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Generalized biomass equations for the main aboveground biomass components of maritime pine across contrasting environments

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Abstract

· *Introduction* In order to predict the biomass of aerial components of maritime pine stands (*Pinus pinaster* Ait.), generalized allometric equations were developed using data collected from the southern and northern margins of its geographical area.
· *Methods* The data comprised biomass values divided into foliage, branch, stem and minor components collected from 26 trees in Tunisia and 152 trees in France. Some trees were taken from plots receiving fertilisation and irrigation. The equation $W = aD^b$, where W is the biomass, D the stem diameter and a and b are fitted parameters, explained 98% of the variations in the total aerial biomass. The addition of tree age reduced significantly the residual sum of squares for the foliage component. This model explains 79% of the variations in foliage biomass observed.
· *Results* To a lesser extent, the age variable also improved the stem and branch models that explain 98% and 71% of the observed sum of squares, respectively. Site variables such as the stocking density, stand basal area, fertilisation or annual precipitation did not reduce the residual sum of squares, suggesting that their putative effects are conveyed through tree growth rate.

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1 Introduction

Using allometric equations for estimating biomass and carbon stocks in forests on the basis of simple variables measured in forest inventories is a convenient method long employed by foresters and scientists (Ter-Mikaelian and Korzukhin 1997; Zianis et al. 2005). Allometric equations used for trees are essentially power functions of the stem diameter at a given height (Crow and Laidly 1980; Zianis and Mencuccini 2003; Kajimoto et al. 2006; Muukkonen 2007; Socha and Wezyk 2007). The rationale of such a model was analysed in terms of proportionality of the relative growth rate between stem diameter, height and compartment and total biomass (Enquist 2002). These equations have been applied to predict the total biomass and its aboveground and belowground components (Baldwin et al. 1997; Makela and Vanninen 1998; Ritson and Sochacki 2003). Additional variables such as the height or age of the trees have been shown to improve the predictability of site-specific models (Porté et al. 2002; Trichet et al. 2008; Wang 2006; King et al. 2007).

The calibration of biomass equations to be generalized over large regions needs to be based upon a sample of site and climate conditions that encompasses the range of environmental conditions covered. Among the environmental factors under consideration, the nutrient and water availabilities and the social status of trees are known to modify the growth rate and the tree and crown shape, respectively. Whether allometric relationships vary accord-

ing to such factors is under debate. They may therefore be taken into account when constructing allometric equations to estimate biomass or carbon stocks over large areas.

Generalized biomass equations constructed from a dataset including different sites have been established for different European and North American tree species in order to calculate biomass and carbon stocks across large geographic areas (Schmitt and Grigal 1981; Pastor et al. 1984; Marklund 1987; Lambert et al. 2005). This approach can also be used to evaluate the generality of biomass allometric equations and identify the site factors which may modify such relationships. For instance, Muukkonen (2007) explained that 64–99% of the total aboveground biomass and its components for five broadleaved and coniferous species in Europe with models only based upon the diameter at breast height. Also, the generalized foliar biomass of *Pinus strobus* based only upon the stem diameter developed by Levia (2008) explained 97% of its variance.

In this study, we have examined biomass equations for maritime pine, *Pinus pinaster* Ait., a European southern pine species that has a natural area extending from North Africa to South of France and which grows in a climate ranging from Mediterranean to temperate Atlantic. It is mainly used for wood, biomass and pulp production and covers 4 million hectares in southern Europe. Some site-specific allometric equations have been established for this species in France (Lemoine et al. 1986; Porté et al. 2000; 2002; Trichet et al. 2008), Spain (Merino et al. 2005) and Australia (Ritson and Sochacki 2003), but no attempt has yet been made to generalise these equations on a larger scale. The aim of this study was to generalize allometric equations for maritime pine across much of its natural growing range in Europe and North Africa.

2 Material and methods

2.1 Sites

Our analysis is made on 178 maritime pine (*P. pinaster* Ait.) trees sampled on nine sites spread between the northern (France) and southern (Tunisia) limits of its natural area. Table 1 summarises the main site and stand characteristics.

In France, the biomass data were collected from four managed even-aged stands where 152 trees were felled on different dates between 1996 (Bray site) and 2004 (Hermitage-L12). One of the sites, Hermitage-L, was sampled at the ages of nine (2001) and 12 (2004), respectively. Hermitage-L is a fertilisation–irrigation experiment which was begun in 1997 and which is described by Trichet et al. (2008). It comprises four complete randomised blocks where two levels of irrigation and three levels of fertilisation are combined. These treatments were applied

annually from 1997 to 2008. The trees sampled in this site were taken from the six different treatment combinations, including the control plots, and were pooled in six composite plots. All other stands were managed according to regional guidelines with 5-year periodic thinnings between the ages of 15 and 35 and the final clearcut at the age of 40 to 50.

In Tunisia, 26 trees were sampled from six different plots located in the northern mounts forming the Mediterranean littoral. The sites cover a range of soils from podzolic soils (Malloula 1 and 2) to brown luvic (Tbeinia) and calcareous sands on ancient dunes (Saounia, Ouechtata, Rimel). The forest stand at Malloula was naturally regenerated and is a mixture of different age classes and species, whereas the five other stands were artificially regenerated. No thinning, fertilisation or irrigation was applied in Tunisian stands.

2.2 Biomass and tree measurements

In each plot, a sample of trees was chosen to cover the observed range of trunk diameter at breast height (1.30 m). The protocol for collecting trees on the French sites is described in detail by Porté et al. (2002), Bert and Danjon (2006) and Trichet et al. (2008) for the Bray, Bilos and Hermitage-L site, respectively. Trees sampled were felled and separated into biomass components. Subsamples of each component were then dried at 65°C and weighed. On Tunisian sites, branch and foliage biomasses were estimated by applying values of water content and needle to branch ratio measured on one representative branch per whorl to the fresh weight of the total branch+foliage of each whorl. This was then summed over the entire crown. The total bud and cone biomass was estimated with the same method. For each whorl, the ratio of their biomass to the total branch biomass was measured on a representative branch, applied to the rest of the whorl branches, and then summed over the crown. The trunk was cut into 1-m-long logs that were weighed immediately. The wood and bark dry weights were then determined from the bark to wood ratio and humidity content determined in the laboratory from a stem disk taken from the middle of the log. Biomass values are all dry weights at 65°C.

3 Models

In order to keep the model as simple as possible, we first tested the allometric general equation:

$$W_{i,j} = a_i D_j^{b_i} + e_{i,j}, \qquad (1)$$

where $W_{i,j}$ is the biomass of compartment i of tree j (kilograms per tree), a_i and b_i are model parameters to fit by non-linear regression, D_j the diameter at breast height

Table 1 Main environmental and dendrometric characteristics of sampled forest stands

Site	Berganton	Bilos	Bray	Herm. L9	Herm. L12	Malloula 1	Malloula 2	Ouechtata	Rimel	Saouania	Tbeinia
Number of plots	1	1	1	6	6	1	1	1	1	1	1
Sample size (trees plot^{-1})	10	12	10	4	16	2	2	6	10	2	4
Location (lat, lon)	44°42′ N 0°46′ W	44°29′43″N 0°57′09″W	44°42′ N 0°46′W	44°42′ N 0°46′ W	44°42′ N 0°46′ W	36° 56′50″N 8°42′27″ E	36° 57′07″ N 8°41′47″ E	36° 59′12″ N 8°58′09″ E	37° 17′48″ N 10° 0′21″ E	36° 58′12″ N 8°53′26″ E	36° 46′26″ N 8° 46′16″ E
Elevation (m)	56	38	61	58	58	195	232	116	41	67	499
Annual rainfall (mm)	930	930	930	930	930	1,068	1,094	925	627	940	1,281
Mean annual temperature (°C)	12.5	12.5	12.5	12.5	12.5	17.5	17.4	17. 8	18.1	18	16.3
Stand area (ha)	17	60	16	7	7	77	93	52.6	80.5	74	24
Plot area (ha)	0.198	9	4.70	1	1	1	1	1	1	1	1
Mean plot density (ha^{-1})	334	223	621	1,144	836	758	441	792	332	791	834
Mean D (m)	0.3844	0.38	0.2603	0.1368	0.1841	0.1421	0.1213	0.1465	0.1720	0.1817	0.2476
Basal area (m^{2}ha^{-1})	38.76	25.2	33.8	17.26	27.32	13.860	7.23	17.32	8.23	24.37	42.10
Mean height (m)	20.8	20.3	17.6	8.8	10.5	5.3	7.4	8.5	7.0	9.8	15.6
Mean tree age (year)	32	50	26	9	12	31	28	31	35	35	40
Fertilization[a]	2	1	2	1, 2, 3, 4	1, 2, 3, 4	1	1	1	1	1	1
Irrigation[b]	0	0	0	0 or 1	0 or 1	0	0	0	0	0	0

See Trichet et al. (2008) for additional details

[a] Fertilisation level code: *1* control, *2* one unique input at plantation of 60 to 80 kg P as P$_2$O$_5$, *3* annual input of 20 to 50 kg P, *4* annual input of complete fertiliser (N, P, K, Ca, Mg and micronutrients)

[b] Irrigation level code: *0* natural rainfall, *1* annual input of 450 to 550 mm year^{-1}

(meter) and $\varepsilon_{i,j}$ the error term. In order to give an even weight to every plot sampled, each observation was weighted by $1/n$, where n is the number of trees sampled. For normalising the error distribution, we used a transformed form of Eq. 1 multiplying the two sides of equation by D_j^{-2} as follows:

$$W_{i,j}.D_j^{-2} = \left(a_i D_j^{bi} + e_{i,j}\right).D_j^{-2} \qquad (2)$$

We checked the residual distribution homogeneity visually and its normality with the Kolmogorov–Smirnov's test. Following Parresol (1999), it would be mathematically more exact to optimise the power value of the transforming variable D_j (Ritson and Sochacki 2003; Saint-Andre et al. 2005; Antonio et al. 2007). Fixing this value at −2 allows a correct normality of model residuals and did not substantially affect the values estimated for model parameters a and b. Two additional explanatory variables, the total tree height, H_i, and tree age, A_i, were added to the model Eq. 2 as follows:

$$W_{i,j}.D_i^{-2} = \left(a_i D_i^{bi} H_j^{ci} + e_{i,j}\right).D_i^{-2} \qquad (3)$$

$$W_{i,j}.D_i^{-2} = \left(a_i D_i^{bi} A_j^{di} + e_{i,j}\right).D_i^{-2} \qquad (4)$$

The influence of additional effects, such as the annual amount of water precipitated (rainfall+irrigation), fertilisation level, latitude, or stand structure variables (stocking density and basal area), was analysed on the model residual values retained for each biomass component (Eqs. 2, 3 or 4). Statistical analyses were carried out using the NLIN and GLM procedures of the statistical software package SAS version 9.2.

4 Results

The range of data collected for subsequent analysis can be visualised in Fig. 1.

The model predictions and observed data shown in Fig. 2 and Table 2 give the parameter values together with their asymptotic errors and normality test results. Only the results of the weighted model with standardised residuals (Eqs. 2, 3 and 4) are shown. The standardised residual graphs included in the Fig. 1 graphs do not visually reveal a systematic departure from homoscedasticity. The models used for individual biomass components and total aboveground biomass were not constrained a priori for fulfilling the additivity criteria (Parresol 2001). However, the linear regression equation between the total biomass estimate and the sum of the biomass components has a slope of 1.016 (R^2=0.999) so that both estimates are consistent, and the
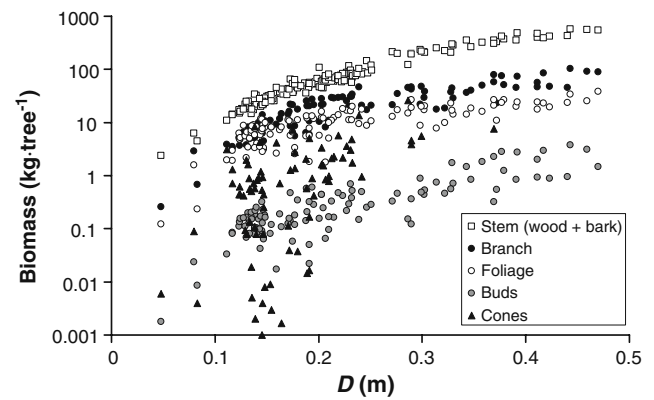

Fig. 1 Biomass values of aboveground components in relationship with diameter at breast height (D) for the entire data set obtained. Y-axis is on a logarithmic scale

additivity of the obtained predictive equations is verified a posteriori (Fig. 3).

For the main biomass components, the model asymptotic sum of squares reach 80% to 98% of the total sum of squares. Asymptotic errors on parameters a, b, c and d are correspondingly small (Table 2). The allometric Eq. 1 with only D sufficed to capture the aboveground biomass variations among sites and trees. For the other main biomass components—branch, stem, and foliage—the sum of squares of the standardised residual was significantly reduced when the age was introduced in the model (Eq. 3) and so for stemwood, the tree height (Eq. 4; Table 2). Residual distribution was not significantly different from the normal distribution for the main biomass compartments.

Tree age has the strongest effect on the needle biomass: the addition of the tree age variable to the model reduces the residual sum of squares (Table 2) by one quarter, the model sum of squares rising from 71% to 79% of the total sum of squares. The age effect is negative for foliage and branches, indicating that older trees support less foliage and branch biomasses than younger trees of the same stem diameter. Conversely, the age effect is positive for the stem biomass model, which is consistent with the wood density increase and age-related change in biomass allocation observed with age in most pine tree species.

The between-site variation of the aboveground biomass–D relationship is not visually significant. Similarly, the visual examination of residual graphs for the stem, branch and aboveground components does not reveal any trend according to the climate variables, air temperature or annual rainfall+irrigation (see examples for aboveground biomass and foliage in Figs. 4 and 5). The geographic location also has no effect. The analysis of the environmental and stand structure effects on back-transformed residuals (Table 3) shows that only the fertilisation level had a statistically significant effect. This effect only concerned the branch and
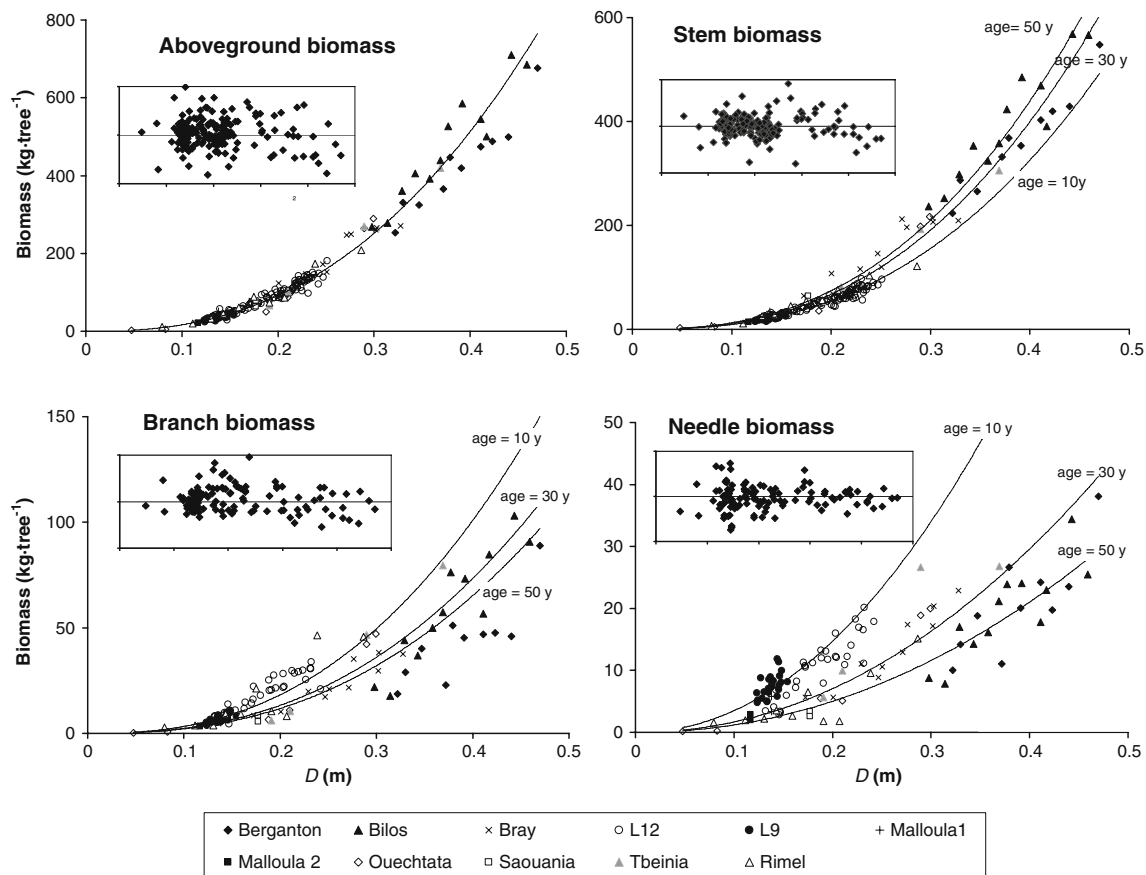
Fig. 2 Allometric best models fitted for the stem, branch, needle and total aboveground compartment together with observed data. The effect of tree age was introduced as: $W = aD^b\mathrm{Age}^c$ apart from the aboveground biomass model where it was not significant. The *curves* show model prediction at the age of 10, 30 and 50, respectively

stem biomass and was actually due to the data collected from one French site only, Le Bray. Therefore, a measurement bias at this particular site cannot be excluded. This analysis otherwise confirms that the allometric models shown in Fig. 3 capture the potential effects of site, climate and fertilisation on the *D*–biomass relationship.

It is noteworthy that fertilisation and annual amount of precipitation+irrigation significantly affect the residual of the simplest allometric model (Eq. 1) for the foliage and branch compartments (not shown). For a given *D*, the trees fertilised annually with phosphorus or a complete nutrient addition (class 3 and 4), as well as the trees receiving higher rainfall, have a higher branch and needle biomass than control plots or trees grown on plots fertilised only before stand regeneration (class 1 and 2, respectively). Since the branch and needle residuals of the allometric model with a tree age effect (Eq. 3) show no more significant effect of fertilisation or precipitation, we can conclude that the latter effects are accounted for by the interaction of the allometric model with tree age. The increase in water and nutrient availabilities created by

fertilisation and rainfall or irrigation impacts the trees in that a given stem diameter is reached at a younger age, i.e. faster growth. Introducing height as a supplement variable only reduces the residual sum of squares of the stem model, and this effect is marginal.

5 Discussion

Our dataset assembles the data available so far in France and Tunisia; the southern and northern limits of the geographical area of maritime Pine, respectively. This does not include the Lemoine et al. (1986) data, as it unfortunately could not be recovered, and it excludes trees younger than 8 years old that have not yet developed a bole free of branches. The oldest tree collected was 53 years old, and our conclusions are therefore limited to the age range of 8 to 53 years old and to the diameter range shown in Fig. 1. The dataset includes manipulation experiments in France where the foliar nitrogen content and annual precipitation were augmented to values 60% higher than the maximum

Table 2 Values of parameters of the allometric equations fitted to the biomass data set collected over ten sites across France and Tunisian sites ($n=178$ trees), together with their asymptotic standard error (smaller font)

Component	Model	a		b		c		d		Sum of squares		Normality (p value K–S test)
										Total	Residual	
Buds	aD^b	9	2	2.17	1.79					873	242	0.13
Cones	aD^b	171	92	2.71	0.52					154,245	73,660	<0.01
Needle	aD^b	142	33	1.65	0.11					1,105,270	241,992	>0.15
	$aD^b H^d$	1,131	683	2.09	0.22			−0.57	0.21		222,402	>0.15
	$aD^b age^c$	**1,916**	**428**	**2.07**	**0.09**	**−0.67**	**0.05**				**80,428**	**>0.15**
Branch wood	aD^b	509	74	2.19	0.08					2,285,826	275,719	0.06
	$aD^b H^d$	6,849	3,663	2.81	0.19			−0.66	0.18		244,849	0.05
	$aD^b age^c$	**1,883**	**543**	**2.47**	**0.09**	**−0.29**	**0.06**				**221,425**	**0.14**
Stem	aD^b	5,041	260	2.70	0.04					52,593,167	1,725,507	0.01
	$aD^b H^d$	334	166	2.17	0.08			0.59	0.09		1,272,376	0.01
	$aD^b age^c$	**2,225**	**215**	**2.56**	**0.03**	**0.19**	**0.02**				**1,119,912**	**0.02**
Stemwood	aD^b	4,846	303	2.82	0.04					30,603,380	1,069,968	0.08
	$aD^b H^d$	317	184	2.19	0.10			0.70	0.11		794,748	0.12
	$aD^b age^c$	**2,319**	**414**	**2.67**	**0.05**	**0.16**	**0.04**				**867,771**	**0.09**
Stembark	aD^b	419	46	2.20	0.06					1,518,394	117,543	<0.01
Total aboveground	**aD^b**	**5,013**	**202**	**2.48**	**0.03**					105,700,000	**1,896,108**	**>0.15**
	$aD^b H^d$	3,177	858	2.38	0.07			0.12	0.07		1,864,507	0.11
	$aD^b age^c$	4,445	408	2.46	0.03	0.03	0.02				1,873,048	>0.15

Total and residual sum of squares of each model are given and p value of the Kolmogorov-Smirnov's test of normality for the residual distribution (p values lower than .05 indicate a departure from a normal distribution). The parameter values of the models shown in Fig. 1 are in bold

observed in natural conditions: 1.6 (0.9) mg N g needle dry matter^{-1} and 1,500 (900) mm year^{-1} for the fertilised (control) nitrogen foliar content and irrigated (control) annual precipitation, respectively (Trichet et al. 2008). Thus, this range covers most of the natural conditions of the natural geographical area for this species, apart from the driest conditions in central Spain where precipitations as low as 500 mm year^{-1} are observed.
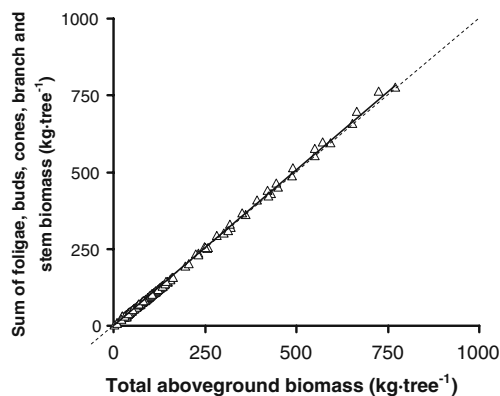

Fig. 3 Plot of the sum of predicted values of the biomass components versus total aboveground biomass estimates (1:1 *line/broken line*; linear regression *bold line*). Values are produced by the models retained and corresponding values are given in *bold font* in Table 1

Following previous surveys, we have chosen to analyse the allometric equation introducing a two-way biomass equation based upon the diameter at breast height and at either age or tree height (Zianis and Mencuccini 2003; Antonio et al. 2007; Cienciala et al. 2006; Peichl and Arain 2007; Hu and Wang 2008; Kaitaniemi and Lintunen 2008; Pajtik et al. 2008). Each of these variables is currently being measured by National Forest Inventories across Europe, thus enabling our results to be used for estimating biomass and carbon stocks in maritime pine forests. It is argued that tree age is difficult to measure, but we stress the fact that it is relatively easy to estimate for pines up to 40 years by visual analysis of the stem. In addition, the age effect on biomass estimates is small beyond that age: the derivation of Eq. 3 shows that an error of 5 years on the tree age would then lead to a bias of 2%, 3%, and 5% on the stem, branch and foliage biomasses, respectively.

The generalized biomass equation modelled for the aboveground part appeared to be unique and unaffected by site conditions (rainfall regime, climate, soil type), silvicultural practices (stocking density, fertilisation) or geographical provenance (Antonio et al. 2007), contrary to studies showing that biomass allometric equations are climate-specific (Callaway et al. 1994; Delucia et al. 2000; Lopez-Serrano et al. 2005). We think the cause of this discrepancy is that these latter surveys were based upon a
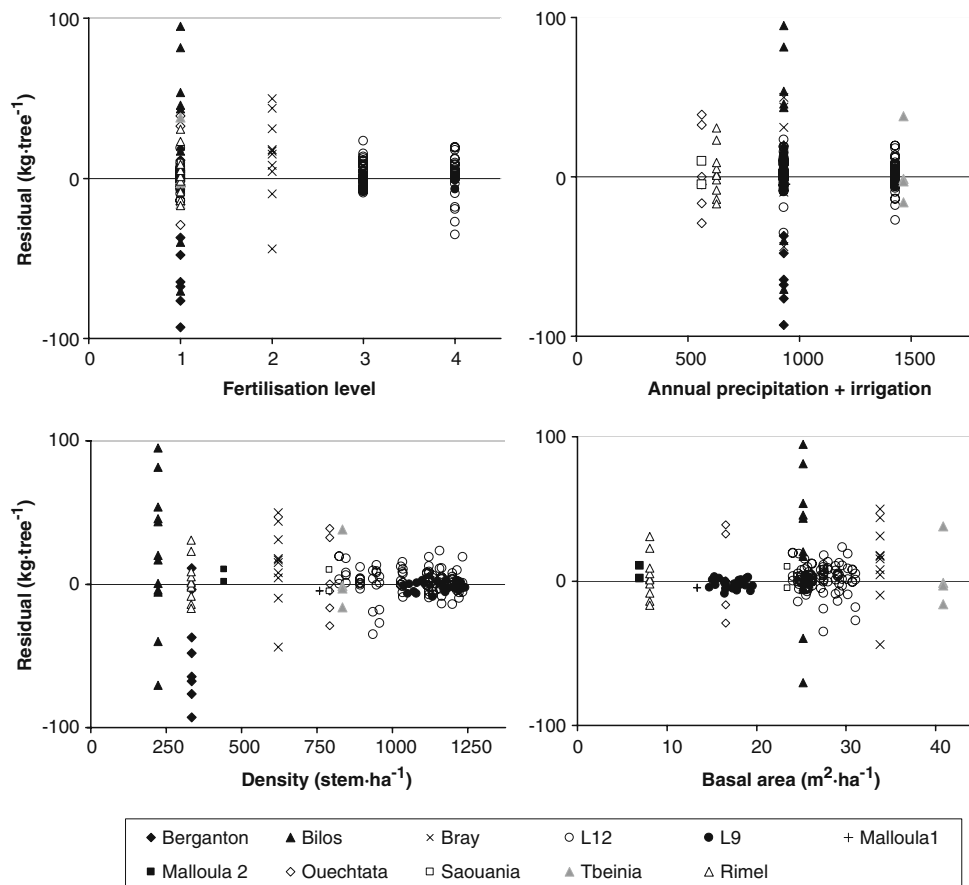
Fig. 4 Plots of the raw residual values of allometric model of aboveground biomass shown in Fig. 1 against environmental and stand variables: fertilisation level, annual precipitation+irrigation, stocking density and basal area

limited number of contrasted sites with regards to e.g. the precipitation regime. The strength of this aboveground biomass–D relationship suggests that it may be used for inventorying biomass and carbon stock using inventory data across the whole species area, regardless of the site and climate conditions. A noticeable exception was however reported by Ritson and Sochacki (2003) for wind effects in southwestern Australia, where trees grown in open spaces were found to be slightly denser and heavier than trees

located in closed stands. For estimating biomass and carbon stock, generalized biomass equations may be advantageous over volume equations that need highly uncertain conversion and expansion factors (Nabuurs et al. 2004; Vallet et al. 2006). The model fit to the above aboveground and stem biomass explains 97% of the variance observed in the data set used, a value currently reached in similar studies (Cienciala et al. 2006; Muukkonen 2007). We observe that a unique D–biomass relationship holds

Table 3 Determination coefficients (R^2) of linear models including effects of fertilisation level, annual precipitation, stocking density and basal area on the residuals of best allometric models (Eq. 1 or 3) selected for the main biomass components (shown in Fig. 1)

	Allometric model equation	Effects			
		Fertilisation	Precipitation	Basal area	Stocking density
Foliage	(4)	n.s.	n.s.	n.s.	n.s.
Branch	(4)	n.s.	0.09	n.s.	n.s.
Stem	(4)	n.s.	0.14	n.s.	n.s.
Aboveground	(2)	n.s.	n.s.	n.s.	n.s.

Each effect was tested separately

n.s. not significant
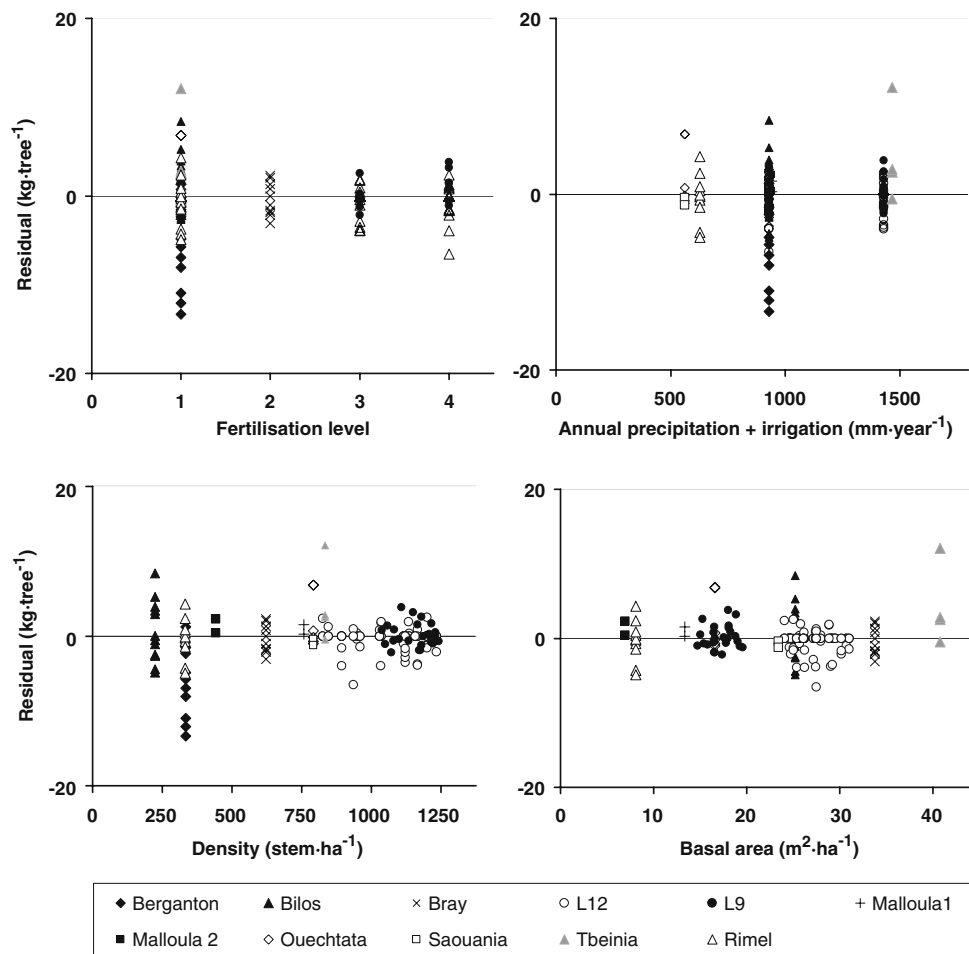
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Fig. 5 Plots of the raw residual values of allometric model of foliage biomass shown in Fig. 2 against environmental and stand variables: fertilisation level, annual precipitation + irrigation, stocking density and basal area

only for the total aboveground biomass whereas additional variables are required for estimating component biomass albeit with a higher error (Antonio et al. 2007). This may support the hypothesis of an invariant allometric relationship due to mechanical constraint, i.e. a given stem thickness must be reached for supporting a given mechanical stress (Niklas and Spatz 2004). Since maritime pine essentially grows over littoral areas exposed to strong winds, it would be interesting to investigate the allometry for pines exposed at different wind regimes.

In addition, we show that the age of tree brings a significant amount of additional information for estimating the biomass of the stem, foliage and branch compartments, confirming previous findings on this species reported in site-specific studies by Porté et al. (2002), Ritson and Sochacki (2003) and Balboa-Murias et al. (2006). A changing allometry scheme with age has also been reported in boreal species (Bond-Lamberty et al. 2002) or Eucalyptus (Saint-Andre et al. 2005; Antonio et al. 2007) and pine

species (Socha and Wezyk 2007). Mathematically, it implies that the linear relationship between the relative growth rates of stem radius and biomass components has an intercept proportional to 1/age. In other words, it allows for a changing allocation into foliage, stem and branch component along the tree development whereas model Eq. 2 implies a constant proportionality between the relative growth rates of plant parts whatever the tree age. Such an age effect is not surprising for maritime Pine whose growth is constrained by a strong age-related effect on hydraulic architecture, and therefore, a diminishing foliage/sapwood ratio with age (Delzon et al. 2004; Niklas and Spatz 2004).

It is important to account for age effect on foliage, branch and stem allometry because this species exhibits a large range of growth rates across the area from Europe to Tunisia, where it can be either grown naturally in unmanaged forests or artificially in intensively managed stands with site preparation, fertilisation and periodic thinning. At this spatial scale, the tree age and size become weakly correlated: a given diameter at breast height can be

reached at a large range of ages. The supplementary information brought by age in the allometric model is also shown indirectly by the asymptotic correlation coefficients between model parameters, a, b and c in Eq. 3 that are weaker than between a, b and d of Eq. 4 (data not shown).

It is noteworthy that age explains entirely the effects of fertilisation and precipitation on the model residuals for the foliage and branch compartments. This suggests that nutrition and water affect the growth rate, but not the tree ontogeny itself. It also suggests that the higher foliage and branch biomass in fertile sites result essentially from a faster growth and not a change in the fundamental morphometric model of the species (Trichet et al. 2008). Gower et al. (1993) on *Pinus resinosa* and *Pinus ponderosa* came to the same conclusion, as well as Coyle and Coleman (2005) for irrigated and fertilised cottonwood clones and sycamore. We are aware that a number of other authors report a significant interaction of environmental and stand variables on the allometry of coniferous species (Beets and Madgwick 1988; Callaway et al. 1994; Delucia et al. 2000 among others). We conclude that for the case of maritime Pine—a shade-intolerant species with a limited social position range—tree age is a variable that may well capture most of these effects.

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