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Developing a framework for growth modelling in a managed southern black beech forest

Elias Ganivet^{1*}, Elena Moltchanova² and Mark Bloomberg¹

Abstract

Background: A model of individual tree growth using simple predictors in a managed black beech (*Fuscospora solandri* (Hook.f.) Heenan & Smissen) forest could provide a useful tool for predicting future stand characteristics.

Methods: Data from permanent sample plots were used to develop a framework for modelling individual tree growth in Woodside forest, a managed black beech forest in north Canterbury (New Zealand). We tested three mixed-effect models to identify effects of sites, treatment (thinnings), individual tree size and competition on tree growth rates.

Results: A power function amended with variables specifying stand basal area and thinning treatment was best suited for black beech, explaining about 55% of the variation in growth rates. Treatment history (thinnings), as well as the individual tree size and the stand basal area, strongly affected tree diameter growth. Only 3% of the variation in diameter growth rates was explained by plot-specific effect which was less than observed in earlier studies.

Conclusions: All predictor variables (management history, individual tree diameter and stand basal area) are quite simple to measure in the field and could be easily used to predict diameter increments in managed or unmanaged forests. A limitation of our study was that available growth data in Woodside were from small plots, focused on a small number of trees and a narrow range of diameters. However, our results are a good starting point, providing a promising framework for further modelling of tree growth in Woodside forest from new permanent plot data.

Keywords: Mixed-effect models, Woodside forest, Black beech forest, Forest management, New Zealand

Background

New Zealand's native forests cover in total over 6.6 million hectares, with beech forests (dominated by *Fuscospora* and *Lophozonia* species) being the most widespread (Wiser et al. 2011). The beech species constitute the largest native timber resource remaining in New Zealand, accounting for 88% of the annual allowable harvest from all indigenous forests under Forests Act requirements (Richardson et al. 2011). Harvesting these forests while maintaining or enhancing their non-extractive benefits has been a controversial issue over the last few decades (Benecke 1996; Mason 2000). As a consequence, native forest harvest is highly regulated,

with only a small part of New Zealand's privately owned forest covered by sustainable management plans approved by the Ministry for Primary Industries (Donnelly 2011).

Understanding the factors influencing tree growth is a critical task in forest ecology and management. Long-term vegetation monitoring through permanent plots is widely used to provide an insight into regeneration behaviour and vegetation dynamics as well as growth and mortality patterns (Bakker et al. 1996). Data from permanent plots allow study of the effects of many factors on tree growth through mathematical models, providing useful tools for forest management (Alder 1995; Boot and Gullison 1995; Alder 2002). In this study, we use data from permanent sample plots in a mono-specific black beech forest (*Fuscospora solandri* (Hook.f.) Heenan & Smissen) to develop predictive models of

* Correspondence: ganivet.elias@gmail.com

¹Department of Land Management and Systems, Faculty of Agribusiness and Commerce, Lincoln University, Lincoln 7640, New Zealand
Full list of author information is available at the end of the article

diameter growth, excluding tree height and mortality rates in our analysis.

Tree growth varying with ontogeny is a well-recognised concept in ecology (Clark and Clark 1999; Poorter et al. 2005; Herault et al. 2011). It has been suggested that tree growth rate could be mechanistically related to size by an invariant power law (Enquist et al. 1999; Enquist 2002). This approach has been already used in New Zealand for describing the relationship between the size of an individual and its growth rate (Richardson et al. 2009, 2011). However, the assumption that tree growth rate is only dependent on tree size is suspect, because it is obvious that other factors such as competition and site productivity also influence tree growth (Coomes 2006; Reich et al. 2006; Muller-Landau et al. 2006).

Moreover, while power-law-based approaches only allow a monotonic increase or decrease of growth (Coomes and Allen 2007; Richardson et al. 2009, 2011), some studies argue for hump-shaped growth trajectories, with species attaining their maximum growth rate at intermediate size (Davies 2001; Herault et al. 2011; Easdale et al. 2012). Describing the relationship between the size of an individual and its growth rate has been a debate over the last decade, with authors proposing either one approach or the other (Enquist et al. 1999; Coomes and Allen 2007, 2009; Enquist et al. 2009; Richardson et al. 2011; Herault et al. 2011).

In this study, we aimed to identify which approach is best suited for modelling the relationship between tree size and tree growth rate of a managed black beech forest in New Zealand. We used multilevel (i.e. mixed) modelling approaches to account for the nested structure of our dataset (trees grouped within plots). Following earlier studies (Coomes and Allen 2007; Easdale et al. 2012), the basal area of the larger neighbours (B_L) and all neighbours (B_T) was also added to the model to describe competitive effects of such neighbours on growth. Because taller neighbours intercept light first, the basal area of larger neighbouring trees has been often used as a proxy of competition for light. By similar reasoning, basal areas of all neighbouring trees can be used as proxy of above- and below-ground competition (competition for nutrients/water and competition for light).

In New Zealand, some studies have already modelled growth of beeches (Harcombe et al. 1997; Richardson et al. 2011; Coomes et al. 2012; Easdale et al. 2012) and other native species (Kunstler et al. 2009). However, they only focused on unmanaged stands, which does not give information about silvicultural management impacts on growth processes. This study aims to develop a framework for modelling individual tree growth using simple

predictors in a managed black beech forest where harvesting and thinning take place. Such a model could provide a useful tool to predict future stand structure from simple field measurements of tree diameter and stocking.

Methods

Study site

The study was conducted in Woodside, a 121-ha black beech forest privately owned and located in Canterbury in the South Island of New Zealand (Fig. 1). This forest is a part of one of the larger remnants of the formerly extensive Canterbury foothill forests dominated by black beech (Allen et al. 2000). It is a second-growth forest following earlier logging and fire (1860–1910), with management aimed at being an example of sustainable forest management (Allen et al. 2012).

Woodside forest is located at the foothills of the Southern Alps, at an elevation ranging from 400 to 550 m. The climate is windy, with annual precipitation about 1300 mm year⁻¹ and common snowfall in winter. The ecology of the forest is affected by location. Infrequent, heavy, wet snowfalls and recurrent gale-force north-west winds can damage the canopy and potentially expose trees to pests and diseases. The majority of the property is covered by black beech while a smaller area (29 ha) is planted with exotic species (principally *Pinus radiata* D. Don) for wood production. Of the 84 ha of black beech forest, 70 ha are managed with timber harvesting as an objective. The remaining 14 ha are managed as a reserve with no timber harvesting. The management regime involved aims to work with the ecological processes that naturally determine the forest structure.

Data collection

We analysed data from eight rectangular permanent plots of different sizes established by the owner between 2002 and 2006 across the 70 ha of managed black beech forest (Table 1). No plots were established in the unmanaged reserve areas. All black beech trees inside the permanent plots with a diameter at breast height (DBH) ≥ 1 cm had been identified by the owner. The DBH of each tree had been measured and recorded, and trees had been tagged with a permanent number using a metal tag and wire. All the plots had been re-measured by the owner at least once, providing DBH increment data for a small sample of trees in Woodside. Six plots had been thinned and pruned, while two plots had received no silvicultural treatments (Table 1).

The annual growth rate (AGR in cm year⁻¹) for all live trees ≥ 1 cm DBH was defined as the change in DBH between two measurements, divided by the number of

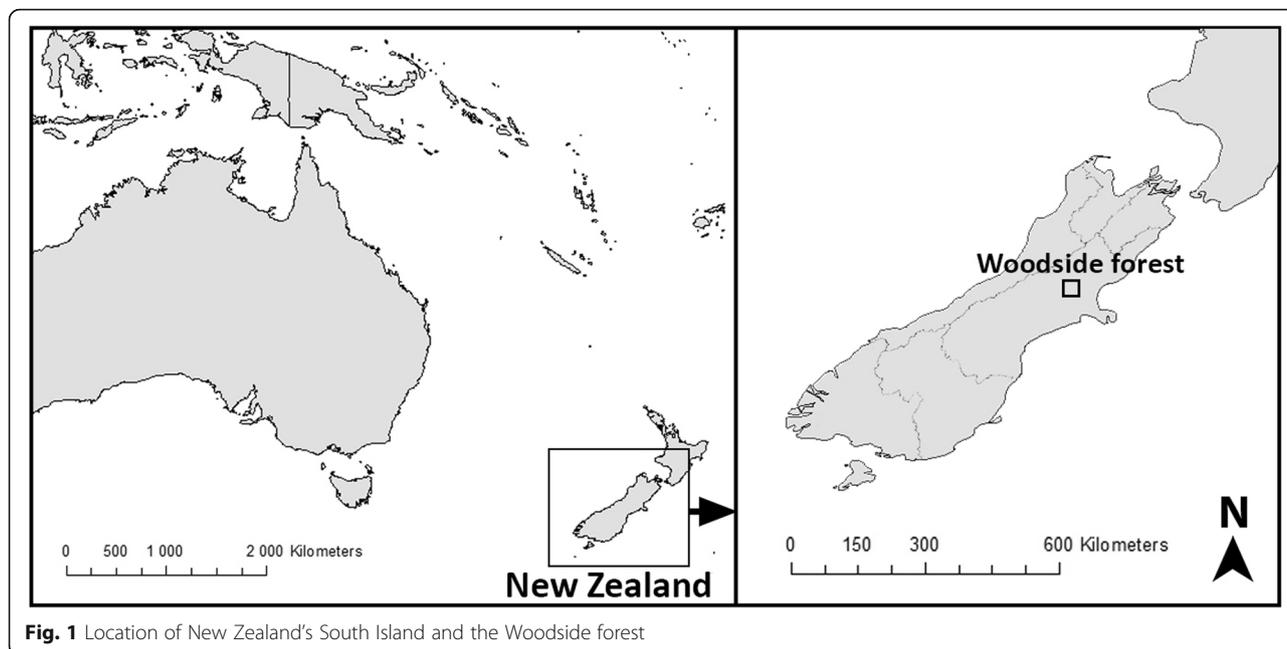


Fig. 1 Location of New Zealand's South Island and the Woodside forest

years between measurements. Some values were excluded from the analysis following Richardson et al. (2011) to account for possible errors in the dataset (during measurements, recording or data entry). We assumed negative growth $>0.2 \text{ cm year}^{-1}$ and positive growth $>1.5 \text{ cm year}^{-1}$ to be erroneous, and these values were removed from the dataset prior to analysis. Finally, stand structure parameters of the plots were used as proxy of competition (Coomes and Allen 2007). A proxy of competition for light was defined as the sum of basal areas of trees that had diameters larger than the target tree within the plots. A proxy of above- and below-ground competition (roots, light, etc.) was defined as the basal area of all trees within the plots, excluding the target stem. Finally, because our data were obtained from eight plots with two different management treatments, thinned (plots 1, 2, 3, 4, 6 and 7) and unthinned (plots 5 and 8), we also included a binary factor in the model to assess the impact of thinning on tree growth rates.

Growth models

We tested three candidate growth models using mixed-effect modelling approaches. Mixed-effect models form a class of model that incorporates multilevel hierarchies in data and can account for the nested structure of our dataset. Allen et al. (2000) found that plot-level variables explained about 40% of the variation in growth rates in Woodside. For that reason, we included the plot-specific effect as a random intercept in all our models.

Power function only (Enquist model)

We first focused on the Enquist growth model (Enquist et al. 1999), also used by Richardson et al. (2011), which models the relationship between tree size and tree growth rate with the following power function:

$$AGR_i = \lambda_1 \times DBH_i^\alpha \tag{M1}$$

which can be linearised as:

Table 1 Size, structure and silvicultural history of the eight permanent plots used for the analysis

Plot	Treatment	Harvesting history	Basal area ($\text{m}^2 \text{ ha}^{-1}$)	Stand density (stems ha^{-1})	Mean DBH (cm)	Plot size (m)
Plot 1	T/P	-	34.8	1594	15.8	8 × 40
Plot 2	T/P	-	16.0	1758	8.6	8 × 32
Plot 3	T/P	1.18 m^3 removed from dead trees in 2002	25.9	875	17.2	8 × 30
Plot 4	T/P	Harvested in 1987	7.9	1344	8.3	8 × 40
Plot 5	-	-	40.6	844	22.3	8 × 40
Plot 6	T/P	1.19 m^3 removed from dead trees in 2005	14.9	2250	8.9	8 × 20
Plot 7	T/P	Harvested in 1992	8.6	2750	6.1	8 × 20
Plot 8	-	-	51.5	2500	15.4	8 × 20

T thinned, P pruned

$$\begin{aligned} \log\text{AGR}_i &= \log\lambda_1 + \alpha\log\text{DBH}_i + \varepsilon_i \\ \text{with } \varepsilon_i &\sim N\left(0, \sigma_{\varepsilon_i}^2\right) \end{aligned} \tag{M1b}$$

with AGR_i the annual growth rate (cm year⁻¹) of the individual tree i ; λ_1 and α the fitted-model parameters; DBH_i the diameter at breast height (cm) of the individual tree i and ε_i the fitted-model residuals.

We then added the binary factor for treatment (thinning) to the model and accounted for possible plot-related variability by specifying the plots as random effects:

$$\begin{aligned} \log\text{AGR}_i &= \log\lambda_1 + \alpha\log\text{DBH}_i + \beta T_i + \phi_{\text{plot}_i} + \varepsilon_i \\ \text{with } \phi_{\text{plot}_i} &\sim N\left(0, \sigma_{\phi_{\text{plot}_i}}^2\right) \text{ and } \varepsilon_i \sim N\left(0, \sigma_{\varepsilon_i}^2\right) \end{aligned} \tag{M1c}$$

with AGR_i the annual growth rate (cm year⁻¹) of the individual tree i ; λ_1 , α and β the fitted-model parameters; DBH_i the diameter at breast height (cm) of the individual tree i ; T_i the treatment effect; ϕ_{plot_i} the plot-specific effect and ε_i the fitted-model residuals. Here, $T_i = 1$ if the observation i comes from an unthinned plot and $T_i = 0$ otherwise.

Power function with competition functions (Coomes model)

The method proposed by Coomes and Allen (2007) adjusts and tests for the possible effect of competition by amending M1 with competition functions (e.g. Canham et al. 2004; Uriarte et al. 2004) as follows:

$$\text{AGR}_i = \frac{\lambda_1 \times \text{DBH}_i^\alpha}{\left(1 + \frac{\lambda_1}{\lambda_2} e^{\lambda_3 B_L}\right) (1 + \lambda_4 B_T)} \tag{M2}$$

which can again be partially linearised, with adjustments for plot effects and for the possible treatment effect as follows:

$$\begin{aligned} \log\text{AGR}_i &= \log\lambda_1 + \alpha\log\text{DBH}_i - \log\left(1 + \frac{\lambda_1}{\lambda_2} e^{\lambda_3 B_L}\right) \\ &\quad - \log(1 + \lambda_4 B_T) + \beta T_i + \phi_{\text{plot}_i} + \varepsilon_i. \\ \text{with } \phi_{\text{plot}_i} &\sim N\left(0, \sigma_{\phi_{\text{plot}_i}}^2\right) \text{ and } \varepsilon_i \sim N\left(0, \sigma_{\varepsilon_i}^2\right) \end{aligned} \tag{M2b}$$

with AGR_i the annual growth rate (cm year⁻¹) of the individual tree i ; λ_1 , λ_2 , λ_3 , λ_4 , α and β the fitted-model parameters; DBH_i the diameter at breast height (cm) of the individual tree i ; B_L the basal area (m² ha⁻¹) of taller neighbours only (proxy of competition for light); B_T the basal area (m² ha⁻¹) of all neighbours (proxy of above- and below-ground competition); T_i the treatment effect; ϕ_{plot_i} the plot-specific effect and ε_i the fitted-model residuals. Again, $T_i = 1$ if the observation i comes from an unthinned plot and $T_i = 0$ otherwise.

Quadratic model of ontogenetic growth trajectories

Finally, we introduced a mathematical model of ontogenetic growth trajectories that has been already described as the tree-size effect (King et al. 2006; Herault et al. 2010). We used the ratio between the individual DBH and the 95th percentile of the DBH values in the black beech population ($\text{DBH}_{95} = 50.46$ cm), estimated using inventory data (Ganivet and Bloomberg, unpubl.). Both the ratio and the squared ratio were included to obtain a flexible mathematical form allowing a monotonic increase, a monotonic decrease or a humped growth trajectory. In order to remain consistent with M1 and M2 and due to strong heteroscedasticity in our data, the logarithm of growth was modelled instead of growth itself.

The quadratic mathematical model of ontogenetic growth trajectories was specified as follows:

$$\begin{aligned} \log\text{AGR}_i &= \lambda_1 + \lambda_2 \frac{\text{DBH}_i}{\text{DBH}_{95}} + \lambda_3 \left(\frac{\text{DBH}_i}{\text{DBH}_{95}}\right)^2 \\ &\quad + \lambda_4 B_T + \lambda_5 B_L + \beta T_i + \phi_{\text{plot}_i} + \varepsilon_i \\ \text{with } \phi_{\text{plot}_i} &\sim N\left(0, \sigma_{\phi_{\text{plot}_i}}^2\right) \text{ and } \varepsilon_i \sim N\left(0, \sigma_{\varepsilon_i}^2\right) \end{aligned} \tag{M3}$$

with AGR_i the annual growth rate (cm year⁻¹) of the individual tree i ; λ_1 , λ_2 , λ_3 , λ_4 , λ_5 and β the fitted-model parameters; B_L the basal area (m² ha⁻¹) of taller neighbours only; B_T the basal area (m² ha⁻¹) of all neighbours; DBH_i the diameter at breast height (cm) of the individual tree i ; DBH_{95} the 95th percentile of the DBH values of black beech; T_i the treatment effect; ϕ_{plot_i} the plot-specific effect and ε_i the fitted-model residuals. Again, $T_i = 1$ if the observation i comes from an unthinned plot and $T_i = 0$ otherwise.

Since the three models (M1c, M2b and M3) had the same response variable, $\log\text{AGR}_i$, they were all compared using the Akaike Information Criterion (AIC). Moreover, while the models M1c and M3 were linear in parameters, the competition model M2b was not. In order to be consistent, all the three models were fitted using the non-linear mixed-effect model function “nlme” from the “nlme” package in R software v.3.2.2 (R Core Team 2015). Finally, out of 305, only 6 observations had AGR values slightly below 0. In order to allow their log to be calculated, these values were all set to 0.01.

Results

In total, 305 black beech trees were used to model the individual annual growth rate (AGR) in Woodside. The average growth rate was 0.5 cm year⁻¹, with wide variation across the plots (Fig. 2). The lowest growth rates were observed for the unthinned plots 5 and 8. The

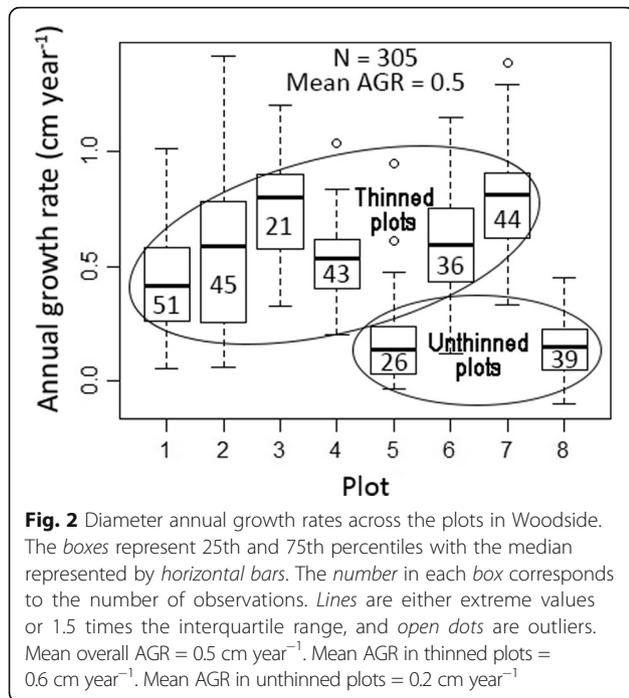


Fig. 2 Diameter annual growth rates across the plots in Woodside. The boxes represent 25th and 75th percentiles with the median represented by horizontal bars. The number in each box corresponds to the number of observations. Lines are either extreme values or 1.5 times the interquartile range, and open dots are outliers. Mean overall AGR = 0.5 cm year⁻¹. Mean AGR in thinned plots = 0.6 cm year⁻¹. Mean AGR in unthinned plots = 0.2 cm year⁻¹

mean AGR for these plots was 0.2 cm year⁻¹ while the thinned plots exhibited a mean AGR of 0.6 cm year⁻¹. Growth rates varied also widely among individual trees of the same size (Fig. 3).

The AIC for each of the models M1c, M2b and M3 was 630.80, 627.64 and 629.08 respectively. The quadratic model of ontogenetic growth trajectories M3 outperformed the power function model M1c but not the power function with competition function model M2b. We then simplified models M2b and M3 using the AIC in a backward selection to choose the most

parsimonious models and avoid over-parameterisation (Legendre and Legendre 1998). The most parsimonious version of the competition model M2b was:

$$\log AGR_i = \log \lambda_1 + \alpha \log DBH_i - \log(1 + \lambda_4 B_T) + \beta T_i + \phi_{plot_i} + \varepsilon_i \tag{M2c}$$

with AGR_i the annual growth rate (cm year⁻¹) of the individual tree i ; λ_1 , λ_4 , α and β the fitted-model parameters; DBH_i the diameter at breast height (cm) of the individual tree i ; B_T the basal area (m² ha⁻¹) of all trees around the target stem (within the entire plot); T_i the treatment effect; ϕ_{plot_i} the plot-specific effect and ε_i the fitted-model residuals.

This final model M2c resulted in AIC = 626.71. Removing the term B_T would result in M1c which would decrease the model fit as evaluated by AIC. The most parsimonious version of the quadratic model M3 was:

$$\log AGR_i = \lambda_1 + \lambda_2 \frac{DBH_i}{DBH95} + \lambda_3 \left(\frac{DBH_i}{DBH95} \right)^2 + \lambda_4 B_T + \beta T_i + \phi_{plot_i} + \varepsilon_i \tag{M3b}$$

with AGR_i the annual growth rate (cm year⁻¹) of the individual tree i ; λ_1 , λ_2 , λ_3 , λ_4 and β the fitted-model parameters; B_T the basal area (m² ha⁻¹) of all neighbours; DBH_i the diameter at breast height (cm) of the individual tree i ; $DBH95$ the 95th percentile of the DBH values of black beech; T_i the treatment effect; ϕ_{plot_i} the plot-specific effect and ε_i the fitted-model residuals.

This final model M3b resulted in AIC = 627.76, which still outperformed the power model M1c but not the competition model M2c. Comparing the residuals for

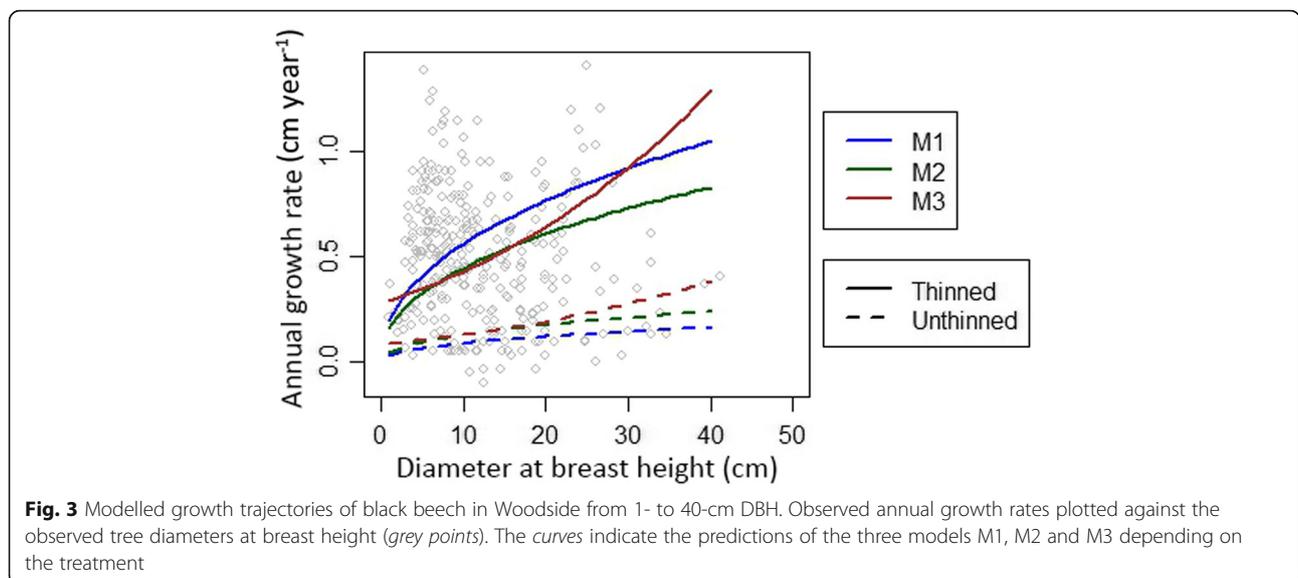


Fig. 3 Modelled growth trajectories of black beech in Woodside from 1- to 40-cm DBH. Observed annual growth rates plotted against the observed tree diameters at breast height (grey points). The curves indicate the predictions of the three models M1, M2 and M3 depending on the treatment

the three models (not shown in the results), the unthinned stands had more variance than the thinned ones. To see whether the growth dynamics were qualitatively different in the two types of stands, we tested the above models for the interaction effect between treatment and DBH. We also tested for plot-specific effects of treatment or DBH, i.e. random slopes. However, none of those features improved any of the three models. The estimated parameters of the final three models are shown in Table 2.

To assess the relative explanatory value of the fixed effects and random intercepts, we evaluated the total variance of the observed response, $\log AGR$, the variance of the random slopes and the residual variance (Table 2). In all three models, about 45% of the variance remained unexplained. In both the competition model M2c and the quadratic model M3b, 51% of the variance was explained by the fixed effects only, against 45% in M1c. The remaining variance explained by the random slopes was only 3% in M2c, 4% in M3b and 9% in M1c.

Trees ranged from 1- to 40-cm DBH in the current dataset, which resulted in the modelled growth rate of black beech exhibiting a dependency on tree size, with growth rates increasing monotonically when diameters increased in the three models (Fig. 3). However, in the quadratic model M3b, the presence of a negative value for the quadratic parameter λ_3 allowed for a hump-shaped response of tree growth to tree diameter. As a mathematical consequence of the low value of λ_3 , the AGR only reached a peak at around 140-cm DBH and then decreased at larger diameters. This was not shown in Fig. 2 as our dataset ranged only up to 40-cm DBH.

The observed influence of treatment was substantial in all three models tested, with reduced AGR in unthinned plots (Fig. 3). Growth trajectories were slightly different

among models, with AGR increasing logarithmically with models M1 and M2 while exponentially (from 0- to 40-cm DBH) with model M3. Also, the rate of increase in AGR was greater for model M1 compared with model M2.

Discussion

Large variability in growth rates was observed in this study (Fig. 3). Consistent with the results of Allen et al. (2000), AGR varied widely among the plots (Fig. 2) proving the necessity of including the plot effect in our modelling approach. Also, as observed by Allen et al. (2000), trees in Woodside exhibited relatively high mean AGR (0.5 cm year^{-1}) compared with what has been found elsewhere, not only for black beech but also the closely related species mountain beech (*Fuscospora cliffortioides* (Hook.f.) Heenan & Smissen) (see Coomes and Allen 2007; Richardson et al. 2011). This could be partly linked to environmental differences (i.e. elevation, climate, soil, etc.). While the Woodside plots were all located at around 500 m in elevation, the other studies usually involved black/mountain beech forests at higher elevations.

However, the high overall mean AGR was due mainly to the thinned plots (mean AGR of 0.6 cm year^{-1}). The mean AGR in unthinned plots 5 and 8 was only 0.2 cm year^{-1} which was consistent with what has been found elsewhere for black and mountain beeches. Thus, it seems the main driver of these differences in AGR would be the silvicultural management occurring at Woodside (i.e. thinning), which aims to improve individual tree growth. The positive impact of thinning on tree growth rates was further confirmed by the three modelling approaches tested. They all presented a significant effect of treatment, with clearly lower growth rates in unthinned stands (Fig. 3). For all models, there was no

Table 2 Summary of the estimated parameters, resulting AIC and relative variance of the response $\log AGR$ explained by the fixed effects, random intercepts and residuals (unexplained) for the three tested models

Model	M1			M2			M3		
	Est.	95%CI	<i>p</i> value	Est.	95%CI	<i>p</i> value	Est.	95%CI	<i>p</i> value
λ_1	0.20	(0.13; 0.30)	<0.001	0.37	(0.20; 0.71)	0.003	-0.66	(-1.07; -0.26)	0.002
α	0.45	(0.31; 0.60)	<0.001	0.45	(0.30; 0.60)	<0.001			
λ_2							2.25	(0.25; 4.25)	0.028
λ_3							-0.42	(-3.28; 2.45)	0.775
λ_4				0.05	(-0.02; 0.12)	0.139	-0.02	(-0.04; -0.01)	0.010
β	-1.84	(-2.34; -1.33)	<0.001	-1.23	(-1.71; -0.75)	<0.001	-1.20	(-1.83; -0.57)	0.007
AIC		630.80			626.71			627.76	
Var. fixed		45%			51%			51%	
Var. intercept		9%			3%			4%	
Var. residuals		46%			46%			45%	

Significant *p* values (*p* value < 0.05) are shown in italic

evidence that the effect of individual size on AGR was different in thinned vs. unthinned stands.

The best model was M2 in terms of AIC, although the differences among the three models were relatively small. Model M2 included a competition function (basal areas of all neighbours), which increased the variance explained by the fixed effects (51%). This result suggests that, as expected, black beech growth depends also on resource availability as an effect of above- and below-ground competition. It was further consistent with results from Coomes and Allen (2007) and other studies that already outlined effects of root competition (Platt et al. 2004), especially for nitrogen (Davis et al., 2004), on mountain beech. The power function model M1 was outperformed by both M2 and M3, supporting other studies that have shown that simplistic power-law functions are not generally the best descriptors of tree growth (Vanclay 1995; Coomes and Allen 2007, 2009; Enquist et al. 2009).

In terms of growth trajectories, our data were best described by M2 which exhibited a monotonic increase of the AGR with increasing diameters (Fig. 3). This result contrasted with other studies in New Zealand (Easdale et al. 2012) and elsewhere (Kohyama et al. 2003; Uriarte et al. 2004; Coates et al. 2009) that reported a hump-shaped response of growth to tree diameter. However, a clear limit of our dataset was the small diameter range (DBH ≤ 40 cm) compared with results from other studies in Woodside that used inventory data of larger diameter trees (Allen et al. 2000; Ganivet and Bloomberg, unpubl.). This lack of growth data for larger trees in the current study may explain the late humped growth response in M3 and why the quadratic model did not perform as well as M2. Maximal growth rates would be expected to be reached at intermediate sizes (around 30–50-cm DBH), while the AGR peaked at around 140-cm DBH in M3 before decreasing. New data with larger tree diameters would be required to re-estimate the parameters and compare M3 with M2. In any case, the monotonic growth trajectory found in this study was consistent with other studies on black and mountain beech (Coomes and Allen 2007; Richardson et al. 2011). Different factors could be relevant to explain this increase in growth with tree ontogeny.

At young stages, lower growth rates could be caused by: (1) black beech trees initially putting energy into height growth rather than diameter growth (Wardle, personal communication); and/or (2) a lack of available resources such as light (Chazdon et al. 1996; Whitmore 1996). Our proxy of competition for light (B_L) did not improve the tested models when used as an explanatory variable. However, light is widely accepted to be one of the main environmental limiting factors for tree growth (Pacala et al. 1996; Smith et al. 1997; Herwitz et al. 2000;

Canham et al. 2004; Uriarte et al. 2004; Wyckoff and Clark 2005), especially for light-demanding species such as black beech (Wardle et al. 1984). Our results suggest that using basal areas of taller trees as proxy of light competition is either not relevant or it needs to be measured at a smaller scale than the whole plot (see Coomes and Allen 2007). Light is more variable in the understorey than in the sub-canopy and canopy, so small-size trees are necessarily more dependent on variation in light availability than large trees (Wright et al. 2010). For larger diameter trees, increase in growth rates could be a consequence of trees reaching canopy status and spreading their crown, which further enhances light capture and growth (Poorter et al. 2006).

The aim of our study was to develop a simple framework that could be used for predictions, rather than explaining all the possible variation in growth rate. A model was successfully developed that explained more than 50% of the variation in growth rates using only few predictors easily measurable in the field (management history, individual tree diameter and stand basal area). However, a substantial fraction of individual variation in growth remained unexplained in all three modelling approaches used. This means other factors not investigated here might contribute to influence the growth of black beech in this managed forest. Depending on the model used, the plot-specific effect only explained 3–9% of the variation in growth rates, which was much less than the 40% found by Allen et al. (2000). However, their analysis did not look for effect of management on tree growth, and it is likely that our variable for treatment included a substantial fraction of the unaccounted plot-specific effect.

In February 2016, a further twelve 0.07-ha permanent plots were established across Woodside forest (Ganivet and Bloomberg, unpubl.). Further growth data from these permanent plots will provide additional data for building a more accurate model for the management of trees in this forest. Moreover, the spatial organisation of trees in the plots were measured, and these data could be used to investigate effects of competition for light at a smaller scale. A final recommendation would be to include mortality rates in the model to improve yield predictions.

Conclusions

Three candidate growth models that could be used for forest management were tested using data from height permanent plots in Woodside forest. The competition model M2 was the best of the models tested, with fixed effects explaining more than 50% of the variation in black beech growth rates. Individual tree size strongly affected the growth of trees, as did the management history and the basal area of the stand although only 3% of

the variation in growth rates remained explained by the plot-specific effect. These predictors are quite simple to measure in the field and could be easily used to predict diameter increments in managed or unmanaged forests. The growth data used focused on a small number of trees, a narrow range of diameters (up to 40 cm only) within a small geographic area, which limited the applicability of the model even though it performed well. Moreover, contrary to our expectations, the method did not produce reliable results when a basal area parameter was used as a proxy of competition for light. However, the results of the current study provide a good starting point for growth modelling of a southern black beech forest and provide a promising framework for further modelling.

Ethics approval and consent to participate

Not applicable

Abbreviations

AGR: Annual growth rate; DBH: Diameter at breast height

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Availability of data and materials

Permanent sample plot data were provided by the landowners (John and Rosalie Wardle). However, they have not consented to making the original measurement data available as an appendix to the report, and this must be obtained by request from the landowners.

Authors' contributions

EG handled the project design, analysis and interpretation of the data and wrote substantial sections of the paper. EM handled the analysis and interpretation of the data. MB supervised the study, including the project design and coordination and assistance with the interpretation of the results and writing the paper. All authors read and approved the final manuscript.

Authors' information

Elias Ganivet: Research and Teaching Assistant in Forestry, Department of Land Management and Systems, Faculty of Agribusiness and Commerce, Lincoln University, Lincoln 7640, New Zealand.
Elena Moltchanova: School of Mathematics and Statistics, University of Canterbury, Christchurch, New Zealand.
Mark Bloomberg: Senior Lecturer in Forestry Management, Department of Land Management and Systems, Faculty of Agribusiness and Commerce, Lincoln University, Lincoln 7640, New Zealand.

Competing interests

The authors declare that they have no competing interests.

Consent for publication

Permanent sample plot data were provided by the landowners (John and Rosalie Wardle), and the analysis and results in this paper are published with their consent.

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Author details

¹Department of Land Management and Systems, Faculty of Agribusiness and Commerce, Lincoln University, Lincoln 7640, New Zealand. ²School of Mathematics and Statistics, University of Canterbury, Christchurch, New Zealand.

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