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Development of a height-diameter model for New Zealand grown tōtara (*Podocarpus totara* G. Benn. ex D. Don)

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Abstract

Background: Robust species-specific height-diameter (H-D) equations are necessary for the estimation and prediction of tree volume, yield, biomass or carbon stocks. In addition, information about height growth characteristics allows for the analysis of stand growth dynamics. But there is a general lack of species-specific growth models for most New Zealand native tree species considered for plantation and wood production. Therefore, the aim of this study was to develop a species- and site-specific H-D model for planted lowland tōtara (*Podocarpus totara* G. Benn. ex D. Don).

Methods: The models were developed using data from 719 individually measured trees aged 11 to 110 years from eight different sites in the North Island of New Zealand. Two different modelling approaches, traditional non-linear and linear mixed effect, were used. The process included selecting, testing, conditioning, and extending a total of 18 different equations by incorporating site-specific tree variables.

Results: The most precise model predicting the H-D relationship was reported by linear mixed-effect models that include diameter at breast height (DBH at 1.4 m, cm) and age (years). The final model had a low root mean square error (RMSE, 0.21, m), mean absolute error (MAE, 0.16, m) and high R^2 (0.94), which slightly increased during validation.

Conclusions: The study demonstrated a robust process and reported the most plausible and parsimonious model to predict *P. totara*'s H-D relationship, which serves as the basis for species-specific growth dynamics. The reported models provide for the first time the opportunity to predict the H-D relationship of planted *P. totara* in New Zealand. This fills a long existing knowledge gap and provides forest growers and managers important decision-making information.

Keywords: *Podocarpus totara*, height-diameter function, indigenous forest, linear mixed-effect model, growth modelling

Introduction

Lowland tōtara (*Podocarpus totara* G. Benn. ex D. Don) is an endemic indigenous conifer species of great cultural significance to Māori (Barstow 1878; Simpson 2017) and is found throughout New Zealand (Colenso 1868; Cheeseman 1871; Krik 1884). The species has been extensively used by European settlers due to its ease of use and the natural durability of its heartwood (Ebbett 1992; Bergin 2009; Page & Singh 2014). This has depleted old-growth indigenous forest in most parts of the country, creating a scarcity of native high-value timber (Bergin & Kimberley 2012). But *P. totara* has excellent potential for plantation

(Smail & Steward 2015), as it can tolerate a wide range of sites (Bergin 2009; Simpson 2017), has proven wood quality (Page & Singh 2014) and promising growth rates (Bergin & Kimberley 2003). Furthermore, it is one of the major species that occurs in nearly all regions of the country (Hinds & Reid 1957).

Recognising its potential, *P. totara* plantations have been established at scale for well over a century (Department of Lands 1909). Apart from using *P. totara* for timber production, it is nowadays also planted throughout New Zealand for other reasons such as forest restoration, to create shelter, or to enhance native faunal biodiversity as a habitat and food source

(Pardy et al. 1992; Bergin & Kimberley 2003). Currently, a mosaic of young and semi-mature *P. totara* and grazed pasture is a characteristic feature of the landscape throughout New Zealand. In the Northland region, prolific *tōtara* regeneration in the pastoral landscapes has coined the term, “farm-totara”. It offers the potential to be managed and improved as a long-term sustainable timber resource (Smaill & Steward 2015; Steward & Quinlan 2019).

While planted *tōtara* on cleared land can be harvested without constraint, existing or regenerating indigenous (native) forest must be managed under the provisions of Part IIIA of the *Forests Act 1949* through Sustainable Forest Management (SFM) Plans or Permits administered by Te Uru Rākau (Forestry New Zealand). These plans require comprehensive pre-harvest inventory estimates of standing merchantable volume (Steward 2020). To ensure a sustainable management of *P. totara*, it is therefore necessary to understand its growth dynamics, especially the relationship between height and diameter (H-D). This is because, accurate H-D functions are fundamental to estimate stand development over time (Temesgen & Gadow 2004).

Due to the cost of data collection, it is common practice in forestry to sample units of target populations and use models to make predictions about the whole population. In this context, H-D models that are based on a limited number of measured tree heights and tree diameters can be constructed and used to predict the heights of all trees in any stand (Mehtätalo 2004; Adame et al. 2008). These H-D models can be used to compute different tree and stand characteristics (Curtis 1967) such as the standing volume of trees and forest stands (Tomppo et al. 2010). Apart from the estimation of merchantable timber, stemwood volume can be used to estimate other parameters, such as biomass or carbon stocks (Albaugh et al. 2009; Jagodziński et al. 2017). Additionally, information about tree height allows for the analysis of future stand growth dynamics (Kulej & Socha 2008; Kazimirović et al. 2024) and can often be integrated into other modelling systems (Härkönen et al. 2019).

In H-D models, height (H) estimates are generally expressed as a function of diameter at breast height (DBH) and may include stand level variables (Liu et al. 2017). DBH-based functions are local and may not adapt well to different site conditions, whereas including stand variables provides a generalised solution (Soares & Tomé 2002). A good H-D model should exhibit monotonic increment, an inflection point, and an asymptote, typically forming sigmoidal (S-shaped) curves (Yuancai & Parresol 2001). This curve is characterised by a lower asymptote from which the growth increases until a maximum point of inflection is reached. Thereafter the growth rate declines towards zero at an upper asymptote (Salas-Eljatib et al. 2021). Limited datasets may necessitate concave curves (Adame et al. 2008).

Furthermore, H-D models must be flexible, biologically interpretable, and accommodate nested-stochastic structures, such as trees within plots (West et al. 1984; Gregorie 1987). Traditional generalised statistical modelling techniques often fall short to adequately

incorporate such structures. Therefore, mixed modelling methods that integrate repeated measurements and explain random variation are nowadays used (Hökkä 1997; Lappi 1997; Bronisz & Mehtätalo 2020). But it is essential to calibrate species-specific functions with appropriate site-specific variables.

To date, several studies have focused on understanding *P. totara* growth dynamics and conditions (Colenso 1868; Ebbett 1992; Bergin & Kimberley 2012). A few studies have attempted to develop growth and yield models, either generic for multiple native tree species (Ellis 1978) or specific to *P. totara* (Bergin & Kimberley 2003). Among these, Bergin and Kimberley (2003) developed height-age and diameter-age relationship equations separately. However, none of these studies have produced an operational H-D model to depict a species- and site-specific relationship of height and diameter for *P. totara*. This significant lack poses a major barrier to have a detailed site- and species-specific growth and yield model for *P. totara*, and hinders efficient forest management and/or timber production planning.

Therefore, the main aim of this study is to develop a fully functional species-specific *P. totara* H-D model. The specific objectives are to: 1) compile the most comprehensive available dataset, 2) condition the best H-D model, and 3) generalise and incorporate site-specificity into the modelling framework by exploring traditional linear, non-linear and mixed-effects approaches.

Methods

Data description

Tree measurements from eight different sites from upper- to mid-latitude in the North Island of New Zealand were used for this study (Figure 1). These sites cover *P. totara* plantations in the Northland, Thames, Bay of Plenty, Hawkes Bay, Gisborne and Taranaki regions. A total of 719 trees were measured for height (H, m) and diameter at breast height (DBH at 1.4 m, cm), with the number of trees per site varying from 19 to 175. Site-specific age (ranging from 11 to 110 years) was recorded from initial plantation notes. Data descriptions are presented in Table 1 and distributions in Figure 2. Tree heights and diameters were initially collected for the investigation of wood density characteristics of plantation-grown *P. totara* (Steward 2019; Steward & McKinley 2019). Consequently, there is likely to be some bias in the data set towards larger diameter stems within each stand assessed.

Model development and evaluation

Selection of the basic height-diameter models

A range of two and three parameter non-linear H-D equations have been reported over time, with some dating back to the early 1920s (Pearl & Reed 1920; Huang et al. 2000; Mehtätalo et al. 2015). For this study, a total of 17 non-linear H-D equations were selected (reported in Supplementary Table S1). Generally, all equations can

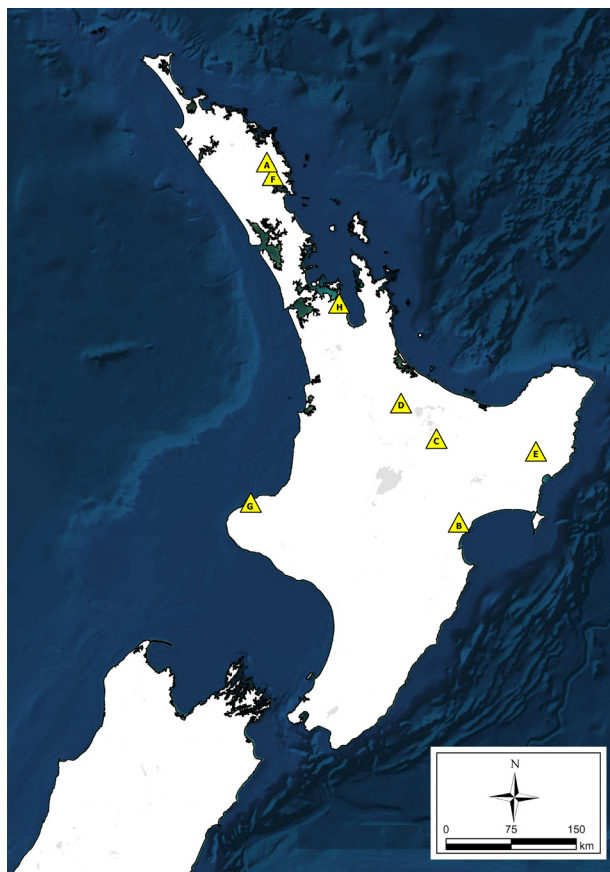


FIGURE 1: Tree-measurement sites.

be mathematically expressed as:

$$H_i = f(\text{DBH}_i, \phi) + \varepsilon_i \quad \text{Equation 1}$$

Where H_i is the i th observation of the dependent variable tree height (H , m), DBH_i is the i th observation of the independent variable tree diameter at breast height

(DBH at 1.4 m, cm), ϕ specific vector parameters to be estimated, and ε is the random error term. Here and elsewhere, i is the i th observation with $i=1,2,\dots,N$.

Each of the 17 equations was independently fitted to individual tree data through nonlinear regression using ordinary nonlinear least squares (NLS) techniques. At this stage, a global least squares solution was considered, and different initial values for the model parameters were provided for the fits. Additionally, all models were initially evaluated based on the magnitude and distribution of residuals to detect any discrepancies (Vanclay 1994; Gadow & Hui 1998). Numerical comparisons were made using root mean square error (RMSE) and Akaike information criterion (AIC, Akaike 1974), as shown in Table 2.

Model generalisation with site-specific variables

Augmenting empirical growth and yield models with stand- or site-specific covariates to enhance biological explainability and localise model projections has been well-adapted (Woollons et al. 1997; Salekin et al. 2021). Similarly, bringing stand- or site-level variables into H-D equations to express variability and improve model generality is feasible (Höckä 1997; Salekin et al. 2020). In the case of re-measured data, spatial and temporal correlation might be expected (Vanclay et al. 1995). However, since this study has only one site re-measured but different trees each time, it is reasonable to assume an absence of such temporal correlation. Regarding spatial correlation, the sites are widely dispersed across different regions, suggesting minimal or no spatial correlation (Zhao et al. 2004).

The set of selected basic H-D equations' parameters were linearly expanded with site-specific variables. Specifically, α , β , and/or γ -parameters were linearly regressed with the following site-specific variables: quadratic mean diameter (QMD, cm), site mean diameter (SMD, cm), individual tree basal area (BA, $\text{m}^2 \text{ha}^{-1}$), and stand age (t , years). Various combinations of these variables were tested in this study. The final model was selected based on models' AIC, RMSE, mean absolute error (MAE), and coefficient of determination (R^2) (Table 2).

TABLE 1: Descriptive statistics of *P. totara* data. max.= maximum, min.=minimum. H_1 and H_2 indicate two repeated measurements in stand H, but using different trees.

Stand	Number of trees	Age (years)	Height (H, m)			Diameter at breast height (DBH at 1.4 m, cm)		
			mean	max.	min.	mean	max.	min.
A	30	63	10.69	12.50	8.50	35.60	61.80	25.50
B	19	52	12.54	15.10	10.00	28.43	33.90	23.10
C	40	53	11.72	14.00	9.00	27.29	42.50	20.60
D	30	57	10.59	16.50	8.00	28.19	46.50	19.50
E	30	68	13.34	17.00	10.50	31.44	43.80	23.50
F	29	110	22.79	25.60	16.00	38.37	53.50	20.20
G	14	79	18.59	23.30	14.00	39.21	69.00	22.60
H_1	253	11	5.50	7.20	2.00	9.60	16.30	1.50
H_2	274	31	12.10	15.70	7.80	18.60	34.40	5.80

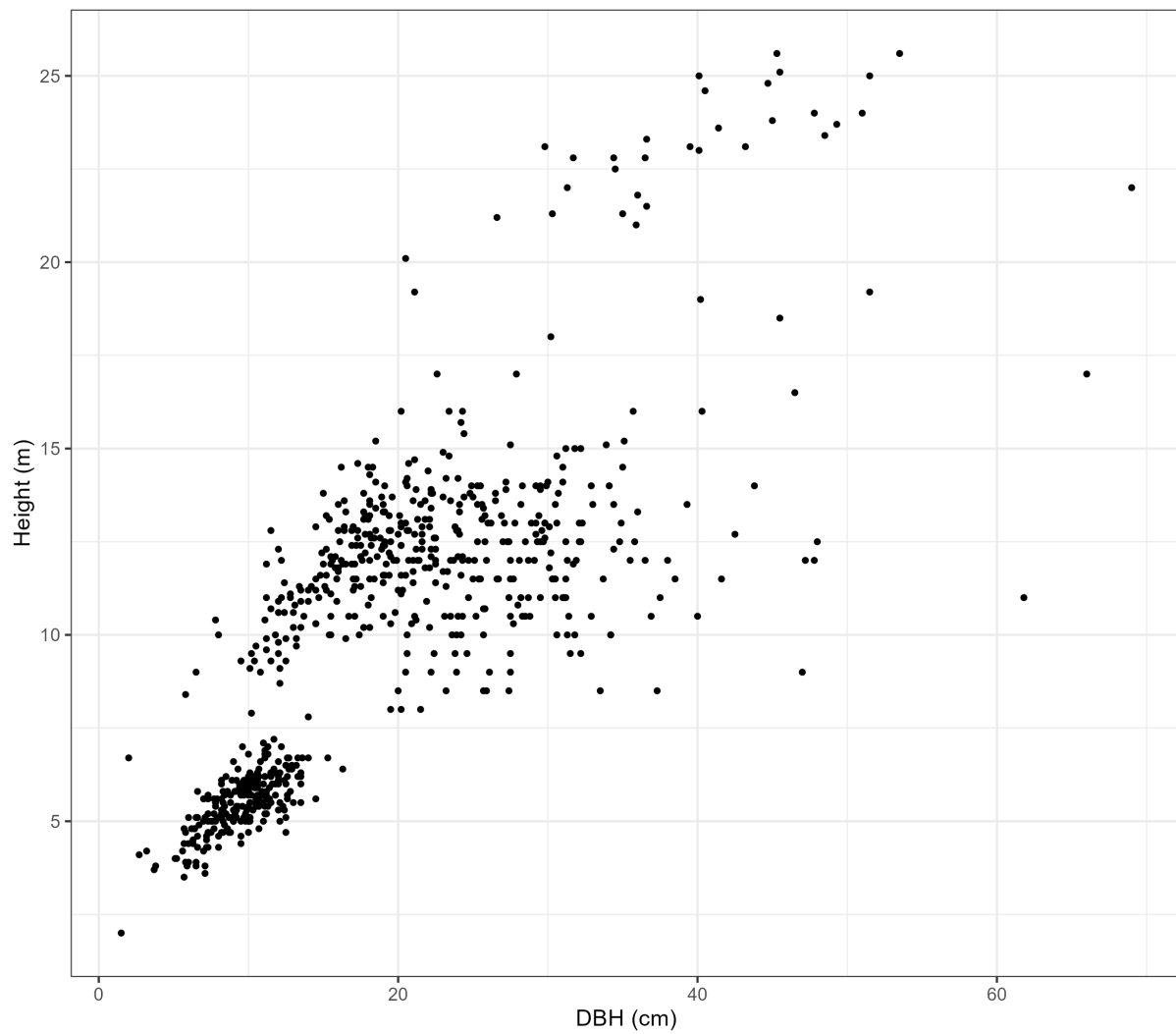


FIGURE 2: Measured tree height (m) and diameter at breast height (DBH at 1.4 m, cm) distribution of the study dataset.

TABLE 2: Model performance evaluation criteria, where est_i is the i th estimated value; obs_i is the i th observational value; n is the number of observations; and p is the number of parameters.

Performance criterion	Unit	Symbolic expression	Mathematical expression	Ideal
Akaike information criterion	-	AIC	$AIC = 2k - 2\ln(\hat{L})$	Lower is better
Root means square error	m	RMSE	$\sqrt{\frac{\sum_{i=1}^n (est_i - obs_i)^2}{n-p}}$	0
Relative root mean square error	m	RRMSE	$\sqrt{\frac{\frac{1}{n} \sum_{i=1}^n (est_i - obs_i)^2}{\sum_{i=1}^n (est_i)^2}}$	0
Mean absolute error	m	MAE	$\sum_{i=1}^n \frac{ est_i - obs_i }{n}$	0
Coefficient of determination	-	R^2	$1 - \frac{\sum_{i=1}^n (est_i - \bar{obs})^2}{\sum_{i=1}^n (obs_i - \bar{obs})^2}$	1

Linear mixed-effect modelling

While the general H-D model presented in Equation 1 can be applied considering all sites as one, the measurements from sites exhibit a hierarchically nested structure, necessitating spatial grouping to adequately describe the relationship in the measured data (Lappi 1997; Adame et al. 2008; Bronisz & Mehtätalo 2020). Therefore, a linear mixed-effect model (LMM) was developed to explain the variation in the H-D relationship by partitioning regression coefficients into fixed and random effects (Equation 2).

$$H_{ij} = f(\text{DBH}_{ij}; \beta_i) + \varepsilon_{ij} \quad \text{Equation 2}$$

where H_{ij} is the j th observation of the dependent variable tree height (H, m) on site i and corresponding diameter at breast height (DBH at 1.4 m) by DBH_{ij} , $f(\text{DBH}_{ij}; \beta_i)$ is the systematic part of the model, and ε_{ij} unexplained residual error.

In this model, different sites were assigned as random effects, while all site-specific variables introduced earlier were treated as fixed effects. The assumptions of data normality and homoscedasticity were assessed graphically and using the Shapiro-Wilk test. Where necessary, data were appropriately transformed through scaled power transformation (Equation 3, Sakia 1992) to meet the assumptions of normality and equal variances, and subsequently back-transformed for graphical presentation. Parameters of this model were estimated using a restricted maximum-likelihood (REML) technique.

$$x^{(\lambda)} = \begin{cases} (x^\lambda - 1)/\lambda & \lambda \neq 0 \\ \log(x) & \lambda = 0 \end{cases} \quad \text{Equation 3}$$

where $x^{(\lambda)}$ is the scaled power transformation of x , and λ is a parameter that defines the curvature of the relationship between x and $x^{(\lambda)}$.

Model evaluation and statistical analysis

All models were evaluated for their mathematical consistency and biological rationality (Weiskittel et al. 2011) through a mixed approach, performing both quantitative and qualitative residual analyses (Kozak & Kozak 2003). The models' goodness-of-fit statistics included Akaike information criterion (AIC), root mean square error (RMSE), relative root mean square error (RRMSE), mean absolute error (MAE), and coefficient of determination (R^2) (Table 2, Huang et al. 2003). Additionally, predicted heights (m) were subjected to a correlation test (r) with measured height (m) to demonstrate the agreement between them.

Model validation is an indispensable part of development (Weiskittel et al. 2011) as it assesses the sensitivity and performance of the model with independent datasets. However, validating forest growth and yield models with appropriate independent datasets is rare and often conducted through alternative

approaches. In this study, a data splitting approach was employed, where the total dataset was divided into fitting and validation datasets at a 75:25 ratio. All model development procedures were conducted using the fitting dataset (75% of the total data). Subsequently, the final models—one extended non-linear and one linear mixed effect—were validated using the validation dataset (25% of the total data) and compared. For validation, the same goodness-of-fit statistics as in Table 2 were used, with the exception of AIC.

The statistical analyses began with an exploratory analysis to assess multi-collinearity among response and dependent variables. It was carried out by inspecting the variance inflation factor (VIF) and employing the procedures outlined in Cook and Weisberg (2009), by comparing the contribution of the most strongly correlated variables towards their residuals. Basic non-linear models were employed with fitting dataset, and subsequently extended with statistically significant variables selected based on goodness-of-fit criteria. A linear mixed-effects model (LMM) was then developed, starting from a null model and progressively adding variables that substantially improved model prediction. Following these processes, final non-linear and linear mixed-effects models were developed.

All statistical analyses, model building and simulations were carried out in the R statistical environment version 4.4.1 (R core team 2022). Finally, model evaluation during fitting and validation were carried in base R with the "Metrics" package (Hammer & Frasco 2018). Besides this, residuals were visually inspected for their normality and variance homogeneity. All the graphical analyses and presentations were performed with the "ggplot2" package (Wickham et al. 2019).

Results

Among the selected non-linear models, four equations exhibited comparatively higher precision (Table S3). Of these, two have two parameters - the first by Näslund (1936) that includes a constant power of 3.75 and second by Schreuder et al. (1979). There were also two equations that contain three parameters - that of Lundqvist (1957) and also that of Pearl and Reed (1920). These models were further extended with site-specific variables, and their fitting parameters are reported in Table S3. The goodness-of-fit statistics indicated that, among the four, the Pearl and Reed (1920) equation extended with individual tree basal area (BA, $\text{m}^2 \text{ha}^{-1}$) and age (t, years) performed with high precision (RMSE = 1.91 m, MAE = 1.50 m, and $R^2 = 0.81$) (Table 3).

However, the linear mixed-effects model (Table 4) with DBH and time outperformed all non-linear models with higher precision (RMSE = 0.21 m, MAE = 0.16 m, and $R^2 = 0.94$) and demonstrated a significantly narrower range (-0.5 to 0.5) and homogeneous residual distribution (Table 4 and Figure 3). Furthermore, Figure 4 illustrated the models' agreement with measured height data, showing that the linear mixed-effects model achieved a similar level of accuracy with a significant correlation coefficient (r) of 0.96.

TABLE 3: Goodness-of-fit statistics for extended non-linear and linear mixed models. Abbreviations are the same as in Table 2. Values within parenthesis were back-transformed statistics.

Model	Fitting statistics					Validation statistics			
	RMSE (m)	RRMSE (m)	MAE (m)	R ²	AIC	RMSE (m)	RRMSE (m)	MAE (m)	R ²
Näslund (1936)	2.15	1.95	1.68	0.76	2369.544	2.35	2.05	1.86	0.72
Schreuder et al. (1979)	2.12	1.76	1.73	0.77	2352.282	2.36	1.96	1.83	0.71
Lundqvist (1957)	2.35	1.97	1.84	0.71	2464.125	2.33	1.94	1.87	0.72
Pearl and Reed (1920)	1.91	1.68	1.50	0.81	2241.116	2.13	1.87	1.66	0.76
Final linear mixed model	0.21(1.3)	0.15 (0.96)	0.16(0.83)	0.94	-30.386	0.93 (1.10)	0.76 (1.04)	0.58(0.82)	0.92

During validation, the goodness-of-fit statistics for all models worsened marginally, but the linear mixed-effects model maintained minimal degradation in precision (Table 3). All models exhibited data clustering and skewness towards more data points.

Discussion

The main aim of this study was to investigate the relationship between height and diameter of planted *P. totara* in New Zealand and develop an appropriate H-D model. A statistically robust and comprehensive process was undertaken, involving the selection, conditioning, and comparison of a total of 17 models, followed by the integration of site-specific parameters to develop the final model. This represents a significant advancement from previous separate time- or age-based height and diameter models (Bergin & Kimberley 2003).

TABLE 4: Final linear mixed-effect model and parameters. Std. Dev. = standard deviation; Std. Error = standard error; $DBH^{\lambda d}$ = scaled-power transformed DBH; $H^{\lambda h}$ = scaled-power transformed H; t = age (year). $\lambda h = 0.28$ and $\lambda d = 0.17$. "Stand" was a random effect.

Model	$H^{\lambda h} = DBH^{\lambda d} + t + (1 Stand)$		
<i>Random effect</i>			
Groups	Name	Variance	Std. Dev.
Stand	Intercept	1.00133	1.00
Residual	-	0.04812	0.21
<i>Fixed effect</i>			
Parameters	Estimate	Std. Error	t value
Intercept	-1.482097	0.36	-4.08
$DBH^{\lambda d}$	0.463137	0.02	17.203
t	0.057722	0.01	35.30

In most forest growth modelling studies, both tree and stand development are strongly linked with the individual tree height-diameter (H-D) relationship (Borders 1989; Hynynen 1995). This is because these features represent important morphometric characteristics (Sims 2022). Moreover, the dominant height of a stand is used to indicate site quality in terms of stand growth and yield capacity (West 2015). Additionally, the height of trees of the same diameter varies as a function of stand stocking and provides a good indication of stand carrying capacity through basal area (Hökkä 1997).

Among the 17 non-linear H-D models tested in this study, 3 parameter Pearl and Reed (1920) equation performed best when integrated with localised site-specific parameters. Although 3 parameter models are often recommended for describing the relationship curve more accurately, they can encounter issues with model convergence (see Mehtätalo et al. 2015). Previous studies have noted these challenges with increasing complexity in non-linear H-D equations (e.g., Hong et al. 2008; Feldpausch et al. 2011). As a result, it is often suggested to use two-parameter equations (Mehtätalo et al. 2015). However, the studied species *P. totara* has some unique features. It demonstrates slower height-growth, particularly in the earlier years, up to approximately age 85 years (Kunstler et al. 2011). Therefore, careful investigation and integration with site-specific variables, as well as consideration of more complex models like the 3 parameter Pearl and Reed (1920) equation, are necessary in this case.

When multiple measurements are taken from individual sampling units and combined altogether as a single dataset, it exhibits a nested stochastic structure (West et al. 1984). It becomes challenging to fully incorporate the variation of sampling residuals through traditional ordinary or non-linear least squares, often leading to biased estimation (West et al. 1986; Schabenberger & Gregoire 1995). The application of mixed-effects modelling approaches provides a statistically flexible framework to explicitly model hierarchical data structures, which has seen increasing

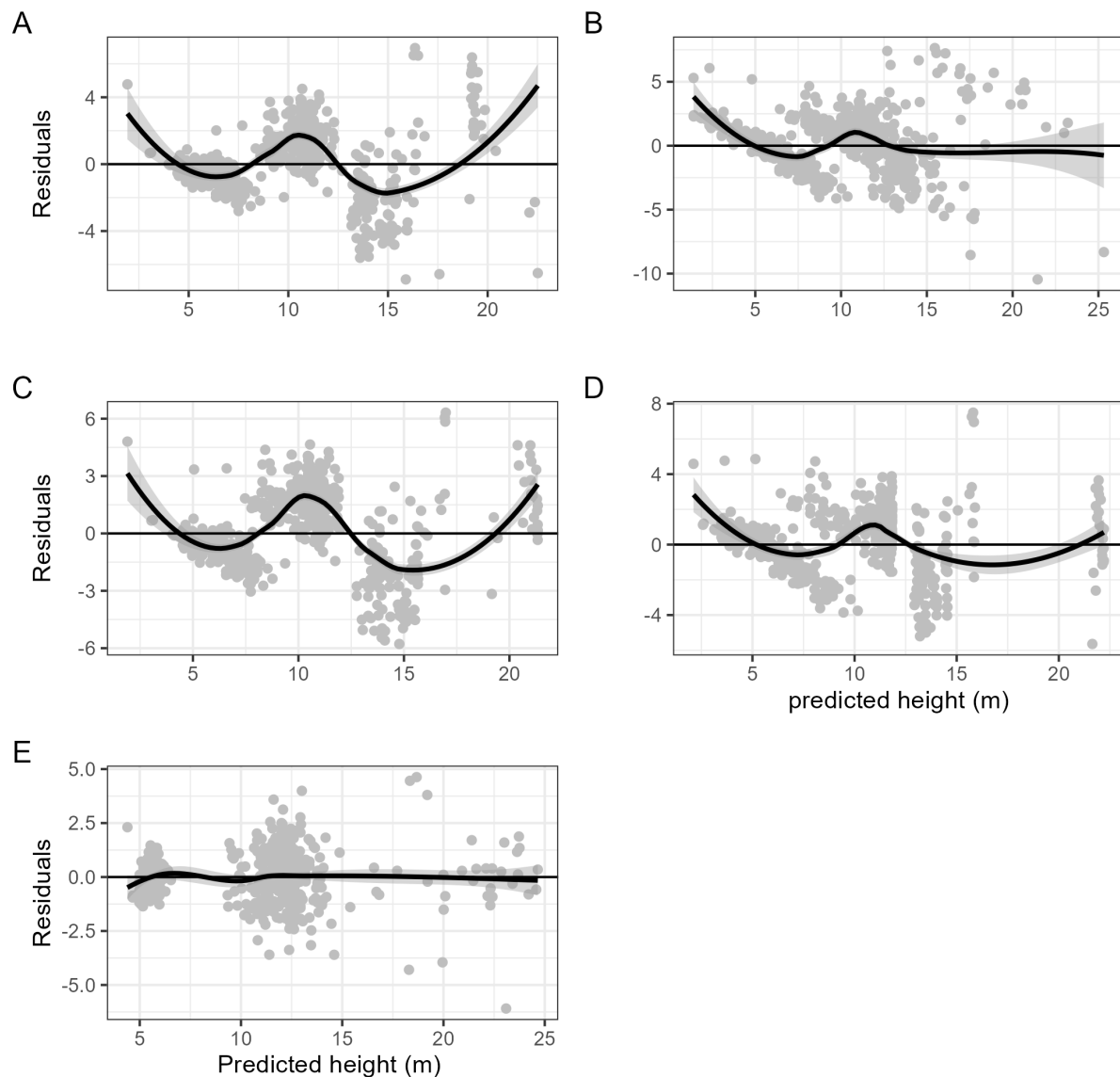


FIGURE 3: Model predicted heights against residuals distribution plots for extended final A) Näslund (1936), B) Schreuder et al. (1979), C) Lundqvist (1957), D) Pearl and Reed (1920) and E) back transformed linear mixed-effect models. Black lines show the model fit line with grey shaded area as confidence intervals at 95%.

use in forest biometry, particularly in modelling height-diameter (H-D) relationships. For instance, Hökkä (1997) applied a linear mixed-effect approach to develop tree height models of *Pinus sylvestris*, *Picea abies*, and *Betula pubescens* in drained peatland of southern Finland. Castedo Dorado et al. (2006) applied a generalised mixed-effect model for the H-D relationship of *P. radiata* in northwest Spain. Most recently, Tian et al. (2022) used it to develop a climate sensitive H-D model for mixed forest in northeast China. Their findings emphasise the importance of explicitly modelling and incorporating hierarchy to effectively integrate complex errors. These previous studies are in line with the finding of this study, where the sampling unit varied with stand, representing variable characteristics.

When integrated with site-specific variables, the models, specifically the Pearl and Reed (1920) and the

final mixed-effect models, demonstrated biological rationality. It is common for the height-diameter (H-D) relationship to vary between sites, thus including site-specific predictor variables in the final models is crucial. For example, Bronisz and Mehtätalo (2020) included basal area and quadratic diameter into an H-D model for *Betula pendula* in post-agricultural land in Poland, while Adame et al. (2008) used basal area and initial height for *Quercus pyrenica* in Spain. In this study, site-specific age (years) and individual tree basal area ($\text{m}^2 \text{ha}^{-1}$) significantly improved the final models. Conversely, Tian et al. (2022) incorporated site-specific climatic variables, and Huang et al. (2000) used eco-region base variables to further extend the models' utility. Given the dataset and scope of this study, extending it to include similar resolutions would not be pragmatic and is therefore considered out of scope.

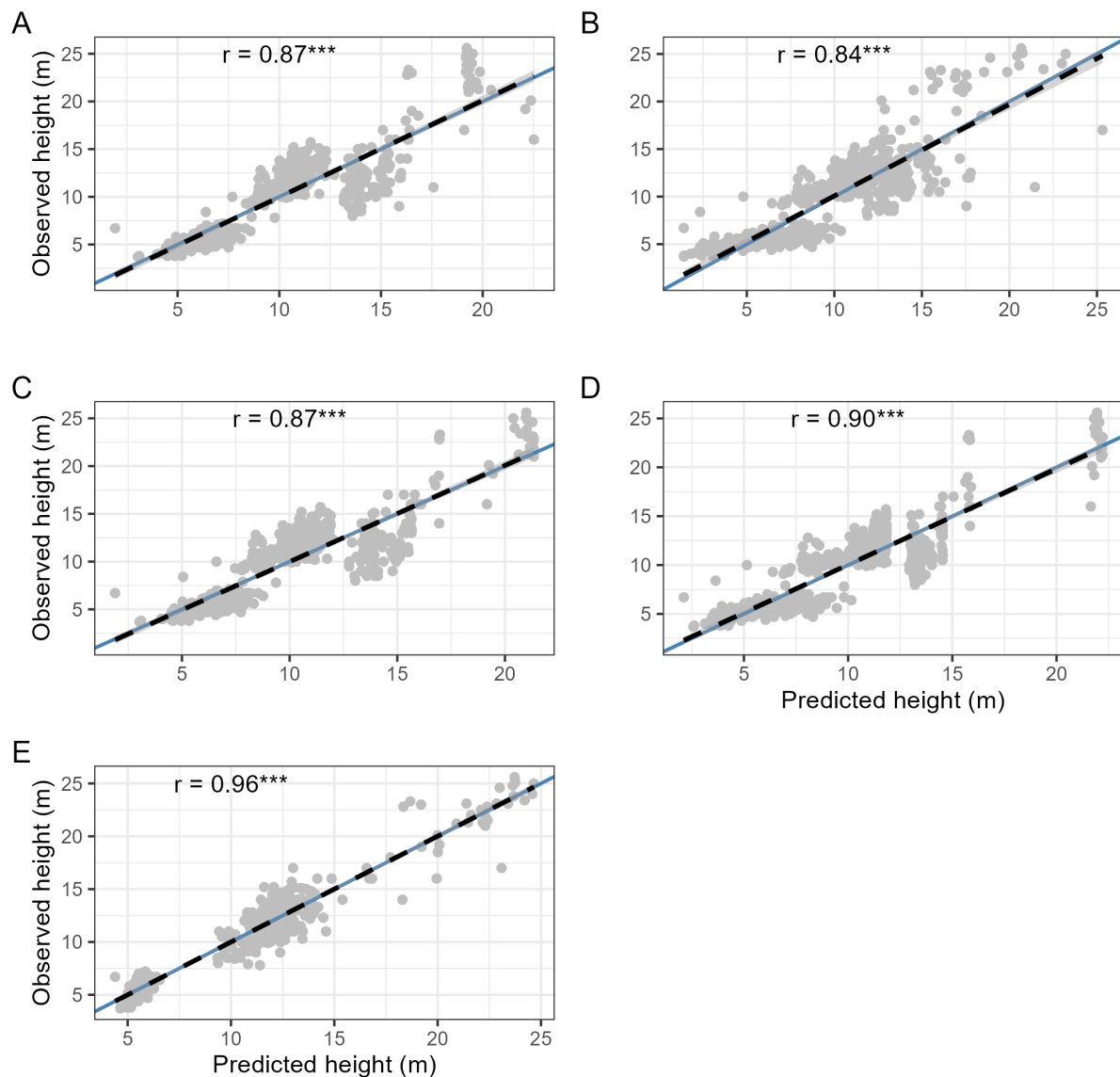


FIGURE 4: Relationship between predicted heights and measured heights (m) and their correlation coefficients (r) for extended final A) Näslund (1936); B) Schreuder et al. (1979); C) Lundqvist (1957); D) Pearl and Reed (1920); and E) back transformed linear mixed-effect model. Black dashed lines show linear fit with grey shaded area as confidence interval at 95%, and steel-blue lines represented ideal intercept and slope line (0, 1).

Tree height and diameter are important basic input variables for growth and yield models (Burkhart & Strub 1974), as they directly contribute to estimate stand volume and site quality as well as describe stand vertical structure (Thornley 1999). Furthermore, measuring tree heights is expensive and time consuming, in comparison to diameter measurements (West 2015). So, any opportunity to estimate them with minimum input and maximum accuracy is useful in operational forestry (Brosfokske et al. 2013), especially with site- and species-species H-D functions described in this study. In addition, such functions can be used to impute missing heights and built comprehensive databases for stand-level growth and yield models (Garber et al. 2009). Based on the range of ages and diameters, functions described

in this study can also be useful for management planning and stocking management. Due to the kind of data used, the suggested H-D functions should neither be used in thinned stands or stands with juvenile spacing or selective logging, nor in model predictions which contain any of these treatments.

As “stand” was used as a random effect in the models, the equations reported here would require fitting to data from stands not included in our study, and the primary finding of this study was that a scaled-power transformed linear mixed effect model was a better fit to the data than non-linear mixed effect models reported elsewhere for height-diameter relationships.

Finally, it should be noted that the study dataset, while comprehensive, may not be the largest or most complete

available. Obtaining a fully orthogonal dataset for such studies is rare. Nonetheless, this dataset represents one of the most complete records of measured *P. totara* data to date. Looking ahead, future efforts could explore developing an even more comprehensive volume equation based on these findings.

Conclusions

This study aimed to develop the first-of-its-kind height-diameter (H-D) model for *P. totara*. The approach and the final models were deemed the most plausible and parsimonious. The model highlighted the integration and localisation of H-D model through site-specific tree morphometric features, e.g., DBH, age and basal area. The reported model in this study provides valuable information and understanding about the height-diameter relationship of planted *P. totara* in New Zealand. This fills a critical gap in the predictive modelling framework for this species and helps growers, managers and investors to make appropriate management decisions, as well as help to estimate the potential economic return.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

SS: conceptualisation, data organisation, formal analyses, reporting, visualisation, writing-original draft, writing-review & edit; CR: data collection, data curation, writing-review & edit, project administration; GS: conceptualisation, data collection, writing-original draft, writing-review & edit.

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References

- Adame, P., del Río, M., & Cañellas, I. (2008). A mixed nonlinear height-diameter model for Pyrenean oak (*Quercus pyrenaica* Willd.). *Forest Ecology and Management*, 256(1-2), 88-98. <https://doi.org/10.1016/j.foreco.2008.04.006>
- Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, 19(6), 716-723. <https://doi.org/10.1109/TAC.1974.1100705>
- Albaugh, T.J., Bergh, J., Lundmark, T., Nilsson, U., Stape, J.L., Allen, H.L., & Linder, S. (2009). Do biological expansion factors adequately estimate stand-scale aboveground component biomass for Norway spruce? *Forest Ecology and Management*, 258(12), 2628-2637. <https://doi.org/10.1016/j.foreco.2009.09.021>
- Barstow, R.C. (1878). The Maori canoe. *Transactions and Proceedings of the New Zealand Institute*, 11, 71-76.
- Bergin, D.O., & Kimberley, M.O. (2003). Growth and yield of totara in planted stands. *New Zealand Journal of Forestry Science*, 33(2), 244-264.
- Bergin, D.O. (2009). *Growth and management of planted and naturally regenerating stand of Podocarpus totara D. Don.* (PhD thesis), University of Waikato, Hamilton, New Zealand.
- Bergin, D.O., & Kimberley, M.O. (2012). Reliability of increment core growth ring counts as estimates of stand age in totara (*Podocarpus totara* D. Don). *New Zealand Journal of Forestry Science*, 42, 131-141.
- Borders, B.E. (1989). Systems of equations in forest stand modeling. *Forest Science*, 35(2), 548-556. <https://doi.org/10.1093/forestscience/35.2.548>
- Bronisz, K., & Mehtätalo, L. (2020). Mixed-effects generalized height-diameter model for young silver birch stands on post-agricultural lands. *Forest Ecology and Management*, 460: 117901. <https://doi.org/10.1016/j.foreco.2020.117901>
- Broszofske, K.D., Froese, R.E., Falkowski, M.J., & Banskota, A. (2013). A review of methods for mapping and prediction of inventory attributes for operational forest management. *Forest Science*, 60(4), 733-756. <https://doi.org/10.5849/forsci.12-134>
- Burkhart, H.E., & Strub, M.R. (1974). A model for simulation of loblolly pine stands. In J. Fries (Ed.), *Growth models for tree and stand simulation* (pp. 128-135). Stockholm, Sweden: Royal College of Forestry.
- Castedo Dorado, F., Diéguez-Aranda, U., Barrio Anta, M., Sánchez Rodríguez, M., & von Gadow, K. (2006). A generalized height-diameter model including random components for radiata pine plantations in northwestern Spain. *Forest Ecology and Management*, 229(1), 202-213. <https://doi.org/10.1016/j.foreco.2006.04.028>
- Cheeseman, T.F. (1871). On the botany of the Titirangi district of the province of Auckland, New Zealand. *Transactions and proceedings of the New Zealand Institute*, 4, 270-284.

- Colenso, W. (1868). On the geographic and economic botany of the North Island of New Zealand. *Transactions and Proceedings of the New Zealand Institute*, 1, 230-283.
- Cook, R.D., & Weisberg, S. (2009). *Applied regression including computing and graphics*. New York, USA: John Wiley & Sons.
- Curtis, R.O. (1967). Height-diameter and height-diameter-age equations for second-growth Douglas-fir. *Forest Science*, 13(4), 365-375.
- Department of Lands. (1909). *Report on state nurseries and plantations*. 44 p. Retrieved on: July 10, 2024.
- Ebbett, R.L. (1992). *Ecological characterisation of dense lowland podocarp forest, Whirinaki Sanctuary*. (MSc thesis), Auckland, New Zealand, University of Auckland.
- Ellis, J.C. (1978). Volume equations for the major indigenous species in New Zealand. *New Zealand Journal of Forestry Science*, 8(2), 267-268.
- Feldpausch, T.R., Banin, L., Phillips, O.L., Baker, T.R., Lewis, S.L., Quesada, C.A., Affum-Baffoe, K., Arets, E.J.M.M., Berry, N.J., Bird, M., Brondizio, E.S., de Camargo, P., Chave, J., Djabbletey, G., Domingues, T.F., Drescher, M., Fearnside, P.M., França, M.B., Fyllas, N.M., Lopez-Gonzalez, G., Hladik, A., Higuchi, N., Hunter, M.O., Iida, Y., Salim, K.A., Kassim, A.R., Keller, M., Kemp, J., King, D.A., Lovett, J.C., Marimon, B.S., Marimon-Junior, B.H., Lenza, E., Marshall, A.R., Metcalfe, D.J., Mitchard, E.T.A., Moran, E.F., Nelson, B.W., Nilus, R., Nogueira, E.M., Palace, M., Patiño, S., Peh, K.S.H., Raventos, M.T., Reitsma, J.M., Saiz, G., Schrodte, F., Sonké, B., Taedoumg, H.E., Tan, S., White, L., Wöll, H., & Lloyd, J. (2011). Height-diameter allometry of tropical forest trees. *Biogeosciences*, 8(5), 1081-1106. <https://doi.org/10.5194/bg-8-1081-2011>
- Gadow, K.V., & Hui, G. (1998). *Modelling forest development*. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Garber, S.M., Temesgen, H., Monleon, V.J., & Hann, D.W. (2009). Effects of height imputation strategies on stand volume estimation. *Canadian Journal of Forest Research*, 39(3), 681-690. <https://doi.org/10.1139/X08-188>
- Gregorie, T.G. (1987). Generalized error structure for forestry yield models. *Forest Science*, 33(2), 423-444. <https://doi.org/10.1093/forestscience/33.2.423>
- Hammer, R., & Frasco, M. (2018). Metrics: Evaluation metrics for Machine Learning. *R package version 0.1.4*.
- Härkönen, S., Neumann, M., Mues, V., Berninger, F., Bronisz, K., Cardellini, G., Chirici, G., Hasenauer, H., Koehl, M., Lang, M., Merganicova, K., Mohren, F., Moiseyev, A., Moreno, A., Mura, M., Muys, B., Olschofsky, K., Del Perugia, B., Rørstad, P.K., Solberg, B., Thivolle-Cazat, A., Trotsiuk, V., & Mäkelä, A. (2019). A climate-sensitive forest model for assessing impacts of forest management in Europe. *Environmental Modelling & Software*, 115, 128-143. <https://doi.org/10.1016/j.envsoft.2019.02.009>
- Hinds, H.V., & Reid, J.S. (1957). Forest trees and timbers of New Zealand. *New Zealand Forest Service Bulletin*, 12, 221.
- Hökkä, H. (1997). Height-diameter curves with random intercepts and slopes for trees growing on drained peatlands. *Forest Ecology and Management*, 97(1), 63-72. [https://doi.org/10.1016/S0378-1127\(97\)00063-7](https://doi.org/10.1016/S0378-1127(97)00063-7)
- Hong, X., Mitchell, R.J., Chen, S., Harris, C.J., Li, K., & Irwin, G.W. (2008). Model selection approaches for non-linear system identification: a review. *International Journal of Systems Science*, 39(10), 925-946. <https://doi.org/10.1080/00207720802083018>
- Huang, S., Price, D., & Titus, S.J. (2000). Development of ecoregion-based height-diameter models for white spruce in boreal forests. *Forest Ecology and Management*, 129, 125-141. [https://doi.org/10.1016/S0378-1127\(99\)00151-6](https://doi.org/10.1016/S0378-1127(99)00151-6)
- Huang, S., Yang, Y., & Wang, Y. (2003). A critical look at procedures for validating growth and yield models. In A. Amaro, D. Reed & P. Soares (Eds.), *Modelling forest systems* (pp. 271-292). Cambridge, USA: CABI International. <https://doi.org/10.1079/9780851996936.0271>
- Hynynen, J. (1995). Predicting the growth response to thinning for Scots pine stands using individual-tree growth models. *Silva Fennica*, 29(3), 225-246. <https://doi.org/10.14214/sf.a9210>
- Jagodziński, A.M., Zasada, M., Bronisz, K., Bronisz, A., & Bijak, S. (2017). Biomass conversion and expansion factors for a chronosequence of young naturally regenerated silver birch (*Betula pendula* Roth) stands growing on post-agricultural sites. *Forest Ecology and Management*, 384, 208-220. <https://doi.org/10.1016/j.foreco.2016.10.051>
- Kazimirović, M., Stajić, B., Petrović, N., Ljubičić, J., Košanin, O., Hanewinkel, M., & Sperlich, D. (2024). Dynamic height growth models for highly productive pedunculate oak (*Quercus robur* L.) stands: explicit mapping of site index classification in Serbia. *Annals of Forest Science*, 81(1), 15. <https://doi.org/10.1186/s13595-024-01231-0>
- Kozak, A., & Kozak, R. (2003). Does cross validation provide additional information in the evaluation of regression models? *Canadian Journal of Forest Research*, 33(6), 976-987. <https://doi.org/10.1139/x03-022>
- Krik, T. (1884). On the flowering plants of Stewart Island. *Transactions and proceedings of the New Zealand Institute*, 17, 213-228.

- Kulej, M., & Socha, J. (2008). Effect of provenance on the volume increment of grand fir (*Abies grandis* Lindl.) under mountain conditions of Poland. *Journal of Forest Science*, 54(1), 1-8. <https://doi.org/10.17221/794-JFS>
- Kunstler, G., Allen, R.B., Coomes, D.A., Canham, C.D., & Wright, E.F. (2011). *SORTIE/NZ model development*. Lincoln, New Zealand: Landcare Research New Zealand Ltd.
- Lappi, J. (1997). A longitudinal analysis of height/diameter curves. *Forest Science*, 43(4), 555-570. <https://doi.org/10.1093/forestscience/43.4.555>
- Liu, M., Feng, Z., Zhang, Z., Ma, C., Wang, M., Lian, B.-l., Sun, R., & Zhang, L. (2017). Development and evaluation of height diameter at breast models for native Chinese Metasequoia. *PLOS ONE*, 12(8), e0182170. <https://doi.org/10.1371/journal.pone.0182170>
- Lundqvist, B. (1957). On the height growth in cultivated stands of pine and spruce in Northern Sweden. *Medd Fran Statens Skogforsk*, 47(2), 1-64.
- Mehtätalo, L. (2004). A longitudinal height-diameter model for Norway spruce in Finland. *Canadian Journal of Forest Research*, 34(1), 131-140. <https://doi.org/10.1139/x03-207>
- Mehtätalo, L., de-Miguel, S., & Gregoire, T.G. (2015). Modeling height-diameter curves for prediction. *Canadian Journal of Forest Research*, 45(7), 826-837. <https://doi.org/10.1139/cjfr-2015-0054>
- Näslund, M. (1936). Skogsförsöksanstaltens gallringsförsök i tallskog. *Meddelanden från Statens Skogsförsöksanstalt*.
- Page, D., & Singh, T. (2014). Durability of New Zealand grown timbers. *New Zealand Journal of Forestry*, 58(4), 7-11.
- Pardy, G.F., Bergin, D.O., & Kimberley, M.O. (1992). Survey of native tree plantations. *New Zealand Forest Service Bulletin*, 175, 24 p.
- Pearl, R., & Reed, L.J. (1920). On the rate of growth of the population of the United States since 1790 and its mathematical representation. *Proceedings of the National Academy of Sciences*, 6, 275-288. <https://doi.org/10.1073/pnas.6.6.275>
- R core team. (2022). R: A language and environment for statistical computing *R Foundation for Statistical Computing*.
- Sakia, R.M. (1992). The box-cox transformation technique: A review. *Journal of the Royal Statistical Society. Series D*, 41(2), 169-178. <https://doi.org/10.2307/2348250>
- Salas-Eljatib, C., Mehtätalo, L., Gregoire, T.G., Soto, D.P., & Vargas-Gaete, R. (2021). Growth equations in forest research: Mathematical basis and model similarities. *Current Forestry Reports*, 7(4), 230-244. <https://doi.org/10.1007/s40725-021-00145-8>
- Salekin, S., Mason, E.G., Morgenroth, J., & Meason, D.F. (2020). A preliminary growth and yield model for *Eucalyptus globoides* Blakely plantations in New Zealand. *New Zealand Journal of Forestry Science*, 50. <https://doi.org/10.33494/nzjfs502020x55x>
- Salekin, S., Mason, E.G., Morgenroth, J., Bloomberg, M., & Meason, D.F. (2021). Hybrid height growth and survival model for juvenile *Eucalyptus globoides* (Blakely) and *E. bosistoana* (F. Muell) in New Zealand. *Forest Ecology and Management*, 490, 119074. <https://doi.org/10.1016/j.foreco.2021.119074>
- Schabenberger, O., & Gregoire, T.G. (1995). A conspectus on estimating function theory and its applicability to recurrent modeling issues in forest biometry. *Silva Fennica*, 29(1): 5546. <https://doi.org/10.14214/sf.a9197>
- Schreuder, H.T., Hafley, W.L., & Bennett, F.A. (1979). Yield prediction for unthinned natural slash pine stands. *Forest Science*, 25, 25-30.
- Simpson, P. (2017). *Totara: A natural and cultural history*. Auckland, New Zealand: Auckland University.
- Sims, A. (2022). Tree and its measurement. In A. Sims (Ed.), *Principles of National Forest Inventory Methods: Theory, Practice, and Examples from Estonia* (pp. 19-35). Cham, Switzerland: Springer International Publishing.. https://doi.org/10.1007/978-3-031-06405-0_3
- Smaill, S., & Steward, G.A. (2015). Totara research at Scion. *Indigena, February 2015*, 6-8.
- Soares, P., & Tomé, M. (2002). Height-diameter equation for first rotation eucalypt plantations in Portugal. *Forest Ecology and Management*, 166(1), 99-109. [https://doi.org/10.1016/S0378-1127\(01\)00674-0](https://doi.org/10.1016/S0378-1127(01)00674-0)
- Steward, G.A. (2019). To the heart of the matter - heartwood content in tōtara. *New Zealand Journal of Forestry*, 64(2), 37-41.
- Steward, G.A., & McKinley, R.B. (2019). Indigenous plantations - implications for wood quality. *New Zealand Journal of Forestry*, 64(2), 42-45.
- Steward, G.A., & Quinlan, P. (2019). Tōtara industry pilot project: a fresh look at familiar Northland species. *New Zealand Tree Grower*, November 2019, 30-33.
- Steward, G.A. (2020). Harvesting native trees - estimated versus recovered volumes. *New Zealand Journal of Forestry*, 64(4), 11-17.
- Temesgen, H., & Gadow, V.K. (2004). Generalized height-diameter models-an application for major tree species in complex stands of interior British Columbia. *European Journal of Forest Research*, 123(1), 45-51. <https://doi.org/10.1007/s10342-004-0020-z>

- Thornley, J.H.M. (1999). Modelling stem height and diameter growth in plants. *Annals of Botany*, 84(2), 195-205. <https://doi.org/10.1006/anbo.1999.0908>
- Tian, D., Jiang, L., Shahzad, M.K., He, P., Wang, J., & Yan, Y. (2022). Climate-sensitive tree height-diameter models for mixed forests in Northeastern China. *Agricultural and Forest Meteorology*, 326: 109182. <https://doi.org/10.1016/j.agrformet.2022.109182>
- Tomppo, E., Schadauer, K., McRoberts, R.E., Gschwantner, T., Gabler, K., & Ståhl, G. (2010). National Forest Inventories. In E. Tomppo, T. Gschwantner, M. Lawrence & R.E. McRoberts (Eds.), *National Forest Inventories: Pathways for Common Reporting* (pp. 1-18). Dordrecht: Springer Netherlands. <https://doi.org/10.1007/978-90-481-3233-1>
- Vanclay, J.K. (1994). *Modelling forest growth and yield - Application to mixed tropical forests*. Wallingford, UK: CAB International.
- Vanclay, J.K., Skovsgaard, J.P., & Pilegaard Hansen, C. (1995). Assessing the quality of permanent sample plot databases for growth modelling in forest plantations. *Forest Ecology and Management*, 71(3), 177-186. [https://doi.org/10.1016/0378-1127\(94\)06097-3](https://doi.org/10.1016/0378-1127(94)06097-3)
- Weiskittel, A.R., Hann, D.W., Kershaw Jr, J.A., & Vanclay, J.K. (2011). *Forest growth and yield modeling*: Oxford, UK: John Wiley & Sons. <https://doi.org/10.1002/9781119998518>
- West, P.W., Ratkowsky, D.A., & Davis, A.W. (1984). Problems of hypothesis testing of regressions with multiple measurements from individual sampling units. *Forest Ecology and Management*, 7(3), 207-224. [https://doi.org/10.1016/0378-1127\(84\)90068-9](https://doi.org/10.1016/0378-1127(84)90068-9)
- West, P.W., Davis, A.W., & Ratkowsky, D.A. (1986). Approaches to regression analysis with multiple measurements from individual sampling units. *Journal of Statistical Computation and Simulation*, 26(3-4), 149-175. <https://doi.org/10.1080/00949658608810962>
- West, P.W. (2015). Stand measurement. In P. W. West (Ed.), *Tree and forest measurement* (pp. 71-95). Cham, Switzerland: Springer International Publishing. https://doi.org/10.1007/978-3-319-14708-6_8
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pederse, T.L., Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seidel, D.P.S.V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., & Yutani, H. (2019). Welcome to the tidyverse. *Journal of Open Source Software*, 4(43): 1686. <https://doi.org/10.21105/joss.01686>
- Woollons, R.C., Snowdon, P., & Mitchell, N.D. (1997). Augmenting empirical stand projection equations with edaphic and climatic variables. *Forest Ecology and Management*, 98(3), 267-275. [https://doi.org/10.1016/S0378-1127\(97\)00090-X](https://doi.org/10.1016/S0378-1127(97)00090-X)
- Yuancai, L., & Parresol, B.R. (2001). Remarks on height-diameter modeling. *Research Note SE-10*. U.S. Asheville, NC, USA: Department of Agriculture, Forest Service, Southeastern Forest Experiment Station. <https://doi.org/10.2737/SRS-RN-10>
- Zhao, D., Borders, B., & Wilson, M. (2004). Individual-tree diameter growth and mortality models for bottomland mixed-species hardwood stands in the lower Mississippi alluvial valley. *Forest Ecology and Management*, 199(2), 307-322. <https://doi.org/10.1016/j.foreco.2004.05.043>

SUPPLEMENTARY TABLES

TABLE S1: Height-diameter equations for evaluation. α , β and γ are model parameters. *x is a variable constant, see Zhao et al. (2006).

Parameters	Equation no.	Form	References
Two-parameters	1	$H = 1.4 + \alpha DBH^\beta$	Stoffels and van Soest (1953)
	2	$H = \frac{\alpha DBH}{\beta + DBH}$	Bates and Watts (1980)
	3*	$H = 1.4 + \left(\frac{DBH}{\alpha + \beta DBH} \right)^x$	Näslund (1936)
	4	$H = 1.4 + \alpha + \beta \frac{1}{DBH}$	Rymer-Dudzińska (1978)
	5	$H = 1.4 + \alpha e^{\left(\frac{\beta}{DBH} \right)}$	Schumacher (1939)
	6	$H = 1.4 + e^{\alpha + \frac{\beta}{DBH + 1}}$	Schreuder et al. (1979)
	7	$H = 1.4 + \frac{\alpha DBH}{\beta + DBH}$	Wykoff et al. (1982)
	8	$H = 1.4 + \frac{DBH^2}{\alpha + (\beta DBH)^2}$	Meyer (1940)
	9	$H = 1.4 + 10^\alpha DBH^\beta$	Burkhart and Strub (1974)
	10	$H = 1.4 + \frac{\alpha DBH}{(DBH + 1)} + \beta DBH$	Watts (1983)
	11	$H = 1.4 + \alpha \left(\frac{DBH}{1 + DBH} \right)^\beta$	Strand (1959)
Three-parameters	12	$H = \alpha + \beta DBH + \gamma DBH^2$	Staebler (1954)
	13	$H = 1.4 + \frac{DBH^2}{\alpha + \beta DBH + \gamma DBH^2}$	Strand (1959)
	14	$H = 1.4 + \alpha e^{-\beta DBH^{-\gamma}}$	Lundqvist (1957)
	15	$H = 1.4 + \frac{\alpha}{1 + \beta DBH^\gamma}$	Huang et al. (2000)
	16	$H = 1.4 + \alpha (1 - e^{-\beta DBH^\gamma})$	Yang et al. (1978)
	17	$H = 1.4 + \frac{\alpha}{1 + \beta e^{-\gamma DBH}}$	Pearl and Reed (1920)

TABLE S2: Model goodness-of-fit statistics. Bold faces indicate relatively better models.

Equation no.	RMSE	AIC
1	2.686	2598.692
2	2.623	2573.189
3	2.572	2552.028
4	3.142	2768.192
5	2.584	3409.368
6	2.57	2550.949
7	2.623	2573.189
8	2.614	2569.456
9	2.578	2554.313
10	2.686	2598.692
11	2.765	2629.924
12	2.604	2566.205
13	2.573	2553.449
14	2.572	2553.058
15	2.576	2554.648
16	2.602	3420.674
17	2.631	2577.538

TABLE S3: Fitting parameters for extended non-linear models

Reference	Extended non-linear model	Parameters	Estimate	Std. error	t value	p-value
Näslund (1936)	$H = 1.4 + \left(\frac{DBH}{(\alpha_0 + \alpha_1 t) + (\beta_0 + \beta_1 BA) DBH} \right)^{3.75}$	α_0	1.645047	0.09	17.80	< 2e-16 ***
		α_1	-0.026616	0.01	-17.57	< 2e-16 ***
		β_0	0.510516	0.01	69.06	< 2e-16 ***
		β_1	-0.113352	0.03	-3.21	0.00114 **
Schreuder et al. (1979)	$H = 1.4 + e^{\frac{(\beta_0 + \beta_1 t)}{DBH + 1} (\alpha_0 + \alpha_1 BA)}$	α_0	2.48553	0.05	45.83	< 2e-16 ***
		α_1	0.88390	0.26	3.35	0.00863 ***
		β_0	-11.83716	0.67	-17.44	< 2e-16 ***
		β_1	0.20939	0.01	17.08	< 2e-16 ***
Lundqvist (1957)	$H = 1.4 + (\alpha_0 + \alpha_1 t; BA) e^{-\beta DBH^\gamma}$	α_0	11.30233	0.56	19.83	< 2e-16 ***
		α_1	0.47574	0.04	11.18	< 2e-16 ***
		β	134.15597	85.12	1.57	0.116
		γ	2.26565	0.30	7.43	4.07e-13 ***
Pearl and Reed (1920)	$H = 1.4 + \frac{(\alpha_0 + \alpha_1 BA + \alpha_2 t)}{1 + \beta e^{-\gamma DBH}}$	α_0	8.6312406	0.27	31.52	< 2e-16 ***
		α_1	-3.1672226	3.51	-0.90	0.0368601 **
		α_2	1.0231736	0.01	2602.34	< 2e-16 ***
		β	24.6507805	6.76	3.64	0.000294 ***
		γ	0.3240744	0.02	11.07	< 2e-16 ***

References for Supplementary Tables

- Bates, D.M., & Watts, D.G. (1980). Relative curvature measures of nonlinearity. *Journal of the Royal Statistical Society: Series B (Methodological)*, 42(1), 1-16. <https://doi.org/10.1111/j.2517-6161.1980.tb01094.x>
- Burkhardt, H.E., & Strub, M.R. (1974). A model for simulation of loblolly pine stands. In J. Fries (Ed.), *Growth models for tree and stand simulation* (pp. 128-135). Stockholm, Sweden: Royal College of Forestry.
- Huang, S., Price, D., & Titus, S.J. (2000). Development of ecoregion-based height-diameter models for white spruce in boreal forests. *Forest Ecology and Management*, 129, 125-141. [https://doi.org/10.1016/S0378-1127\(99\)00151-6](https://doi.org/10.1016/S0378-1127(99)00151-6)
- Lundqvist, B. (1957). On the height growth in cultivated stands of pine and spruce in Northern Sweden. *Medd Fran Statens Skogforsk*, 47(2), 1-64.
- Meyer, H.A. (1940). A mathematical expression for height curves. *Journal of Forestry*, 38(5), 415-420.
- Näslund, M. (1936). Skogsförsöksanstaltens gallringsförsök i tallskog. *Meddelanden från Statens Skogsförsöksanstalt*.
- Pearl, R., & Reed, L.J. (1920). On the rate of growth of the population of the United States since 1790 and its mathematical representation. *Proceedings of the National Academy of Sciences*, 6, 275-288. <https://doi.org/10.1073/pnas.6.6.275>
- Rymer-Dudzińska, T. (1978). Stałe krzywe wysokości dla drzewostanów sosnowych (Uniform height curves for pine stands). *Zeszyty Naukowe Szkoły Głównej Gospodarstwa Wiejskiego Akademii Rolniczej w Warszawie, Rozprawy Naukowe*, 102, 1-19.
- Schreuder, H.T., Hafley, W.L., & Bennett, F.A. (1979). Yield prediction for unthinned natural slash pine stands. *Forest Science*, 25, 25-30.
- Schumacher, F.X. (1939). A new growth curve and its applications to timber yield studies. *Journal of Forestry*, 37, 819-820.
- Staeble, G.R. (1954). *Standard computations for permanent sample plots*. Washington, WA, USA, United States Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station.
- Stoffels, A., & van Soest, J. (1953). The main problems in sample plots. *Nederlandsch Boschbouw-Tijdschrift*, 25, 190-199.
- Strand, L. (1959). The accuracy of some methods for estimating volume and increment on sample plots. *Meddelelser fra det Norske Skogforsoksvesen*, 15(4), 278-392.
- Watts, S.B. (1983). *Forestry handbook for British Columbia* (4th ed.). Forestry Undergraduate Society.
- Wykoff, W.R., Crookston, N.L., & Stage, A.R. (1982). *User's guide to the stand prognosis model*. General Technical Report INT-GTR-133. Ogden, UT, USA: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 112 p. <https://doi.org/10.2737/INT-GTR-133>
- Yang, R.C., Kozak, A., & Smith, J.H.G. (1978). The potential of Weibull-type functions as flexible growth curve. *Canadian Journal of Forest Research*, 8, 424-431. <https://doi.org/10.1139/x78-062>
- Zhao, W., Mason, E.G., & Brown, J. (2006). Modelling height-diameter relationships of *Pinus radiata* plantations in Canterbury, New Zealand. *New Zealand Journal of Forestry*, 51(1), 23-27.