

# Height growth-rate at a given height: A mathematical perspective for forest productivity

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## ABSTRACT

Understanding the height growth of trees is a fundamental component for scientific knowledge and management of forest ecosystems. The height of dominant trees at a reference-age, commonly known as the site-index, is the most widely used forest productivity indicator globally. Yet, it has been criticized for its restricted applicability to monospecific and even-aged forests, making it unreliable for natural forests or mixed-species where there is not a single meaningful age. Here, I develop a mathematical perspective for using height growth-rate at a reference-height as a new type of site index. I provide the mathematical basis for the proposed index and illustrate its application by fitting a nonlinear mixed-effects differential equation model to tree height growth data of three *Nothofagus* species in southern Chile. The proposed index allows us to foresee and analyze growth patterns, not only by representing growth-rates as a function of time but also of size. In doing so, the proposed index makes tree growth and productivity analyses accessible to a broader community of researchers.

## 1. Introduction

As a society, we demand forest management practices to promote a sustainable provision of services. Management should rely on both models and indices that provide quantitative information about ecological, social, and economic conditions of forest systems. Understanding the relationships between environmental factors and tree growth had been a significant endeavour of forest scientists. A key feature of forest ecosystems is the potential of sites to produce a given amount of plant biomass. This property is known as forest site productivity (Bontemps and Bouriaud, 2013; Skovsgaard and Vanclay, 2008). While in forest plantation management the term productivity is associated with wood volume, it is generally understood as being the capacity to produce plant biomass. Site productivity determined is by inherent features of the habitat, such as climate, soil properties (i.e., physical, chemical, and biological), and topography.

Forest site productivity assessment is critical for both forest dynamics understanding and forest management planning (Oliver and Larson, 1996). Just as growth is a crucial factor in forest management, site quality is the crucial factor in determining growth (Assmann, 1970; Spurr, 1952). Besides, any sound silvicultural decision should take into account site productivity and conditions (Daniel et al., 1979). As tree growth depends on site productivity, the configuration and composition of forests are too. In consequence, the change in forest structure

through time is affected by productivity; therefore, productivity also affects forest dynamics.

The most common measure of forest site quality is the dominant height of a stand at a specified reference age. This measure, or index, has the advantage of being independent of stand density (Carmean, 1975; García, 2005; Hägglund, 1981; Skovsgaard and Vanclay, 2008; Tesch, 1980), and is widely known as “site index” (Skovsgaard and Vanclay, 2008; van Laar and Akça, 2007; Weiskittel et al., 2011), although other indices had received the same name. Henceforth, I refer to it as a “traditional site index” or simply TSI. Although TSI is used widely for the above reasons, it had received criticism (Gaiser and Merz, 1951; Mader, 1963; Monserud, 1984; 1987; 1988; Sammi, 1965; Vincent, 1961; Wykoff and Monserud, 1988). A significant limitation of TSI is that it is exclusively an even-aged concept (Monserud, 1984; Skovsgaard and Vanclay, 2008), given that it is calculated based on height-age. Therefore, its use is limited for natural forests or mixed-species stands, where there are not a single meaningful age.

Although dominant height growth is a good proxy of site productivity and is accurate enough for management purposes, I stress that the TSI concept could be refined. Likewise, the use of height growth-rate at a reference-height as a site index, henceforth termed GRSI, seems to be suitable on quantitative grounds, providing more insights to our ecological understanding of forest dynamics. I focus here on a quantitative approach for deriving a growth-rate index and only cover

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the essential mathematical aspects. Some other related details are covered in the pioneer studies of forest modelling by Leary and Skog (1972), García (1983) and the most recent ones by Pommerening and Muszta (2015, 2016). I examine and show the theoretical model-based foundations for the use of GRSI as an alternative to TSI. In the present article, I aim at showing the use of height-growth rate at a given height as a potential site index from a mathematical perspective. First, I provide the mathematical grounds on which is based and derived the GRSI. Meanwhile, the second part applies the concept of GRSI to real data from the Andean *Nothofagus* temperate forests in southern Chile, by fitting a non-linear mixed-effects height growth model to three species.

## 2. Methods

### 2.1. Mathematical basis

I illustrate the concept starting from a simple individual-growth model, known as the monomolecular model

$$\frac{dy}{dt} = \beta(\alpha - y), \quad (1)$$

where  $\alpha$  is the upper asymptote or maximum level of the state variable  $y$  and  $\beta$  is a parameter that governs the rate of change (Schabenberger and Pierce, 2002). The state variable  $y$  can be any measure of individual sizes, such as mass, length, volume, or height, among others. However, a more flexible form of the monomolecular model is achieved by a power transformation (García, 1983), so having

$$\frac{dy^\gamma}{dt} = \beta(\alpha^\gamma - y^\gamma), \quad (2)$$

with  $\gamma$  acting as a shape parameter. In addition, solving  $\frac{dy^\gamma}{dt} = \frac{dy^\gamma}{dy} \frac{dy}{dt}$  and after some algebraic manipulation, Eq. (2) renders

$$\frac{dy}{dt} = \frac{\beta\alpha^\gamma}{\gamma} y^{(1-\gamma)} - \frac{\beta}{\gamma} y. \quad (3)$$

Eq. (3) is equivalent to the well-known von Bertalanffy's growth-rate model (von Bertalanffy, 1957; García, 1983):

$$\frac{dy}{dt} = \eta y^m - \kappa y, \quad (4)$$

with  $\frac{\beta\alpha^\gamma}{\gamma} = \eta$ ,  $1 - \gamma = m$ , and  $\frac{\beta}{\gamma} = \kappa$ . I use Eq. (2) as a baseline individual growth-rate model. It is worth noting that although other models and parametrizations can be used (Bontemps and Duplat, 2012; García, 2008; Grosenbaugh, 1965), this model form had shown good behaviour in several tree growth studies (Birch, 1999; Salas et al., 2008; Zeide, 1993). In the sequel, I shall use Eq. (2) as a baseline or skeleton growth-rate model. I aim to develop a new type of site index; therefore, I use this baseline model as such, but the procedure can be expanded to other growth-rate models, indeed. Furthermore, I am not pursuing here to find the best prediction model, but only in using a growth-rate model that behaves reasonably well.

By solving Eq. (2) under some assumptions (see Appendix A), I obtain:

$$y_t = \alpha \left\{ 1 - \left[ 1 - \left( \frac{y_0}{\alpha} \right)^\gamma \right] \exp[-\beta(t - t_0)] \right\}^{1/\gamma}, \quad (5)$$

which if  $t_0 = h_0 = 0$  can be reduced to (see Appendix B):

$$y_t = \alpha \{ 1 - e^{-\beta t} \}^{1/\gamma}. \quad (6)$$

Hereafter, I change the general state-variable  $y$  for a specific one: height ( $h$ ) of dominant (i.e., belonging to the main canopy) trees. The rationale for this choice is based upon the fact that the height growth of dominant trees is relatively unaffected by forest density. As pointed out by Walters et al. (1989), it provides a practical and efficient means to index site quality on occupied sites, even in stands that have undergone

prescribed thinnings or changes in density (i.e., disturbances). Therefore, differences in dominant height (at a reference-age) can be attributed to differences in site productivity (Daniel et al., 1979; Skovsgaard and Vanclay, 2008). In this context, Eq. (6) becomes a useful solution of Eq. (2) because it is especially suitable for modelling height growth of even-aged forest populations (e.g., forestry plantations) because stand age ( $t$ ) is easily measured (García, 1983). Meanwhile, Eq. (5) is suitable for native forest populations where we can use the period of length ( $t - t_0$ ), and the state variables at both the beginning and the end are needed (Salas et al., 2008).

Given that the traditional site index is the dominant height at a reference-age (Skovsgaard and Vanclay, 2008), by substituting this reference-age ( $t_r$ ) in the model (6), the represented height corresponds to the site index ( $S$ ). From here, I can re-arrange the equation in such a way that I obtain a new height growth function that depends on not only the parameters and time but also on the reference-age and site index. Mathematically, the curve equations for different sites differ only in the value of one scalar parameter (García, 1983). For example, if in (6) the parameter  $\beta$  change with site index, I can reparametrize it and obtain

$$h_t = \alpha \left\{ 1 - \exp \left[ \ln \left\{ 1 - \left( \frac{S}{\alpha} \right)^\gamma \right\}^{t/t_r} \right] \right\}^{1/\gamma}. \quad (7)$$

Eq. (7) depicts height growth depending on the parameters, the reference-time and the site index. We obtain a height growth curve for each  $S$  in Eq. (7), and the series of curves, are called a family of site index curves (Clutter et al., 1983).

### 2.2. Deriving a growth-rate based site productivity index

I start by taking the derivative of the growth function (6) for height, which gives

$$\frac{dh}{dt} = \frac{\alpha\beta}{\gamma} [1 - e^{-\beta t}]^{\frac{1}{\gamma}-1} (e^{-\beta t}). \quad (8)$$

This differential equation (DE) is a function of time ( $t$ ); however, I would prefer to have it as a function of the state variable,  $h$ . The resulting model can be applied wherever that is no information about stand age or when information on stand age is not meaningful such happens in uneven-aged stands. Raising both sides of (6) by  $\gamma$  and with little algebra (see detailed steps of this derivation in Appendix B) I obtain

$$\frac{dh}{dt} = \left( \frac{\beta}{\gamma} \right) h \left[ \left( \frac{\alpha}{h} \right)^\gamma - 1 \right], \quad (9)$$

a DE as a function of  $h$  and free of  $t$ , therefore being an autonomous differential equation (Boyce and DiPrima, 2003). Based on this, I propose a new type of site index based on the use of height growth-rate at a reference-height, instead of tree height growth at a reference-age, as in TSI. To build a system of "site index" curves, as I showed with Eq. (7), I start from (9) and define a new site index  $S$  as the time-derivative of  $h$  evaluated at a reference-height  $h_r$ ,

$$S = \left( \frac{\beta}{\gamma} \right) h_r \left[ \left( \frac{\alpha}{h_r} \right)^\gamma - 1 \right]. \quad (10)$$

Then, solving (10) for  $\beta$  and replacing it into (9) yields an expression of the growth rates as a function of height and site index as follows,

$$\frac{dh}{dt} = \left( \frac{S}{h_r} \right) h \left[ \left( \frac{\alpha}{h} \right)^\gamma - 1 \right] \left[ \left( \frac{\alpha}{h_r} \right)^\gamma - 1 \right]^{-1} \quad (11)$$

The height growth-rate model (Eq. (11)) not only depends on the height  $h$  and the parameters but also the site index  $S$  and the reference-height  $h_r$ . In the following, I illustrate the use of this new site index concept by fitting a height growth model to real data.

## 2.3. Application example

### 2.3.1. Data

I used stem analysis data of sample trees of the native species *Nothofagus dombeyi* (coigüe), *N. alpina* (raulí), and *N. obliqua* (roble) selected from sample plots established in secondary forest of roble-raulí-coigüe in south-central Chile between the 36° and 41°30' South latitude. The number of plots by species is 30, 53, and 62, for coigüe, raulí, and roble, respectively, and having between three and four sample trees per plot. These stands are mature forests, mixed-species, and naturally regenerated after some disturbances. Further ecological aspects of these forests can be found in [Veblen et al. \(1981, 1980\)](#). Data were collected in different research projects but compiled and summarized by [Salas \(2011\)](#), in studies involving one or two species of the roble-raulí-coigüe forest type ([Donoso, 1995](#)). Dominant trees were selected for stem analysis, provided they were healthy and of good form, of seed origin, and belonging to the upper canopy. After measuring diameter at breast height ( $d$ ) and total height ( $h$ ), the selected trees were felled, and cross-sectional discs were obtained at stump height (10–40 cm), breast-height (1.3 m), plus other discs evenly spaced between breast-height and total height. Rings were counted in the laboratory. Heights and ring counts from cross-section discs were used to reconstruct height growth as in [Salas and García \(2006\)](#).

### 2.3.2. Statistical model

For my purposes, I re-write (5) as follows

$$h = \alpha \{1 - [1 - (h_0/\alpha)^\gamma] e^{-\beta(t-t_0)}\}^{1/\gamma}, \quad (12)$$

where  $h$  represents tree height at time  $t$ . As pointed out by [Salas et al. \(2008\)](#), this height increment model (12) has the following properties; It does not depend on age; it can be used with data having different period lengths, and can predict height increment for different period lengths. To account for temporal correlation and the hierarchical structure of the data, I fit Eq. (12) in a non-linear mixed-effects framework, by adding random-effects to the  $\beta$  parameter, as follows

$$h_{ijk} = \alpha \{1 - [1 - (h_{ij(k-1)}/\alpha)^\gamma] \exp[-(\beta + b_i + b_{ij})(t_{ijk} - t_{ij(k-1)})]\}^{1/\gamma} + \varepsilon_{ijk},$$

$$b_i \sim N(0, \sigma_1^2), b_{ij} \sim N(0, \sigma_2^2), \varepsilon_{ijk} \sim N(0, \text{Var}[\varepsilon_{ijk}]), \text{Var}[\varepsilon_{ijk}] = \sum \varepsilon_{ijk} = \sigma^2 \delta_{Gijk}^2, \quad (13)$$

where:  $h_{ijk}$  is the height for the  $i$ th tree within the  $j$ th plot at the  $k$ th temporal measurement and  $h_{ij(k-1)}$  is the height of the same tree at time  $k-1$ , or simply at the beginning of the period  $\Delta t = t_{ijk} - t_{ij(k-1)}$ . The stochastic element  $\varepsilon_{ijk}$  of Eq. (13) is added to represent that growth is not deterministic, except on its expected value. I fitted the non-linear mixed-effects models (Eq. (13)) by maximum likelihood, followed by the best linear unbiased predictors of the random effects ([Robinson, 1991](#)). I used variance functions to model the variance structure of the within-stratum ( $G$ ) errors, where the coefficient  $\delta$  changes for each  $G$ -stratum ([Pinheiro and Bates, 2000](#)). Since the data come from different studies, I used this information as the stratum for the residual variance modelling, as recommended by [Salas et al. \(2008\)](#), therefore, the model was fitted allowing a different variance for the error term. Notice that I prefer to use this model instead of other variants (e.g., adding random-effects to  $\alpha$ ) because it has been shown a better performance in previous studies ([Stage, 1963](#); [García, 2005](#); [Salas and García, 2006](#)).

## 3. Results

The collected data span trees from young ages to adulthood (having between 19 and 103 years), as well as from small trees to taller ones (between 7 to 37 m, [Table 1](#)). Furthermore, the observed height growth

**Table 1**

Tree and cross-section level variables summary for the *Nothofagus dombeyi*, *N. alpina*, and *N. obliqua* data.  $d$  is diameter at breast height,  $h$  is total height,  $age$  is total age, and  $bha$  is breast-height age.

Species	Statistic	$d$	$h$	$age$	$bha$
		(cm)	(m)	(yr)	(yr)
<i>N. dombeyi</i> ( $n = 107$ )	Minimum	5.3	9.9	21	15
	Maximum	60.2	33.7	71	68
	Mean	26.6	19.9	41.3	37.7
	Median	26	20.8	40	37
	CV(%)	19	16.6	15.8	17.3
<i>N. alpina</i> ( $n = 169$ )	Minimum	5.3	7.1	19	17
	Maximum	49.9	31.2	81	76
	Mean	24.9	20.3	45.9	42.2
	Median	25	21	46	42
	CV(%)	16.2	15.1	17	18.4
<i>N. obliqua</i> ( $n = 155$ )	Minimum	7.3	7.9	14	13
	Maximum	59.1	37	103	94
	Mean	28.8	22.6	45.2	41
	Median	28	22.3	42	38
	CV(%)	19.4	18.3	19.2	19.3

series (grey lines in [Fig. 2a–c](#)) depict a large growing conditions variability, by showing different growth rates and asymptotes among species. Upon the above, the sample offered an array of height growth patterns of dominant trees suitable to represent different forest productivities.

Both the estimated parameters of the model (13) and their respective variance estimates, shown biologically consistent values, e.g., for the asymptote ([Table 2](#)). The variance in height growth between trees of the same plots ( $\hat{\sigma}_2^2$ ) is low because they having growing under similar conditions. I plot the resulting behaviour of the model (11) by using the parameter estimates of their respective mixed-effect model per species, the parameter estimates of their respective mixed-effect model per species ([Table 2](#)), a reference-height of 10 m, and by setting four site index values: 0.3, 0.5, 0.7, and 0.9 m/yr. I show this for the *N. dombeyi* model in [Fig. 1](#) only, the other species behave similarly.

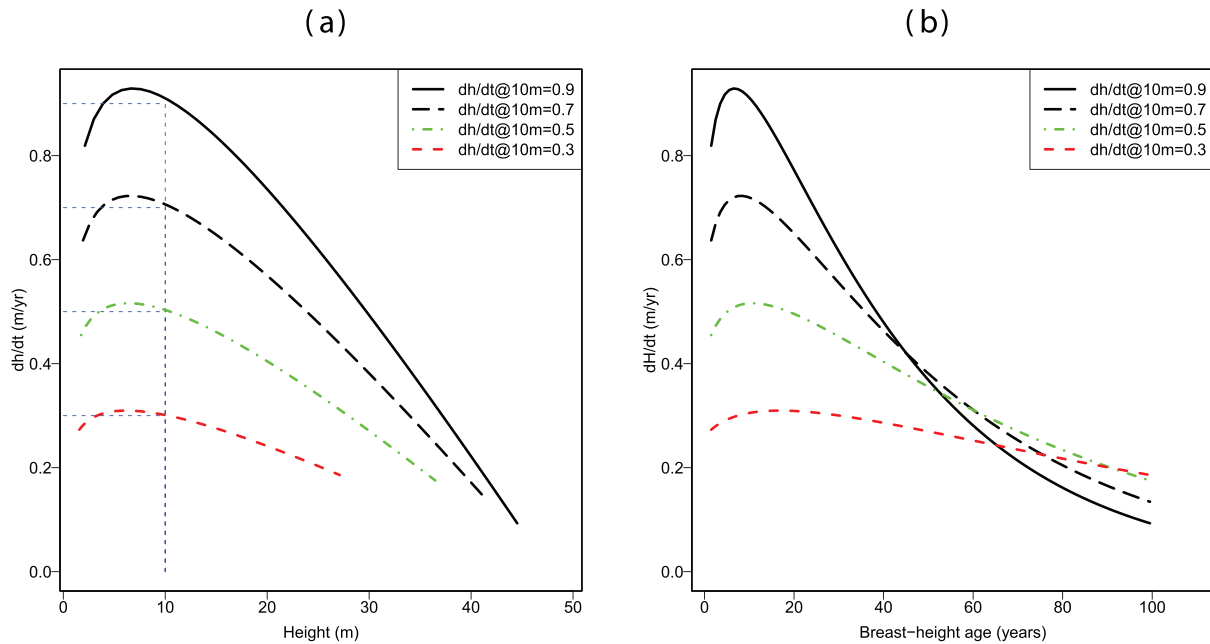
With a focus on building a simple-continuous time dynamical system where the DE of height is a function of both the estimated parameters and the site index, I assumed an initial height of 1.3 m and an initial time of 0.5 yr ([Salas, 2011](#)). Using height growth-rates versus the state variable (i.e., height) rather than versus time (i.e., breast-height age) allows us to differentiate among sites easily ([Fig. 1](#)). The site index curves derived from the proposed model (Eq. (13) and parameters in [Table 2](#)) demonstrated being able to capture the observed height growth series ([Fig. 2a–c](#)) for *N. dombeyi*, *N. alpina*, and *N. obliqua*, respectively.

I computed the time of maximum annual growth-rate ( $t^*$ ) based on

**Table 2**

Parameters estimated for the tree height growth model (13) by species. Estimates of the variance components of the mixed-effects model are also provided.

Parameter	Species		
	<i>N. dombeyi</i>	<i>N. alpina</i>	<i>N. obliqua</i>
Coefficient			
$\hat{\alpha}$	47.740	40.696	52.716
$\hat{\beta}$	0.015	0.018	0.015
$\hat{\gamma}$	0.821	0.770	0.766
Variance			
$\hat{\sigma}_1^2$	0.003565	0.0039122	0.0044702
$\hat{\sigma}_2^2$	9.80560E-4	5.9777E-6	8.231E-7
$\hat{\sigma}$	0.79649	0.98708	0.97354



**Fig. 1.** Behaviour of the proposed height growth model for *Nothofagus dombeyi*. (a) Height growth-rate versus the state variable (height) and (b) versus time (breast-height age) for different site indices: height growth-rate at a reference height of 10 m.

the proposed models, as a biological application of the current approach, because this time should depend on the autoecological features of the species. As expected,  $t^*$  is smaller for trees on good sites than those on poor sites (Table 3); the better the sites, the shorter the period elapsed to reach the maximum growth-rate. I argue that the value of  $t^*$  could also be used as an indicator of the shade-tolerance level of the species, in the sense that the more shade-intolerant a species is, the smaller  $t^*$  would be. For instance, *N. dombeyi* is the most shade-intolerant species among the *Nothofagus* being studied here (Donoso et al., 2006) with lower  $t^*$  for all site indices than the other species. In the same context, *N. alpina* is more shade-tolerant than *N. obliqua* (Donoso, 1995), therefore having a higher  $t^*$ .

#### 4. Discussion

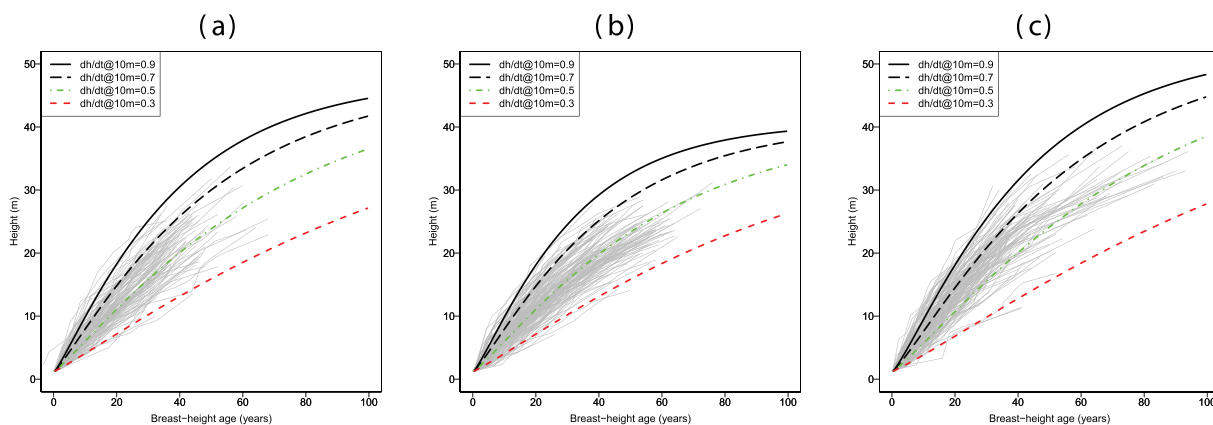
I presented the development of a forest site index based on the dominant trees height growth-rate at a reference-height, termed GRSI. This index is an alternative to the traditional site index (TSI), based on tree height at a reference-age. I explored the behaviour of the GRSI by using an autonomous DE as a baseline model, which is a growth-rate

**Table 3**

Time of maximum height growth-rate,  $t^*$ , by species depending on site productivity. Site index corresponds to the height growth-rate when the tree is 10 m tall.

Site index (m/yr)	$t^*$ (yr)		
	<i>N. dombeyi</i>	<i>N. alpina</i>	<i>N. obliqua</i>
0.3	16.5	25.0	21.5
0.5	10.3	15.2	13.4
0.7	7.7	11.4	10.6
0.9	6.5	9.5	8.5

equation only depending on the state variable  $h$  and not on time. Being the site index model built in this way has the potential for being applied to forests where there is not a single meaningful age, such as uneven-aged forests, and not only for even-aged stands, a drawback of the TSI. The non-use of age in a growth model has been advocated earlier by Spurr (1952), who stated that the ideal method of predicting forest growth should not have age as the primary variable. Other authors



**Fig. 2.** Tree height growth series of dominant trees and site index curves. Grey lines join successive observations of height on the same tree. The GRSI curves were obtained by solving the differential equation (Eq. (11)) based on tree height growth-rate at a reference-height of 10 m. Each column of the panel shows the corresponding curves for *Nothofagus dombeyi* (a), *N. alpina* (b), and *N. obliqua* (c), respectively.



encouraged related ideas (Monserud, 1984; 1987; 1988; Stage, 1959; 1963). Because of the proposed approach does not require age to be measured (i.e., free-of-time), could be suitable for natural stands with all types of structure.

There is a biological basis for thinking that growth is not determined by age. For instance, Bond et al. (2007) studied height growth development from a physiological perspective and demonstrated that size, not age, drives developmental changes in height growth in the conifer *Pseudotsuga menziesii*. The proposed height growth model (Eq. (13)) is both height-reference ( $h_r$ ) and site index ( $S$ ) invariant: neither parameter estimates depend on  $h_r$ , nor on  $S$ . To use  $h_r$  different from 10 m, as used here, a user will only need to replace  $h_r$  and  $S$  of choice in (11), and to depict height growth curves according to these values. Although other approaches can be used to derived site index curves (e.g., Lappi and Bailey, 1988), the proposed site index remains as a useful and alternative tool.

Further details need attention to use the proposed site index in practice. I presented here a height growth model based on dominant trees, which is assumed to represent well the dominant height growth of a forest (García, 2005). However, in practice, careful assessment of dominant trees must be taken into account before being used for site productivity estimation (Raulier et al., 2003; Salas and García, 2006). Besides, It is not an easy task to measure height increment with sufficient accuracy (Sterba, 1982), in the sense that we must measure the height at two times. Although for some coniferous species that form whorls at each growing season, their height increments could be easily obtained (Oliver and Larson, 1996; Stage, 1963). Regardless, I suggest measuring the periodic annual increment in height ( $pa_{h_r}$ ) as an approximation to the growth-rate for a random sample of suitable trees within sample plots. Besides, special care has to be taken for using the GRS for shade-tolerant species, which usually experiment erratic height growth patterns. On this regard, we could choose a representative species and sampling them carefully (Nyland, 1996).

The reference-height is other detail. As pointed out above, this height is user-defined; therefore, It is arbitrary. Not only  $h_r$  should be too low to bypass the establishment period of juvenile trees (Husch, 1956), but also too high to avoid measuring sample trees. Regardless, the use of 10 m for the studied species, It is a compromise between a size after which I expect dominant trees were overcoming the first intense competition period after establishment and an achievable height to be easily measured. Further details could arise, indeed. For instance, how the GRSI could be applied in mixed-species stands. I suggest sampling the same trees used to estimate the dominant height (i.e., the average height of the 100 largest trees in 1 ha, van Laar and Akça, 2007). Later, the estimation of a stand-level GRSI has to consider the sample plot-sizes, like the one proposed by García (1998). Future research is required to oversee other practical issues.

Time of maximum height growth-rate could be used as a quantitative proxy for the shade-tolerance level of species. *N. dombeyi* is the most shade-intolerant species among the *Nothofagus* being studied here (Donoso et al., 2006), which is in agreement with the  $t^*$  values derived from the proposed models. According to the photosynthesis measured features in a controlled experiment by Read and Hill, (1985), *N. alpina* is the most shade-tolerant species among the ones here. Indeed, the results support this when comparing *N. dombeyi* versus *N. obliqua*. Furthermore, these findings could also support that *N. dombeyi* is a more pioneer species than *N. obliqua*, as reported by

Bögelein et al. (2018). Similar trends had been observed by Puente et al. (1979) and Veblen et al. (1980) when analyzing tree population structure of *N. alpina*, *N. obliqua*; and tree seedlings of *N. alpina* and *N. dombeyi*, respectively. Moreover, the results point out that the maximum height growth-rate occurs five and two years earlier for *N. dombeyi* than *N. alpina* in the poorest and best site indices, respectively. This sort of information is important for silvicultural research (Soto et al., 2017; Soto and Puettmann, 2018) and restoration efforts (Bannister et al., 2018).

## 5. Concluding remarks

A new type of forest site index is introduced: height growth-rate at a reference height (GRSI), with a stronger emphasis in the mathematical details than into the practical ones. The concept is exemplified by fitting a growth-rate model to data of dominant trees, and by depicting the corresponding site index curves. I presume that many researchers will decide to model site index in the traditional way (TSI) or use different quantitative approaches for nonstatistical/nonmathematical reasons, at least until the theoretical and practical consequences of these courses of action become better determined. For those who seek to use a different approach, I suggest the GRSI as a suitable alternative to model site productivity. The proposed approach goes beyond the current traditional site index concept, providing a growth-rate basis for comparing site productivity. Indeed, assessing forest site productivity is a complicated matter, and a single index cannot summarize all, but I aimed at providing a novel quantitative-oriented approach.

## Credit Author Statement

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## Declaration of Competing Interest

The author declares that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Mathematical derivation of the base-growth model

The differential equation used here as a baseline growth-rate model is

$$\frac{dy'}{dt} = \beta(\alpha' - y'). \quad (\text{A.1})$$

Integrating (A.1) between  $t_0$  and  $t_1$  gives the value of the variable  $y$  at  $t_1$  (that is,  $y_1$ ), in terms of  $y_0$  (value of the variable  $y$  at time  $t_0$ ) and the period

length  $t_1 - t_0$ . The derivation is as follows. First, I integrate separating the terms of the DE

$$\int_{y_0^\gamma}^{y_1^\gamma} \frac{1}{(\alpha^\gamma - y^\gamma)} dy^\gamma = \int_{t_0}^{t_1} \beta dt, \quad (\text{A.2})$$

then, solving the integral

$$-\ln |\alpha^\gamma - y^\gamma| \Big|_{y_0^\gamma}^{y_1^\gamma} = \beta t \Big|_{t_0}^{t_1} + \varphi, \quad (\text{A.3})$$

$$\ln |\alpha^\gamma - y^\gamma| \Big|_{y_0^\gamma}^{y_1^\gamma} = -\beta t \Big|_{t_0}^{t_1} + \varphi, \quad (\text{A.4})$$

where  $\varphi$  is an arbitrary constant of integration. Now, I evaluate the integral

$$\ln |\alpha^\gamma - y_1^\gamma| - \ln |\alpha^\gamma - y_0^\gamma| = -\beta(t_1 - t_0) + \varphi, \quad (\text{A.5})$$

$$\ln \left| \frac{\alpha^\gamma - y_1^\gamma}{\alpha^\gamma - y_0^\gamma} \right| = -\beta(t_1 - t_0) + \varphi, \quad (\text{A.6})$$

then, taking the exponential at both sides:

$$\exp \left[ \ln \left| \frac{\alpha^\gamma - y_1^\gamma}{\alpha^\gamma - y_0^\gamma} \right| \right] = e^{-\beta(t_1 - t_0)} e^\varphi, \quad (\text{A.7})$$

$$\left| \frac{\alpha^\gamma - y_1^\gamma}{\alpha^\gamma - y_0^\gamma} \right| = e^{-\beta(t_1 - t_0)} e^\varphi, \quad (\text{A.8})$$

or

$$\frac{\alpha^\gamma - y_1^\gamma}{\alpha^\gamma - y_0^\gamma} = \pm e^\varphi e^{-\beta(t_1 - t_0)}, \quad (\text{A.9})$$

where I can make  $\psi = \pm e^\varphi$ , then  $\psi$  is also an arbitrary (nonzero) constant of integration, then

$$\frac{\alpha^\gamma - y_1^\gamma}{\alpha^\gamma - y_0^\gamma} = e^{-\beta(t_1 - t_0)} \psi, \quad (\text{A.10})$$

$$\alpha^\gamma - y_1^\gamma = (\alpha^\gamma - y_0^\gamma) e^{-\beta(t_1 - t_0)} \psi, \quad (\text{A.11})$$

multiplying by -1

$$y_1^\gamma = \alpha^\gamma - (\alpha^\gamma - y_0^\gamma) e^{-\beta(t_1 - t_0)} \psi, \quad (\text{A.12})$$

and reordering,

$$y_1^\gamma = \alpha^\gamma - \{ \alpha^\gamma e^{-\beta(t_1 - t_0)} - y_0^\gamma e^{-\beta(t_1 - t_0)} \} \psi, \quad (\text{A.13})$$

$$y_1^\gamma = \alpha^\gamma \left\{ 1 - \left[ e^{-\beta(t_1 - t_0)} - \left( \frac{y_0^\gamma}{\alpha^\gamma} \right) e^{-\beta(t_1 - t_0)} \right] \right\} \psi, \quad (\text{A.14})$$

$$y_1^\gamma = \alpha^\gamma \left\{ 1 - \left[ e^{-\beta(t_1 - t_0)} \left( 1 - \left[ \frac{y_0}{\alpha} \right]^\gamma \right) \right] \right\} \psi, \quad (\text{A.15})$$

which finally integrates to

$$y_1 = \alpha \left\{ 1 - \left[ 1 - \left( \frac{y_0}{\alpha} \right)^\gamma \right] e^{-\beta(t_1 - t_0)} \right\}^{1/\gamma} \psi^{1/\gamma}. \quad (\text{A.16})$$

Expression (A.16) contains all possible solutions of the continuous-time DE (Eq. (A.1)), which is called the general solution [Boyce and DiPrima \(2003\)](#). Notice, however, that I can find infinitely many solutions of the DE corresponding to the infinitely many values that the arbitrary constant  $\psi$  in (A.16) might have, that is to say, I can generate an infinite family of solutions from a DE ([Boyce and DiPrima, 2003](#)). Furthermore, from different DEs I can arrive at the same solution or integrated form, depending on their parameter values. Both situations were not specified clearly by some of the studies working with DEs in ecological applications ([McDill and Amateis, 1993](#); [Tomé et al., 2006](#)).

If I allow  $\psi = 1$ , the general solution (A.16) becomes

$$y_1 = \alpha \left\{ 1 - \left[ 1 - \left( \frac{y_0}{\alpha} \right)^\gamma \right] e^{-\beta(t_1 - t_0)} \right\}^{1/\gamma}, \quad (\text{A.17})$$

and more generally if I make  $t_1 = t$  then (A.17) becomes

$$y_t = \alpha \left\{ 1 - \left[ 1 - \left( \frac{y_0}{\alpha} \right)^\gamma \right] e^{-\beta(t - t_0)} \right\}^{1/\gamma}, \quad (\text{A.18})$$

a solution of the continuous-time DE (A.1), having expressed this solution analytically, or in a closed-form. Several authors have previously reported

Eq. (A.18) in the context of height growth models (García, 1983; Salas and García, 2006). Notice that in most forestry applications  $t_0 = y_0 = 0$  (García, 1983). Then, the growth function becomes the wrongly-called “Chapman-Richards” function (Pienaar and Shiver, 1984; Pienaar and Turnbull, 1973; van Laar and Akça, 2007) and the most used parameterization of this model:

$$y_t = \alpha \{1 - e^{-\beta t}\}^{1/\gamma}. \quad (\text{A.19})$$

## Appendix B. Obtaining the growth-rate index

From

$$\frac{dh}{dt} = \frac{\alpha\beta}{\gamma} [1 - e^{-\beta t}]^{\frac{1}{\gamma}-1} (e^{-\beta t}), \quad (\text{B.1})$$

and by raising (6) by  $\gamma$

$$h^\gamma = \alpha^\gamma [1 - e^{-\beta(t)}], \quad (\text{B.2})$$

I can solve that either

$$[1 - e^{-\beta(t)}] = \left(\frac{h}{\alpha}\right)^\gamma, \quad (\text{B.3})$$

or

$$e^{-\beta(t)} = 1 - \left(\frac{h}{\alpha}\right)^\gamma, \quad (\text{B.4})$$

now, substituting (B.3) and (B.4) in (B.1)

$$\frac{dh}{dt} = \frac{\alpha\beta}{\gamma} \left[\left(\frac{h}{\alpha}\right)^\gamma\right]^{\frac{1}{\gamma}-1} \left[1 - \left(\frac{h}{\alpha}\right)^\gamma\right], \quad (\text{B.5})$$

this derivative can be algebraically simplified as follows.

$$\frac{dh}{dt} = \frac{\alpha\beta}{\gamma} \left[\left(\frac{h}{\alpha}\right)^{1-\gamma}\right] \left[1 - \left(\frac{h}{\alpha}\right)^\gamma\right], \quad (\text{B.6})$$

now, solving and reordering

$$\frac{dh}{dt} = \frac{\alpha\beta}{\gamma} \left[\left(\frac{h}{\alpha}\right)^{1-\gamma} - \left(\frac{h}{\alpha}\right)^{1-\gamma} \left(\frac{h}{\alpha}\right)^\gamma\right], \quad (\text{B.7})$$

$$= \frac{\alpha\beta}{\gamma} \left[\left(\frac{h}{\alpha}\right)^{1-\gamma} - \left(\frac{h}{\alpha}\right)^{1-\gamma+\gamma}\right], \quad (\text{B.8})$$

$$= \frac{\alpha\beta}{\gamma} \left(\frac{h}{\alpha}\right)^{1-\gamma} - \frac{\alpha\beta}{\gamma} \left(\frac{h}{\alpha}\right), \quad (\text{B.9})$$

$$= \frac{\beta}{\gamma} \alpha \left(\frac{h}{\alpha}\right)^{1-\gamma} - \frac{\beta}{\gamma} (h), \quad (\text{B.10})$$

$$= \frac{\beta}{\gamma} \left[\alpha \left(\frac{h^{1-\gamma}}{\alpha^{1-\gamma}}\right) - h\right], \quad (\text{B.11})$$

$$= \left(\frac{\beta}{\gamma}\right) h [\alpha \cdot \alpha^{-(1-\gamma)} \cdot h^{-\gamma} - 1], \quad (\text{B.12})$$

$$= \left(\frac{\beta}{\gamma}\right) h [\alpha^{1-1+\gamma} \cdot h^{-\gamma} - 1], \quad (\text{B.13})$$

$$= \left(\frac{\beta}{\gamma}\right) h \left[\frac{\alpha^\gamma}{h^\gamma} - 1\right], \quad (\text{B.14})$$

which, finally yields

$$\frac{dh}{dt} = \left(\frac{\beta}{\gamma}\right) y \left[\left(\frac{\alpha}{h}\right)^\gamma - 1\right]. \quad (\text{B.15})$$

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