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PRELIMINARY GROWTH AND YIELD MODELS FOR EVEN-AGED CUPRESSUS LUSITANICA AND C. MACROCARPA PLANTATIONS IN NEW ZEALAND

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ABSTRACT

Preliminary stand growth and yield models were constructed for even-aged *Cupressus lusitanica* Mill. and *C. macrocarpa* Hartw. plantations in New Zealand. Models that predict mean top height, basal area, initial basal area, post-thinning basal area, mortality, and total standing volume per hectare were fitted to permanent sample plot data biased towards younger ages. A wide range of height growth rates were observed, with site index estimates ranging from 15 to 35 m mean top height at age 30. Basal area models predicted greater basal area growth for *C. macrocarpa*. Exponential models predicted different rates of *C. macrocarpa* mortality in the North and the South Islands of New Zealand. All suitable data were used to fit models, preventing separation of independent validation data. The models were tested as a system of equations by comparing total standing volume predictions with data used to fit the models. Volume predictions were relatively imprecise, but unbiased overall across the range of available data.

Keywords: growth and yield model; stand growth; difference equation; non-linear mixed model; *Cupressus macrocarpa*; *C. lusitanica*.

INTRODUCTION

Even-aged *Cupressus lusitanica* (Mexican cypress) and *C. macrocarpa* (Monterey Cypress) plantations have been established in most regions of New Zealand (Miller & Knowles 1990). Over the last two decades, the New Zealand Forest Research Institute has developed a database of repeated measurements of tree diameter, height, and crown height from permanent sample plots within *C. lusitanica* and *C. macrocarpa* stands and silvicultural regime trials around New Zealand for growth and yield model development.

To date, published research on New Zealand-grown cypress has consisted mostly of evaluations of wood properties, wood quality and utilisation, genetics, and forest health.

- The attractive, scented, naturally durable cypress timbers have been used for exterior cladding, interior mouldings and panelling, boat building, and contemporary furniture making (Haslett 1986).
- Cypress timber utilisation (Somerville 1993) and drying studies (Haslett *et al.* 1985) have been performed.

- McKinley *et al*. (2000) reported whole-tree basic wood density for *C. lusitanica* and *C. macrocarpa* in New Zealand.
- *Cupressus lusitanica* and *C. macrocarpa* progeny trials were established in New Zealand the 1980s, and genetic parameters have been reported (Gea & Low 1997).

New Zealand-grown cypress is susceptible to cypress canker (*Seiridium unicorne* (Cooke & Ellis) Sutton and *S. cardinale* (Wagener) Sutton & Gibson) infection (Nicholas & Hay 1990) which Van der Werff (1988) found to be distributed across most New Zealand regions. Self & Chou (1994) assessed the influence of pruning on canker in *C. lusitanica.* The future role of cypress species in New Zealand will depend very much on the degree of canker, which does not appear to have stabilised.

Somerville (1993) studied the growth and utilisation of *C. macrocarpa* on one site in New Zealand. In a spacing trial in Tanzania, Malimbwi *et al*. (1992) found no significant differences in age-19 *C. lusitanica* height or wood properties between treatments. Even-aged *C. lusitanica* stand growth and yield has been modelled in Central America (Hughell & Chaves 1990; Jansen & Groenendijk 1994) and in eastern Africa (Pukkala & Pohjonen 1993; Ngugi *et al*. 2000; Teshome & Petty 2000). These studies confirmed that cypress stand height and basal area growth follows a sigmoid pattern. Sigmoidal functions commonly used to model biological growth include the Chapman-Richards (Richards 1959; Pienaar & Turnbull 1973), Gompertz (Winsor 1932), Hossfeld II (Hossfeld 1822, cited by Peschel 1938), and Schumacher (Schumacher 1939) functions, and the cumulative form of the 3-parameter Weibull probability density function (Weibull 1939; Yang *et al*. 1978). These equations are shown in yield form with yield (Y) as a function of age (T):

Chapman-Richards: $Y = a(1 - e^{-bT})^c$

Hossfeld II: $Y = \dfrac{aT^c}{b + T^c}$

Gompertz: $Y = ae^{-(e^{(c-bT)})}$

Schumacher: $Y = ae^{(-bT^c)}$

Weibull: $Y = a(1 - e^{-bT^c})$

Allowing the asymptote (a) or slope (b) parameter to change between sample plots or pairs of consecutive measurements gives families of curves that reflect growth differences between sites, ages, or management. This "local" parameter can be replaced by yield at age T_1 when the yield form is arranged in difference form to predict yield at age T_2. The anamorphic difference form with local asymptote gives curves with a common slope parameter and different asymptotes across the range of input values. The polymorphic form with local slope gives curves with different slopes that converge at one upper asymptote (Clutter *et al*. 1983). Polymorphic forms are renowned for superior representation of variability in site and other factors influencing biological growth (Mason & Whyte 1997; Ngugi *et al*. 2000). Starting values (yield at T_1) are needed for difference equation projections. Site index, the height of dominants at a given base age, or height-age data reflect local site quality, and provide starting values for height growth projections. Initial stand basal area starting values depend on site quality, stocking, and age. Initial basal area models can be developed to provide starting values for stand basal area models when actual young stand data are limited to stocking and age.

Natural competition-induced mortality has been modelled using the –3/2 power law of self-thinning (Yoda *et al.* 1963) or the size-density reference curve proposed by Reineke (1933). Woollons (1998) observed episodic mortality within even-aged *Pinus radiata* D. Don plantations in New Zealand, modelling this phenomenon with a combination of stochastic and empirical non-linear models that predict the probability of mortality occurring in any given time period, and the rate of mortality if its occurrence was predicted. Mortality models influence predictions of mean stand diameter based on stocking and stand basal area.

Thinning models that predict basal area reductions for a given stocking reduction are designed to reflect the predominant thinning strategy. Basal area reduction would be proportional to stocking reduction under a geometric thinning regime. Removal of smaller stems during thinning from below reduces basal area proportionally less than stocking. Unlike tree-level growth models that predict total standing volume as the sum of individual tree volumes, some stand-level growth models make predictions of total standing volume from predicted stand basal area and mean top height (e.g., Candy 1989).

This paper outlines the development of preliminary stand-level growth and yield models for even-aged *C. lusitanica* and *C. macrocarpa* plantations based on New Zealand sample plot and silvicultural field trial data. The five sigmoid functions listed above were evaluated as mean top height and stand basal area models. Initial basal area, post-thinning basal area, mortality, and volume models were also developed. These models can be used in combination to predict total standing volume per hectare and quadratic mean diameter based on actual starting data and prescribed thinning regimes. The data, model-fitting methodologies, resultant models, and their limitations are discussed.

METHODS

Data

Stand-level data were extracted from the New Zealand Forest Research Institute Permanent Sample Plot System (Pilaar & Dunlop 1990). The per-hectare summary data consisted of 1897 plot measurements from 166 *C. lusitanica* and 163 *C. macrocarpa* sample plots (Table 1). Mean top height and mean top diameter were calculated respectively as the average height and diameter of the 100 largest-diameter stems/ha. Basal area was

TABLE 1–*Cupressus lusitanica* and *C. macrocarpa* measurement data summary (n = 1897).

		Age (years)	Stocking (stems/ha)	Mean top height (m)	Mean top diameter (cm)	Basal area (m^2/ha)	Volume (m^3/ha)
C. lusitanica (n=1041)	Mean	12.7	687.1	12.3	26.2	21.9	132.6
	s.d.	9.5	421.3	5.8	11.6	17.2	158.7
	Min.	3.0	72.0	3.6	4.4	0.2	0.5
	Max.	70.0	2566	35.5	71.0	102.9	1029.8
C. macrocarpa (n=856)	Mean	17.1	821.3	13.6	27.6	28.8	206.0
	s.d.	14.2	580.5	7.9	14.4	27.1	294.8
	Min.	3.0	32.0	2.3	3.5	0.2	0.5
	Max.	74.3	4950	37.8	77.6	165.6	2106.5

calculated as the hectare sum of cross-sectional stem area at breast height 1.4 m. Total standing volume per hectare (inside bark) was calculated as the sum of individual tree volumes predicted by a tree volume equation. A height-diameter regression predicted total tree height for sample plot stems without height data. Mean annual volume increment (MAI) was calculated for each measurement within each sample plot. Maximum age and MAI data are listed in Table 2 by geographic region.

TABLE 2–*Cupressus lusitanica* and *C. macrocarpa* sample plot count, maximum age, and mean annual volume increment (MAI) by geographic region of New Zealand.

Region		*C. lusitanica*			*C. macrocarpa*		
		No. plots	Max. age	Max. MAI (m^3/ha)	No. plots	Max. age	Max. MAI (m^3/ha)
North Island	Northland	34	41	19.3	4	42	17.2
	Auckland	6	8	11.0	-	-	-
	Bay of Plenty	47	41	24.6	20	39	15.6
	Waikato	33	67	19.8	23	61	22.6
	Gisborne	20	31	20.3	3	4	6.3
	Hawke's Bay	10	28	26.0	-	-	-
	Taranaki	1	32	19.6	1	33	29.0
	Wanganui/Manawatu	3	31	17.5	10	34	20.0
	Wellington	3	13	18.5	6	51	22.9
	All regions	157	67	26.0	67	61	29.0
South Island	Nelson	1	13	11.4	8	36	4.7
	West Coast	8	14	9.2	7	16	18.9
	Canterbury	-	-	-	21	55	16.9
	Otago	-	-	-	53	72	36.1
	Southland	-	-	-	7	18	16.4
	All regions	9	14	11.4	96	72	36.1

Analysis

Models that predict mean top height, basal area, post-thinning basal area, mortality, initial basal area, and volume were fitted to *C. lusitanica* and *C. macrocarpa* data. All data from older plots were required for model fitting, preventing separation of independent validation data. Candidate models were evaluated in terms of accuracy and precision of predictions. The best models were tested in combination by comparing actual data and predicted values for the last measurement in each plot, using data from the first plot measurement as starting values.

Anamorphic and polymorphic difference forms of the five candidate sigmoid functions were fitted to pairs of consecutive mean top height and stand basal area measurements through Gauss-Newton non-linear least squares regression analysis executed by the SAS statistical analysis software PROC NLIN procedure (SAS Institute Inc. 1989). Functions were also fitted to the repeated sample plot measurements as mixed models using the SAS macro NLINMIX (Littell *et al.* 1996) where, for each sample plot, a random error term entered the asymptote (*a*) or slope (*b*) parameter of anamorphic and polymorphic forms respectively. The y-intercept (H_0) of the mean top height model was set to 0.3 m to reflect average seedling height at planting. The influence of pruning intensity on basal area growth was not modelled.

Basal area model starting values that covered a wide range of site qualities were obtained by predicting age-5 basal area for sample plots with stockings around 1100 stems/ha using the basal area model and actual basal area and age data for starting values. Initial basal area models that predict starting basal area values for an average site as a function of stocking and age were fitted as multiple linear and non-linear regression models to data from unthinned young (age 5–10) stands.

Average tree size and stand density data were plotted on logarithmic scales, and examined for density-dependent self-thinning patterns. Stocking and age data were organised into pairs of consecutive measurements. Models that predict stocking reduction from natural mortality and non-catastrophic windthrow, post-thinning basal area from stocking before and after thinning and pre-thinning basal area, and total standing volume from mean top height and stand basal area were fitted as non-linear least squares regression models.

Individual models were tested for goodness of fit across all pairs of measurements, across the range of predicted values, ages, and stockings, and by comparing predictions of the last measurement based on the first measurement for each sample plot. Prediction errors were calculated in real terms, as the mean difference between predicted and actual values. Errors were summarised as the average and standard deviation of all prediction errors, and as the mean error sum of squares (RMSE) calculated as the sum of squared errors divided by the number of degrees of freedom. The coefficient of determination (R^2) was calculated for each model, adjusted for degrees of freedom, as

$$R^2_{adj.} = 1 - \frac{SSE / df_{Error}}{SST / df_{Total}}$$

where SSE = error sum of squares;
SST = total sum of squares;
df_{Total} = n–1 observations or consecutive pairs of time series data;
df_{Error} = n–k–1 where k = number of explanatory variables in multiple linear regression models, or the number of model parameters in non-linear regression models including the number of fixed effects in non-linear mixed models.

Overall model significance tests (F-tests) consistently returned probabilities of for the model F-value, failing to exceed the critical F-statistic (Pr.>F) of <0.0001; they were therefore not reported. Individual models were considered for further testing only when individual parameter estimates were statistically significant at the 95% level of confidence. This criterion was met when the t-value for linear model parameter estimates exceeded the critical t-statistic (Pr.>t) of 0.05, or when the approximate 95% confidence interval for non-linear model parameter estimates did not include zero.

The most suitable individual models were applied in combination as a system of equations to predict standing volume per hectare and quadratic mean diameter at the last measurement for all sample plots with stocking, mean top height, and basal area data. Predicted quadratic mean stand diameter was calculated as the diameter of a stem with average basal area for any predicted stocking and basal area per hectare. Data from the first measurement in each sample plot were used as model starting values, permitting comparison of the latest measurement data with model predictions of mean top height, basal area, thinning, mortality, volume, and diameter for that age. Volume model predictions were based on predicted mean top height and basal area. Actual and predicted final measurements from a range of starting ages were compared to examine the influence of starting age and projection period length on model predictions. Minimum starting ages of 3 (all data), 5, 10, 15, and 30 were tested; data from the first measurement above the minimum starting age were used as starting values for each sample plot. Actual and predicted volume growth was depicted graphically for six *C. lusitanica* and six *C. macrocarpa* sample plots with a long history of re-measurement.

The models were applied in combination to demonstrate total standing volume and quadratic mean diameter development in managed stands. Projections were based on age-5 starting values for *C. lusitanica* and *C. macrocarpa* at 1100 stems/ha located on relatively good and average sites, defined as the ninetieth and fiftieth percentiles of available height and basal area data, respectively. Thinning to three final crop stockings (200, 400, and 800 stems/ha) at age 10 was simulated to demonstrate the predicted influence of stocking on volume and average tree size to age 35.

Results

Mean Top Height Model

Models fitted to mean top height data for individual species did not improve overall prediction accuracy and precision when compared with models fitted to data from both species combined. The polymorphic Chapman-Richards mixed mean top height model with local slope (b) exhibited the least prediction error and greatest precision across all measurement pairs, stockings, and ages, and when predicting mean top height of the last measurement for each sample plot. The polymorphic difference form with local slope predicts mean top height H_2 at age T_2 dependent on starting values of mean top height H_1 and age T_1 (Equation 1).

$$H_2 = a\left[1 - \left\{1 - \left[\frac{H_1 - 0.3}{a}\right]^{\frac{1}{c}}\right\}^{\left(\frac{T_2}{T_1}\right)}\right]^{c} + 0.3 \qquad (1)$$

Parameter estimates (and their standard errors) for the polymorphic Chapman-Richards model ($R^2 = 0.99$) were

$a = 44.2944$ (0.9) $b = 0.03131$ (0.001) $c = 1.1166$ (0.01)

Mean top height at age 30 (site index) was predicted for all height-age data. Average site index estimates for each cypress species sampled within each forest were summarised by species, and by species on the North and South Islands (Table 3). Mean top height growth curves that approximately encompass the range of site index estimates for all forests are shown in Fig. 1.

Mean top height model fit statistics across all pairs of measurements and by plot, from the first to last plot measurement, were calculated (Table 4). Prediction errors were plotted against predicted mean top height values (Fig. 2).

TABLE 3–Summary statistics for average forest site index estimates. Forest-level averages for industrial plantations and farm woodlots were calculated from site index estimates for each height-age data pair from all plots on the forest.

	C. lusitanica			*C. macrocarpa*		
	New Zealand	North Island	South Island	New Zealand	North Island	South Island
n	46	42	4	47	20	27
Min.	14.5	14.5	15.4	14.8	19.7	14.8
Twenty-fifth percentile	23.0	23.8	18.4	22.0	24.5	21.1
Mean	25.8	26.3	20.7	23.9	25.9	22.4
Seventy-fifth percentile	29.3	29.4	22.9	25.6	27.1	24.0
Max.	34.0	34.0	26.3	31.6	31.6	28.6

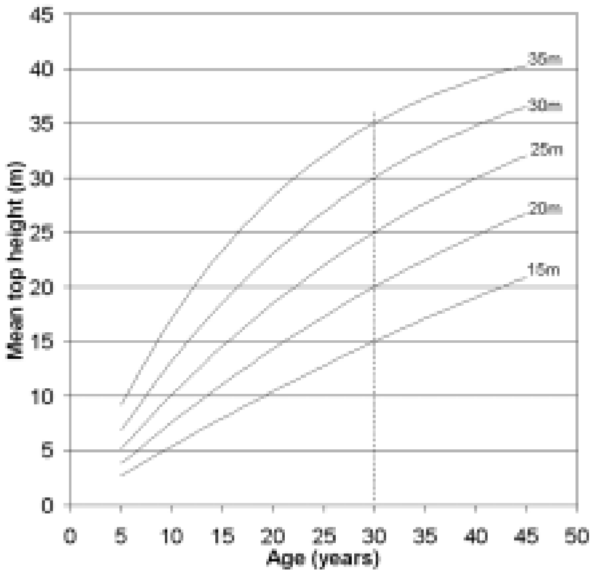

FIG. 1–Mean top height-age curves for *C. lusitanica* and *C. macrocarpa*. Site index defined as mean top height (m) at base age 30 years.

TABLE 4–Mean top height model error statistics for measurement pairs and entire plot history. Errors expressed in real terms: predicted-actual (m). RMSE = mean error sum of squares.

	All pairs	By plot	
		C. lusitanica	*C. macrocarpa*
n	1570	166	154
Mean error (m)	–0.059	–0.25	–0.46
s.d. of errors	0.468	1.05	1.10
RMSE	0.223	1.19	1.45

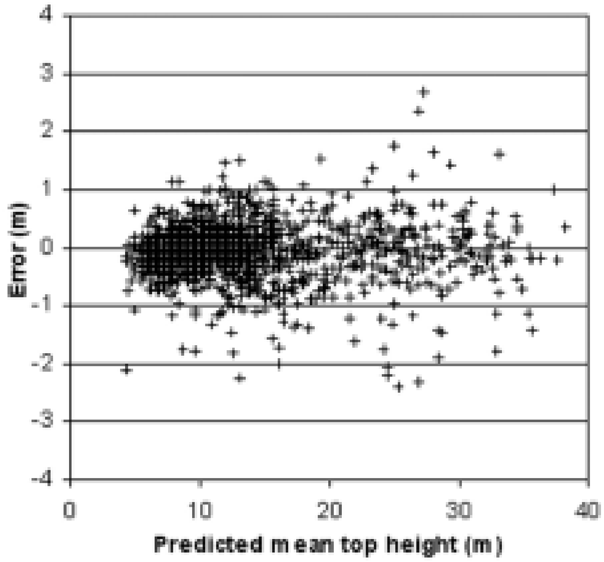

FIG. 2–Chapman-Richards polymorphic mean top height model error chart (n=1570).

Basal Area Model

All difference and mixed models of *C. lusitanica* and *C. macrocarpa* basal area growth fitted the data poorly and made unreasonable predictions. Site index predicted for each plot was incorporated into basal area models, but did not improve predictions. Coefficients for age when basal area at breast height (1.4 m) was zero were not significant. Model fit was improved by discarding measurements above age 60, and *C. macrocarpa* plots from the Rotoehu Forest spacing trial in the Bay of Plenty, where high levels of cypress canker infection and mortality were observed. Of all models tested, the polymorphic Schumacher basal area model, fitted in difference form with the slope parameter *b* isolated (local) in the algebraic difference formulation, exhibited the lowest mean prediction error and RMSE for each species. The model also made the most accurate and precise predictions of basal area at the last measurement based on the first measurement in each sample plot. The polymorphic difference form predicts basal area BA_2 at age T_2 dependent on starting values of basal area BA_1 and age T_1 (Equation 2).

$$BA_2 = a^{1-\left(\frac{T_2}{T_1}\right)^c} BA_1^{\left(\frac{T_2}{T_1}\right)^c} \tag{2}$$

Parameter estimates (and their standard errors) for the polymorphic Schumacher basal area model (R^2=0.99) were

C. lusitanica	a = 151.1 (9.8)	c = –0.8231 (0.03)
C. macrocarpa	a = 248.7 (19.2)	c = –0.7842 (0.03)

Model fit statistics were calculated for measurement pairs and plots used to fit the model (Table 5). Prediction errors were plotted against predicted basal area for all *C. lusitanica* and *C. macrocarpa* data pairs (Fig. 3).

TABLE 5–Basal area model error statistics for all measurement and plot pairs. Errors expressed in real terms: predicted-actual.

	All pairs		By plot	
	C. lusitanica	*C. macrocarpa*	*C. lusitanica*	*C. macrocarpa*
n	884	742	166	157
Mean error (m^2/ha)	–0.046	0.093	–0.62	0.29
s.d. of errors	1.083	1.782	4.40	6.66
RMSE	1.177	3.191	20.0	45.0

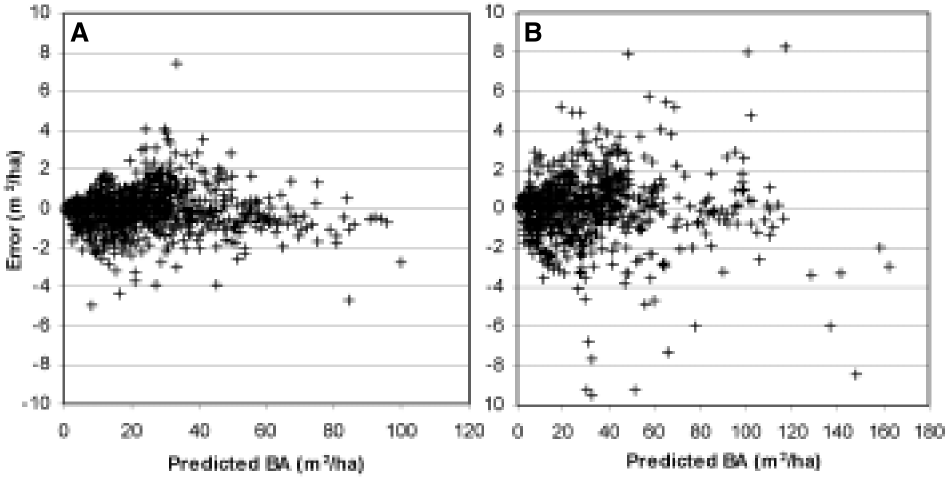

FIG. 3–Schumacher polymorphic *C. lusitanica* (A) (n=884) and *C. macrocarpa* (B) (n=742) basal area model error chart.

Initial Basal Area Model

Annual basal area increments in young unthinned stands increased with age in some plots and decreased in others. As result, non-linear models fit the data poorly. Skewed stocking data were log transformed. A multiple linear regression of basal area as a function of age T and the natural logarithm of stocking predicts basal area BA for a defined age T and stocking N within an average unthinned stand between 200 and 2000 stems/ha between ages 5 and 10 years (Equation 3).

$$BA = a + bT + cLn(N) \qquad (3)$$

Parameter estimates (and their standard errors) for the multiple linear regression (R^2=0.48) were

C. lusitanica $a = -59.6840$ (4.07) $b = 2.9238$ (0.19) $c = 7.8847$ (0.53)

C. macrocarpa $a = -76.8092$ (5.53) $b = 3.2940$ (0.24) $c = 9.5498$ (0.72)

The performance of the model was evaluated in terms of mean prediction error and RMSE (Table 6). Prediction errors were plotted against predicted initial basal area (Fig. 4).

TABLE 6–Initial basal area model error statistics. Errors expressed in real terms: predicted-actual.

n	700
Mean error (m^2/ha)	0.0002
s.d. of errors	5.82
RMSE	34.1

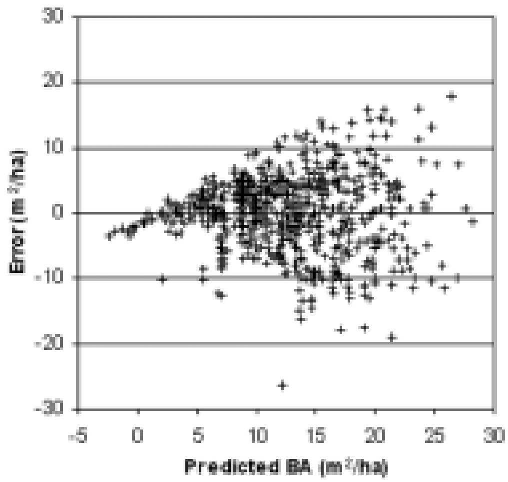

FIG. 4–Initial basal area model error chart (n=700).

Thinning Model

The thinning model predicts post-thinning basal area (BA_2) as a function of pre-thinning basal area (BA_1) and stocking before (N_1) and after (N_2) thinning (Equation 4).

$$BA_2 = BA_1 \left(\frac{N_2}{N_1} \right)^a \tag{4}$$

The parameter estimate (and its standard error) for the power model ($R^2 = 0.98$) were $a = 0.706$ (0.013). Model fit statistics were calculated for predictions across all thinned basal area data pairs (Table 7). Ratios of post- to pre-thinning stocking and basal area data and model predictions, and prediction errors plotted against predicted post-thinning basal area, are shown in Fig. 5.

TABLE 7–Thinning model error statistics. Errors expressed in real terms: predicted-actual.

n	107
Mean error (m^2/ha)	–0.146
s.d. of errors	0.946
RMSE	0.916

Mortality Model

The most satisfactory model in terms of goodness-of-fit to both species- and Island-specific data, an exponential function, predicts stocking N_2 at age T_2 from stocking N_1 and

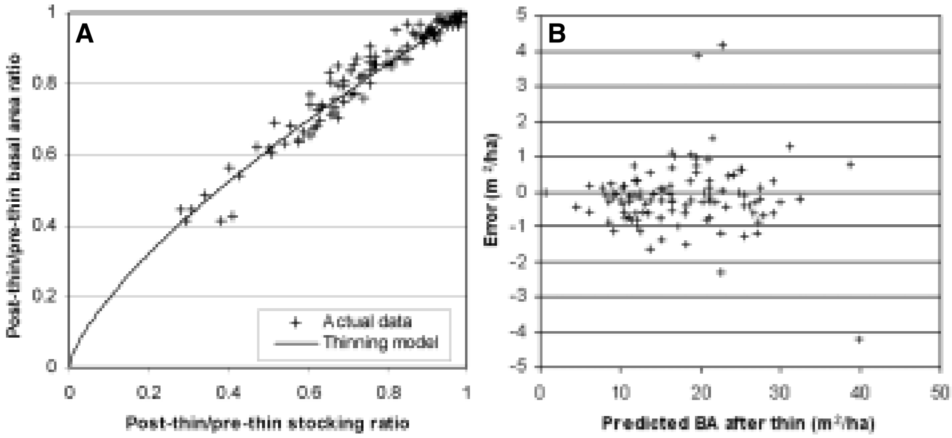

FIG. 5–Ratio of post- to pre-thinning stocking and basal area data and thinning model predictions (A) and thinning model error chart (B) (n=107).

age T_1 for each cypress species on the North and South Islands of New Zealand (Equation 5).

$$N_2 = N_1 e^{a(T_2 - T_1)} \tag{5}$$

Parameter estimates and their standard errors for national and Island-specific models (R^2 >0.99 for all models) are given in Table 8. Larger t-values indicate greater statistical significance of the parameter estimates. Parameter estimates for North and South Island *C. macrocarpa* differed by more than two standard errors, and were considered significantly different. North and South Island *C. lusitanica* parameter estimates did not differ significantly from the New Zealand *C. lusitanica* estimate (Table 8).

Mortality model fit statistics were calculated for functions fitted to all data, separate species, and to data from the North and South Islands of New Zealand (Table 9). Predictions from age-5 starting data (Fig. 6) and prediction errors (Fig. 7) were plotted for the Island- and species-specific models.

TABLE 8–Mortality model parameter estimates, standard errors and t-statistics by species and Island; n = No. pairs of consecutive stocking data. Significance levels: *=99%; **=99.9%.

	C. lusitanica				*C. macrocarpa*			
	n	Estimate	s.e.	t	n	Estimate	s.e.	t
New Zealand	888	–0.00976**	(0.0009)	–11	745	–0.00385**	(0.0004)	–11
North Island	874	–0.00968**	(0.0008)	–16	324	–0.0283**	(0.002)	–15
South Island	14	–0.0154*	(0.007)	–3.1	421	–0.00255**	(0.0003)	–6.2

TABLE 9–Mortality model error statistics for models fitted to all data, for each species, and each island of New Zealand (n=1633). Errors expressed in real terms: error = predicted-actual.

	All data	Separate species	Separate species by island
Mean error (stems/ha)	6.534	4.771	1.558
s.d. of errors	30.40	30.37	28.24
RMSE	966.7	945.2	801.4

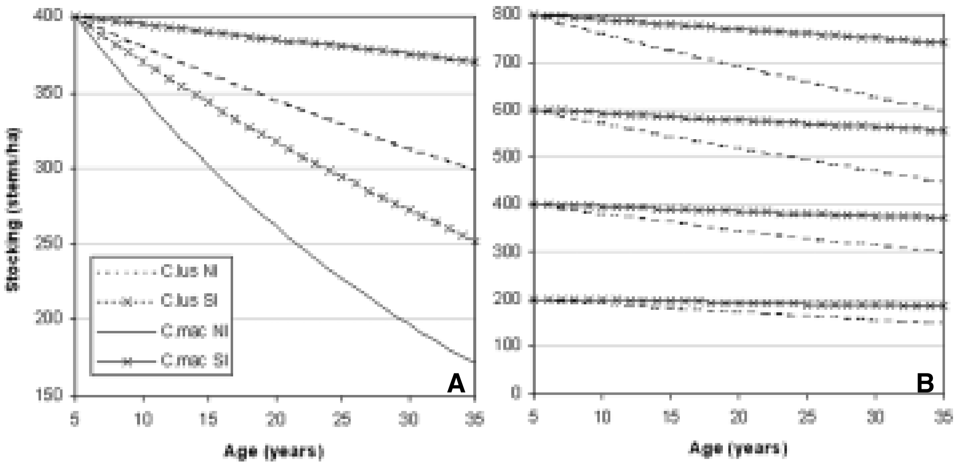

FIG. 6–New Zealand island- and species-specific mortality model predictions for 400 stems/ha at age 5 (A), and North Island *C. lusitanica* and South Island *C. macrocarpa* stands with 200, 400, 600, and 800 stems/ha at age 5 (B).

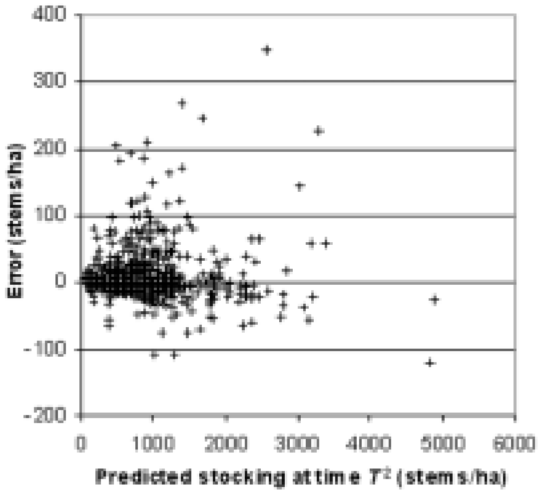

FIG. 7–New Zealand island- and species-specific mortality model prediction error chart (n=1633).

Volume Model

The most satisfactory volume model, proposed by Candy (1989) for *P. radiata* in Tasmania, was fitted by non-linear least squares, predicting total standing volume V as a function of basal area BA and mean top height H (Equation 6).

$$V = e^{(a + bLn(H) + cLn(BA))} \quad (6)$$

Parameter estimates (and their standard errors) for the volume model ($R^2 = 0.999$) were

$a = -0.5815$ (0.0053) $b = 0.8863$ (0.0025) $c = 0.9791$ (0.0015)

Volume model fit statistics were calculated for all data, and for each species (Table 10). Prediction errors were plotted against predicted standing volume (Fig. 8).

TABLE 10–Volume model error statistics. Errors expressed in real terms: predicted-actual.

	All data	*C. lusitanica*	*C. macrocarpa*
n	1895	1041	854
Mean error (m^3/ha)	0.02	0.44	–0.49
s.d. of errors	6.24	4.93	7.51
RMSE	38.9	24.5	25.5

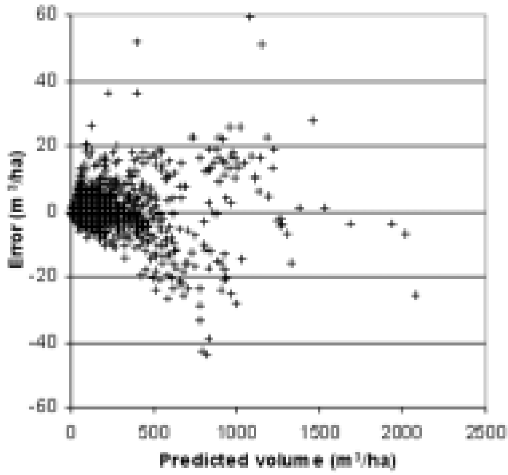

FIG. 8–Volume model error chart (n=1895).

Testing Model Predictions

Volume prediction error statistics were calculated for each minimum starting age in real and percentage terms, as the mean and standard deviation of all prediction errors, minimum and maximum error, and RMSE for the last measurement from *n* sample plots (Table 11).

TABLE 11–*Cupressus lusitanica* and *C. macrocarpa* total standing volume (m^3/ha) prediction error statistics for the last measurement in each sample plot predicted from minimum starting ages of 3, 5, 10, 15, and 30 years. Errors expressed in real (m^3/ha) and percentage terms.

Min. start age	n	Error (m^3/ha)	Error (%)	s.d. (m^3/ha)	s.d. (%)	min. (m^3/ha)	min. (%)	max. (m^3/ha)	max. (%)	RMSE (m^3/ha)	RMSE (%)
C. lusitanica											
3+	166	–5.0	–4.2	35	23	–145	–90	98	52	1262	457
5+	150	–4.0	–0.7	36	20	–145	–79	98	52	1373	332
10+	88	–9.1	–1.2	38	14	–145	–43	98	27	1616	200
15+	47	–18.5	–4.3	40	9	–145	–33	98	22	2166	112
30+	13	–27.0	–4.3	40	6	–109	–17	30	5	3611	85
C. macrocarpa											
3+	155	–4.1	–2.4	55	28	–350	–94	170	70	3088	785
5+	150	–4.0	–1.	56	26	–350	–94	170	70	3190	677
10+	112	0.9	3.8	61	17	–350	–56	162	62	3827	333
15+	53	–16.6	–3.0	80	17	–350	–56	162	40	7292	334
30+	31	–4.8	0.8	89	12	–350	–22	152	37	9253	178

Volume prediction errors were plotted against projection period length for all plots in percentage terms (Fig. 9). Model predictions of total standing volume were compared with data from six *C. lusitanica* (Fig. 10) and six *C. macrocarpa* (Fig. 11) sample plots with a long history of remeasurement. The predicted influence of site quality and final crop stocking on standing volume and average tree size development is demonstrated in Fig. 12. The models predict greater total standing volume and quadratic mean diameter development in *C. macrocarpa* stands than in *C. lusitanica* stands, based on starting values for relatively good and average sites (Fig. 12). The ninetieth percentile (7.5 m) and average (5.5 m) of all mean top height data were used as age-5 starting values to represent relatively good and average sites, respectively. Basal area starting values were based on the ninetieth percentile and average basal area in unthinned *C. lusitanica* and *C. macrocarpa* stands with approximately 1100 stems/ha at age 5 years (Table 12).

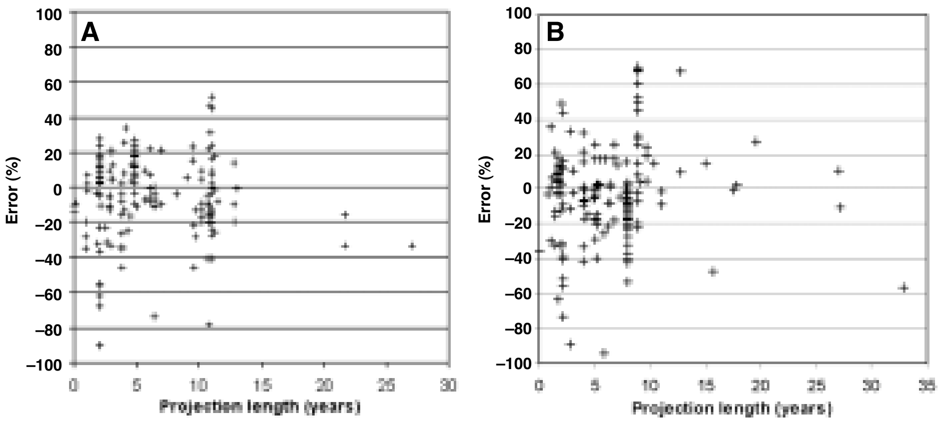

FIG. 9–Influence of projection period length on percentage errors for *C. lusitanica* (A) (n=166) and *C. macrocarpa* (B) (n=155) volume predictions at the last measurement for all plots (n=321).

DISCUSSION

Stand-level variables such as mean top height could not be calculated in some instances because of missing data. Thinning was recorded only at some measurements. Thus, individual models were fitted to different numbers of data, giving different degrees of freedom and operating ranges. Minimum and maximum stand-level data define the model operating range for each species (Table 1). Projections are not recommended where very few data were available — above 2000 stems/ha, starting below age 5, and to later ages, especially beyond age 45 and age 60 for *C. lusitanica* and *C. macrocarpa* respectively.

The range of site index estimates for sample plots across New Zealand (approx. 15–35 m at age 30), obtained using the polymorphic Chapman-Richards mixed mean top height model, showed that height growth varied widely between stands (Fig. 1). Height-age data for *C. lusitanica* plantations in Ethiopia also varied widely between sample plots, with both greater (12–27 m at age 15— Teshome & Petty 2000) and lower (15–25 m at age 30 — Pukkala & Pohjonen 1993) rates of height growth reported. Jansen & Groenendijk (1994) used the Chapman-Richards equation to describe *C. lusitanica* height growth in Costa Rica;

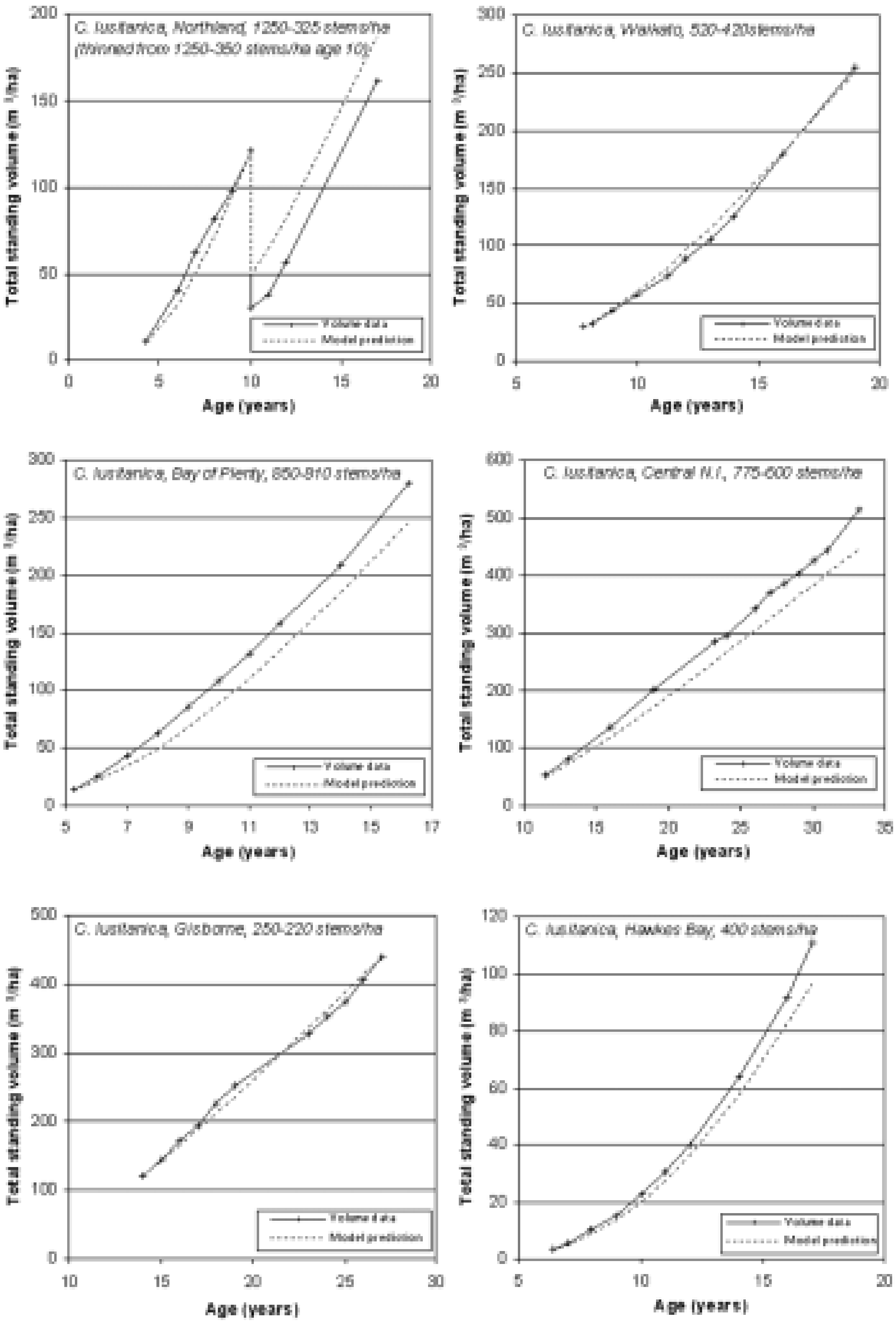

FIG. 10–*Cupressus lusitanica* total standing volume (m^3/ha) data and model predictions for six North Island plots. Stocking (stems/ha) data given for beginning and end of projection period.

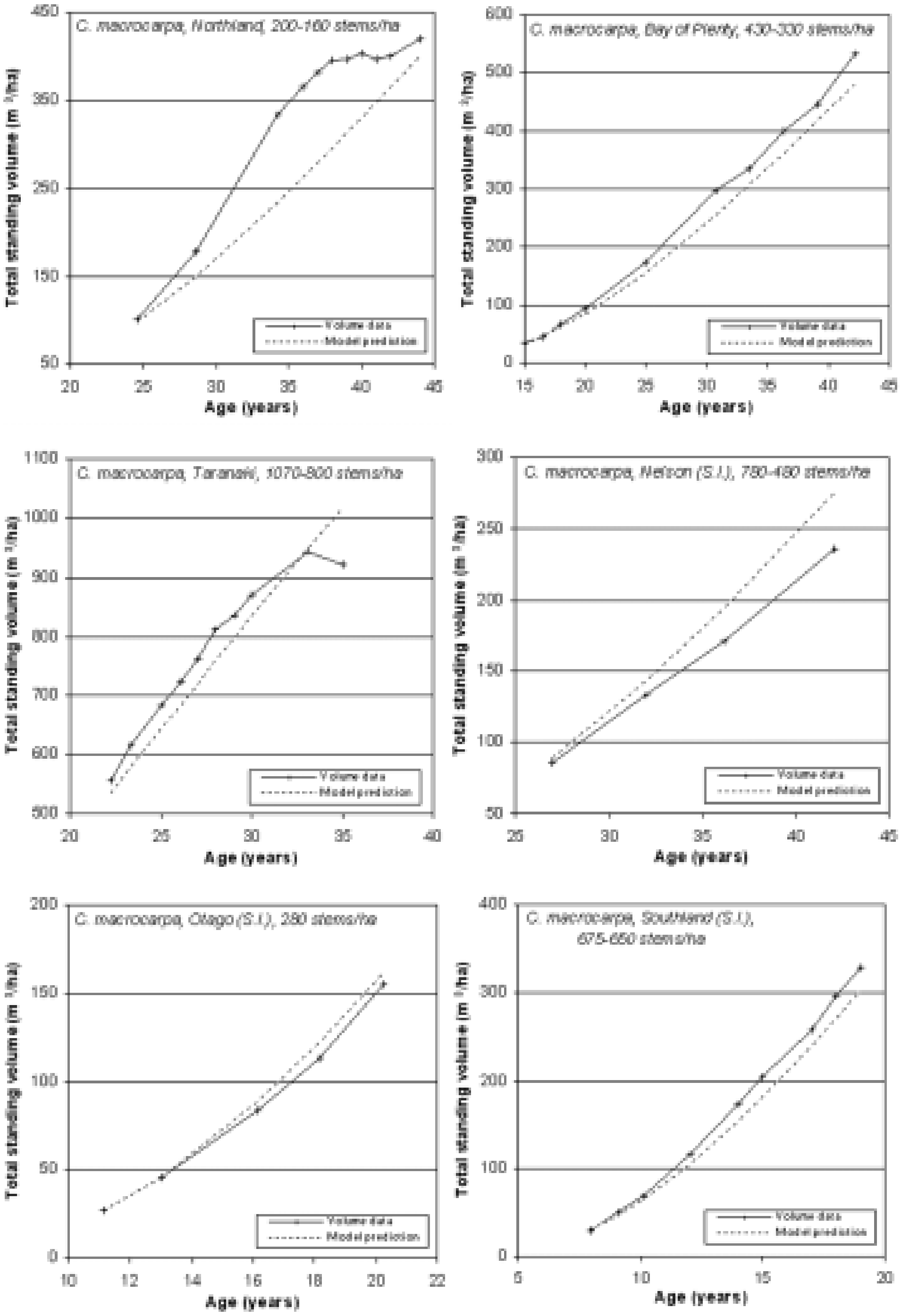

FIG. 11–*Cupressus macrocarpa* total standing volume (m^3/ha) data and model predictions for three North Island and three South Island (S.I.) sample plots. Stocking (stems/ha) data given for beginning and end of projection period.

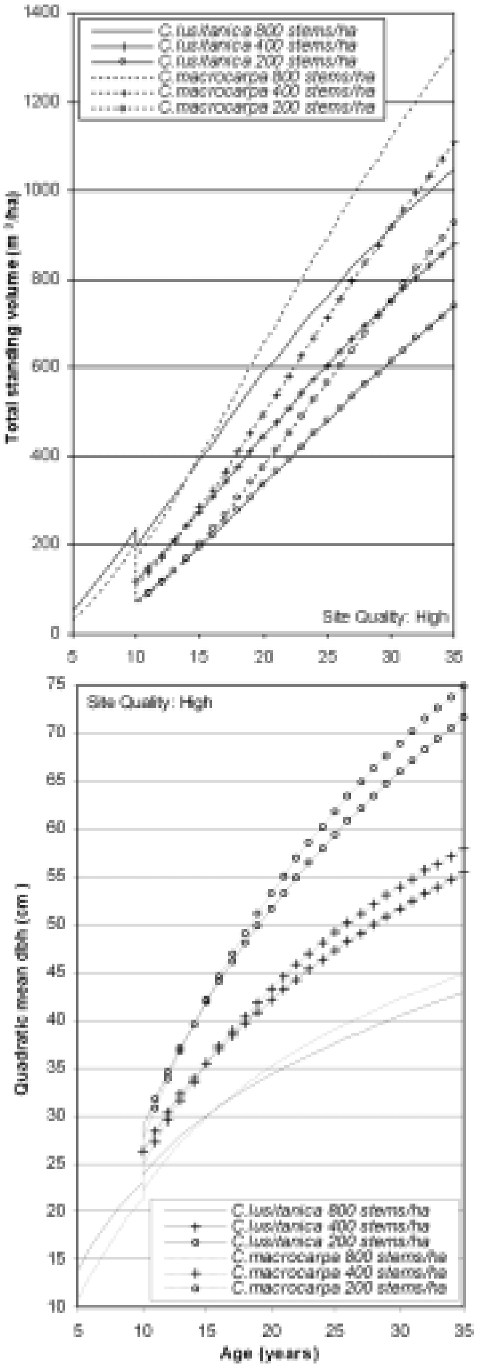

FIG. 12–Total standing volume (m^3/ha) and quadratic mean diameter (cm) predictions for *C. lusitanica* and *C. macrocarpa* stands starting at 1100 stems/ha at age 5, thinned to three final crop stockings (200, 400, and 800 stems/ha) at age 10. Site quality "High" and "Average" represent the ninetieth percentile and the mean of height and basal area data, respectively.

Teshome & Petty (2000) and Ngugi *et al*. (2000) used the Schumacher equation to describe *C. lusitanica* height growth in East Africa.

All models fitted to the basal area data, including the best-fitting polymorphic Schumacher model, had large standard errors for fitted asymptote parameter estimates, indicating that more (older) data were needed to develop robust basal area models. The Schumacher equation has also been used to describe *C. lusitanica* basal area growth in Kenya (Ngugi *et al*. 2000). The basal area models apply to pruned stands because the data originated predominantly from stands that received some level of clear-bole pruning. Too few post-thinning data were available to model thinning response. The basal area model assumes that post-thinning basal area growth is equivalent to the growth of stands with the same age and basal area as the residual thinned stand. The thinning function predicts a lower percentage decrease in basal area for a given percentage stocking reduction, with an associated increase in mean stand diameter. The data and model reflect the pre-commercial "thinning from below" or "thinning to waste" strategy where larger, healthier, more vigorous stems are favoured through removal of smaller stems (Fig. 5).

Unlike data presented by Reineke (1933) for even-aged stands of native and exotic tree species growing in California, no clear upper limit of size-density relations was detected. Either too few data from fully stocked stands were available, or external factors such as cypress canker and wind were pre-empting density-dependent mortality within cypress plantations. Stocking reduction data where the cause of mortality was attributed to windthrow were separated from all other stocking reduction data. Approximately one-third of all *C. lusitanica* mortality (33.5%) was ascribed to wind; the number of *C. macrocarpa* stems killed by wind, expressed as a percentage of all mortality, was low (2.9%). Non-linear mortality models fitted all data poorly. Incorporation of aspect and elevation did not improve mortality predictions. The analysis revealed significantly different rates of mortality between the Islands of New Zealand. An exponential model gave the most satisfactory predictions when fitted to data from the North and South Islands. The number of data, and thus reliability of predictions, varied widely between regions for both species. The mortality model parameter estimates imply that mortality rates vary between species and Islands (Fig. 6; Table 8). While higher mortality was predicted for *C. lusitanica* on average over New Zealand, *C. macrocarpa* mortality rates were consistently higher in North Island regions where both species were represented.

The wide range of basal area estimates (Table 12) for cypress stands with approximately 1100 stems/ha at age 5 years, implies that the high error variance and low R^2 (0.48) for the initial basal area model (Fig. 4; Table 6) could be ascribed largely to differences in site quality. Since basal area growth in young stands varied widely between sites, local basal area and age data should provide less biased starting values than the national average

TABLE 12–Predicted age-5 basal area (m^2/ha) starting values by species for about 1100 stems/ha on relatively good, above-average, average, and poor sites (n=62).

	Ninetieth percentile	Seventy-fifth percentile	Fiftieth percentile	Twenty-fifth percentile
C. lusitanica (n=30)	16.8	15.6	9.6	5.3
C. macrocarpa (n=32)	10.0	7.8	6.2	4.7

predicted by the initial basal area model. The ninetieth, seventy-fifth, fiftieth, or twenty-fifth percentiles of age-5 basal area could be used as starting values for 1100 stems/ha planted on relatively good, above-average, average, and poor sites respectively (Table 12).

Comparing actual and predicted final measurements for each sample plot tested model predictions; the earliest measurement data above a range of minimum starting ages from each plot were used as starting values (Table 11). Overall, volume predictions were within 5% of actual values on average for each cypress species, for each starting age tested, but prediction errors for individual plots were highly variable (Fig. 9). The variability in prediction errors decreased with increasing starting age. This result may be an artifact of the paucity of data from older stands, but implies that the oldest available data should be used for starting values. Large minimum and maximum errors across the range of starting ages were traced back to basal area model prediction errors. Even the most satisfactory basal area model could not completely account for the wide range of growth rates. This variability was reflected in the large standard errors for the asymptote parameter estimates, which differed significantly between species. The basal area models should be assigned highest priority for revision once more data are obtained.

The projections of standing volume and tree diameter development in *C. lusitanica* and *C. macrocarpa* stands demonstrate the important influence of site quality and final crop stocking on stand growth and yield. The models predicted greater volume and tree size development in *C. macrocarpa* stands than in *C. lusitanica* stands of equivalent stocking (Fig. 12). Part of this difference was related to the starting values, which were based on a small number of young stands and differed between species (Table 12); however, the analysis of basal area data showed that the *C. macrocarpa* stands sampled exhibited more rapid basal area growth to later ages for any given stocking. The greatest volume growth (MAI) was recorded in *C. macrocarpa* stands on the North and South Islands (Table 2). However, maximum regional MAI is likely to be under-estimated because of the small sample sizes, and because of the sampling bias towards young or thinned stands that were still approaching maximum MAI. The greatest MAI (36.1 m^3/ha) was recorded in Otago *C. macrocarpa* standing at 1300 stems/ha at age 58. Most data originated from central North Island and Otago sample plots and silvicultural field trials (Table 2).

Models were fitted to a dataset lacking older data from fertile farm sites. Some data were collected from older stands with little genetic improvement, but most data came from young silvicultural field trials and plantations with few plot measurements. As can be seen from the summary statistics provided in Table 1, the data were not normally distributed but were skewed toward younger ages and lower stand-level parameters. While the model parameters were correctly estimated given the data at hand, they may not be efficient due to sampling bias towards younger ages, fertile sites, and improved planting stock. Inefficient parameter estimates could lead to serious prediction errors over long projection periods to later ages. Data were not available for both cypress species in some regions (Table 2), and so the preliminary models do not apply to all regions of New Zealand. All suitable data were required for model fitting, preventing separation of independent validation data. Comparing predictions with data used to fit the models tested but did not rigorously validate the preliminary models. Independent data should be collected from new sample plots within older stands, and by taking later measurements within existing *C. lusitanica* and *C. macrocarpa* permanent sample plots, for model validation and revision.

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