

Article

Stand-Level Components of a Growth and Yield Model for *Nothofagus* Mixed Forests from Southern Chile

Sebastian Palmas ¹^[b], Paulo C. Moreno ²^[b], Wendell P. Cropper Jr. ¹^[b], Alicia Ortega ³ and Salvador A. Gezan ⁴,*^[b]

- ¹ School Forest Resources and Conservation, University of Florida, Gainesville, FL 32611, USA; palmasforest@gmail.com (S.P.); wcropper@ufl.edu (W.P.C.J.)
- ² Centro de Investigación en Ecosistemas de la Patagonia (CIEP), Camino Baguales s/n, Coyhaique 5951601, Chile; paulo.moreno@ciep.cl
- ³ Instituto de Bosques y Sociedad, Facultad de Ciencias Forestales y Recursos Naturales, Universidad Austral de Chile, Campus Isla Teja, Valdivia 5110566, Chile; aortega@uach.cl
- ⁴ VSN International, Hemel Hempstead HP2 4TP, UK
- * Correspondence: salvador.gezan@vsni.co.uk

Received: 29 June 2020; Accepted: 24 July 2020; Published: 27 July 2020



Abstract: Reliable information on stand dynamics and development is needed to improve management decisions on mixed forests, and essential tools for this purpose are forest growth and yield (G&Y) models. In this study, stand-level G&Y models were built for cohorts within the natural mixed second-growth Nothofagus-dominated forests in Chile. All currently available (but limited) data, consisting of a series of stratified temporary and permanent plots established in the complete range of this forest type, were used to fit and validate these models. Linear and nonlinear models were considered, where dominant stand age, number of trees, and the proportion of basal area of Nothofagus species resulted in significant predictors to project future values of stand basal area for the different cohorts (with $R^2 > 0.51$ for the validation datasets). Mortality was successfully modeled ($R^2 = 0.79$), based on a small set of permanent plots, using the concept of self-thinning with a proposed model defined by the idea that, as stands get closer to a maximum density, they experience higher levels of mortality. The evaluation of these models indicated that they adequately represent the current understanding of dynamics of basal area and mortality of Nothofagus and companion species in these forests. These are the first models fitted over a large geographical area that consider the dynamics of these mixed forests. It is suggested that the proposed models should constitute the main components of future implementations of G&Y model systems.

Keywords: RORACO; stand basal area; mortality model; second growth; self-thinning; projection

1. Introduction

Computational tools such as growth and yield (G&Y) models can be used by forest professionals to plan and implement management strategies at the local or regional scale. For instance, knowledge of growth dynamics, such as basal area growth and mortality, can be combined with forest inventories to determine timber production and examine the potential impacts of alternative management and harvesting regimes on the value and sustainability of the forest [1].

Growth and yield (G&Y) models for mixed forests were first developed during the 20th century, more than 150 years after such models were first implemented on commercial tree plantations [2]. Most models for mixed forest stands are limited and mainly focused on North American and European forests. In contrast to mono-specific plantations, mixed forests present additional complexity,



where often specific equations are required for each species. In addition, dealing with natural mixed forests presents difficulties on the establishing and remeasuring of inventory plots often over a wide geographical range, resulting in time-consuming and costly efforts. Furthermore, there is a need to unambiguously identify tree species and to sample over a range of forest conditions [1]. Hence, this has resulted in limited datasets, with few high-quality sample plots for the development and testing of growth and yield models in most mixed forests, often lacking long-term remeasurements.

G&Y models can be classified as stand-(whole) or individual-(tree) level [1–3], depending on the modeling units. Stand-level models are those in which the modeling units are aggregated parameters such as basal area, stocking, and site productivity. Individual-level models can keep track of each tree as a unique entity in the stand providing detailed information on tree size, diameter distributions, and individual mortality probabilities [3,4]. Building individual-level models is complicated because parameterization requires more data than stand-level models. But individual-tree models, particularly for mixed forests, provide the greater flexibility often required for these complex systems. While not providing a high level of detail, stand-level models have the advantage of being more robust for long-term projections than individual models [2] and they can be complemented with remotely sensed data [5]. As a compromise between these two model levels, tree species can be grouped into cohorts with shared biological responses, such as similar growth rates or light requirements [6]. Hence, defining cohorts of commercially important species and a cohort of companion (secondary tree species within the forest type) species can be particularly useful to construct stand-level models in mixed forests with cohorts that provide further granularity with the advantage of requiring less data than individual-level models.

One of the most interesting mixed temperate forests in South America are those dominated by the beeches *Nothofagus alpina* (raulí), *N. obliqua* (roble), and *N. dombeyi* (coigüe), which are native species of Chile and Argentina often present in a mixed forest type known locally as RORACO (for the first letters of the *Nothofagus* species). The RORACO forest type is considered as secondary forests established after disturbances, e.g., in treefall gaps, after volcanic activities and landslides [7,8]. These disturbances are often responsible for the establishment of even-aged RORACO stands dominated by these three shade-intolerant species, followed by the gradual establishment of shade-tolerant companion species [9]. This cohort of secondary species can be composed of *Gevuina avellana*, *Persea lingue*, *Lomatia hirsuta*, *Eucryphia cordifolia*, *Drymis winteri*, and *Laurelia phillippiana*, to name a few.

The RORACO forest type is present approximately between the 36° and 42° S latitudes in both the Chilean Andes and the coastal mountain range [9] with some fragments in Argentina, specifically the Neuquén Province [10]. The RORACO forest type covers 1.96 million hectares, around 10% of the native forested area of Chile [11], and it represents a little over 45% of the sawtimber volume from native species for the country [12]. Conversion to shrublands and exotic tree plantations has caused a trend in reduction in the last three decades of this forest type [13]. In addition, insect defoliator outbreaks present a threat to *Nothofagus* forests, with increasing vulnerability due to climate change [14]. Therefore, tools such as G&Y models are urgent and important to improve management and sustainability of the RORACO forest type.

Currently, the availability of G&Y models for this forest type is limited, except for preliminary work presented by Ortega and Gezan [15]. However, the three dominant species, and particularly *N. alpina*, have been the focus of many models for elements such as tree volume [16], taper equations [17], dominant height and site index [18–20], diameter increment [4,21,22], and mortality [23,24]. These models are useful contributions, but they often apply to subpopulations and specific environmental or limited geographical distribution.

Given the spatial, temporal, and budgetary limitation on collecting information for this forest type in Chile, it is not surprising that at the present time no serious attempt has been made to build a complete, representative, and consistent modeling system for this important resource. Therefore, the main objective of this study was to build some of the components of a growth and yield model system for the natural mixed forests of the RORACO forest type in Chile. These models use one source of currently available, but still limited, information from temporary and permanent plots established in the complete range of this forest type. The specific objectives included to fit and validate stand-level models for (1) basal area according to the cohorts of *Nothofagus* and companion species, (2) changes over time in the proportion of *Nothofagus* trees in a stand, and (3) tree mortality that considers the concept of self-thinning. These models should constitute the main component of future implementations of G&Y systems for this resource.

2. Materials and Methods

2.1. Data Description

The data for this study originated from three independent sets of sampling series, i.e., two temporary plot (TP1 and TP2) and one permanent plot (PP) series. All plots were established in second growth RORACO forests in Chile, and they are located between the 36° and 42° S latitude. The TP1 and TP2 series were established by the Universidad Austral de Chile between 1999 and 2000 (see [15] for original sampling methodology). The TP1 and TP2 series were sampled according to a stratification representative of the RORACO forest type based on the latest national forest inventory [11]. The TP1 data had a total of 50 plots with an area of 250 m² formed by a conglomerate of two subplots. Meanwhile, the TP2 data had a total of 120 rectangular plots with areas ranging between 250 and 500 m². In contrast, the PP series consisted of three sites under silvicultural thinning measured between 1980 and 1999 with each site remeasured up to four times [25]. However, for the latter, only the subset of plots without treatment (i.e., controls), low thinning (less than 5% of removed basal area), and girdling treatments were considered in the present study. Hence, the PP series dataset consisted of 48 plots with 183 unique measurements, providing several growth and mortality periods. A map of the locations of plots of these three datasets are presented in Figure 1.

For all plots, trees above 5 cm of diameter at breast height (DBH, cm) were inventoried for DBH and total height (H, m). The *Nothofagus* species were identified and the rest was recorded as companion species. For all plots, the following stand-level variables were calculated: dominant age at breast height (AGE, years), dominant height (HD, m), site index (SI, m), total basal area (BA, m² ha⁻¹), and total number of trees (NHA, trees ha⁻¹). Quadratic diameter (DQ, cm) was measured and defined as the diameter of the tree with average basal area. Dominant age at breast height (AGE) is defined as the average age of 100 trees per hectare with the largest DBH. Dominant height (HD) is the average total height of the thickest 100 trees per hectare. Site index (SI) is the stand dominant height at 20 years (see [26] for further details). Additionally, for each of the cohorts, basal area for *Nothofagus* and companion species (NHAN and NHAC, respectively, trees ha⁻¹) were calculated. Finally, the proportion of basal area and number of trees of *Nothofagus* (PBAN, PNHAN) and companion species (PBAC, PNHAC) were also obtained. To study the effect of geographic location in growth and productivity, all plots were assigned to their growth zone (ZONE) (further details on zoning are presented in [26]).

In order to focus on stands that were dominated by *Nothofagus* species, only those plots with PBAN > 0.6 were selected for this study. Summary statistics of these plots are presented in Table 1. Additionally, the dominant species (DOM-SP) of a given plot was defined as the *Nothofagus* species that had more than 70% of BA. In terms of composition, the TP1 and TP2 data are primarily of *N. dombeyi* but all dominant species are present; however, the PP data contains only plots dominated by *N. alpina* (Table 2).



Figure 1. Map of the location of plots within the natural distribution of forest type RORACO (shaded area) for the permanent plots (PP) and temporary plots (TP1 and TP2). Growth zones (1–4) are also identified.

Variable	TP1 ($n = 50$)		TP2 (<i>n</i> = 120)		PP $(n = 48, m = 183)$	
	Mean (SE)	Range	Mean (SE)	Range	Mean (SE)	Range
AGE	39.76 (1.89)	14.21-67.9	39.58 (1.54)	12.71-86.81	41.08 (0.60)	25–51
HD	21.29 (0.84)	9.99-34.65	21.84 (0.66)	7.83-42.40	23.49 (0.46)	15.25-37
SI	10.40 (0.42)	3.61-17.13	11.09 (0.39)	1.81-23.01	10.62 (0.32)	6.15-17.24
BA	47.41 (2.53)	14.48-98.42	41.75 (1.46)	9.54-86.28	40.91 (0.59)	13.35-69.82
NHA	2442 (150)	880-5560	2514 (123)	200-5600	1277 (38)	340-3560
DQ	16.81 (0.77)	7.74-30.41	16.74 (0.75)	6.78-70.42	22.17 (0.40)	10.38-40.87
BAN	42.17 (2.34)	13.9-89.57	36.30 (1.31)	8.76-85.99	38.67 (0.57)	12.66-63.83
BAC	5.24 (0.85)	0.00-23.10	5.45 (0.56)	0.00 - 26.40	2.24 (0.17)	0.00 - 15.44
NHAN	1826 (135)	280-5560	1784 (106)	200-5040	1127 (32)	160-2880
NHAC	616 (88)	0.00-3040	730 (69)	0.00 - 3480	150 (12)	0.00-1180
PNHAN	0.75 (0.03)	0.23-1.00	0.72 (0.02)	0.18 - 1.00	0.89 (0.01)	0.47 - 1.00
PNHAC	0.25 (0.03)	0.00-0.77	0.28 (0.02)	0.00-0.82	0.11 (0.01)	0.00-0.53
PBAN	0.89 (0.02)	0.61 - 1.00	0.88 (0.01)	0.60 - 1.00	0.95 (0.00)	0.63-1.00
PBAC	0.11 (0.02)	0.00-0.39	0.12 (0.01)	0.00 - 0.40	0.05 (0.00)	0.00-0.37

Table 1. Mean (standard error (SE)) and range of stand variables between plot series.

Note. TP1: Temporary Plot 1, TP2: Temporary Plot 2, and PP: Permanent Plot series. *n* is the number of plots and *m* is the number of measurements, m = n in TP1 and TP2. AGE: dominant age (years), HD: dominant height (m), SI: site index (m), BA: total basal area (m² ha⁻¹), NHA: total number of trees (trees ha⁻¹), DQ: mean quadratic diameter (cm), BAN: basal area of *Nothofagus* species (m² ha⁻¹), BAC: basal area of companion species (m² ha⁻¹), NHAN: number of *Nothofagus* species trees (trees ha⁻¹), NHAC: number of trees of companion species (trees ha⁻¹), PNHAN: proportion number of trees of *Nothofagus* species (0–1), PNHAC: proportion number of trees of companion species (0–1).

Table 2. Number of plots classified by dominant species (DOM-SP) for the Temporary Plot 1 (TP1), Temporary Plot 2 (TP2), and Permanent Plot (PP) series. *N*. = *Nothofagus*.

Series	N. alpina	N. dombeyi	N. obliqua	Mixed	Total
TP1	6	21	14	9	50
TP2	8	49	20	23	120
PP	41	0	0	7	48

2.2. Model Description

2.2.1. Basal Area

To predict basal area for the two cohorts, BAN and BAC, this study fitted two independent models. All three *Nothofagus* species were combined into the same cohort based on reported low levels of differentiation between the species [26]. Given the limitation of the data, the TP1 and TP2 plots were used as training data, whereas only PP plots were used as validation data. Hence, validation is focused on the performance of *N. alpina*, which is a limitation. As more long-term data become available, further validations are possible. For BAN and BAC, linear models were fitted using a log transformation of these responses with different combinations of predictors, including AGE, HD, SI, NHA, NHAN, NHAC, PBAN, and PBAC. These predictors were considered in their original units or transformed using the functions of natural logarithm, inverse, square of the inverse, and square root of the inverse. ZONE for each stand was evaluated separately with no interactions with other predictors. To assist with model selection, a backward selection procedure was implemented based on a significance level set to $\alpha = 0.05$, and models with variance inflation factors (VIFs) larger than four in any of their predictors were discarded. It is assumed that the BAN and BAC form the total stand basal area; hence, BA = BAN + BAC.

To estimate the future values of BAN and BAC given a starting condition, the prediction equations fitted above were derived into projection models by differentiating with respect to age following the methodology described by Clutter [27]. This study defined projection models as those that use current stand conditions to project parameter values into the future; hence, this methodology converted yield

models into compatible growth equations using the same model parameters. Simultaneous fitting of prediction and projection equations was not possible given that the TP1 and TP2 datasets contained only temporary plots, where projection models require basal area growth data measured over intervals. To evaluate these models, the PP series data, consisting of 217 growth intervals, were used, but note that this dataset, as indicated earlier, is dominated by *N. alpina* stands.

2.2.2. Proportion of Nothofagus Trees

To predict the proportion of trees corresponding to the *Nothofagus* cohort (PNHAN), a linear model was fitted based on the logit transformation of PNHAN using, as similar to the basal area fit, the TP1 and TP2 plots as training data and the permanent plot measurements from PP as validation data. The same predictors (and their transformations) used in the BA model were tested and a final model was selected using a backward selection procedure as indicated above. As stated before, all *Nothofagus* species were combined into a single cohort given their similarity in biological behavior.

2.2.3. Mortality

Given the limitations on long-term mortality data that adequately represent all dominant species, we followed a two-step procedure in this study. First, coefficients from Reineke's self-thinning models [28] were first obtained. These were then used to fit a proposed nonlinear model defined by the concept that, as stands get closer to a maximum density, they experience higher levels of mortality.

In a previously published study using the information from TP1 and TP2 [24], the following self-thinning expression was fitted [28]:

$$\ln(\text{NHA}) = \alpha + \beta \, \ln(\text{DQ}) \tag{1}$$

where ln() is the natural logarithm and α and β are the parameters to estimate; NHA and DQ were described previously. The above model was obtained to stands dominated by *N. alpina*, *N. obliqua*, or *N. dombeyi*, separately, and parameters are reported by [24]. However, a single slope ($\beta = -1.41$) was found for all three species but with different intercepts (11.61, 11.37, and 11.76, respectively). The above model can be used, together with the current density value (NHA₀), to estimate the current maximum (or limiting) quadratic diameter (DQ_{0max}), as follows:

$$DQ_{0max} = \exp\left(\frac{\ln(NHA_0) - \alpha}{\beta}\right)$$
(2)

Here, DQ_{0max} is interpreted as the maximum stand quadratic diameter that is allowed at a density of NHA₀. Hence, the model from Equation (2) implies that, as the current quadratic diameter (DQ_0) approaches DQ_{0max} , there is an increase in mortality and that stands dominated by the same species respond to the self-thinning rule evenly.

For the second step, the 217 growth intervals from the PP series were used to fit the following proposed nonlinear mortality model that uses both the current conditions (NHA₀, DQ₀ and its DQ_{0max}), as follows:

$$\ln(\text{NHA}_1) = \ln(\text{NHA}_0) \left(1 - (\theta \ \Delta t) \left(\frac{\text{DQ}_0}{\text{DQ}_{0\text{max}}} \right) \right)$$
(3)

where θ is the parameter to estimate and can be interpreted as a maximum mortality rate when the stand is at DQ_{0max}, and Δt is the years between growth intervals.

2.2.4. Model Evaluation

Predictions and projections for the model of basal area of *Nothofagus* and companion species, proportion of *Nothofagus* trees, and mortality were evaluated by calculating the following goodness-of-fit

measures: R^2_{emp} , RMSE%, and Bias%, which are detailed below. These measures were obtained for the training and validation datasets providing two assessments of the models.

$$R_{\rm emp}^2 = 1 - \sum_{i=1}^{n} (y_i - \hat{y}_i)^2 / \sum_{i=1}^{n} (y_i - \overline{y}_i)^2$$
(4)

RMSE% =
$$100 \times \sqrt{\sum_{i=1}^{n} (y_i - \hat{y}_i)^2 / \overline{y}_i}$$
 (5)

Bias% =
$$100 \times \sum_{i=1}^{n} (y_i - \hat{y}_i)^2 / (n \, \overline{y}_i)$$
 (6)

where y_i and \hat{y}_i are the ith observed and predicted (or projected) value, respectively; \bar{y} is the mean response observed value; and *n* is the number of observations.

All linear and nonlinear models were fitted using the statistical software R version 3.3.2 [29]. To detect multicollinearity between predictors (see Table 1), variance inflation factors (VIFs) were checked. All goodness-of-fit statistics were evaluated using the back-transformed response variables to their original units. Because the models for BAN and BAC use the natural logarithm transformation, their back-transformed estimates were adjusted using the correction, i.e., $\hat{y}_i^* = \hat{y}_i \exp(\sigma^2/2)$, where σ^2 is the mean square error. For graphical outputs, relative residuals were used, which were defined as the difference between observed and predicted values divided by the mean observed value. As an additional check, projection models were evaluated by using all 217 possible growth intervals within the PP data; here, the earlier plot measurement was used as the initial conditions to perform the simulations, and these were projected over the growth interval. Then, the later measurement was used to contrast observed against predicted values. For this dataset, the time between growth intervals ranged between 2 and 12 years.

3. Results

3.1. Basal Area

For all plots considered in this study, the average total BA for *Nothofagus* and companion species corresponded to 38.48 and 3.41 m² ha⁻¹, respectively. BAN ranged from 12.66 to 89.57 m² ha⁻¹, and BAC from 0.00 to 26.40 m² ha⁻¹.

The final selected models for BA of Nothofagus and companion species were as follows:

$$\ln(\text{BAN}) = \hat{\beta}_0 + \hat{\beta}_1 \ln(\text{AGE}) + \hat{\beta}_2 \ln(\text{SI}) + \hat{\beta}_3 \ln(\text{NHA}) + \hat{\beta}_4 \ln(\text{PBAN})$$
(7)

$$\ln(BAC) = \hat{\beta}_0 + \hat{\beta}_1 \ln(AGE) + \hat{\beta}_2 \ln(PNHAN) + \hat{\beta}_3 \ln(PBAN)$$
(8)

The logarithmic transformation of the predictors returned the best results and had the additional advantage that it derives the projection models easily (see below). For the selected models, all final predictors showed low VIF values (<2.1), reflecting negligible levels of multicollinearity between them. The resulting fitted model for BAN had $R^2_{emp} = 0.54$, and the fitted model for BAC had a higher R^2_{emp} with a value of 0.85 (Table 3). The prediction of total basal area had an $R^2_{emp} = 0.56$. This moderate correlation reflects the wide range of conditions found in these forests. All models presented negligible bias (<1%). Both BAN and BAC models had good goodness-of-fit measures with the PP validation data (Table 3), where the BAN, BAC, and BA predictions returned slightly unfavorable higher Bias% values when compared to the training data, but these were all lower than 4%.

According to the estimated coefficients (Table 4), AGE was positively associated with both BAN and BAC (with slope coefficients of 1.21 and 0.09, respectively). Hence, as the stand gets older basal area increases, with a larger effect for the *Nothofagus* cohort. For BAN, the positive coefficients for SI (0.65) and NHA (0.52) indicate that better site quality and higher levels of stocking result in higher *Nothofagus* basal area. In the BAC model, PNHAN and PBAN have negative coefficients (-0.22 and

-1.87, respectively) indicating that higher proportions of *Nothofagus* species abundance affect the amount of basal area of companion species.

Model	Prediction		Projection	Prediction		Projection
	Training	Validation	Tojection	Training	Validation	Tojection
	BAN			BA		
п	150	51	217	150	51	217
R^2_{emp}	0.54	0.51	0.80	0.56	0.50	0.84
RMSE%	27.31	13.63	9.04	26.29	13.36	7.83
Bias%	-0.29	2.25	-5.24	-0.16	1.69	-4.51
	BAC			PNHAN		
п	150	183	217	150	183	
R^2_{emp}	0.85	0.89	0.94	0.68	0.56	
RMSE%	44.6	41.68	33.52	16.92	8.07	
Bias%	0.86	-3.72	12.48	-1.50	3.46	

Table 3. Goodness-of-fit measures for models for the basal area of *Nothofagus* species (BAN, Equations (7) and (9)), basal area of companion species (BAC, Equations (8) and (10)), total basal area (BA), and the proportion of number of *Nothofagus* species trees (PNHAN, Equation (11)).

Note: The TP1 and TP2 series were used as training data and the PP series as validation data. Validation data for the BAN and PNHAN models only include stands with known AGE.

Table 4. Parameter estimate, standard error (SE) and variance inflation factor (VIF) for models of basal area of *Nothofagus* species (BAN, Equations (7) and (9)), basal area of companion species (BAC, Equations (8) and (10)), and the proportion of number of *Nothofagus* species trees (PNHAN, Equation (11)). All model parameters were found to be significant (p < 0.001).

Model	eta_0	β_1	β_2	β_3	eta_4
BAN					
Estimate	-6.16977	1.21163	0.65197	0.51841	1.24957
SE	0.71314	0.07496	0.06801	0.0529	0.17498
VIF		2.06	1.53	2.10	1.25
BAC					
Estimate	1.99503	0.09436	-0.21578	-1.87264	
SE	0.08904	0.02513	0.04885	0.12278	
VIF		1.23	3.62	3.27	
PNHAN					
Estimate	-7.13684	10.29084	-0.01404		
SE	0.55383	0.56703	0.00429		
VIF		1.02	1.02		

Note: The TP1 and TP2 series were used for training.

Predicted BAN and BAC values corresponded well with observed values in both training and validation data (Figures 2 and 3). However, this correspondence decreased with larger observed BAN and BAC values, and some under-prediction was found for observed BAN values above 75 m² ha⁻¹. Similar results were found for BA, as this mostly corresponds to *Nothofagus* species basal area (Figure 2C). Normality and heterogeneity of residuals were also checked without important departures from these assumptions.

Both basal area equations were used to derive their compatible projection equations. These models project future values (BAN_1 and BAC_1) based on the current stand conditions (BAN_0 and BAC_0 , respectively). These are as follows:

$$BAN_{1} = BAN_{0} \left(\frac{AGE_{1}}{AGE_{0}}\right)^{\hat{\beta}_{1}} \left(\frac{NHA_{1}}{NHA_{0}}\right)^{\hat{\beta}_{3}} \left(\frac{PBAN_{1}}{PBAN_{0}}\right)^{\hat{\beta}_{4}}$$
(9)

$$BAC_{1} = BAC_{0} \left(\frac{AGE_{1}}{AGE_{0}}\right)^{\hat{\beta}_{1}} \left(\frac{PNHAN_{1}}{PNHAN_{0}}\right)^{\hat{\beta}_{2}} \left(\frac{PBAN_{1}}{PBAN_{0}}\right)^{\hat{\beta}_{3}}$$
(10)

where the β coefficients are the same parameters from the fitted Equations (8) and (9).

For the evaluation of the projection equations using the validation dataset, all basal area models showed excellent goodness-of-fit measures (all with $R^2_{emp} > 0.94$). The relative residuals obtained over time for BAN, BAC, and BA projections (Figure 4A–C) are centered around zero for shorter projections (i.e., low bias), whereas they tend to depart for increasing projection times (i.e., under-estimate). For projections under 6 years, the BAN model returned relative residuals lower than 10% and were centered about zero. After 6 years, the relative residuals reached higher values with a tendency to under-predict basal area. The BAC model had residuals centered around zero with no notable deviations even at 12 years of projections. However, there were some projections with residuals over 30%, which are not of relevant concern because of the low proportion of basal area from the companion cohort in the sampled plots.



Figure 2. Observed vs. predicted values for (**A**) basal area of *Nothofagus* species (BAN, Equation (7)); (**B**) basal area of companion species (BAC, Equation (8)); (**C**) total basal area, BA = BAN + BAC; and (**D**) the proportion of number of trees per hectare of *Nothofagus* species (PNHA, Equation (3)). All panels are from the Temporary Plot series (TP1 and TP2).



Figure 3. Observed vs. predicted values for (**A**) basal area of *Nothofagus* species (BAN, Equation (7)); (**B**) basal area of companion species (BAC, Equation (8)); (**C**) total basal area, BA = BAN + BAC; and (**D**) the proportion of number of trees per hectare of *Nothofagus* species (NHA, Equation (3)). All plots use the Permanent Plot (PP) series.



Figure 4. Relative residuals for different simulation years in projections of (**A**) basal area of *Nothofagus* species (BAN, Equation (9)); (**B**) basal area of companion species (BAC, Equation (10)); (**C**) total basal area, BA = BAN + BAC; and (**D**) number of trees per hectare (NHA, Equation (3)) using the PP data as validation.

3.2. Proportion of Nothofagus Trees

For the plots considered in this study, the average proportion of *Nothofagus* species trees corresponded to 82%, where most of them presented values greater than 72%. The final selected model for PNHAN was the following:

$$logit(PNHAN) = ln\left(\frac{PNHAN}{1 - PNHAN}\right) = \hat{\beta}_0 + \hat{\beta}_1 PBAN + \hat{\beta}_2 AGE$$
(11)

For the training data, this model had reasonable goodness-of-fit measures with $R^2_{emp} = 0.68$ and Bias% = -1.50. Additionally, predicted PNHAN values tended to correspond with observed values, but high levels of uncertainty still existed (Figure 2D). Moreover, for PP validation data, these measures were $R^2_{emp} = 0.56$ and Bias% = 3.46. The predictions for PNHAN tended to have less uncertainty with higher observed PNHAN, as observed in Figure 3D.

The estimated parameters of this model are shown in Table 4. The slope coefficient for PBAN (10.29) reflects the high association between this predictor and PNHAN (these predictors present a correlation of 0.89). For AGE, its coefficient (-0.01) indicates a reduction of PNHAN with increasing stand age, reflecting the pioneer behavior of *Nothofagus* species and the gradual establishment of companion species over time. These selected predictors all show low VIF values (<1.02).

3.3. Mortality

Among the remeasured plots from the PP data, the observed annual mortality rates had an average of 3.0% with a maximum of 14.2%. Their patterns were consistent over time for most plots evidenced from the parallel trajectories, as shown in Figure 5A.

The fitted nonlinear model had a good fit with $R^2_{emp} = 0.79$, RMSE% = 18.46 and Bias% = -2.80. The single parameter estimate corresponded to $\theta = 0.003595746$ (SE = 0.000213), indicating that, for future projections, the estimated number of trees will always be smaller than the current condition. The predicted mortality values had good correspondence with observed ones over the entire range of the data (Figure 5B) and with relative residuals ranging from -30% to 30% (Figure 4D). While these residuals may be considered as large model uncertainty, the fact that residuals are generally centered around zero, even after 12 years of projection, suggests a good overall accuracy.



Figure 5. (**A**) Quadratic diameter (DQ) vs. number of trees per hectare (NHA) trajectories of measured stands of the PP series. The dashed line is the DQ_{max} for *N. alpina*. (**B**) Observed vs. projected values of number of trees.

4. Discussion

The fitted model for BAN presented here is biologically realistic as it accounts for stand age, productivity, and stocking using AGE, SI, and NHA, respectively. These are common predictors

found in other reported *Nothofagus* species growth models [30]. In the present study, the effect of productive growth geographic zones (ZONE) on basal area growth was not significant, which is likely to be the result of the incorporation of site index (SI) in the model, an in situ stand parameter that describes that productivity. However, other studies have found that growth zone is a significant component [4,24,30–32]. Additional future data should allow exploring these responses further together with the evaluation of effects of other environmental and biological factors that may affect *Nothofagus* species growth, such as light conditions, elevation, and nitrogen availability [22,33,34]. The fitted BAN models resulted in moderate correlations for the training and validation datasets (<0.54). This reflects the level of heterogeneity found on these forests, with many aspects that might influence the accuracy of this model, such as uncertainty on determining age, anthropic alterations, variable climate at plant establishment, etc.

The model for the proportion of *Nothofagus* trees reflects the pioneer behavior of the *Nothofagus* species [7], evidenced by the negative coefficient related to dominant age. It also shows the increasing establishment of the companion (shade-tolerant) species as the stand gets older, reflecting some gradual forest succession.

The self-thinning rule, which has been mostly applied in pure stands with some examples in mixed forest stands [24], worked successfully here to predict mortality. This natural self-thinning is occurring in stands as young as 25 years of dominant age, 15 years earlier than shown in stands dominated by *N. obliqua* [8]. Additional long-term measurements of permanent plots should allow the use of more widely tested stand-level mortality models, such as the ones presented by Thapa and Burkhart [35].

Based on the mortality and basal area projection models, it is possible to propose a flow that builds a simple simulation system of equations that can realistically project BAN values into the future for RORACO forests. To illustrate this system, simulated stands dominated only by *Nothofagus* species (i.e., PBAN equal to 1), with an initial BAN of 15 m² ha⁻¹, stand age of 15 years, SI of 10 m, and several initial NHAN values are presented in Figure 6. These simulated stands showed that basal area patterns grow asymptotically with larger BAN growth rates for forests with fewer initial trees (Figure 5A). Furthermore, as expected, higher initial tree densities resulted in higher rates of mortality (Figure 6B) following the patterns described by the proposed mortality model.



Figure 6. Model projections of 60 years of basal area of *Nothofagus* species (BAN, Equations (3) and (9)) with a different initial number of trees per hectare (NHA). Projections are based on an initial BAN of 15 m² ha⁻¹, the dominant age of 15 years, SI of 10 m, and PBAN of 1. (**A**) Dominant age vs. BAN trajectories. (**B**) DQ vs. NHA trajectories. The dashed line is the DQ_{max} line for *N. alpina*.

In this study, the basal area models for the two cohorts (*Nothofagus* and companion species) were assumed to be independent. This assumption can be challenged by studies that suggest that additive effects allow higher yields of *Nothofagus* species when companion species are present [36,37]. However, the choice of independent growth models is supported by research that showed a lack of correlation

between basal area of *Nothofagus* and companion species [38]. Furthermore, the sum of our proposed models accurately estimates total basal area (BA), but further measurements should allow for a better evaluation of these hypotheses.

The use of cohorts for G&Y models presents additional flexibility, and it is a reasonable compromise between whole-stand models and single-tree models [1,6], particularly for mixed forests, providing some additional granularity on the construction of these models. The similarity on growth behaviors of *N. alpina* and *N. dombeyi* [31] and the reliability of stand-level projections presented in this study justified the grouping of these species into a single cohort. In addition, there is evidence of low differentiation among these species, as reported in a multivariate analysis that used the same dataset from the current study [26] and from other authors indicating that stands dominated by either *N. alpina* or *N. obliqua* do not greatly differ in the total basal area or canopy height [30]. While it could be useful to have individual stand models for each of the *Nothofagus* species for further granularity, the present limitations of the dataset (which has not adequately represented each species) is likely to affect the accuracy of the final fitted models.

Unfortunately, the permanent plot (PP) series is, at present, our only currently available source of remeasured data to fit and validate the proposed *Nothofagus* species models, and its main limitations is that it is dominated by *N. alpina*. Hence, further improvements to our proposed models can only be achieved with additional permanent plots that better represent the other *Nothofagus* species, and that span over a wider geographical range. This lack of time series is particularly relevant for mortality that, in this case, was based on Reineke's expression and not on repeated measurements of the same plot.

Regardless of these limitations, these models represent critical components of growth and yield models for the natural mixed forests of the RORACO forest type in Chile, and importantly they are using information from stratified temporary and permanent plots established in its complete geographical range.

5. Conclusions

For this study, several stand-level models were built to improve the predictability of stand dynamics for natural mixed secondary forests of the RORACO forest type in Chile. Stand mortality was successfully modeled with a function defined by the concept that, as stands get closer to a maximum density, they experience higher levels of mortality. To our knowledge, these are the first broadly applicable growth and yield models for the RORACO forest type with dynamics of both companion species and *Nothofagus* cohorts. These models can be incorporated as part of a system of modules for a growth and yield simulator of this forest type. This system could also include local conditions and model operational thinning. The models reported here constitute simple and valuable tools to support management decisions for this resource in Chile.

Author Contributions: Conceptualization, S.A.G.; methodology, S.P., P.C.M., and S.A.G.; software, S.P., P.C.M., and S.A.G.; validation, S.P.; formal analysis, S.P.; data curation, S.P., P.C.M., and S.A.G.; writing—original draft preparation, S.P.; writing—review and editing, S.P., P.C.M., W.P.C.J., A.O., and S.A.G.; supervision, S.A.G.; project administration, A.O. and S.A.G.; funding acquisition, A.O. and S.A.G. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by FONDEF (Chile), grant number D9711065, and S.P. was funded by a scholarship from the School of Forest Resources and Conservation, IFAS, University of Florida (USA).

Acknowledgments: The authors greatly acknowledge the team of technicians and students that helped on the establishment and measurement of the majority of the plots used in this study. P.M. thanks the financial support of Programa Regional CONICYT R17A10002 Laboratorio Ecoclimático. In addition, we would like to thank reviewers for their important contribution to improvements of this manuscript.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

References

- 1. Vanclay, J. Modelling Forest Growth and Yield: Applications to Mixed Tropical Forests; CAB International: Wallingford, UK, 1994; p. 312.
- 2. Porte, A.; Bartelink, H.H. Modelling mixed forest growth: A review of models for forest management. *Ecol. Model.* **2002**, *150*, 141–188. [CrossRef]
- Liu, J.; Ashton, P.S. Individual-based simulation models for forest succession and management. *For. Ecol. Manag.* 1995, 73, 157–175. [CrossRef]
- 4. Moreno, P.C.; Palmas, S.; Escobedo, F.J.; Cropper, W.P.; Gezan, S.A. Individual-tree diameter growth models for mixed Nothofagus second growth forests in southern Chile. *Forests* **2017**, *8*, 506. [CrossRef]
- 5. Wulder, M.A.; White, J.C.; Fournier, R.A.; Luther, J.E.; Magnussen, S. Spatially explicit large area biomass estimation: Three approaches using forest inventory and remotely sensed imagery in a GIS. *Sensors* **2008**, *8*, 529–560. [CrossRef] [PubMed]
- 6. Reed, K.L. An ecological approach to modelling the growth of forest trees. For. Sci. 1980, 26, 33–50.
- 7. Veblen, T.T.; Schlegel, F.M.; Escobar, B. Structure and dynamics of old-growth Nothofagus forests in the Valdivian Andes, Chile. *J. Ecol.* **1980**, *68*, 1–31. [CrossRef]
- 8. Donoso, C. Bosques templados de Chile y Argentina. In *Variación, Estructura y Dinámica;* Editorial Universitaria: Santiago, Chile, 1993; p. 483.
- 9. Veblen, T.T.; Donoso, C.; Kitzberger, T.; Rebertus, A. Ecology of southern Chilean and Argentinean Nothofagus forests. In *The Ecology and Biogeography of Nothofagus Forests*; Veblen, T., Hill, R., Read, J., Eds.; Yale University Press: New Haven, CT, USA, 1996; pp. 293–353.
- Sabatier, Y.; Azpilicueta, M.; Marchelli, P.; Gonzalez-Penalba, M.; Lozano, L.; Garcia, L.; Martinez, A.; Gallo, L.; Umana, F.; Bran, D.; et al. Distribución natural de Nothofagus alpina y Nothofagus obliqua (Nothofagaceae) en Argentina, dos especies de primera importancia forestal de los bosques templados norpatagónicos. *B. Soc. Argent. Botánica* 2011, 46, 131–138.
- 11. CONAF (Corporación Nacional Forestal, CL). Catastro de los Recursos Vegetacionales Nativos de Chile: Monitoreo de Cambios y Actualizaciones, Periodo 1997–2011; Ministerio de Agricultura: Santiago, Chile, 2011; p. 25.
- 12. INFOR (Instituto Forestal, CL). Bosque Nativo. In *Área de Información y Economía Forestal;* Ministerio de Agricultura: Santiago, Chile, 2016; p. 42.
- Zamorano-Elgueta, C.; Rey-Benayas, J.M.; Cayuela, L.; Hantson, S.; Armenteras, D. Native forest replacement by exotic plantations in southern Chile (1985–2011) and partial compensation by natural regeneration. *Forest Ecol. Manag.* 2015, 345, 10–20. [CrossRef]
- 14. Paritsis, J.; Veblen, T. Dendroecological analysis of defoliator outbreaks on Nothofagus pumilio and their relation to climate variability in the Patagonian Andes. *Glob. Change Biol.* **2011**, *17*, 239–253. [CrossRef]
- 15. Ortega, A.; Gezan, S.A. Cuantificación de crecimiento y proyección de calidad en Nothofagus. *Bosque* **1998**, *19*, 123–126. [CrossRef]
- Muller-Using, S.; Muller-Using, B.; Martin, M.; Grosse, H.; Mujica, R. Estado Actual y Propuestas Silvicolas para los Renovales de Nothofagus en la Zona Centro Sur de Chile; Informe Tecnico 190: Reporte de Practicas Silvicolas; Instituto Forestal: Santiago, Chile, 2012.
- 17. Gezan, S.A.; Moreno, P.C.; Ortega, A. Modelos fustales para renovales de roble, raulí y coigue en Chile. *Bosque* **2009**, *30*, 61–69. [CrossRef]
- Esse, C.; Donoso, P.J.; Gerding, V.; Navarro, C.; Encina-Montoya, F. Modelling dominant height and site index in different edaphoclimatic zones of Nothofagus dombeyi secondary forest in the Andes of south-central Chile. *South For.* 2014, *76*, 1–8. [CrossRef]
- Salas-Eljatib, C.; Garcia, O. Modelling height development of mature Nothofagus obliqua. *For. Ecol. Manag.* 2006, 229, 1–6. [CrossRef]
- 20. Trincado, G.; Kiviste, A.; Von Gadow, K. Preliminary site index models for native roble (Nothofagus obliqua) and raulí (N. alpina) in Chile. *N. Z. J. For. Sci.* **2002**, *32*, 322–333.
- 21. Attis-Beltrán, H.; Chauchard, L.; Dezzotti, A.; Martínez-Pastur, G. Modelo de crecimiento diamétrico de Nothofagus alpina y su relación con el de Nothofagus obliqua y Nothofagus dombeyi en los bosques naturales de la Patagonia argentina. *Bosque* **2018**, *39*, 107–117. [CrossRef]
- Chauchard, L.; Sbrancia, R. Modelos de crecimiento diamétrico para Nothofagus obliqua. *Bosque* 2003, 24, 3–16. [CrossRef]

- 23. Bahamóndez, C.; Martin, M. Modelo de estimación de la competencia y mortalidad individual para renovales de roble y raulí. *CIFOR* **1996**, *10*, 153–163.
- 24. Gezan, S.A.; Ortega, A.; Andenmatten, E. Diagramas de manejo de densidad para renovales de roble, raulí y coigue en Chile. *Bosque* 2007, *28*, 97–105. [CrossRef]
- 25. Puente, M.; Penaloza, R.; Donoso, C.; Paredes, R.; Núñez, P.; Morales, R.; Engdahl, O. Estudio de Raleo y Otras Técnicas para el Manejo de Renovales de Raulí y Roble. Segunda Fase: Informe de Avance de Instalación de Ensayos de Raleo en Renovales de Raulí. Informe de Convenio 30; Proyecto CONAF/PNUD/FAO-CHI/76/003; Facultad de Ciencias Forestales, Universidad Austral de Chile: Valdivia, Chile, 1980; p. 59.
- Moreno, P.C.; Gezan, S.A.; Palmas, S.; Escobedo, F.J.; Cropper, W.P. Exploring stand and tree variability in mixed Nothofagus second-growth forests through multivariate analyses. *Bosque* 2018, 39, 397–410. [CrossRef]
- 27. Clutter, J.L. Compatible growth and yield models for loblolly pine. *For. Sci.* **1963**, *9*, 354–371.
- 28. Reineke, L. Perfecting a stand-density index for even-aged forests. J. Agric. Res. 1933, 46, 627–638.
- 29. R Core Team. R: A Language and Environment for Statistical Computing; R Foundation for Statistical Computing: Vienna, Austria, 2016.
- 30. Lusk, C.; Ortega, A. Vertical structure and basal area development in second-growth Nothofagus stands in Chile. *J. Appl. Ecol.* **2003**, *40*, 639–645. [CrossRef]
- 31. Echeverria, C.; Lara, A. Growth patterns of secondary Nothofagus obliqua-N. alpina forests in southern Chile. *Forest Ecol. Manag.* **2004**, *195*, 29–43. [CrossRef]
- 32. Esse, C.; Donoso, P.J.; Gerding, V.; Encina-Montoya, F. Determination of homogeneous edaphoclimatic zones for the secondary forests of Nothofagus dombeyi in central-southern Chile. *Cienc. Investig. Agrar.* **2013**, *40*, 351–360. [CrossRef]
- Soto, D.P.; Jacobs, D.F.; Salas, C.; Donoso, P.J.; Fuentes, C.; Puettmann, K.J. Light and nitrogen interact to influence regeneration in old-growth Nothofagus-dominated forests in south-central Chile. *For. Ecol. Manag.* 2017, 384, 303–313. [CrossRef]
- 34. Walter, C.; Prez, C.A.; Thomas, F.M. Weather or weathering? Growth of Nothofagus dombeyi on volcanic soils differing in nitrogen and phosphorus concentrations. *J. Plant Ecol.* **2016**, *9*, 596–607. [CrossRef]
- 35. Thapa, R.; Burkhart, H.E. Modelling stand-level mortality of loblolly pine (Pinus taeda L.) using stand, climate, and soil variables. *For. Sci.* **2015**, *61*, 834–846. [CrossRef]
- Danescu, A.; Albrecht, A.T.; Bauhus, J. Structural diversity promotes productivity of mixed, uneven-aged forests in southwestern Germany. *Oecologia* 2016, 182, 319–333. [CrossRef]
- 37. Donoso, P.J.; Soto, D.P. Does site quality affect the additive basal area phenomenon? Results from Chilean old-growth temperate rainforests. *Can. J. Forest Res.* **2016**, *46*, 1330–1336. [CrossRef]
- 38. Donoso, P.J.; Lusk, C.H. Differential effects of emergent Nothofagus dombeyi on growth and basal area of canopy species in an old-growth temperate rainforest. *J. Veg. Sci.* 2007, *18*, 675–684. [CrossRef]



© 2020 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (http://creativecommons.org/licenses/by/4.0/).