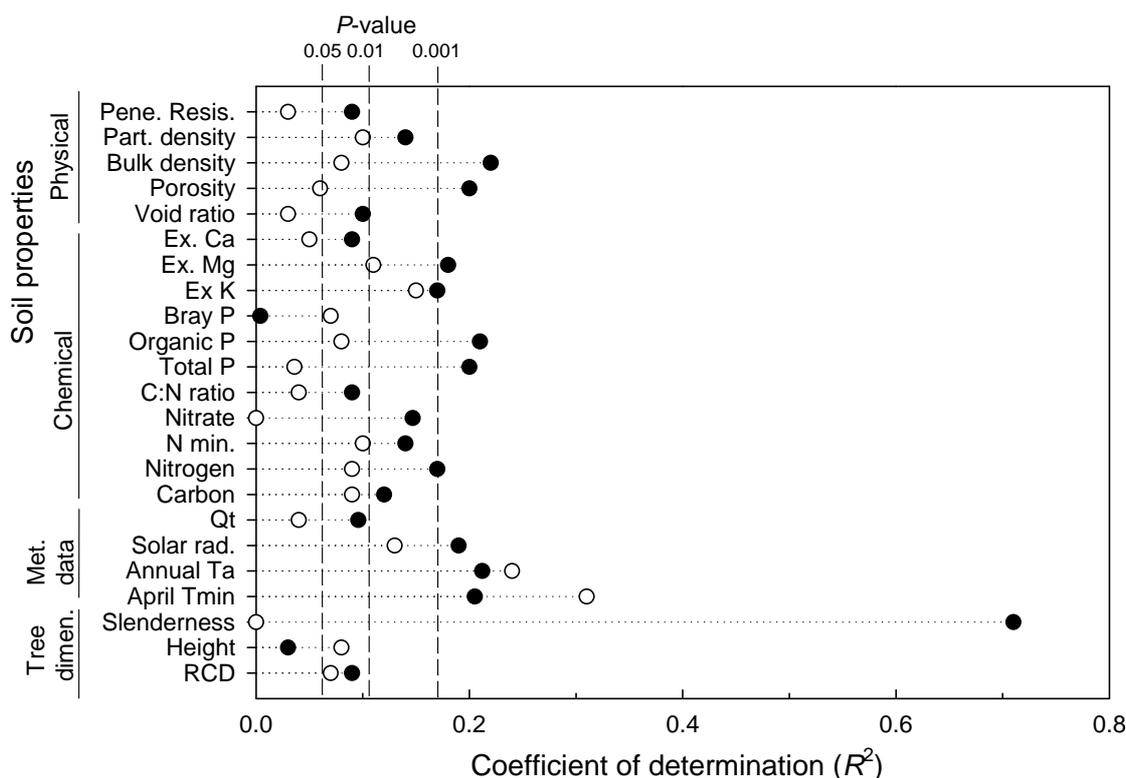


Figure 4. Horizontal point plot showing the strength of correlations between independent variables and modulus of elasticity before (closed circles) and after stem slenderness (open circles) was added to the model. The lower x-axis shows the coefficient of determination, while the upper x-axis shows significance levels at $P=0.05$, 0.01 and 0.001 .

After correction had been made for stem slenderness, air temperature had the strongest influence of the variables examined (Fig. 4). Mean minimum air temperature during April, T_{\min} , exhibited the strongest correlation with E , and a positive linear relationship best described this relationship (Fig. 5). Addition of N mineralisation as a negative linear relationship (Fig. 5) to the model that included stem slenderness and T_{\min} accounted for a further 3% of the variance in E . As addition of further variables did not significantly improve this model, or add more than 3% of the variance, these were the final three variables selected to describe E . This model significantly differed between the weed control treatments, with values for the plots with weed control being slightly under-predicted while those with no weed control were slightly over-predicted. This was attributable to a significant interaction (see Fig. 5 for interaction) between stem slenderness and weed control ($P=0.0049$), which when included in the model did not markedly improve the R^2 ,

but did account for treatment differences, resulting in an unbiased fit for both treatments (Fig. 6a).

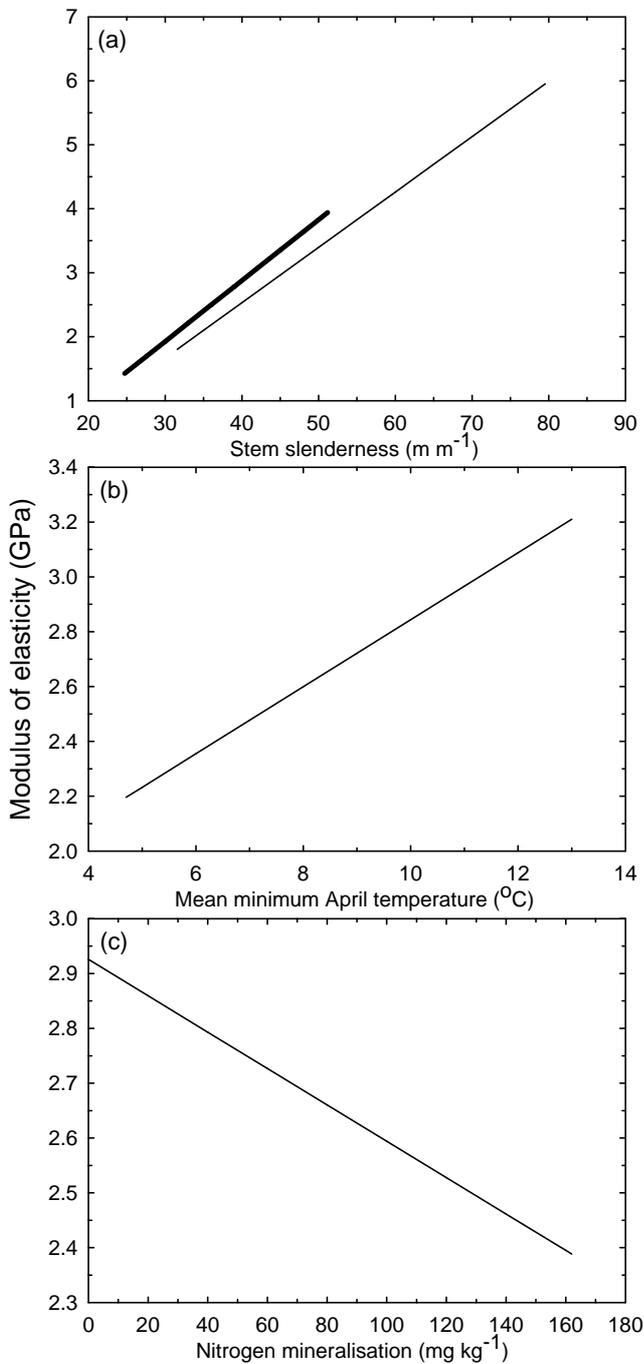


Figure 5. Partial response curves for modulus of elasticity plotted against (a) stem slenderness for plots without (thin line) and with weed control (thick line) (b) mean minimum April air temperature and (c) net N mineralisation. For each partial response curve, all other variables were held at mean values when the response curve was generated, within the dataset range for each variable.

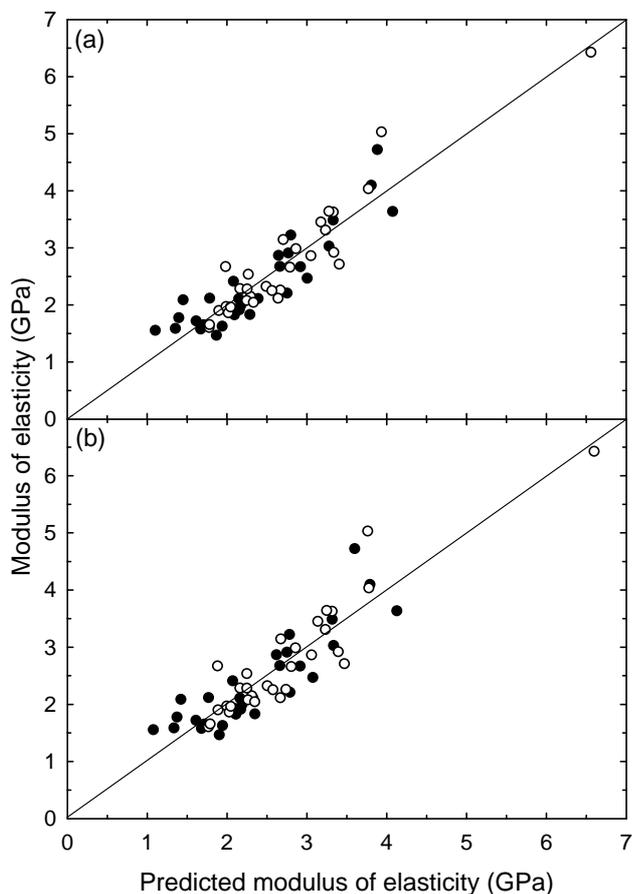


Figure 6. Relationship between predicted and actual modulus of elasticity for (a) the fitting and (b) validation datasets.

The equation and coefficients used for the final model are described in Table 3. Residuals for this model exhibited little apparent bias with predicted values, or any of the independent variables in the model (data not shown). The variance inflation factor did not exceed 1.10 for any of the independent variables (Table 3), indicating that multicollinearity was within acceptable bounds. The results from the one-at-a-time validation indicated that the final model was relatively unbiased, and accurate, with the predicted values accounting for 82% of the variance in the actual E (Fig. 6b).

Table 3. Summary of statistics for the final predictive model of modulus of elasticity. Parameter values and variable partial R^2 and cumulative R^2 values (in brackets) are shown. For the significance category, the F values and P categories from an F -test, are shown, with asterisks ***, **, respectively representing significance at $P = 0.001$ and 0.01 . The variance inflation factor (VIF) is also shown.

Equation: Modulus of elasticity = $a + bS + cT_{\min} + dN + eS$ (for no weed control only)						
Para.	Value	Variable	Units	R^2	Significance	VIF
a	-1.64					
b	0.095	Slenderness (S)	$m\ m^{-1}$	0.71 (0.71)	143.9***	1.10
c	0.115	Mean minimum April air temp. (T_{\min})	$^{\circ}C$	0.80 (0.09)	26.4***	1.04
d	-0.00332	Net N mineralisation (N)	$mg\ kg^{-1}$	0.83 (0.03)	10.0**	1.06
e	-0.00865	Slenderness (S)	$m\ m^{-1}$	0.86 (0.03)	8.6**	-

At the tree level, a mixed-effects model which included site as a random effect and stem slenderness as a fixed effect indicated that after site effects were removed, slenderness had a significant positive influence on E of trees within the site ($P < 0.0001$; F value = 343). Similar analyses with other structural variables indicated significant, although considerably weaker, relationships between E and tree height ($P < 0.0001$; F value = 10), root collar diameter ($P < 0.0001$; F value = 113), green crown height ($P < 0.0001$; F value = 24) and ratio of green crown to total height ($P < 0.0001$; F value = 41).

The final multiple regression model developed for stem slenderness accounted for 54% of the variance in the data. This model included negative linear correlations with radiation transmitted through the canopy, (Q_t), total soil phosphorus, and positive linear relationships with maximum air temperature during January and soil C:N ratio, which had respective partial R^2 values of 0.24, 0.17, 0.07, and 0.05. Addition of all variables significantly improved the model at $P = 0.05$, and plots of residuals against independent variables and predicted values exhibited little apparent bias (data not shown). The variance inflation factor did not exceed 1.45 for any of the variables added to the model.

Path Analysis

The final path analysis model is shown in Figure 7. For the final model, an acceptable level of model fit to the data was demonstrated by all goodness of fit indices (all > 0.9) and the chi-square ratio ($p = 0.24$). None of the normalised residuals exceeded 1.30 in absolute magnitude. All variables used in the multiple regression model for slenderness had a significant direct influence on stem slenderness in the final path analysis model. The only one of these variables found to have a significant ($P = 0.05$) direct influence on E , beyond the indirect influence via stem slenderness, was below-canopy radiation. The analysis also showed that all variables included in the final multiple regression model for E , had a significant direct influence on this variable. However, none of these variables was found to indirectly influence E through a significant direct influence on stem slenderness.

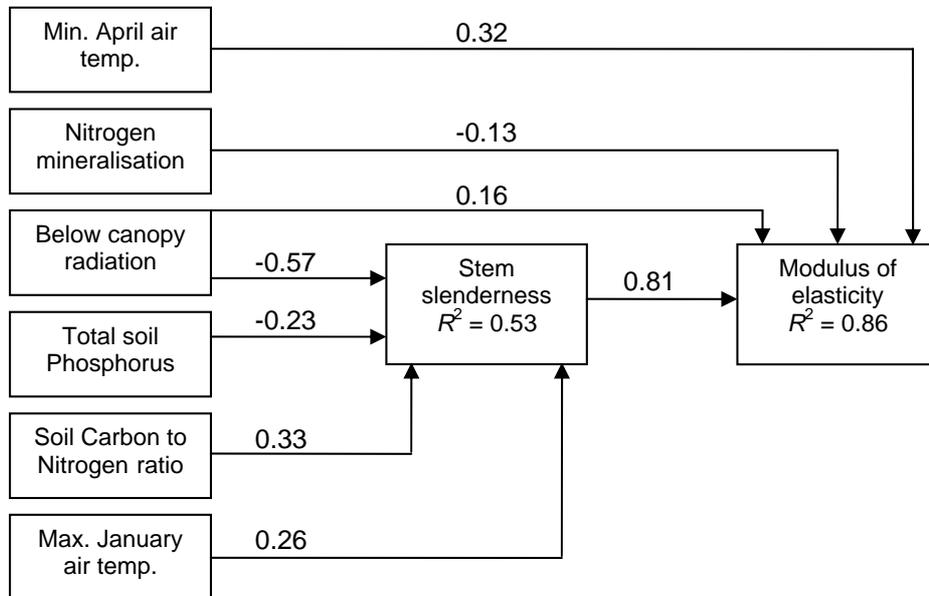


Figure 7. Final path analysis model, with significant ($P < 0.05$) pathways shown. Values next to each line give the path coefficient for that pathway. The amount of variance (R^2) explained for each endogenous variable is shown.

Examination of the path coefficients show that stem slenderness had a positive direct effect on E that considerably exceeded the strength of other directly related variables. The direct effect of mean minimum temperature during April had a moderate positive influence on E . Although both N mineralisation and below-canopy radiation had significant direct effects on E , the magnitude of the path coefficients for both variables was low. Stem slenderness was most sensitive to below-canopy radiation, which had a reasonably strong negative direct influence on this variable. Soil C:N ratio had a moderate positive direct influence on slenderness. The effect of mean maximum January air temperature and total soil phosphorus on stem slenderness were significant, but somewhat lower in magnitude. The final models explained 86% of the variance in E , and 53% of the variance in stem slenderness.

DISCUSSION

This study highlights the importance of stem slenderness and air temperature as key determinants of juvenile modulus of elasticity for *P. radiata*. In conjunction with N mineralisation, these variables were able to explain a large proportion of the variation in E between weed control treatments and sites that covered very broad climatic and edaphic gradients.

Stem slenderness had the dominant influence on E . At the site level this was clearly apparent from the bivariate correlations (Fig. 4), where stem slenderness accounted for over three-fold more variance in E than any other variable. Both the multiple regression model and path analysis reinforced the dominance of stem slenderness as the key determinant of E . Analysis undertaken at both the site and tree levels strongly suggests that the less significant effects of diameter and height on E are mediated through stem slenderness.

The strong influence of stem slenderness on E found here is part of an emerging theme in the wood quality literature. Across a broad environmental gradient in eastern Canada, stem slenderness was found to be the most closely related variable to E for *Picea mariana* (Liu *et al.*, 2007). The dominant influence of stem slenderness on E has also been noted in spacing trials at single sites for both *P. radiata* (Waghorn, 2007a; Lasserre *et al.*, 2008) and *Pinus taeda* (Roth *et al.*, 2007), where gradients in environment have been created using a wide stand density range.

The mechanism by which slenderness affects E was not explicitly examined in this study. However, it can be shown that for a given mass, a more slender tree will have a greater level of compressive stress in its stem (Niklas, 1994, p164). It is hypothesised that trees are able to sense and respond to this higher level of compressive stress and produce new wood with higher E , possibly by manipulating the angle of cellulose microfibrils in the secondary cell wall. This increase in E not only acts to reduce the compressive strains experienced by the stem, but in turn also acts to increase the critical compressive stress that the tree stem can withstand before buckling occurs. This type of thigmomorphogenic response to mechanical stresses caused by self-imposed or dynamic loads commonly occurs in a large number of tree species (Jaffe, 1973), including *P. radiata* (Jacobs, 1954).

The significant direct influence of air temperature on E may be mediated through regulation of latewood development. Analyses show that E was most strongly correlated with minimum air temperature in mid-autumn. Given that latewood with high E is forming during this period (Watt *et al.*, 2005), it follows that sites with warmer temperatures and increased growth rates over this month will develop a greater percentage of high E latewood, and as a consequence higher overall stem E .

The path analysis extended the multiple regression modelling by partitioning cause and effect. These results clearly show that stem slenderness has the strongest direct influence on E , with the path coefficient for this variable exceeding that of all other direct relationships by over two-fold. Another key result from this analysis was that T_{\min} and N mineralisation have a direct effect on E that is not significantly mediated through, or is independent of, slenderness.

The path analysis and multiple regression models clearly identify below-canopy radiation, air temperature and site fertility as key driving variables of slenderness. The sensitivity of slenderness to below-canopy radiation is consistent with previous research (Albrekston and Valinger, 1985; Nilsson and Albrekston, 1993; Vanninen and Mäkelä, 2000). This response is likely to be a survival mechanism whereby greater carbon allocation to height growth under high levels of shading enable trees to avoid being overtopped. The significant direct influence of total soil phosphorus and soil C:N ratio on slenderness concurs with our current understanding of fertility influences on allometry, which typically have a greater influence on tree diameter than height.

These results provide considerable insight into how environment regulates E . Low fertility sites with warm air temperatures and either a high canopy leaf area index, or high levels of woody weed competition, are most likely to produce trees with high stem slenderness and high E . Conversely, sites that are cool over summer and autumn and high in fertility, with low levels of intra- or inter-specific competition for light are likely to produce trees with low stem slenderness and low E .

The results demonstrate the strong and significant influence of weed competition on E , and provide a cohesive mechanistic explanation of how weed competition influences E . The significant positive influence of weed competition on E at 83% of the sites examined here concurs with previous research at a dryland site with woody weed competition (Watt *et al.*, 2005). Our results clearly show that this increase was primarily attributable to the shading caused by weeds, that through significant reductions in below-canopy radiation, resulted in increases in slenderness. This result suggests that the effect of short herbaceous weeds on E are likely to be less pronounced than that of tall woody weeds that compete more strongly for light, over a longer period (Richardson *et al.*, 1996).

This theory also accounts for the anomalous reductions in E caused by weed competition at five of the thirty sites. All of these sites had grass competition. Consequently, compared to sites where weed competition increased E , reductions in below-canopy radiation attributable to the weed understory were considerably less pronounced at these five sites (71 vs. 36% of Q_t of the weed free control). These anomalies were also partly attributable to plots with weeds at these sites having **an higher total phosphorus???** than the weed free control (18% gain), which contrasted with the other 25 plots, in which weed competition induced a 6% reduction in total phosphorus. Consequently, compared to the 25 sites where weed competition induced significant ($P<0.001$) increases of 29% in slenderness, at the anomalous five sites slenderness was not significantly affected ($P=0.12$), and only increased by 7% relative to the weed-free control.

Our findings suggest that the often reported gains in productivity resulting from control of weeds need to be balanced against concomitant reductions in key wood properties such as E to optimise end product value. Decision support tools such as the recently developed Vegetation manager (Watt *et al.*, in prep.) could be used to quantify accurately how differing intensities of weed competition impact not only growth (diameter, height), but also *via* the relationship with stem slenderness identified here, modulus of elasticity. This type of analysis could be used to optimise the duration and intensity of weed control treatments on crop volume and value. Such an analysis is likely to be particularly important in situations (such as warm regions) where E is sufficiently high to allow the cutting of structural grade timber within the juvenile core.

Using data from the same site series, a previous study developed a model of E using trees grown at very high densities ($40,000 \text{ stems/ha}^{-1}$) over short time periods (four years) to expedite stand development and compress the rotation length (Watt *et al.*, 2006). Using this experimentation in miniature design, the main determinants of E were very similar to those found in this study. The final multiple regression model including positive relationships with stem slenderness and mean minimum air temperature during March. Sentence??? The similarity of these results with our study highlights the utility of experimentation in miniature as a valid approach for rapid identification of drivers of wood properties, across broad environmental gradients.

CONCLUSION

This study has highlighted that E varies widely across environmental gradients and is significantly affected by the level of weed competition. A large proportion of this site and treatment variation was attributable to positive relationships with stem slenderness and air temperature and a negative relationship with N mineralisation. Stem slenderness was found to be negatively related to below-canopy radiation and site fertility, and positively related to air temperature. Low corewood values for E commonly limit structural timber utilisation in fast-growing conifers. Consequently, accurate determination of juvenile wood E across environmental gradients using models such as those described here will enable sites to be closely matched to management regimes and clonal material to optimise product outturn and value.

ACKNOWLEDGEMENTS

We are indebted to the numerous forest companies and private owners for providing sites for the trial series, and Hugh Wilde, Trevor Webb, Amy Taylor, Wim Rijkse and Malcolm Mcleod who assisted in selection, identification and classification of soils. The help of technicians at the Landcare Research Environmental Chemistry Laboratory in analysing samples is gratefully acknowledged. The help of Robyn Simcock, John Dando, Murray Davis and George Estcourt in obtaining measurements used in this study is appreciated. We also gratefully acknowledge the assistance of Loretta Garrett in providing trial data. This project was funded by the New Zealand Site Management Co-operative and the New Zealand Foundation for Research Science and Technology under Contract No. C04X0304, 'Protecting and Enhancing the Environment through Forestry'.

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