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General above-stump volume and biomass functions for *Pinus radiata, Eucalyptus globulus* and *Eucalyptus nitens*

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ABSTRACT

Accurate estimations of stem volume and tree component biomass are of paramount importance for the study and management of forests. In Chile, the most important commercial tree species are *Pinus radiata*, *Eucalyptus globulus* and *Eucalyptus nitens*, which are successfully planted in other parts of the world. Available individual-tree allometric models are typically local models which do not include age or stand scale covariates and rely solely on stem diameter outside bark at breast height (DBH) and, in some cases, total tree height (H). We used data from 1571 trees across the distribution of the three species in Chile to develop general individual-tree equations for stem volume inside and outside bark, and biomass components (dead branch, live branch, foliage, bark and stem wood inside and outside bark). Our models include DBH or DBH and H as predicting variables, as well as stand-level variables like age, basal area and stand density. General allometric models that include stand-level variables have not been previously reported for *P. radiata*, *E. globulus* and *E. nitens*. Given the broad area of inference in our data, the models are applicable over a large geographical area and a variety of stand ages and characteristics and can be used to support management decisions or integrated in stand-level productivity models to enhance the accuracy and precision of model outputs. The collective effort behind this study is a remarkable example of cooperation across researchers and practitioners in order to address complex questions in a transdisciplinary world.

1. Introduction

Most of the 2.3 million ha of planted forests in Central and South Central Chile are found between 33.55° and 47.27° S [1]. There are 1.89 million ha of *Pinus radiata* D. Don, and 1.02 million ha of *Eucalyptus*, primarily *Eucalyptus globulus* Labill., *E. nitens* H. Deane & Maiden, and *E. nitens x E. globulus* hybrids [2]. Most of these plantations are intensively managed and total annual production is 31.9 million m^3 $year^{-1}$ for *P. radiata* and 15.3 million m^3 $year^{-1}$ for *Eucalyptus*, with 50% destined for pulp production [1]. These three exotic species are preferred because of their high yield and plasticity to adapt to the broad range of site conditions throughout the country [3,4] and they are the main raw material for the Chilean pulpwood industry, dimension lumber and plywood mills (mainly *P. radiata*) [5].

Currently, Chile has about 1.6 million ha of eroded soils that could be afforested [6]. Another driver of afforestation is the evolving interest in using plant-derived biomaterials and biocomposites, as they provide an alternative for replacing fossil fuel and non-renewable materials [7–11].

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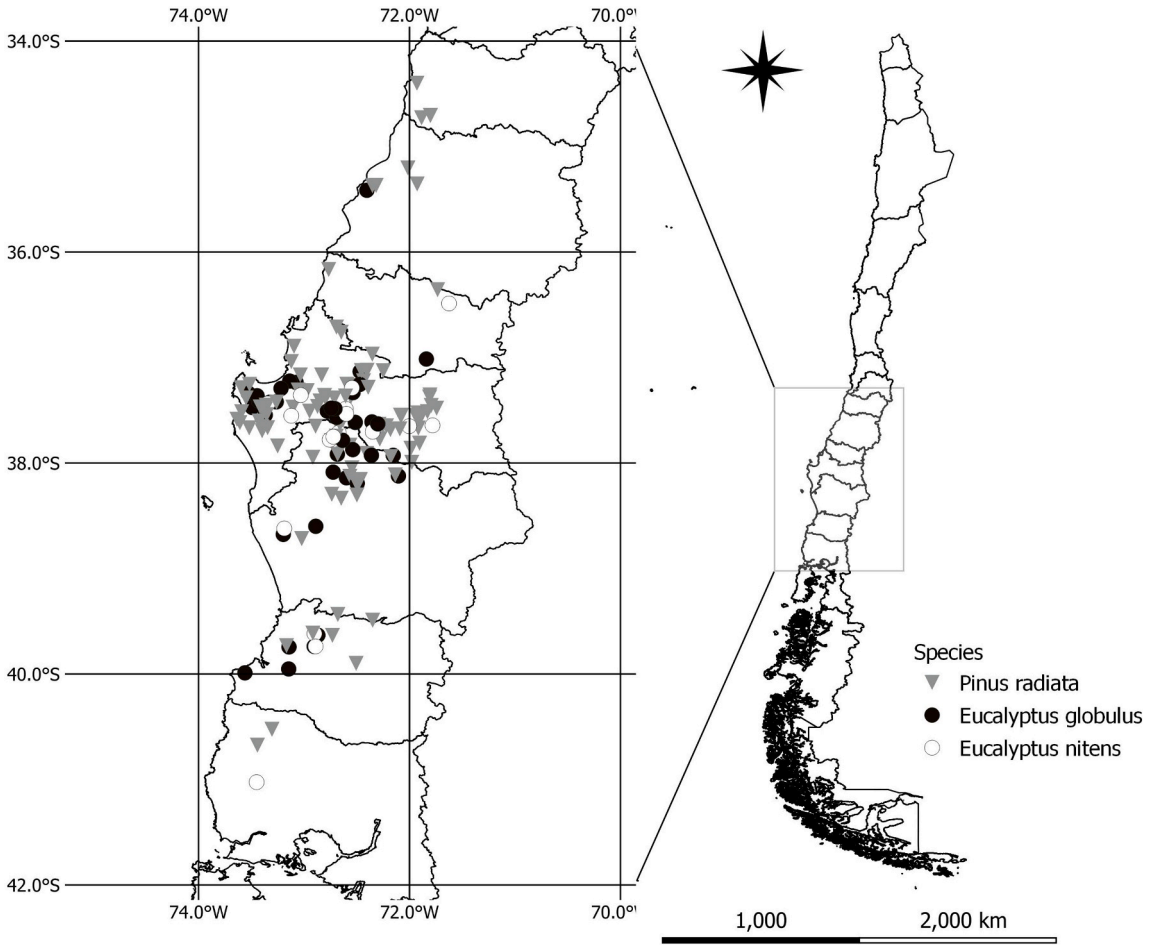

Fig. 1. Location of the sampling sites for *E. globulus* (filled circle), *E. nitens* (open circle) and *P. radiata* (grey triangle) trees growing in central Chile. Map includes administrative divisions (regions) of the country.

Additionally, Chile is committed to be carbon neutral by 2050 [12]. One way to meet that commitment would be to increase the planted area of fast-growing species such as *P. radiata, E. globulus* and *E. nitens*.

Robust estimates of volume and biomass are needed at the general and local scale for these species to quantify wood production, biomass for any sub products, and carbon sequestration and emissions [13,14]. Local models are functions developed for the specific conditions where the trees were sampled and are, generally, restricted to the age, density and site characteristics of the evaluated stand(s) [15]. The inclusion of stand-level variables such as age, basal area and density into these models is not common, and only a few of these models are available in the literature for fast growing species [16–18]. However, there are a large number of local models that only include DBH or DBH and HT as predictors (e.g. Refs. [19–24]). For *P. radiata*, pioneering work developing local models was completed in the 1980s in New Zealand and Australia [25,26], with additional efforts continuing more recently [27,28]. For *E. globulus* and *E. nitens* there are early works reporting local models [29]. Individual-tree models of volume are commonly used in forestry and several models exist in the literature for *P. radiata, E. globulus* and to a lesser extent for *E. nitens* [30–34].

Destructive sampling of trees for allometric biomass functions is labor intensive and functions are usually developed from a relatively small number of trees. In an extensive review of biomass equations in Europe [35], reported that 75% of studies sampled less than 50 trees, which limited use of those equations to the specific geographic and stand characteristics where the functions were developed. When biomass estimates are needed for conditions outside the range of the sampled trees, the estimates can vary greatly depending on the equations used [36,37]. This is especially true when examining crown components due to architecture and allometry changes related to age, stand management and site conditions [38–41].

Geographically generalized models are predictive equations fitted from data combined from many sites rather than a single location, and are commonly applicable over a wide range of stand conditions [42]. A number of generalized allometric functions for different tree species are available [35,43–50], but most studies reported equations that relied solely on DBH as a predictor, and only a few used DBH and H as predictors. Work by Forrester [50] used DBH along with stand (AGE, trees ha^{-1} (TPH), and basal area (BA)), location (latitude) and climate (mean annual temperature and total annual rainfall) attributes in their generalized functions for biomass and leaf area for European tree species. This represents a significant improvement in predictive ability; however, a similar range of location and climate data are not readily available for many sites.

Using this geographically generalized approach [17,18], developed equations for *P. taeda, P. elliottii, and P. palustris* trees growing in the southeastern United States. These general biomass functions were the basis for all biomass and net primary productivity (NPP) estimates reported for *P. taeda* across the southeastern United States by the PINEMAP project (http://pinemap.org/) [51,52]. Similarly, the alternative parameterization of the 3-PG model for *P. taeda* and *P. elliottii* [53,54] used this same approach so that NPP could be allocated to foliage as a function of stand AGE and BA, instead of tree DBH as in the original model version. Finally, this approach was used for tree biomass estimates for the growth, yield and carbon balance models for *P. taeda* [55], *P. elliottii* [56] and *P. palustris* [18,57] stands in the southeastern United

Table 1
Summary statistics of measured *P. radiata, E. globulus* and *E. nitens* trees.

Species	Attribute	Unit	n	Mean	Std Dev	Minimum	Maximum
E. globulus	AGE	year	414	5.8	3.8	1.00	18.0
	DBH	cm	414	11.0	6.5	0.42	35.8
	H	m	414	12.3	7.2	1.74	34.1
	TPH	ha^{-1}	396	1672	1351	333	9011
	BA	$m^2\ ha^{-1}$	396	14.9	11.0	0.36	55.8
	BOLE	kg	411	60.5	109.7	0.10	1005.1
	WOOD	kg	363	59.2	101.7	0.00	885.1
	BARK	kg	363	8.2	13.6	0.00	120.0
	BRANCH DEAD	kg	104	2.4	2.6	0.01	14.2
	BRANCH LIVE	kg	414	7.1	8.6	0.00	75.0
	FOLIAGE	kg	414	5.7	7.6	0.02	71.5
	TASB	kg	411	73.9	122.0	0.29	1100.9
	VOB	m^3	298	0.13	0.21	0.00036	1.7
	VIB	m^3	328	0.12	0.18	0.00024	1.4
E. nitens	AGE	year	345	5.6	3.4	1.5	16.3
	DBH	cm	345	15.0	6.5	1.7	34.5
	H	m	345	15.8	7.1	3.16	38.8
	TPH	ha^{-1}	321	1310	416	683	3333
	BA	$m^2\ ha^{-1}$	321	23.1	13.2	0.9	62.7
	BOLE	kg	342	101	128	3.53	762.1
	WOOD	kg	295	91.9	117.2	3.03	706.4
	BARK	kg	295	9.4	10.7	0.39	55.7
	BRANCH DEAD	kg	209	4.7	4.6	0.02	42.3
	BRANCH LIVE	kg	345	11.6	9.4	0.74	45.6
	FOLIAGE	kg	345	9.6	6.1	0.74	32.2
	TASB	kg	342	137	224	0.65	823
	VOB	m^3	190	0.18	0.24	0.00481	1.2
	VIB	m^3	190	0.16	0.22	0.00396	1.1
P. radiata	AGE	year	764	9.9	6.6	1.3	24.3
	DBH	cm	764	17.0	12.2	0.8	53.6
	H	m	764	13.5	10.6	1.3	39.0
	TPH	ha^{-1}	740	971	445	181	1667
	BA	$m^2\ ha^{-1}$	663	19.5	17.1	0.2	65.9
	BOLE	kg	764	123.1	196.5	0.08	1171.8
	WOOD	kg	764	112.2	179.7	0.05	1029.7
	BARK	kg	764	10.8	17.7	0.01	166.0
	BRANCH DEAD	kg	196	12.9	16.6	0.00	114.9
	BRANCH LIVE	kg	764	21.3	51.5	0.03	532.2
	FOLIAGE	kg	764	12.2	20.5	0.00	178.9
	TASB	kg	764	164.9	260.1	0.24	1883
	VOB	m^3	728	0.31	0.47	0.00001	3.0
	VIB	m^3	651	0.30	0.44	0.00009	2.8

AGE: tree age (yrs.); DBH: diameter outside-bark at 1.3 m height (cm); H: total tree height (m); TPH: trees per hectare (ha^{-1}); BA: basal area ($m^2\ ha^{-1}$); BOLE: above-stump stem over bark biomass (kg); WOOD: above-stump stem wood inside bark biomass (kg); BARK: above-stump stem bark biomass (kg); BRANCH DEAD: total dead branch biomass (kg); BRANCH LIVE: total living branch biomass (kg); FOLIAGE: total living leave/needle biomass (kg); TASB: total above-stump biomass (kg); VOB: stem volume outside bark (m^3); VIB: stem volume inside bark (m^3).

States (https://carboncenter.ifas.ufl.edu/models.shtml).

The goal of this study was to develop a set of general individual-tree-level equations to estimate stem volume and above-stump dry mass by component for *E. globulus, E. nitens* and *P. radiata* trees using a dataset that covers a large geographic area across a wide range of ages and stand characteristics in Chile. The specific objectives were: 1) develop general functions for the selected species to estimate tree stem volume and above-stump dry mass from DBH alone, 2) determine if including HT in these functions increased precision and accuracy of estimations, and 3) assess if including stand level variables produced further improvements in the estimation functions. These equations, will allow for reliable estimates of volume and biomass components using readily available stand attributes as covariates. At the same time, the equations will permit a variety of ecological, silvicultural and economic applications, including regional assessments of NPP, economic evaluations, carbon budgets for life cycle analysis, and multi-scale analysis of carbon exchange between forests and the atmosphere of these three broadly planted species.

2. Materials and methods

2.1. Data description

The dataset used to estimate the parameters for stem volume and individual-tree above-stump biomass equations for *E. globulus*, *E. nitens* and *P. radiata* trees was obtained from previously published site-age-specific allometric functions in Chile (*E. globulus*: [58–60]; *E. nitens* [32,61]; *P. radiata*: [59,62,63]). Additional unpublished data was provided by Bioforest S.A., Forestal Mininco SpA, Universidad de Chile, and Universidad de Concepción (Supplemental Table 1). The dataset had 414 *E. globulus*, 344 *E. nitens* and 763 *P. radiata* trees measured at 44 (*E. globulus*), 27 (*E. nitens*) and 94 (*P. radiata*) sites, respectively.

The data represented a variety of silvicultural inputs (planting density, soil preparation, fertilization, weed control and thinning), site characteristics (physiographic region, soil type, and climate), genetics, and developmental stages which integrated changes in allometry due to silviculture, site quality and stand age. Site descriptions and sampling procedures are detailed in the previously mentioned publications. The method for biomass sampling used by Bioforest S.A. followed procedures described in Ref. [64]. The sampling procedure used by Forestal Mininco SpA is provided in the Supplemental Materials. In all cases, destructive

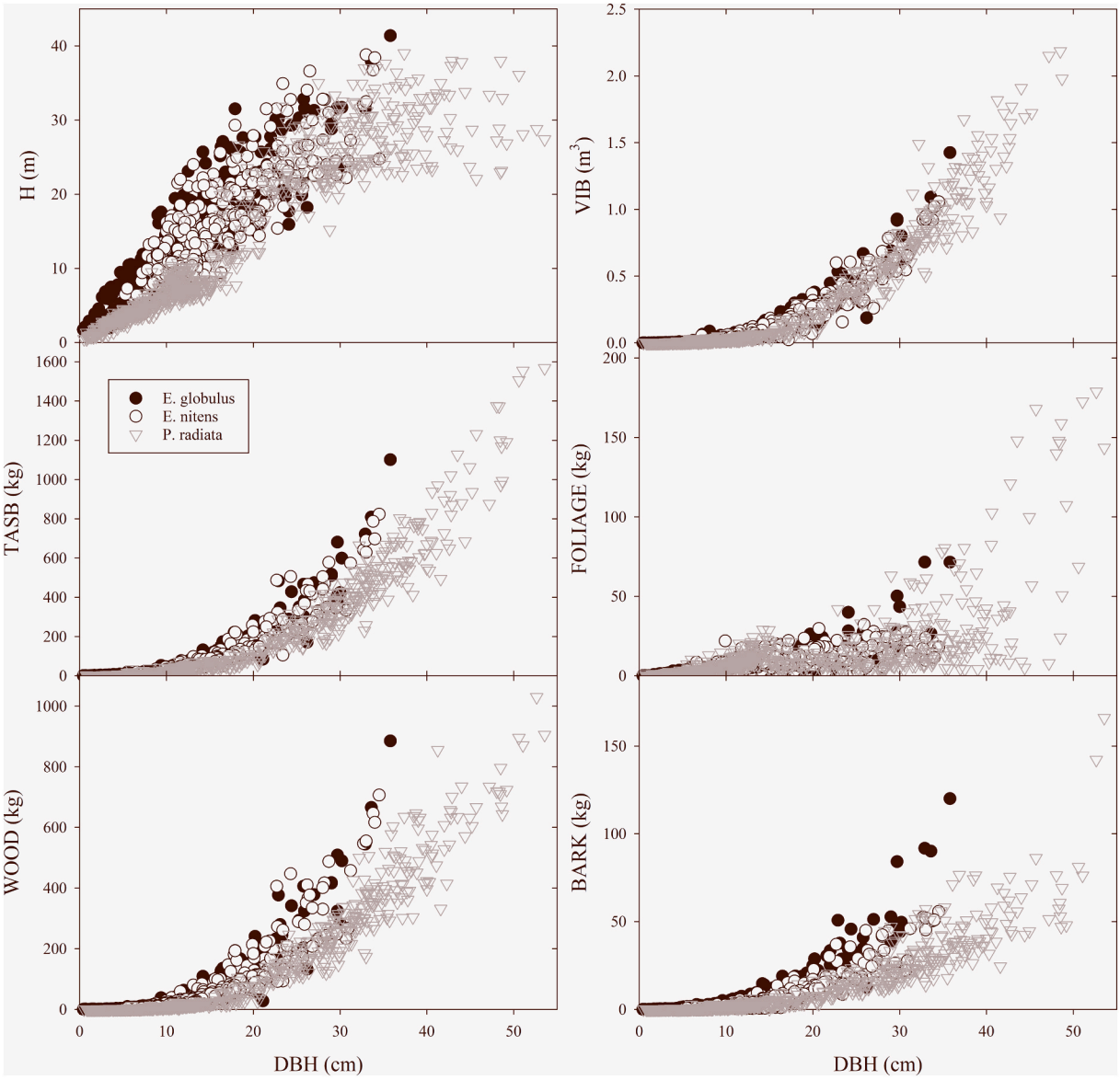

Fig. 2. Relationship between DBH and a) Height (H, m), b) stem volume inside bark (VIB, m^3), c) total tree above-stump biomass (TASB, kg), d) living foliage biomass (FOLIAGE, kg), e) stem wood biomass (WOOD, kg) and f) bark biomass (BARK, kg) for *E. globulus* (filled circle), *E. nitens* (open circle) and *P. radiata* (grey open triangle) trees growing in central Chile.

sampling was carried out. Trees were selected to cover the range of sizes in each study (Supplemental Table 1).

Data were collected across the species planted range in Chile (Fig. 1), spanning 750 km from North to South, and included trees from 1 to 18 (*E. globulus*), 2 to 16 (*E. nitens*) and 1 to 24 (*P. radiata*) years old, with diameter outside-bark at 1.3 m height (DBH, cm) and total height (H, m) ranging between 0.4 and 53.6 cm and 1.3–39.0 m, respectively (Table 1). The climate ranged between Csb (warm-summer Mediterranean climate) and Cfb (Temperate oceanic climate) in the Köppen-Geigen classification system, with rainfall between 660 and 2280 mm $year^{-1}$, and mean annual temperatures between 10.4 and 14 °C (http://explorador.cr2.cl/).

The dataset contained tree-level attributes, including DBH, H, and dry weight of each above-ground tree biomass component: living foliage (FOLIAGE, kg); living branches (BRANCH LIVE, kg); dead branches (BRANCH DEAD, kg); stem wood (WOOD, kg), stem bark (BARK, kg), stem wood + bark (BOLE, kg) and whole-tree above-stump biomass (TASB, the sum of all components in kg) (Fig. 2). Total stem volume inside (VIB, m^3) and outside (VOB, m^3) bark were measured on a large portion of trees. The dataset included trees per hectare (TPH, ha^{-1}), basal area (BA, m^2 ha^{-1}) and stand age (AGE, years) of the plots where the trees were sampled. BA and TPH were not available for 3 stands of *E. globulus*, 8 stands of *E. nitens* and 12 stands of *P. radiata*. Site index (SI) was not available as a stand-level variable.

2.2. Model description

We defined two sets of general equations to estimate stem volume and above-stump biomass.

Set I. When only DBH is known:

Table 2
Parameter estimates and fit statistics of the selected general biomass/volume functions for *E. globulus* trees growing in Central Chile.

Model Set	Component	Model	Parameter	Parameter Estimate	SE	Adj-R2	RMSE	CV%
I	BARK	$= a_1(\mathrm{DBH}^{a_2})(e^{a_3\mathrm{DBH}})$	a1	0.130607	0.060618	0.941	3.86	46.8
			a2	1.131006	0.220595			
			a3	0.075832	0.009764			
	BOLE	$= a_1(\mathrm{DBH}^{a_2})(e^{a_3\mathrm{DBH}})$	a1	0.342106	0.187620	0.936	33.75	50.1
			a_2	1.702719	0.258677			
			a_3	0.049857	0.011264			
	BRANCH DEAD	$= a_1(\mathrm{DBH}^{a_2})$	a_1	0.09959	0.068561	0.578	2.27	95.8
			a_2	1.219806	0.239195			
	BRANCH LIVE	$= a_1(\mathrm{DBH}^{a_2})(e^{a_3\mathrm{DBH}})$	a_1	0.009039	0.007892	0.802	4.95	70.0
			a_2	2.994792	0.431950			
			a_3	−0.06962	0.020650			
	FOLIAGE	$= a_1(\mathrm{DBH}^{a_2})(e^{a_3\mathrm{DBH}})$	a_1	1.314606	0.493097	0.810	4.14	72.3
			a_2	−0.054680	0.193362			
			a_3	0.113085	0.010292			
	TASB	$= a_1(\mathrm{DBH}^{a_2})(e^{a_3\mathrm{DBH}})$	a_1	0.557618	0.239515	0.954	32.52	39.8
			a_2	1.617432	0.204393			
			a_3	0.047241	0.009049			
	VIB	$= a_1(\mathrm{DBH}^{a_2})(e^{a_3\$\mathrm{DBH}})$	a_1	0.000264	0.000139	0.950	0.05	39.6
			a_2	2.068258	0.246409			
			a_3	0.031232	0.010596			
	VOB	$= a_1(\mathrm{DBH}^{a_2})(e^{a_3\mathrm{DBH}})$	a_1	0.000465	0.000232	0.960	0.05	38.1
			a_2	1.824236	0.233181			
			a_3	0.044735	0.009980			
	WOOD	$= a_1(\mathrm{DBH}^{a_2})(e^{a_3\mathrm{DBH}})$	a_1	0.254099	0.148175	0.930	31.15	52.6
			a_2	1.786217	0.274803			
			a_3	0.046079	0.011944			
II	BARK	$= d_1(\mathrm{DBH}^{d_2})(\mathrm{H}^{d_3})(\mathrm{AGE}^{d_4})(\mathrm{TPH}^{d_5})$	d_1	0.004364	0.001547	0.948	2.78	33.8
			d_2	2.071563	0.06406			
			d_3	0.273967	0.057676			
			d_4	0.298372	0.078234			
			d_5	0.093087	0.033115			
	BOLE	$= d_1(\mathrm{DBH}^{d_2})(\mathrm{H}^{d_3})(\mathrm{AGE}^{d_4})(\mathrm{TPH}^{d_5})(\mathrm{BA}^{d_6})(e^{d_7\mathrm{DBH}})$	d_1	0.003898	0.00152	0.983	13.14	21.7
			d_2	2.321142	0.209594			
			d_3	1.038031	0.046402			
			d_4	0.257876	0.048079			
			d_5	0.161819	0.026729			
			d_6	−0.251826	0.032363			
			d_7	−0.017924	0.010119			
	BRANCH DEAD			N.S.				
	BRANCH LIVE			N.S.				
	FOLIAGE	$= d_1(\mathrm{DBH}^{d_2})(\mathrm{H}^{d_3})(\mathrm{AGE}^{d_4})(\mathrm{TPH}^{d_5})(\mathrm{BA}^{d_6})$	d_1	6.403755	4.795997	0.868	2.77	48.4
			d_2	2.247151	0.093171			
			d_3	−1.176093	0.13304			
			d_4	−0.351671	0.091768			
			d_5	−0.41339	0.087346			
			d_6	0.30665	0.091043			
	TASB	$= d_1(\mathrm{DBH}^{d_2})(\mathrm{H}^{d_3})(\mathrm{AGE}^{d_4})(\mathrm{TPH}^{d_5})(\mathrm{BA}^{d_6})$	d_1	0.019456	0.00475	0.981	15.97	21.6
			d_2	2.034478	0.041875			
			d_3	0.815449	0.046442			
			d_4	0.175586	0.045349			
			d_5	0.156443	0.025501			
			d_6	−0.263418	0.033411			
	VIB	$= d_1(\mathrm{DBH}^{d_2})(\mathrm{H}^{d_3})(\mathrm{AGE}^{d_4})(\mathrm{TPH}^{d_5})$	d_1	0.000026527	0.00000626	0.978	0.03	22.6
			d_2	2.255064	0.047468			
			d_3	0.776047	0.041808			
			d_4	−0.121198	0.052974			
			d_5	0.047035	0.022239			
	VOB	$= d_1(\mathrm{DBH}^{d_2})(\mathrm{H}^{d_3})(\mathrm{AGE}^{d_4})(\mathrm{TPH}^{d_5})$	d_1	0.000042559	0.000010817	0.978	0.03	22.2
			d_2	2.144704	0.050672			
			d_3	0.493211	0.048396			
			d_4	0.240327	0.070618			
			d_5	0.048796	0.022153			
	WOOD	$= d_1(\mathrm{DBH}^{d_2})(\mathrm{H}^{d_3})(\mathrm{AGE}^{d_4})(\mathrm{TPH}^{d_5})(\mathrm{BA}^{d_6})(e^{d_7\mathrm{DBH}})$	d_1	0.00237	0.001017	0.983	12.24	20.7
			d_2	2.405302	0.231153			
			d_3	1.123469	0.049442			
			d_4	0.268161	0.051676			
			d_5	0.162929	0.028277			
			d_6	−0.270647	0.034278			
			d_7	−0.023319	0.011148			

DBH: diameter outside-bark at 1.37 m height (cm); AGE: tree/stand age (yrs.); H: total tree height (m); TPH: trees per hectare (ha^{-1}); BOLE: above-stump stem over bark biomass (kg); WOOD: above-stump stem wood inside bark biomass (kg); BARK: above-stump stem bark biomass (kg); BRANCH DEAD: total dead branch biomass (kg); BRANCH LIVE: total living branch biomass (kg); FOLIAGE: total living leave/needle biomass (kg); TASB: total above-stump biomass (kg); VOB: stem volume outside bark (m^3); VIB: stem volume inside bark (m^3). *e* is the base of the natural logarithm; SE: standard error; Adj-R^2: adjusted coefficient of determination; RMSE: root mean square error (kg); CV%: coefficient of variation percent (100•RMSE/mean); N.S.: Non-significant. For all parameter estimates $p < 0.05$.

For *E. nitens* (Table 3), models to estimate BRANCH DEAD that use only DBH (set I) improved when H, AGE, BA and/or TPH were included (set II). For example, for FOLIAGE, Adj-R^2 increased from 0.84 to 0.92, RMSE decreased from 4.3 to 3.1 kg, and CV decreased from 48 to 35%. When significant, the parameter estimate for TPH was always negative. For crown components, the parameter estimate for AGE was negative. Similar to *E. globulus*, for stem components the parameter estimate for AGE was positive. For stem components, the parameter estimate for BA was negative.

For *E. globulus*, selected models using DBH were:

$$\text{BRANCH DEAD} = a_1\$(\text{DBH}^{a_2}) + \varepsilon_i \quad (1)$$

$$\text{FOLIAGE, BARK, BOLE, BRANCH LIVE, WOOD, TASB, VIB, VOB} = a_1\$(\text{DBH}^{a_2})\$\exp(a_3\$\text{DBH}) + \varepsilon_i \quad (2)$$

For *E. nitens*, selected models using DBH were:

$$\text{BARK, BOLE, BRANCH LIVE, BRANCH DEAD, WOOD} = a_1\$(\text{DBH}^{a_2}) + \varepsilon_i \quad (3)$$

$$\text{FOLIAGE, TASB, VIB, VOB} = a_1\$(\text{DBH}^{a_2})\$\exp(a_3\$\text{DBH}) + \varepsilon_i \quad (4)$$

For *P. radiata*, selected models using DBH were:

$$\text{BARK, BRANCH DEAD,} = a_1\$(\text{DBH}^{a_2}) + \varepsilon_i \quad (5)$$

$$\text{FOLIAGE, BOLE, BRANCH LIVE, WOOD, TASB, VIB, VOB} = a_1\$(\text{DBH}^{a_2})\$\exp(a_3\$\text{DBH}) + \varepsilon_i \quad (6)$$

where a_1, a_2 and a_3 are curve fit parameter estimates, exp is the base of the natural logarithm and ε_i is the error term, with $\varepsilon_i \sim N(0, \sigma_i^2)$. The models in eqs. (2), (4) and (6), were proposed by Ruark et al. [65], and include a second parameter for the independent predictor DBH. This model form is called the variable allometric ratio model.

Set II: When DBH, H, AGE, BA and TPH are known:

When DBH and H are known, AGE, TPH and BA were evaluated as covariates to improve the volume/biomass equations. Stand ontogeny, competition and productivity were represented by these variables, which could affect the volume/biomass-diameter relationships [66].

Model fitting was carried out for all equations that include AGE, TPH and/or BA in addition to DBH. Within each species, for each biomass/volume component, we selected models with significant parameter estimates for AGE TPH and/or BA with the lowest Akaike Information Criterion (AIC). Additionally, the variance inflation factor (VIF) was monitored to detect multicollinearity among explanatory variables. Variables included in the model with VIF larger than 5 were discarded, as suggested by Neter et al. [67].

For *E. globulus*, selected models using DBH, H, AGE, BA and TPH were:

$$\text{BARK, BOLE, VIB, VOB} = d_1\$(\text{DBH}^{d_2})\$(\text{H}^{d_3})\$(\text{AGE}^{d_4})\$(\text{TPH}^{d_6}) + \varepsilon_i \quad (7)$$

$$\text{FOLIAGE, BOLE, WOOD, TASB} = d_1\$(\text{DBH}^{d_2})\$(\text{H}^{d_3})\$(\text{AGE}^{d_4})\$(\text{BA}^{d_5})\$(\text{TPH}^{d_6}) + \varepsilon_i \quad (8)$$

For *E. nitens*, selected models using DBH, H, AGE, BA and TPH were:

Table 3
Parameter estimates and fit statistics of the selected general biomass/volume functions for *E. nitens* trees growing in Central Chile.

Model Set	Component	Model	Parameter	Parameter Estimate	SE	Adj-R^2	RMSE	CV %
I	BARK	$= a_1(\mathrm{DBH}^{a_2})$	a_1	0.004442	0.000981904	0.926	3.88	41.3
			a_2	2.654239	0.067549			
	BOLE	$= a_1(\mathrm{DBH}^{a_2})$	a_1	0.017167	0.004099	0.920	42.74	48.1
			a_2	2.983411	0.072243			
	BRANCH DEAD	$= a_1(\mathrm{DBH}^{a_2})$	a_1	0.050396	0.027894	0.665	3.77	80.8
			a_2	1.554082	0.175182			
	BRANCH LIVE	$= a_1(\mathrm{DBH}^{a_2})$	a_1	0.164156	0.039373	0.818	5.99	56.4
			a_2	1.514616	0.077465			
	FOLIAGE	$= a_1(\mathrm{DBH}^{a_2})(e^{a_3\mathrm{DBH}})$	a_1	0.160723	0.104663	0.844	4.27	47.6
			a_2	1.677415	0.336344			
			a_3	−0.033038	0.017454			
	TASB	$= a_1(\mathrm{DBH}^{a_2})(e^{a_3\mathrm{DBH}})$	a_1	0.250158	0.169785	0.946	40.23	36.3
			a_2	1.947679	0.316885			
			a_3	0.031938	0.013484			
	VIB	$= a_1(\mathrm{DBH}^{a_2})(e^{a_3\mathrm{DBH}})$	a_1	0.000006366	0.000006971	0.955	0.06	36.0
			a_2	3.758513	0.498331			
			a_3	−0.038217	0.020086			
	VOB	$= a_1(\mathrm{DBH}^{a_2})(e^{a_3\mathrm{DBH}})$	a_1	0.000007712	0.000008253	0.955	0.06	35.4
			a_2	3.752262	0.487762			
			a_3	−0.040009	0.019719			
	WOOD	$= a_1(\mathrm{DBH}^{a_2})(e^{a_3\mathrm{DBH}})$	a_1	0.082485	0.092665	0.918	42.55	46.3
			a_2	2.195113	0.515938			
			a_3	0.033895	0.021218			
II	BARK	$= d_1(\mathrm{DBH}^{d_2})(\mathrm{H}^{d_3})(\mathrm{AGE}^{d_4})(\mathrm{TPH}^{d_5})(\mathrm{BA}^{d_6})(e^{d_7\mathrm{DBH}})$	d_1	0.000087523	0.000062331	0.974	2.20	23.4
			d_2	2.808464	0.282627			
			d_3	0.44043	0.075733			
			d_4	0.805418	0.048188			
			d_5	0.439448	0.05444			
			d_6	−0.548319	0.050207			
			d_7	−0.033457	0.011615			
	BOLE	$= d_1(\mathrm{DBH}^{d_2})(\mathrm{H}^{d_3})(\mathrm{AGE}^{d_4})(\mathrm{TPH}^{d_5})(\mathrm{BA}^{d_6})$	d_1	0.002744	0.000959662	0.982	19.74	22.2
			d_2	2.094172	0.049878			
			d_3	0.487031	0.056174			
			d_4	0.821127	0.038342			
			d_5	0.366788	0.045716			
			d_6	−0.347305	0.040488			
	BRANCH DEAD			N.S.				
	BRANCH LIVE	$= d_1(\mathrm{DBH}^{d_2})(\mathrm{H}^{d_3})(\mathrm{AGE}^{d_4})(\mathrm{TPH}^{d_5})$	d_1	0.050032	0.030361	0.897	4.50	42.3
			d_2	2.919136	0.112846			
			d_3	−1.351304	0.141022			
			d_4	−0.13189	0.086624			
			d_5	0.178883	0.069998			
	FOLIAGE	$= d_1(\mathrm{DBH}^{d_2})(\mathrm{H}^{d_3})(\mathrm{AGE}^{d_4})(e^{d_7\mathrm{DBH}})$	d_1	0.072938	0.03623	0.917	3.12	34.7
			d_2	2.936419	0.274802			
			d_3	−0.623554	0.13718			
			d_4	−0.549475	0.085051			
			d_7	−0.036916	0.013208			
	TASB	$= d_1(\mathrm{DBH}^{d_2})(\mathrm{H}^{d_3})(\mathrm{AGE}^{d_4})(\mathrm{TPH}^{d_5})(\mathrm{BA}^{d_6})(e^{d_7\mathrm{DBH}})$	d_1	0.009976	0.00506	0.982	22.65	20.4
			d_2	1.833053	0.190156			
			d_3	0.302354	0.056012			
			d_4	0.672656	0.037811			
			d_5	0.414755	0.042847			
			d_6	−0.359789	0.040989			
			d_7	0.014065	0.007908			
	VIB	$= d_1(\mathrm{DBH}^{d_2})(\mathrm{H}^{d_3})(\mathrm{AGE}^{d_4})(\mathrm{TPH}^{d_5})(\mathrm{BA}^{d_6})$	d_1	5.25049E-07	5.29264E-07	0.975	0.04	26.1
			d_2	2.150834	0.088535			
			d_3	0.65500	9.11E-02			
			d_4	0.542939	0.071969			
			d_5	0.628911	0.132311			
			d_6	−0.315796	0.061456			
	VOB	$= d_1(\mathrm{DBH}^{d_2})(\mathrm{H}^{d_3})(\mathrm{AGE}^{d_4})(\mathrm{TPH}^{d_5})(\mathrm{BA}^{d_6})$	d_1	7.69439E-07	7.43701E-07	0.977	0.05	24.9
			d_2	2.108641	0.084475			
			d_3	0.67536	0.087846			
			d_4	0.552991	0.068893			
			d_5	0.618798	0.127158			
			d_6	−0.353583	0.058624			
	WOOD	$= d_1(\mathrm{DBH}^{d_2})(\mathrm{H}^{d_3})(\mathrm{AGE}^{d_4})(\mathrm{TPH}^{d_5})(\mathrm{BA}^{d_6})$	d_1	0.002365	0.000923652	0.981	19.98	21.7
			d_2	2.105216	0.055477			
			d_3	0.488155	0.062077			
			d_4	0.825722	0.042662			
			d_5	0.356064	0.051176			
			d_6	−0.325455	0.045202			

DBH: diameter outside-bark at 1.37 m height (cm); AGE: tree/stand age (yrs.); H: total tree height (m); TPH: trees per hectare (ha^{-1}); BOLE: above-stump stem over bark biomass (kg); WOOD: above-stump stem wood inside bark biomass (kg); BARK: above-stump stem bark biomass (kg); BRANCH DEAD: total dead branch biomass (kg); BRANCH LIVE: total living branch biomass (kg); FOLIAGE: total living leave/needle biomass (kg); TASB: total above-stump biomass (kg); VOB: stem volume outside bark (m^3); VIB: stem volume inside bark (m^3). *e* is the base of the natural logarithm; SE: standard error; Adj-R^2: adjusted coefficient of determination; RMSE: root mean square error (kg); CV%: percent coefficient of variation (100•RMSE/mean); N.S.: Non-significant. For all parameter estimates $p < 0.05$.

$$\text{FOLIAGE} = d_1\$(\text{DBH}^{d_2})\$(\text{H}^{d_3})\$(\text{AGE}^{d_4}) + \varepsilon_i \quad (9)$$

$$\text{BRANCH LIVE} = d_1\$(\text{DBH}^{d_2})\$(\text{H}^{d_3})\$(\text{AGE}^{d_4})\$(\text{BA}^{d_5}) + \varepsilon_i \quad (10)$$

$$\text{BARK, BOLE, TASB, WOOD, VIB, VOB} = d_1\$(\text{DBH}^{d_2})\$(\text{H}^{d_3})\$(\text{AGE}^{d_4})\$(\text{BA}^{d_5})\$(\text{TPH}^{d_6}) + \varepsilon_i \quad (11)$$

For *P. radiata*, selected models using DBH, H, AGE, BA and TPH were:

$$\text{BARK, VIB, VOB} = d_1\$(\text{DBH}^{d_2})\$(\text{H}^{d_3})\$(\text{AGE}^{d_4}) + \varepsilon_i \quad (12)$$

$$\text{BOLE, BRANCH LIVE} = d_1\$(\text{DBH}^{d_2})\$(\text{H}^{d_3})\$(\text{AGE}^{d_4})\$(\text{TPH}^{d_6}) + \varepsilon_i \quad (13)$$

$$\text{WOOD} = d_1\$(\text{DBH}^{d_2})\$(\text{H}^{d_3})\$(\text{AGE}^{d_4})\$(\text{BA}^{d_5}) + \varepsilon_i \quad (14)$$

$$\text{FOLIAGE, TASB} = d_1\$(\text{DBH}^{d_2})\$(\text{H}^{d_3})\$(\text{AGE}^{d_4})\$(\text{BA}^{d_5})\$(\text{TPH}^{d_6}) + \varepsilon_i \quad (15)$$

where d_1 to d_6 are curve fit parameter estimates and ε_i is the error term, with $\varepsilon_i \sim N(0, \sigma_i^2)$. For BRANCH LIVE of *E. globulus* and BRANCH DEAD of all three species, AGE, BA and TPH were not significant.

Two additional model sets were analysed using subsets of the available variables (set III when DBH, AGE, BA and TPH are known and set IV when DBH and H are known). These additional models were developed using the same procedures as those used for set I and set II. The model forms, model evaluation and resulting parameter estimates are available in the Supplemental Materials.

2.3. Model fitting and evaluation

All statistical analyses were performed using SAS 9.4 (SAS Inc., Cary, NC, USA). For all parameter estimates reported, non-linear model fitting was carried out using PROC NLIN. We used $p < 0.05$ to indicate significance for all parameters. As sampling plots had ten or less trees, we assumed that trees were from spatially independent locations and a plot effect was not included in the analysis. The predictive ability of all equations was evaluated using a 10-fold cross validation [67], where the dataset was randomly split into 10 subsets with approximately equal numbers of observations. Two measures of accuracy were used to evaluate the goodness-of-fit between the observed and predicted values for each variable: (i) root mean square difference (RMSD) and (ii) mean bias error (Bias).

The equations for TASB and VIB were compared against models reported in the literature. For TASB, the models used for *E. globulus* were from Refs. [29,59,68]; for *E. nitens*, the models tested were from Refs. [32,61,69]; for *P. radiata*, the models tested were from Refs. [27,28,30]. For VIB, the models tested for *E. globulus* were from Refs. [34,70,71]; for *E. nitens*, the models tested were from Refs. [32,70,72]; for *P. radiata*, the models tested were from Refs. [4,30,73]. Specific model forms from these citations are presented in Supplemental Table 2. Of these [28,34,68,72,74], used data from outside Chile. After splitting the dataset into AGE classes (<5, 5–10, 10–15, 15–20, 20–25, >25 yrs), mean bias and RMSE were computed for TASB and VIB estimations within each AGE class and compared against our two fitted models: set I and set II.

3. Results

The model parameter estimates for set I and set II to estimate above-stump biomass for *E. globulus, E. nitens* and *P. radiata* trees growing in central Chile are reported in Tables 2–4, respectively. All parameter estimates were significant at $p < 0.05$.

3.1. Model fitting

For *E. globulus* (Table 2), models to estimate crown components (FOLIAGE, BRANCH LIVE, BRANCH DEAD) using DBH (set I) improved when H, AGE, BA and/or TPH were included (set II). For example, for BOLE, Adj-R^2 increased from 0.94 to 0.98, RMSD decreased from 33.8 to 17.4 kg, and CV decreased from 50 to 29%, respectively. The parameter estimates for AGE and TPH were negative for crown components. For stem components, parameter estimates for AGE and BA were positive.

The *P. radiata* dataset included 207 pruned and 557 unpruned trees. Covariance tests showed no effect of pruning on the relationship between DBH and above-ground tree components ($p > 0.084$). Based on those results, we combined data for pruned and unpruned *P. radiata* trees for all analyses. For *P. radiata* (Table 4), models to estimate biomass using DBH (set I) were improved when H, AGE, BA and/or TPH were included (set II). For example, for FOLIAGE, Adj-R^2 increased from 0.71 to 0.91, RMSD decreased from 13.0 to 7.6 kg, and CV decreased from 108 to 63%, respectively. A gain in accuracy and precision was found for WOOD, where Adj-R^2 increased from 0.97 to 0.98, RMSD decreased from 39.7 to 32.0 kg, and CV decreased from 33 to 27%. The parameter estimate for AGE was positive for stem components but negative for FOLIAGE and BRANCH LIVE. When significant, the parameter estimate for TPH was always negative.

3.2. Model evaluation

Scatterplots of the residuals against the predicted values for VIB, FOLIAGE and TASB in set I revealed significant heteroscedasticity (filled symbols in Fig. 3). When H, AGE, BA and/or TPH were included (set II), the variability of VIB, FOLIAGE and TASB was similar across the range of predicted values (open symbols in Fig. 3).

There was good agreement between observed and predicted values across all biomass/volume components for all three species (Table 5). For models using DBH (set I), bias ranged between a 2.0% underestimation for BOLE (*E. globulus*) and a 6.0% overestimation for FOLIAGE (*P. radiata*). All estimates agreed better with observed values when the stand variables were included (set II). For example, for FOLIAGE, RMSD was reduced from 69.4, 46.8 and 104.8% (model F1, Table 5), to 51.5, 33.4 and 65.2% (model F2, Table 5), for *E. globulus, E. nitens* and *P. radiata*, respectively.

3.3. Comparison against other published equations

Predicted values for TASB and VIB of our models were within the range of variation for estimations using other published equations (Table 6). Even though there was no trend in over or under estimating

Table 4
Parameter estimates and fit statistics of the selected general biomass/volume functions for *P. radiata* trees growing in Central Chile.

Model Set	Component	Model	Parameter	Parameter Estimate	SE	Adj-R^2	RMSE	CV %
I	BARK	$= a_1(DBH^{a_2})$	a_1	0.004619	0.000927596	0.899	6.82	60.2
			a_2	2.50564	0.054785			
	BOLE	$= a_1(DBH^{a_2})(e^{a_3 DBH})$	a_1	0.001459	0.000829245	0.967	43.44	33.3
			a_2	3.969343	0.218656			
			a_3	−0.044247	0.005942			
	BRANCH DEAD	$= a_1(DBH^{a_2})$	a_1	0.006755	0.00618	0.680	13.67	80.3
			a_2	2.295863	0.253521			
	BRANCH LIVE	$= a_1(DBH^{a_2})(e^{a_3 DBH})$	a_1	6.273507	4.585796	0.725	30.02	140.3
			a_2	−0.846227	0.280942			
			a_3	0.143974	0.008403			
	FOLIAGE	$= a_1(DBH^{a_2})(e^{a_3 DBH})$	a_1	5.541743	2.021442	0.713	13.05	107.5
			a_2	−0.665094	0.154904			
			a_3	0.112145	0.00596			
	TASB	$= a_1(DBH^{a_2})(e^{a_3 DBH})$	a_1	0.09253	0.039606	0.969	55.52	32.2
			a_2	2.351906	0.165304			
			a_3	0.007509	0.004553			
	VIB	$= a_1(DBH^{a_2})(e^{a_3 DBH})$	a_1	0.00002097	0.000011519	0.972	0.09	29.9
			a_2	3.201269	0.215926			
			a_3	−0.018156	0.006235			
	VOB	$= a_1(DBH^{a_2})(e^{a_3 DBH})$	a_1	0.00002043	0.000009946	0.973	0.09	30.1
			a_2	3.271279	0.191839			
			a_3	−0.021104	0.005577			
	WOOD	$= a_1(DBH^{a_2})(e^{a_3 DBH})$	a_1	0.000841805	0.000491368	0.967	39.64	33.3
			a_2	4.152645	0.224278			
			a_3	−0.04958	0.006076			
II	BARK	$= d_1(DBH^{d_2})(H^{d_3})(AGE^{d_4})$	d_1	0.004945	0.001159	0.901	6.73	59.5
			d_2	2.626233	0.062745			
			d_3	−0.522274	0.112229			
			d_4	0.424583	0.104805			
	BOLE	$= d_1(DBH^{d_2})(H^{d_3})(AGE^{d_4})(TPH^{d_5})$	d_1	0.199515	0.037072	0.978	35.69	27.4
			d_2	1.875255	0.040046			
			d_3	0.416989	0.05878			
			d_4	0.280078	0.049796			
			d_5	−0.209954	0.015519			
	BRANCH DEAD			N.S.				
	BRANCH LIVE	$= d_1(DBH^{d_2})(H^{d_3})(AGE^{d_4})(TPH^{d_5})$	d_1	292.344166	175.890208	0.887	19.52	91.2
			d_2	2.7308	0.111124			
			d_3	0.431767	0.163426			
			d_4	−2.145004	0.156042			
			d_5	−1.124987	0.061755			
	FOLIAGE	$= d_1(DBH^{d_2})(H^{d_3})(AGE^{d_4})(TPH^{d_5})(BA^{d_6})$	d_1	1088.923259	545.42398	0.914	7.59	62.5
			d_2	2.474284	0.092097			
			d_3	−1.167848	0.133912			
			d_4	−1.395843	0.136509			
			d_5	−1.12768	0.057917			
			d_6	0.580936	0.093129			
	TASB	$= d_1(DBH^{d_2})(H^{d_3})(AGE^{d_4})(TPH^{d_5})(BA^{d_6})$	d_1	1.167004	0.249436	0.980	47.77	27.7
			d_2	2.096774	0.043131			
			d_3	0.184611	0.062956			
			d_4	−0.080569	0.051159			
			d_5	−0.342082	0.024709			
			d_6	0.085402	0.036148			
	VIB	$= d_1(DBH^{d_2})(H^{d_3})(AGE^{d_4})$	d_1	0.000042928	0.000004735	0.983	0.07	23.3
			d_2	2.053005	0.035751			
			d_3	0.740721	0.051029			
			d_4	0.076777	0.042441			
	VOB	$= d_1(DBH^{d_2})(H^{d_3})(AGE^{d_4})$	d_1	0.000057449	0.000005824	0.983	0.07	24.0
			d_2	2.053076	0.033591			
			d_3	0.659522	0.047783			
			d_4	0.110575	0.039839			
	WOOD	$= d_1(DBH^{d_2})(H^{d_3})(AGE^{d_4})(TPH^{d_5})$	d_1	0.147622	0.026934	0.978	32.05	26.9
			d_2	1.862379	0.0393			
			d_3	0.47691	0.05782			
			d_4	0.27406	0.048877			
			d_5	−0.197239	0.015167			

DBH: diameter outside-bark at 1.37 m height (cm); AGE: tree/stand age (yrs.); H: total tree height (m); TPH: trees per hectare (ha^{-1}); BOLE: above-stump stem over bark biomass (kg); WOOD: above-stump stem wood inside bark biomass (kg); BARK: above-stump stem bark biomass (kg); BRANCH DEAD: total dead branch biomass (kg); BRANCH LIVE: total living branch biomass (kg); FOLIAGE: total living leave/needle biomass (kg); TASB: total above-stump biomass (kg); VOB: stem volume outside bark (m^3); VIB: stem volume inside bark (m^3). *e* is the base of the natural logarithm; SE: standard error; Adj-R^2: adjusted coefficient of determination; RMSE: root mean square error (kg); CV: coefficient of variation (100•RMSE/mean); N.S.: Non-significant. For all parameter estimates $p < 0.05$.

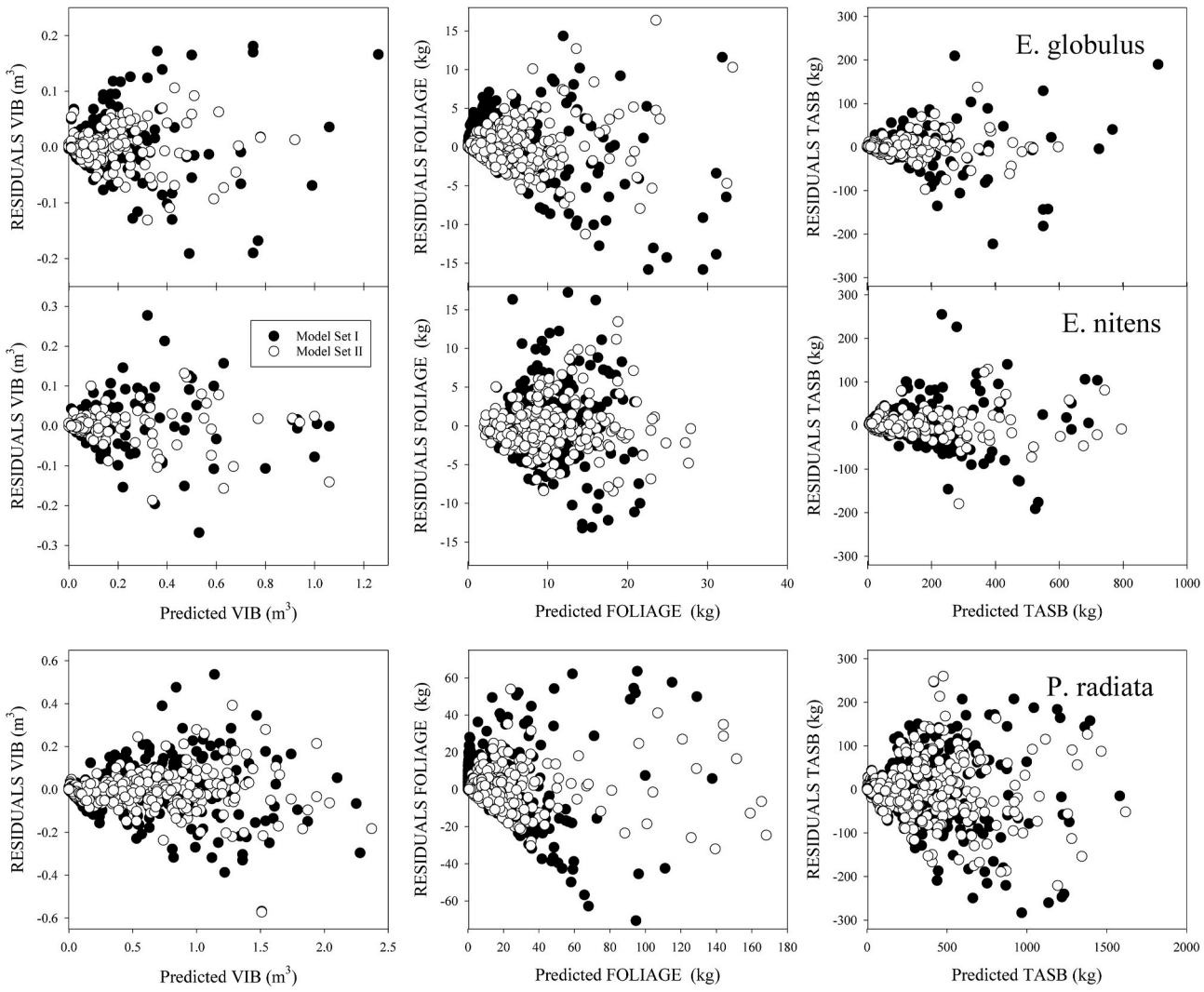

Fig. 3. Model evaluation of biomass/volume models for *E. globulus* (upper panel), *E. nitens* (center panel) and *P. radiata* (bottom panel). Residuals versus predicted values using a model that includes only DBH as an explanatory variable (filled circle; Model Set I) and a model that includes DBH, H and stand parameters AGE, BA and/or TPH as explanatory variables (open circle, Model Set II) for VIB (stem volume inside bark; left), FOLIAGE (total living foliage biomass; center), and TASB (total above-stump biomass; right).

TASB or VIB at different ages, a larger RMSD (as a percent of observed value) was observed for younger trees (age class <5 years) when using our models. For TASB computed using model T1, Bias ranged from a 17% under prediction for 10–15 years old *E. nitens* to a 22% over prediction for 5–10 years old *P. radiata*. With model T2, Bias for TASB ranged from a 13% under prediction for <5 years old *P. radiata* to an 11% over prediction for 10–15 years old *P. radiata* (Table 6). For VIB, using model VI1, Bias ranged from a 9% under prediction for 10–15 years old *E. nitens* to a 47% over prediction for <5 years old *E. globulus*. When using model VI2 for VIB, Bias ranged between a 14% under prediction for 5–10 years old *P. radiata* to a 13% over prediction for <5 years old *E. globulus*.

4. Discussion

The general biomass/volume functions for *E. globulus, E. nitens* and *P. radiata* trees reported here were developed using trees from a large geographical area in central Chile (Fig. 1), spanning a wide variety of ages and stand characteristics (Table 2), and including a broad range of soils, climate and stand productivity reported for all three species. This dataset gives us confidence that the functions can be used on variety of sites and management conditions for planted forests of these species to provide reliable estimates of volume and biomass components using readily available stand attributes.

Model selection will be dependent on data availability and level of precision required by users. The functions will be useful for the direct study and management of these species in a variety of economic and ecological applications including estimating timber value, forest ecosystem carbon stock, bioenergy production [58,76–78], understory abundance and diversity (as LAI can be inferred from foliage biomass and specific leaf area [79]), fire hazard [80,81], soil erosion [82] and nutrient dynamics [83,84]. Similarly, forest growth models which incorporate biomass allocation based on allometric principles such as 3-PG [85], or on estimates of LAI such as SWAT [86] or WaSSI [87], may be improved by the use of these more robust and flexible functions [52–54].

The relationships between DBH and VIB were similar for all three species; in the case of FOLIAGE, both Eucalypts behave quite similarly, in contrast to *P. radiata* that shows a high variability for larger trees, particularly for DBH over 30 cm (Fig. 2). This is likely related to the greater range in planting density, thinning and pruning regimes that are used to manage *P. radiata* for products from pulp wood to saw timber compared to *E. globulus* and *E. nitens* which are managed mainly for pulp production with no density management after planting [88].

Table 5
Summary of model evaluation statistics using 10-fold cross validation for biomass/volume estimations for *E. globulus, E. nitens* and *P. radiata* trees.

Species	Component	Model ID	Explanatory Variables	$\overline{O}$	$\overline{P}$	RMSD		Bias	
E. globulus	BARK	B1*	DBH	8.25	8.37	3.59	(43.6)	−0.11	(-1.4)
		B2	DBH, H, AGE, TPH	7.28	7.23	2.59	(35.6)	0.05	(0.7)
	BOLE	BO1*	DBH	60.32	61.53	30.69	(50.9)	−1.21	(-2.0)
		BO2*	DBH, H, AGE, TPH, BA	53.64	53.00	13.02	(24.3)	0.64	(1.2)
	BRANCH DEAD	BD1	DBH	2.33	2.34	1.99	(85.7)	−0.02	(-0.7)
		BD2		AGE, TPH and BA non-significant					
	BRANCH LIVE	BL1*	DBH	7.03	6.89	4.59	(65.2)	0.14	(2.0)
		BL2		AGE, TPH and BA non-significant					
	FOLIAGE	F1*	DBH	5.71	5.65	3.97	(69.4)	0.06	(1.1)
		F2	DBH, H, AGE, TPH, BA	5.21	5.22	2.68	(51.5)	−0.01	(-0.2)
	TASB	T1*	DBH	73.59	74.49	29.55	(40.2)	−0.89	(-1.2)
		T2	DBH, H, AGE, TPH, BA	66.26	66.00	16.24	(24.5)	0.26	(0.4)
	VIB	VI1*	DBH	0.12	0.12	0.04	(37.3)	0.00	(-0.9)
		VI2	DBH, H, AGE, TPH	0.11	0.11	0.02	(23.1)	0.00	(-0.2)
	VOB	VO1*	DBH	0.13	0.13	0.05	(35.8)	0.00	(-0.8)
		VO2	DBH, H, AGE, TPH	0.11	0.11	0.03	(23.4)	0.00	(0.8)
	WOOD	W1*	DBH	59.24	60.39	30.25	(51.1)	−1.15	(-1.9)
		W2*	DBH, H, AGE, TPH, BA	53.05	52.60	12.24	(23.1)	0.45	(0.8)
E. nitens	BARK	B1	DBH	9.39	9.50	3.67	(39.0)	−0.10	(-1.1)
		B2*	DBH, H, AGE, TPH, BA	9.02	9.03	2.47	(27.4)	−0.02	(-0.2)
	BOLE	BO1	DBH	89.37	88.46	41.38	(46.3)	0.91	(1.0)
		BO2	DBH, H, AGE, TPH, BA	84.94	84.80	20.55	(24.2)	0.14	(0.2)
	BRANCH DEAD	BD1	DBH	9.39	9.50	3.67	(39.0)	−0.10	(-1.1)
		BD2		AGE, TPH and BA non-significant					
	BRANCH LIVE	BL1	DBH	10.57	10.67	5.94	(56.2)	−0.10	(-0.9)
		BL2	DBH, H, AGE, TPH	10.53	10.68	4.39	(41.6)	−0.15	(-1.4)
	FOLIAGE	F1*	DBH	8.95	8.97	4.19	(46.8)	−0.02	(-0.2)
		F2*	DBH, H, AGE	8.95	8.92	2.99	(33.4)	0.03	(0.4)
	TASB	T1*	DBH	111.42	111.59	38.70	(34.7)	−0.17	(-0.2)
		T2*	DBH, H, AGE, TPH, BA	106.74	105.78	24.30	(22.8)	0.97	(0.9)
	VIB	VI1*	DBH	0.16	0.16	0.06	(35.0)	0.00	(-0.2)
		VI2	DBH, H, AGE, TPH, BA	0.15	0.15	0.04	(27.2)	0.00	(-1.2)
	VOB	VO1*	DBH	0.18	0.18	0.06	(34.1)	0.00	(-0.1)
		VO2	DBH, H, AGE, TPH, BA	0.17	0.17	0.05	(26.4)	0.00	(-1.0)
	WOOD	W1*	DBH	92.02	92.53	40.79	(44.3)	−0.52	(-0.6)
		W2	DBH, H, AGE, TPH, BA	88.46	88.61	20.37	(23.0)	−0.14	(-0.2)
P. radiata	BARK	BA1	DBH	11.18	11.32	6.63	(59.3)	−0.13	(-1.2)
		BA2	DBH, H, AGE	11.18	11.36	6.49	(58.0)	−0.18	(-1.6)
	BOLE	BO1*	DBH	128.79	129.02	42.89	(33.3)	−0.23	(-0.2)
		BO2	DBH, H, AGE, TPH	125.94	127.74	34.64	(27.5)	−1.81	(-1.4)
	BRANCH DEAD	BD1*	DBH	17.10	17.32	13.16	(77.0)	−0.22	(-1.3)
		BD2		AGE, TPH and BA non-significant					
	BRANCH LIVE	BL1*	DBH	20.95	20.22	28.62	(136.6)	0.73	(3.5)
		BL2	DBH, H, AGE, TPH	21.15	20.22	18.27	(86.4)	0.93	(4.4)
	FOLIAGE	F1*	DBH	11.99	11.28	12.57	(104.8)	0.72	(6.0)
		F2	DBH, H, AGE, TPH, BA	12.56	12.36	8.18	(65.2)	0.20	(1.6)
	TASB	T1*	DBH	170.57	171.56	55.12	(32.3)	−0.99	(-0.6)
		T2	DBH, H, AGE, TPH, BA	183.47	185.22	46.49	(25.3)	−0.29	(-0.2)
	VIB	VI1*	DBH	0.29	0.30	0.09	(29.6)	0.00	(-0.4)
		VI2	DBH, H, AGE	0.29	0.29	0.07	(22.3)	0.00	(0.1)
	VOB	VO1*	DBH	0.30	0.30	0.09	(29.7)	0.00	(0.2)
		VO2	DBH, H, AGE	0.30	0.30	0.07	(22.9)	0.00	(0.7)
	WOOD	W1*	DBH	117.60	117.65	39.11	(33.3)	−0.05	(0.0)
		W2	DBH, H, AGE, TPH	114.88	116.48	31.03	(27.0)	−1.60	(-1.4)

*: Includes second parameter for DBH (variable allometric ratio model).
DBH: diameter outside-bark at 1.37 m height (cm); AGE: tree/stand age (yrs.); H: total tree height (m); TPH: trees per hectare (ha^{-1}); BARK: above-stump stem bark biomass (kg); BOLE: above-stump stem over bark biomass (kg); BRANCH DEAD: total dead branch biomass (kg); BRANCH LIVE: total living branch biomass (kg); FOLIAGE: total living leave/needle biomass (kg); TASB: total above-stump biomass (kg); VOB: stem volume outside bark (m^3); VIB: stem volume inside bark (m^3); WOOD: above-stump stem wood inside bark biomass (kg); $\overline{O}$: mean observed value; $\overline{P}$: mean predicted value; RMSD: root of mean square difference (same unit as observed value); Bias: mean absolute bias (predicted-observed; same unit as observed value). Values in parenthesis are percentage relative to observed mean.

Particularly in our database, the higher values of foliage come from stands with density lower than 200 TPH, managed as agroforestry systems [62]. In contrast, the relationships between DBH and H, WOOD, BARK and TASB differed among both *Eucalyptus* species and *P. radiata*. For the same DBH, *E. globulus* and *E. nitens* trees trend to be taller with greater biomass than *P. radiata* (Fig. 2). This is likely an effect of lower resistance in the eucalypt xylem transport pathway compared to pine [89], greater wood density [90,91], thicker bark [92,93] or some combination of these factors. Examining species differences in these factors was beyond the scope of our analysis.

The parameter estimate for AGE was positive for stem components, implying that for the same size tree, older trees had, on average, denser wood and bark or a less tapered stem than younger trees. On the other hand, the parameter estimate for AGE was negative for crown components, implying that for the same size tree, older trees allocate less biomass to foliage and branches than younger trees [94]. Working with young *Eucalyptus* hybrids [95], also reported negative values for AGE parameter estimates for crown components, and a positive value for stem. Overall, when AGE was included in the general model (set II) for all of our species, it resulted in a significant improvement in fitting and

Table 6
Comparison of mean absolute bias percent (Bias, %) and root mean square difference percent (RMSD, %) for TASB and VIB estimations using two models reported in this study (Model Set I, using only DBH, and Model Set II, using DB H, H and stand parameters) and three functions reported in the scientific literature (Models 1, 2 and 3) for *E. globulus, E. nitens* and *P. radiata* trees.

Trait	Species	Age class	n	$\overline{O}$	Model Set I		Model Set II		Model 1		Model 2		Model 3	
					Bias	RMSD	Bias	RMSD	Bias	RMSD	Bias	RMSD	Bias	RMSD
TASB	*E. globulus*	<5	208	16.0	18.9	53.1 T1	−8.1	23.4 T2	−128.2	151.1 a1	−17.6	35.2 a2	−13.2	51.7 a3
		5–10	142	78.8	19.8	54.9	3.3	21.1	−8.6	41.2	−14.5	23.3	−29.5	56.7
		10–15	49	210.3	5.9	25.7	−0.6	12.6	−16.7	33.8	−8.9	22.5	−51.3	77.5
		ALL	9	74.4	11.1	45.7	−0.2	20.5	−24.1	55.8	−11.3	34.3	−41.7	114.0
	E. nitens	<5	408	47.9	13.6	27.4 T1	−6.1	23.3 T2	−14.0	23.8 b1	−33.0	38.9 b2	7.1	25.1 b3
		5–10	199	137.3	11.2	31.4	1.2	13.8	6.1	17.0	−7.2	16.6	16.6	30.6
		10–15	97	289.1	−17.0	25.9	0.2	16.3	−7.6	24.6	−13.0	27.6	−8.6	21.2
		ALL	41	110.7	0.2	34.2	−1.0	19.1	−4.2	28.4	−15.6	32.5	4.1	30.1
	P. radiata	<5	6	6.0	−1.8	46.6 T1	−13.5	47.4 T2	136.3	193.6 c1	−46.9	86.2 c2	−43.4	82.5 c3
		5–10	343	31.7	22.0	48.7	8.4	40.1	152.0	179.7	−15.8	41.1	−11.1	41.3
		10–15	245	188.1	16.2	34.0	11.3	27.5	78.9	90.0	14.5	28.2	18.5	30.7
		15–20	249	492.5	−4.0	19.4	−2.6	15.8	22.6	30.7	−10.5	32.6	−9.5	33.7
		20–25	74	508.4	−0.4	19.1	−0.3	16.4	25.9	31.8	8.9	20.3	10.9	21.4
		ALL	141	167.8	0.5	33.3	−0.3	27.1	39.6	61.6	−4.0	47.4	−2.1	49.3
VIB	*E. globulus*	<5	208	0.02	46.7	64.9 VI1	12.8	41.6 VI2	−4.0	35.0 d1	96.0	91.1 d2	−6.2	35.4 d3
		5–10	143	0.11	18.8	46.8	7.5	26.9	3.6	22.4	21.3	29.4	−0.9	22.6
		10–15	51	0.26	−3.4	19.7	−0.9	12.3	3.8	20.4	1.5	17.0	−4.4	20.2
		ALL	9	0.12	6.0	33.4	2.2	20.0	3.0	28.7	13.0	27.4	−3.4	28.6
	E. nitens	<5	411	0.04	21.5	40.2 VI1	2.2	20.0 VI2	−10.7	21.3 e1	−26.4	34.9 e2	−1.3	19.8 e3
		5–10	199	0.13	14.8	37.0	−7.9	20.1	7.6	20.1	16.6	29.6	10.3	22.2
		10–15	99	0.38	−9.4	20.4	4.1	20.8	−4.3	21.8	2.0	22.6	−4.9	20.3
		ALL	42	0.16	−0.3	28.5	−0.4	17.9	−2.5	25.0	1.7	28.1	−1.1	23.9
	P. radiata	<5	6	0.01	9.6	99.7 VI1	−13.8	65.0 V2	1.8	62.8 f1	−168.6	178.6 f2	5.9	66.5 f3
		5–10	346	0.05	24.0	58.4	3.0	30.9	10.4	31.8	−45.8	53.8	7.3	30.8
		10–15	245	0.37	7.4	26.7	2.1	16.5	3.5	16.3	−4.3	17.1	0.8	16.0
		15–20	249	0.75	0.9	16.1	−2.1	12.6	−2.8	13.0	−4.2	13.6	−4.3	13.1
		20–25	74	1.00	−6.2	17.2	1.1	14.0	1.3	14.2	1.9	14.1	−0.8	14.1
		ALL	141	0.29	0.3	32.2	−0.3	24.9	0.4	25.4	−7.3	26.8	−1.6	25.3

Age class: age class (yrs.); n: number of observations; $\overline{O}$: mean observed value (TASB in kg; VIB in m^3); Bias: mean absolute bias (predicted-observed; %); RMSD: root mean square difference (%); TASB: total above-stump biomass; VIB: stem volume inside bark; T1: Equation from Model Set I for TASB; VI1: Equation from Model Set I for VIB; T2: Equation from Model Set II for TASB; VI2: Equation from Model Set II for VIB.
a1: [29]; a2: [59]; a3: [68]; b1: [32]; b2: [75]; b3: [74]; c1: [27]; c2: [30]; c3: [28]; d1: [70]; d2: [71]; d3: [69]; e1: [70]; e2: [32]; e3: [21]; f1: [4]; f2: [30]; f3: [73].

prediction ability of the volume/biomass equations. This result demonstrates the strong effect ontogeny has on tree growth and allometry across species. Wood accumulates on the stem throughout the lifespan of the tree, but FOLIAGE and BRANCHES do not because they are ephemeral, and are also affected by environmental stresses, such as drought or pests, and density management.

Several authors published biomass functions for *E. globulus, E. nitens* and *P. radiata* that were based on DBH as a single predictor variable [29,59], while other authors have reported functions using DBH and H as predictors. For these species, few studies have included AGE [96], AGE and quadratic mean diameter [61] or other stand attributes such as BA or TPH [97] as predictor variables. Working with *E. globulus* in Portugal, António et al. [96] reported an age effect but no effect of stand density or productivity on biomass allometry. Gonzalez-Benecke et al. [17,18] found that including stand attributes, such as AGE, TPH and BA, can improve the estimations of above-ground biomass in southern pines in the southeastern United States by affecting crown and stem morphology and hence the allometry of individual trees. In our study, we followed a similar approach and found comparable results: Stand characteristics used as covariates, in addition to AGE, resulted in significant improvements in model fitting and prediction ability for estimating volume or tree biomass components.

For stem components, when DBH, H, AGE and TPH were known (set II), the parameter estimate for BA was negative, implying that trees of the same size and AGE that are growing on a more productive site (larger BA with the same AGE and TPH), should have either lower wood density or a more tapered stem. The parameter estimates for AGE and TPH were negative for crown components, implying that for the same size trees, older trees or trees growing in high density stands (more intraspecific competition) had less foliage and branches than younger trees or than trees growing in stands with less intraspecific competition. For BRANCH DEAD, H was not significant in set II, implying that canopy closure and crown recession were dependent on stand basal area (and therefore leaf area index). Previous studies found similar patterns for *P. elliottii, P. palustris* and *P. taeda* [17,18].

Milla et al. [98] published an extensive collection of biomass functions for 26 native and 5 introduced forest trees in Chile including the three species used in this study. Those authors presented functions for biomass components (above and below ground), along with the geographic location, number and size of sampled trees, and basic stand characteristics, including AGE and TPH, however, there was no generalization of the functions. Consequently, each equation would be restricted to the original range of sites, ages and tree sizes. Most of the authors of the *E. globulus, E. nitens* and *P. radiata* biomass equations reported in Ref. [98] allowed us to use their datasets in developing our generalized functions.

Biomass stock or carbon sequestration has been quantified for planted *E. globulus* and *E. nitens* [13,88] and *P. radiata* [13,90,99] in Chile using stem volume tables ($m^3\ ha^{-1}$) computed with a growth and yield model and wood density (either age-dependent wood density functions or ranges of wood density depending on age). Espinosa et al. [90] accounted only for BOLE biomass growth, so no crown components were included. Corvalán et al. [88,99] used above-ground biomass partitioning coefficients determined from studies in other countries. Olmedo et al. [13] computed biomass using conversion factors to transform stem volume to total above and below ground biomass. The conversion factors utilized were IPCC standards that only depended on standing volume stock, using the same factors for both *Eucalyptus* species. Our equations allow for an alternative analysis, by including stand attributes to encompass the interactive effects of age, site quality and stand density.

The effects of silvicultural treatments on biomass allometry depend

on site conditions and are often confounded by ontogenetic effects [100]. When evaluating the effects of cultural practices on *P. radiata* biomass allocation, Rubilar et al. [41] concluded that individual tree biomass allometry for 3-4 year-old trees was affected by silvicultural treatment, but the effect depended on site conditions. In traditional growth and yield models, such as MNS Insigne (*P. radiata*) and MNS-Eucasim (*E. globulus* and *E. nitens*) in Chile (http://www.mnssimulacion.cl/), the responses to silvicultural treatments, such as irrigation, competing vegetation control and fertilization, are associated with changes in BA and SI [101]. In our models SI was not included as it was not available for most of the data collected however, we did include AGE and BA which can effectively substitute for SI, and account for variation in competition, resource availability, and inherent stand productivity [17].

Our data included pruned and unpruned *P. radiata* trees and, as noted, our functions were fit combining pruned and unpruned trees because we found no effect of pruning on the relationship between DBH and each above-ground tree component. The lack of a significant pruning effect was likely a result of the combination of our sampling being performed more than two years after pruning [40], and that *P. radiata* foliage lifespan is about 2–2.5 years [102]. Nevertheless, using our functions to estimate crown attributes for trees that were pruned less than 2 years before is not advised. Even though our extensive dataset gives us confidence that the functions can be used over a large variety of sites and management conditions including those outside of Chile, we recommend using these equations within the range of the dataset (Table 2).

The collective effort behind this study is a remarkable example of cooperation across researchers and practitioners. Scientists and extension foresters from five universities and the two largest forest companies in the country worked together, sharing data in order to develop a product that can benefit all of the forest sector in the country and abroad. This cooperative work marks an example of collaboration needed to address complex questions in a transdisciplinary world.

5. Conclusion

This study reports the first set of general equations for stem volume and above-ground biomass equations for *E. globulus*, *E. nitens* and *P. radiata* trees. The precision and accuracy of volume/biomass predictions were improved when easily available stand attributes were incorporated into the general models. When compared with other reported functions for the species, our functions provided the most accurate estimations. Our new equations allow for an alternative analysis, because including stand attributes will encompass the interactive effects of age, site quality and stand density in a more comprehensive manner.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biombioe.2021.106280.

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