

Allometric relationships for branch and tree woody biomass of Maritime pine (*Pinus pinaster* Ait.)

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Abstract

Modelling biomass repartition in a tree is either done using theories regarding carbon transfer and allocation or through empirical repartition coefficients. The latter can be derived from the study of the allometric relationships inside a tree, which reflect the equilibrium between tree structure and biomass. In order to quantify the biomasses of the main aerial compartments (needles, stem wood, stem bark, branch wood and buds) of a Maritime pine tree (*Pinus pinaster* Ait.) and to assess their relationships with tree structure, we undertook some destructive measurements of architecture and biomass. The study of leaf area was presented in a specific paper [Porté et al., Ann. For. Sci. 57 (1) (2000) 73], and the present paper is dealing with the woody compartments (branch wood, stem bark and wood). We collected biomass samples on thirty 5-year-old, sixteen 26-year-old and ten 32-year-old Maritime pines. Allometric equations were developed per site to estimate branch wood biomass. It depended only on the branch basal diameter and the models were very satisfying. Using these equations, we estimated the total branch wood biomass of each sampled tree.

A single relationship for all sites was found to model crown or trunk biomass. A power function of tree diameter at breast height (DBH) and the inverse of tree age was fitted to the branch wood data. A power function of DBH and tree age was used for the stem wood and bark models, which takes into account the differences in vitality with different ages. All models performed quite well. Input variables were easy to measure so that the models could be applied to estimate the aerial biomass of a whole stand, per compartment, over a 20-year-long period. The allometric relationships presented here can be derived to be used as biomass repartition laws, for a 5–30-year-old Maritime pine stand in humid Lande. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: *Pinus pinaster*; Allometry; Biomass; Wood; Bark

1. Introduction

Growth modelling of forest trees covers a wide range of approaches, from functional to empirical ones, from molecular level to stand or more global levels. Regarding tree functioning, the process of carbon allocation is hardly known, therefore modelling was often based on theoretical functional representations such as the pipe-model theory, the

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functional balances or the transport-resistance theory (Valentine, 1985, 1990; Mäkelä, 1986; Thornley, 1991; Dewar et al., 1994). A more empirical approach consisted in determining biomass repartition coefficients (Linder et al., 1984; McMurtrie et al., 1992; Bartelink, 1998). The allometric relationships existing between the different tree compartments express the functional and mechanical equilibrium required for the maintenance and development of each individual tree. Using destructive measurements of biomass and dimensions, statistical laws were determined assuming to be of good help in determining carbon repartition coefficients (Lemoine et al., 1986; Valentine et al., 1994; Kershaw and Maguire, 1995; Bartelink, 1996, 1997; Baldwin et al., 1997).

Most of the studies undertaken on Maritime pine (*Pinus pinaster* Ait.) consisted in characterising the results of assimilate transport and growth processes. Tree height, diameter and biomass increments were determined under different site or environmental conditions. The most accomplished work was done by Lemoine: he first established yield tables (Lemoine and Decourt, 1969). Then, he studied the impacts of silvicultural treatments, such as clearings and stocking density, on tree height and radial growth (Lemoine and Sartolou, 1976; Lemoine, 1980, 1982). He finally built up a stand growth model of trunk volume using allometric relationships established under several stand age and environmental conditions (Lemoine, 1969, 1980, 1991; Lemoine et al., 1986; Salas-Gonzalez, 1995). However, biomass per tree compartments was not estimated, except for one 16-year-old Maritime pine stand (Lemoine et al., 1986).

In order to model Maritime pine growth in terms of tree height, tree diameter and biomass per tree compartment, we undertook destructive measurements on 5-, 26- and 32-year-old pines. The main compartments were the following: stem wood, stem bark, branch wood, branch bark, needles, buds, male flowers, female cones, fine roots and coarse roots. Underground biomass was not regarded during this study. Measurements were done at winter time when no growth phenomena could occur; consequently, it prevented us from studying male flowers. Because of tree fall at cutting, the present study proved not to be relevant for determining the biomass of female cones. For practical technical reasons, branch bark, inner bark and branch wood were integrated into what we

called branch wood. Needles play a crucial role in tree functioning and their specific results were presented in a different paper (Porté et al., 2000). The present paper deals with the woody compartment: stem wood (W_{StW}), stem bark (W_{StBk}) and branch wood (W_{BrW} : wood + inner bark + bark).

This paper first presents how we measured and estimated the amount of woody biomass standing in the aerial part of Maritime pine trees. Then we established relationships between biomasses and dimensions at the branch and tree level. Finally, these models were applied to a whole stand in order to estimate the amounts of biomass per tree compartment and per hectare over a 19-year-long period (8–27-year-old Maritime pines).

2. Materials and methods

2.1. Sites and vegetal material characteristics

Sampled trees originated from three mono-specific *P. pinaster* Ait. even-aged (5-, 26- and 32-year-old) stands located 20 km southwest of Bordeaux, France (44°42'N, 0°46'W). Site conditions were quite similar (Table 1). They had an average annual temperature of 12.5 °C and received an average annual rainfall of 930 mm (1951–1990). All stands were fertilised at planting with 120 units of P_2O_5 . From 1963, the Berganton site was used to study the impacts of fertilisation on tree growth and biomass (Lemoine et al., 1986). Since 1987, the Bray site was intensively studied for carbon and water relations, tree transpiration, energy balance (Berbigier et al., 1991; Granier and Loustau, 1994; Berbigier and Bonnefond, 1995; Loustau et al., 1992a,b, 1997, 1998; Porté and Loustau, 1998; Bosc, 1999). Since 1997, the Hermitage site was used to assess Maritime pine wood mechanical properties (Stokes et al., 1998), root architecture and leaf area characteristics (Danjon et al., 1999; Porté et al., 2000). The present study was achieved in winter 1995–1996 as the Bray pines were 26-year-old and the Berganton pines were 32-year-old, and in winter 1996–1997 while the Hermitage site was 5-year-old. Main stand characteristics at the study time are presented in Table 1. In order to represent the size distribution in the stands, we sampled fourteen 26-year-old trees and ten 32-year-old pines according

Table 1

Main climatic, environmental and dendrometric characteristics of the Berganton, Bray and Hermitage sites at the time of the study

	Hermitage	Bray	Berganton
Location	44°42'N, 0°46'W	44°42'N, 0°46'W	44°42'N, 0°46'W
Elevation (m)	58	61	56
Topography	Flat	Flat	Flat
Soil type	Podzol	Podzol	Podzol
Mean soil depth (cm)	80	70	?
Climate type	Oceanic	Oceanic	Oceanic
Annual rainfall (mm)	930	930	930
Mean annual temperature (°C)	12.5	12.5	12.5
Stand area (ha)	7	16	17
Plot area (ha)	5.51	4.70	0.198
Density (stems ha ⁻¹)	1178	621	334
Tree age (years)	5	26	32
Mean height (m)	3.19 (S.D. = 0.43)	17.63 (S.D. = 1.21)	20.79 (S.D. = 1.40)
Mean diameter (cm)	–	26.03 (S.D. = 4.74)	38.44 (S.D. = 4.76)

to their diameter at breast height (DBH, cm) and thirty 5-year-old trees according to their height. The oldest trees were felled carefully to minimise the damage to the crowns, and the 5-year-old trees were pulled off the ground with a Caterpillar. Each tree was fully analysed within next 3 days.

2.2. Branch architecture and biomass measurements

The diameter of each living branch (D10, cm, measured at the nearest 0.01 cm, diameter at about 10 cm from the bole) was measured with an electronic calliper. One branch per living whorl was randomly selected for more-detailed biomass measurements (93 branches in 1995, 133 branches in 1997). Each branch was separated according to the type of organ (branch wood + bark, needles according to needle age, buds, cones), to the second-order internode which it was part of and to its order of ramification (branch, branch on a branch, etc.). More explanations concerning Maritime pine crown structure can be found in Porté et al. (2000). Each sample was oven-dried at 65 °C as long as required to reach its stable dry weight and weighted.

2.3. Stem height, radial and biomass annual increments

On the ground, the lengths (L_i , nearest 0.5 cm) and the diameters over bark (D_i , measured in the middle of

the growth unit, nearest 0.1 cm) of each annual growth unit of the trunks were measured ($i = 0-n$). One stem disk was taken in the middle of each growth unit to be planned using a surfacing machine and scanned with a 100 or 200 dpi resolution (Scanner HP ScanJet II cx, Software DeskScan II v. 2.3.1.a., Hewlett Packard). The ring width has been measured along four directions (north, south, east, west) using the Windendro software based on image analysis (Windendro 6.11, Regent Gay Instrument, Québec). We called $R_{i,r,azi}$ the radius as measured on growth unit i , until ring r along the azimuth azi . Mean radius until ring r ($R_{i,r}$, cm) was calculated as the quadratic mean of the four measured radii (Pardé and Bouchon, 1988):

$$R_{i,r} = \sqrt{\frac{R_{i,r,north}^2 + R_{i,r,south}^2 + R_{i,r,east}^2 + R_{i,r,west}^2}{4}} \quad (1)$$

$S_{i,r}$ (cm²) is wood area until ring r , on growth unit i :

$$S_{i,r} = \pi R_{i,r}^2 \quad (2)$$

We calculated $V_{i,r}$ (cm³) as the volume until ring r , for growth unit i , that was included between the two slices i and $i + 1$ (sampled on growth units i and $i + 1$). We assumed the volume to be a cone trunk:

$$V_{i,r} = \frac{1}{3} \cdot \frac{1}{2} (L_i + L_{i+1}) \times (S_{i,r} + S_{i+1,r} + \sqrt{S_{i,r} S_{i+1,r}}) \quad (3)$$

Exceptions were made for the two extremes logs: the upper one was considered to be equivalent to a cone of

length $\frac{1}{2}L_0$ and section $S_{0,r}$; the lower one was considered to be equivalent to a cylinder of length $\frac{1}{2}L_n$ and section $S_{n,r}$.

Wood biomasses were then calculated using density measurements done on four cores (north, south, east, west) per growth unit. Cores were sampled from bark to pith. Heartwood and sapwood were separated, their lengths and dry weight (48 h in oven at 65 °C) measured. The volume of the core was estimated as a cylinder of 5 mm diameter. Wood density (kg m^{-3}) was determined as the ratio of the core dry weight to its volume. One-fourth of the bark was taken away from each slice and weighted (48 h in oven at 65 °C). We estimated the area bearing this bark using radius and width measurements of the slice. Specific bark area (SBA, $\text{m}^2 \text{kg}^{-1}$) was estimated as the amount of external wood area to the bark dry weight.

Expansion factors were calculated per stand as the ratio of total aboveground biomass to stem wood biomass (Brown et al., 1989). Foliage biomass per hectare was estimated using the models proposed by Porté et al. (2000) and bud biomass was provided by Porté (unpublished data).

2.4. Statistical analysis

Various linear and non-linear regression models were fitted to the biomass data sets using the SAS software package (SAS 6.11, SAS Institute, Cary, NC, 1989–1995) and SPSS for Windows software (SPSS 7.5, SPSS, Chicago). For the crown woody biomass, fittings were done at the branch level and applied to estimate a second data set of tree branch wood biomass “measurements”. Similar relationships between biomass and structure were then established at the tree level and were finally applied to estimate stand branch wood biomass. For the stem wood and bark, integration consisted only of the last step. The choice of the final

models was based on several criteria: best-fitting on the sample population (characterised with residual sums of square, residual mean square, F -values of regressors, residual plots, relationship estimated—measured values, adjusted R^2 -values), its simplicity (minimum number of regressors) and its possible use as an estimating tool when extrapolating to the total population. Multiple range tests were used to compare mean values (Student–Newman–Keuls). Means with the same letters are considered not to be significantly different at a 5% tolerance level.

3. Results

3.1. Branch woody biomass

The range of branch wood biomass (w_{BrW} , g) was, respectively, 18 and 10 times larger on the 32 (0–5400 g) and 26 (0–3000 g)-year-old pines than on the 5-year-old ones (0–300 g). The branch wood biomass distribution was similar for all stands (Table 2). We observed fifth-order ramifications only on the 32-year-old pines, only on five out of the 10 sampled pines, and on the oldest branches (9–15-year-old). As a whole, fourth- and fifth-order ramifications were representing less than 5% of the branch woody biomass, whereas the main axis biomass was consisting in 72.2, 76.3 and 71.6% of the branch wood biomass, for the 5-, 26- and 32-year-old pines, respectively (Table 2).

Correlations with branch diameter were high for both stands ($R = 0.91$ for the Berganton and Hermitage sites, $R = 0.94$ for the Bray site). A power function of branch diameter (Table 3) provided very satisfying models. Fig. 1 shows measured and estimated branch wood biomass versus branch diameter, as well as a residual plot. Most of the variability was explained and the distribution of residuals

Table 2

Branch wood biomass distribution (in %) according to the shoot ramification order (2: branch, 3: branch on a branch, etc.)^a

Site	Order 2	Order 3	Order 4	Order 5
Berganton	71.6 (4.0)	24.2 (3.3)	4.17 (1.5)	7.19×10^{-2} (1.1×10^{-1})
Bray	76.3 (6.7)	21.8 (5.6)	1.89 (1.8)	0
Hermitage	72.2 (7.5)	26.8 (6.8)	9.37×10^{-1} (1.0)	0

^a Values are mean of measurements on 10, 14 and 30 trees for the 32 (Berganton), 26 (Bray) and 5 (Hermitage)-year-old stands, respectively. Values in parenthesis are standard deviations of the mean.

Table 3

Parameters of the allometric models established to estimate the biomass of branch wood (g) as a function of branch diameter (D10, cm)^a

Site	a_1	a_2	RMS ^b
Berganton	21.228 (1.944)	2.818 (6.130×10^{-2})	92327.16
Bray	26.630 (3.701)	2.736 (0.099)	29155.31
Hermitage	27.892 (1.158)	2.149 (0.063)	367.06

^a The model equation is $a_1 D10^{a_2}$. Values in parenthesis are asymptotic standard deviations on estimated values.^b Residual mean square.

was homogeneous. It only demonstrated a weak underestimation of the higher biomass values (over 1000 g). There was no other significant variable.

Total branch wood biomass of each pine (W_{BrW} , kg) was estimated using these models. The 32-year-old pines developed a mean value of 43.6 kg of branch wood biomass (S.D. = 19.5 kg, max = 88.9 kg, min = 18.6 kg) and the 26-year-old pines 25.2 kg of branch wood biomass (S.D. = 11.3 kg, max = 41.8

kg, min = 8.5 kg), against 2.1 kg for the 5-year-old pines (S.D. = 0.9 kg, max = 4.1 kg, min = 0.1 kg). A power function of DBH (cm) and the inverse of tree age was fitted to this calculated data set (Table 4).

$$W_{BrW} = a_1 \frac{DBH^{a_2}}{age^{a_3}} \quad (4)$$

Adding other variables did not permit to improve the model. Estimated total branch wood biomass versus calculated total branch wood biomass, as well as a residual plot, are presented in Fig. 2. Apart from one slightly outlying point which corresponded to the smallest 5-year-old pine which was considerably overestimated, models were satisfying. The model explained 90% of the observed variability and demonstrated no bias. Although the analysis used weighted least-squares, variance was not fully homogeneous and remained higher when estimating higher values of branch wood biomass.

3.2. Stem biomass estimation

Differences in wood density were higher between the stands than between the types of wood or the growth units, inside the same stand. No relationship was observed with age since the higher density values were observed on the 26-year-old stand, than on the 5-year-old stand and at last on the 32-year-old stand (Table 5). Wood density on the 5-year-old trees was lower than on 26-year-old trees (−13% on the sapwood mean value), but it was close to the values measured on the juvenile wood (3–5-year-old growth units) of some of the adult trees. For the 26- and 32-year-old pines, wood density was a little higher on sapwood than on heartwood, although these differences were only significant for the measurements done

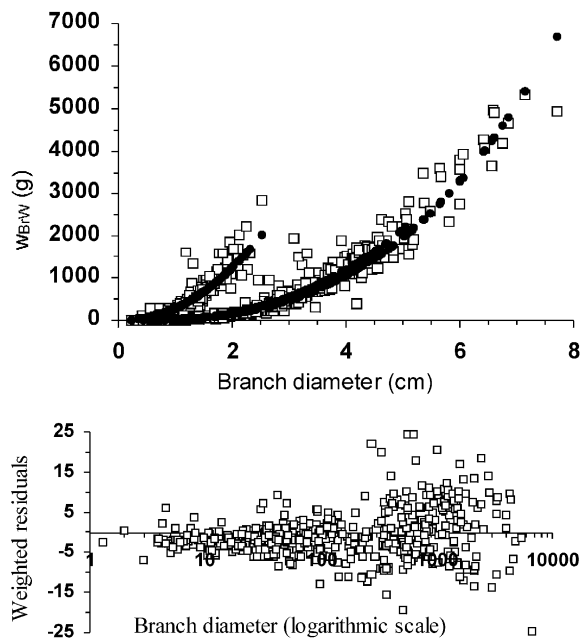


Fig. 1. Measured (\square) and estimated (\bullet) branch wood biomass (W_{BrW} , g) versus branch diameter (D10, cm), for the Hermitage, Bray and Berganton site trees. To ease the lecture of the graph, the Hermitage site biomass values were multiplied by 10. Bottom graph corresponds to weighted residuals plotted against estimated biomass values (logarithmic scale).

Table 4

Parameters of the allometric models established using the data from the three sites to estimate the tree biomass of each woody compartment (kg)^a

	Model	Weight	a_1	a_2	a_3
Stem wood	$a_1 \text{ DBH}^{a_2} \text{ age}^{a_3}$	1/StW	5.922×10^{-3} (8.516×10^{-4})	1.711 (1.297×10^{-1})	1.341 (1.257×10^{-1})
Bark	$a_1 \text{ DBH}^{a_2} \text{ age}^{a_3}$	1/StBk	4.659×10^{-3} (9.597×10^{-4})	1.559 (2.420×10^{-1})	9.864×10^{-1} (2.262×10^{-1})
Branch wood	$a_1 \text{ DBH}^{a_2} / \text{age}^{a_3}$	1/DBH ²	3.775×10^{-2} (1.110×10^{-2})	2.033 (2.566×10^{-1})	8.885×10^{-2} (1.894×10^{-1})

^a Explanative regressors were DBH (cm) and tree age (years). Values in parenthesis are asymptotic standard deviations on estimated values.

on the youngest growth units (4–7- and 6–11-year-old, for the stands, respectively). There was a general vertical trend in both sapwood and heartwood densities: sapwood density increased of 27 and 43%, for the 26- and 32-year-old trees, respectively, from the 4–6-year-old growth units to the 23–25-year-old ones at the bottom of the trees.

Stem wood biomass was ranging from 201 to 487 kg for the 32-year-old sampled pines (mean =

322 kg, S.D. = 82 kg), from 57 to 185 kg for the 26-year-old pines (mean = 134 kg, S.D. = 46 kg), and from 0.059 to 4.4 kg for the 5-year-old ones (mean = 1.7 kg, S.D. = 0.83 kg). On the 5-year-old pines, heartwood was not existing yet. On the 26- and 32-year-old pines, heartwood appeared on growth units older than 4–5 years. Heartwood proportion was then highly variable: according to the age of the growth unit (6–26 or 32 years), it could represent an average of 5–48% of the growth unit biomass. The general tendency was an increase of heartwood proportion when going down along the trunk, with a slight decrease at the real bottom of the tree. In adult trees, bark and inner-bark represented only 15 and 11% of the stem biomass of the 26- and 32-year-old trees, respectively. On young trees, it accounted for almost one-fourth of the stem biomass, more than half of it being constituted of the inner-bark living tissues, only.

Using the data from the three stands, a non-linear relationship between the total compartment biomass and tree DBH (cm) and age (years) was found (Table 4), for both compartments (wood W_{StW} , and bark + inner-bark W_{StBk} , kg):

$$W_{\text{St}} = a_1 \text{ DBH}^{a_2} \text{ age}^{a_3} \quad (5)$$

Figs. 3 and 4 present the estimated values versus the measured values for stem wood and bark, respectively, for all stands data. Because of the discrepancies in absolute values between the younger and older stands, graphs were presented using logarithmic scales. Graphs of weighted residuals versus estimated values were also presented. As for branch wood, the models were overestimating the smallest 5-year-old pine biomasses, but in general models were very satisfying. Most of the variability (99 and 94% for wood and bark, respectively) was explained by tree diameter and age. Tree height was not a significant independent variable. Residuals were quite homogeneously distributed.

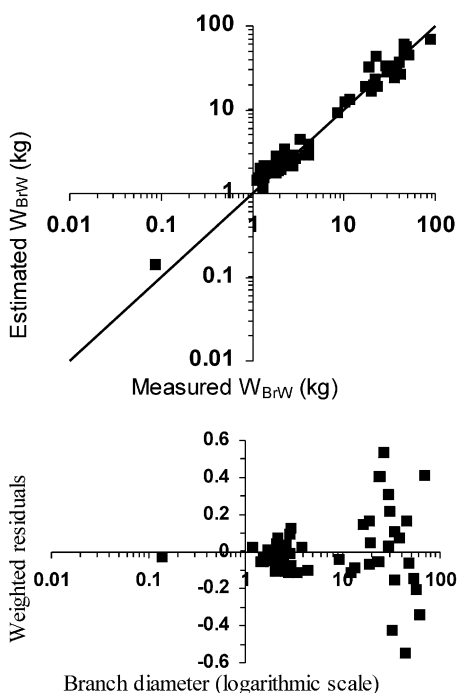


Fig. 2. Estimated total branch wood biomass (W_{BrW} , kg) versus measured total branch wood biomass, for all sites. To ease the lecture of the graph, it was presented using logarithmic scales. The bottom graph corresponds to weighted residuals plotted against estimated biomass values.

Table 5

Mean values of wood density as measured on sapwood and heartwood according to the age of the growth units of the pines from the three sites^a

Growth unit age (years)	Berganton (kg m ⁻³)		Bray sapwood (kg m ⁻³)		Hermitage (kg m ⁻³)
	Sapwood	Heartwood	Sapwood	Heartwood	
1	281 (36)	—	326 (30)	—	434 (58)
2	243 (34)	—	412 (66)	—	394 (40)
3	250 (27)	—	405 (47)	—	371 (40)
4	263 (17)	—	404 a (53)	325 b (45)	372 (28)
5	285 (17)	—	419 a (61)	354 b (32)	—
6	320 a (27)	220 b (33)	412 a (52)	367 b (42)	—
7	328 a (29)	179 b (77)	403 a (36)	367 b (37)	—
8	351 a (29)	249 b (91)	416 a (36)	392 a (40)	—
9	352 a (17)	260 b (55)	431 a (50)	412 a (50)	—
10	347 a (20)	279 b (76)	412 a (36)	407 a (50)	—
11	360 a (18)	301 b (56)	439 a (41)	430 a (42)	—
12	374 a (31)	332 a (78)	435 a (54)	472 a (52)	—
13	368 a (22)	315 b (55)	424 a (51)	451 a (49)	—
14	379 a (19)	364 a (49)	450 a (43)	485 a (48)	—
15	379 a (25)	370 a (38)	468 a (54)	463 a (51)	—
16	380 a (21)	373 a (45)	459 a (48)	462 a (49)	—
17	392 a (18)	381 a (24)	458 a (48)	464 a (43)	—
18	396 a (24)	381 a (24)	478 a (56)	472 a (41)	—
19	403 a (19)	397 a (42)	491 a (43)	488 a (43)	—
20	408 a (23)	367 b (16)	512 a (64)	481 a (52)	—
21	410 a (19)	378 b (29)	501 a (44)	488 a (41)	—
22	408 a (25)	390 a (26)	519 a (79)	485 a (33)	—
23	411 a (20)	383 b (21)	514 a (41)	511 a (31)	—
24	417 a (22)	393 b (21)	519 a (53)	501 a (39)	—
25	413 a (24)	396 a (25)	525 a (61)	509 a (44)	—
26	424 a (28)	403 a (31)	—	—	—
27	433 a (37)	404 b (18)	—	—	—
28	435 a (32)	413 a (27)	—	—	—
29	434 a (35)	422 a (21)	—	—	—
30	444 a (35)	439 a (28)	—	—	—
31	440 a (41)	446 a (44)	—	—	—
Total	372 a (62)	368 a (69)	453 a (67)	445 a (69)	392 (49)

^a Within each stand, significant differences ($\alpha = 5\%$) between heartwood and sapwood were indicated using different letters. Values in parenthesis are standard deviations of the means.

3.3. Stand woody biomass

The woody biomass per tree was estimated based on Eq. (5) using tree DBH and age. Stand woody biomass was estimated (Table 6) for the Hermitage site in 1997 (5-year-old trees) and the Bray and Berganton sites in 1995 (26- and 32-year-old trees). The total Bray woody biomass equalled 21 times the total woody biomass of the Hermitage. Their distributions between the different compartments were quite different. Branch biomass represented 49.3% of

the total woody biomass for the young stand and only 13.2 and 11.4% for the 26- and 32-year-old stands. In the 5-year-old pines, crown and stem compartments were equal whereas the development of adult trees resulted in the predominance of stem wood biomass (75.5 and 78.2% for the 26- and 32-year-old stands, respectively). The proportion of bark did not change significantly with stand age; it was equal 10.3, 11.3 and 11.4% for the 32-, 26- and 5-year-old stand, respectively. Expansion factors (Table 6) were decreasing with stand age, from 4.61 for the

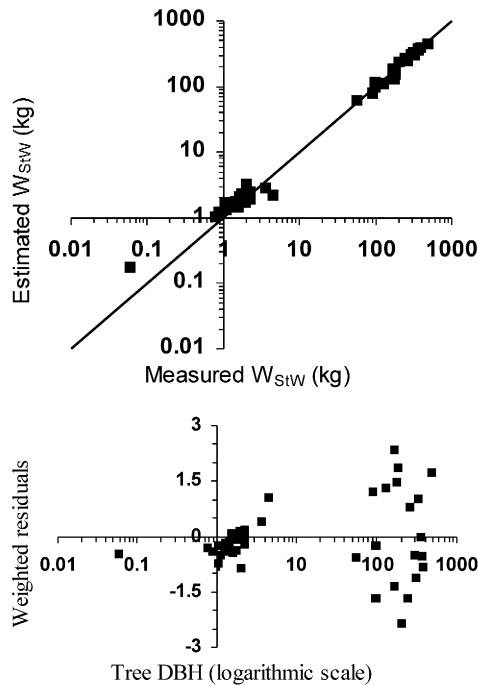


Fig. 3. Estimated stem wood biomass (W_{StW} , kg) versus measured stem wood biomass, for all sites. To ease the lecture of the graph, it was presented using logarithmic scales. The bottom graph corresponds to weighted residuals plotted against estimated biomass values.

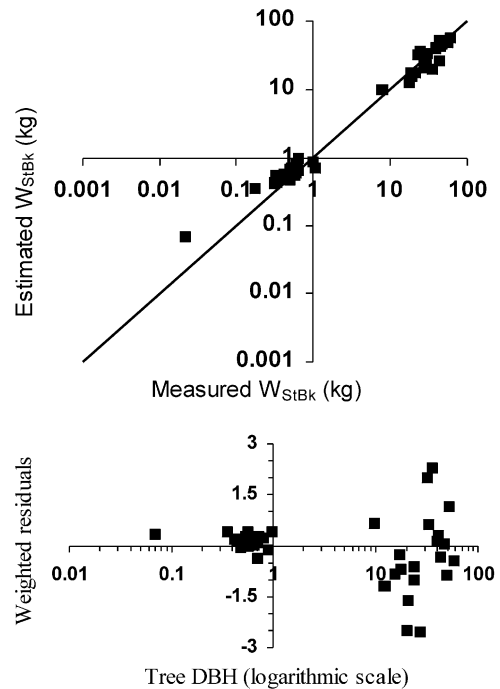


Fig. 4. Estimated stem bark biomass (W_{StBk} , kg) versus measured stem bark biomass, for all sites. To ease the lecture of the graph, it was presented using logarithmic scales. The bottom graph corresponds to weighted residuals plotted against estimated biomass values.

5-year-old stand, to 1.44 and 1.35 for the 26- and 32-year-old stands, respectively.

3.4. Woody biomass immobilisation in a Maritime pine stand over 19 years

The estimation of the evolution of stand woody biomass over 19 years required the knowledge of tree diameters over the same period. We used DBH measurements that were done over 10 years on the Bray site (tree age between 17- and 27-year-old). We had no measurements for 7–17-year-old stands. To estimate the number and diameters of trees that were in the stand, we needed to know which trees had been removed by thinnings. The Bray management history reported thinnings every 5 years (11-, 16-, 21- and 26-year-old) that consisted in removing 31, 25, 25 and 15.4% of the stems. The diameter distribution of the thinned trees was known for the last

two thinnings. Both distributions of thinned trees and the distribution of all trees before thinning could be assimilated to a normal distribution. The distribution of thinned trees was characterised by a mean value μ lower than that of the population before thinning and the same standard deviation σ . When centred and normalised, it corresponded to the following frequency distribution:

$$F_{DBH} = \frac{a}{\sigma\sqrt{2\pi}} \exp\left(-\frac{1}{2}\left(\frac{x-\mu}{\sigma}\right)^2\right) \quad (6)$$

with $a \approx 1$ ($a = 1.0073$, S.D. = 0.0083) and $\mu = 0.6309$ (S.D. = 0.0772). Parameter σ was varying with tree age

$$\sigma = 0.2876 \times \text{age}^{0.8607} \quad (7)$$

This normal function was also used to estimate the centred normalised distribution of tree diameters

Table 6
Stand biomass per compartment (t ha⁻¹)

	Hermitage	Bray	Berganton
Stand age (years)	5	26	32
Density (tree ha ⁻¹)	1178	621	334
Stem wood (t ha ⁻¹) ^a	1.99	78.3	107.0
Stem bark (t ha ⁻¹) ^a	0.58	11.7	14.1
Branch wood (t ha ⁻¹) ^a	2.5	13.7	15.7
Total woody biomass (t ha ⁻¹)	5.1	103.7	136.7
Foliage (Porté et al., 2000) (t ha ⁻¹) ^b	4.0	9.0	7.4
Buds (t ha ⁻¹)	6.0 × 10 ⁻²	0.24	0.28
Total aboveground biomass (t ha ⁻¹)	9.2	113.0	144.5
Expansion factor ^c	4.61	1.44	1.35

^a Stem wood, stem bark + inner bark, and branch wood biomass were estimated in this study.

^b Foliage biomass was estimated from Porté et al. (2000).

^c Expansion factors were estimated as the ratio of total aboveground biomass to stem wood biomass.

for the previous thinnings. Absolute values of mean diameter at these times were estimated from the mean radial growth curve obtained using the pines sampled in winter 1995.

Using the measured or estimated values of tree diameters on the Bray site and the allometric

equations presented in Table 4, we estimated the stand woody biomass per tree compartment from the age of 8 to 27 (Table 7). Stem wood biomass was always predominant, representing 52% of the total wood biomass on the 8-year-old stand to 76% on the 27-year-old stand. Branch wood biomass decreased

Table 7
Estimated stand woody (stem wood, stem bark + inner bark, branch wood) biomass (t ha⁻¹) over 19 years^a

Stand age (years)	Density (tree ha ⁻¹)	Thinning (tree ha ⁻¹)	Stem biomass		Branch biomass (t ha ⁻¹)	Total (t ha ⁻¹)
			Wood (t ha ⁻¹)	Bark (t ha ⁻¹)		
8	1600	–	4.62	1.28	2.88	8.78
9	1600	–	8.10	2.08	4.60	14.8
10	1600	–	11.9	2.87	6.08	20.8
11	1600	500	16.5	3.80	7.67	28.0
12	1100	–	14.1	3.09	5.95	23.1
13	1100	–	18.1	3.82	7.01	29.0
14	1100	–	22.8	4.63	8.14	35.6
15	1100	–	27.9	5.46	9.18	42.5
16	1100	272	33.1	6.30	10.1	49.5
17	828	–	31.4	5.79	8.93	46.1
18	828	–	36.7	6.58	9.75	53.0
19	828	–	42.5	7.45	10.6	60.6
20	828	–	49.0	8.37	11.5	68.9
21	828	207	54.5	9.12	12.1	75.7
22	621	–	48.2	7.86	10.1	66.2
23	621	–	56.6	9.00	11.4	77.0
24	621	–	63.4	9.88	12.1	85.4
25	621	–	70.9	10.8	13.0	94.7
26	621	96	78.3	11.7	13.7	103.7
27	525	–	75.8	11.1	12.7	99.6

^a Estimations were obtained applying the models presented in Table 4 using tree diameter measurements or estimations from age 8 to age 27. Winter time thinning intensities were also indicated.

from 33 to 13% and bark biomass from 15 to 11%, during the 19-year-old long period. On each compartment, we can observe the effect of thinnings: decrease in stand density resulted in a decrease of total biomass per hectare (Table 7). Except from the thinning considerations, stem biomass increased continuously. Growth rates were more important during the two first periods (8–11-year-old: +258% and 12–16-year-old: +135%). During the last periods, the relative stem wood biomass increase was equal to 74 and 62%, respectively (17–21- and 22–26-year-old). We observed the same behaviour for bark, relative growth rates being in average 25% lower than the ones observed for stem wood. Branch wood biomass between two thinnings was slightly increasing, although at a slower rate than stem biomass (166% between 8 and 11, 70% between 12 and 16, 35% between 17 and 21, 36% between 22 and 26 years of age).

4. Discussion

We developed both at the branch and tree levels allometric relationships that linked the compartment biomass to the dimensions of the woody structure that was bearing or constituting each compartment (branch or stem). These dimensions appeared to be almost the same at the branch and tree level, for the three stands and for the different compartments: diameter and age. All relationships were non-linear power functions, displaying either two or three parameters. During the course of this study, many functions were tested to estimate the branch and stem biomass. To select the final model, we considered (1) the goodness of fit based on residuals sum of square, *F*-values of regressors, residual plots, (2) its simplicity and (3) the possible applicability to estimate the stand biomass (see Section 2.4). On Maritime pine, the amount of branch wood biomass was closely related to branch diameter: the bigger the branch, the larger was its biomass. It should be noted that some multivariate linear model including 3–4 variables describing branch lengths and location in the crown performed a little better in terms of total goodness of fit (residual sum of squares) than the one that was finally elected. However, the fitting was not correct for the lowest values: a negative constant value was found that

resulted in estimating negative biomass values for small branches. Moreover, the application of these models was made difficult by the required inputs (branch lengths for branch biomass, sapwood area under the living crown for stem biomass). As a consequence, these multiple linear models could not perform correctly as an extrapolation tool in the field and they were rejected.

Relationships between diameter and biomass are classic relations. Studies regarding woody biomass (stem or branch biomass) were not so numerous as studies demonstrating the link between foliage area and branch or tree diameter but they reached the same conclusions (Lemoine et al., 1986; Bartelink, 1996, 1997; Leonardi et al., 1996; Baldwin et al., 1997; Santa Regina et al., 1997). Bark is an important compartment because its extraction at harvest can deeply influence the stand mineral balance and its sustainability. However, it seemed to constitute an annex compartment in biomass determination studies and we only found one bark biomass determination (Lemoine et al., 1986). Sapwood area or square diameter were sometimes used instead of diameter (Webb and Ungs, 1993; Valentine et al., 1994; Mäkelä et al., 1995; Vanninen et al., 1996). But this was done mainly for foliage area estimations: the functional link between water conducting area and water transpiring area was then introduced into the empirical allometric relationship (Valentine et al., 1994; Margolis et al., 1995). In some studies, variables such as shoot length, foliated length, branch insertion height, crown radius, tree height, etc. were added to increase the fitting (Valentine et al., 1994; Mäkelä et al., 1995; Baldwin et al., 1997; Bartelink, 1996, 1997).

Bartelink (1996) found a relationship between *Pseudotsuga menziesii* (9–39-year-old) stem wood biomass and DBH and tree height which was independent of site age and stand-dependant relationships for branch wood. We always found an age dependency in our models whereas height was not significant: probably, age formed a kind of substitute variable to dominant height which would reflect the site and tree vitality. By establishing one relationship for the three stands, we demonstrated the existence of the same growth equilibrium between young and adult trees growing under equivalent conditions (same site type: humid Lande, hydromorphic soil, with an solid

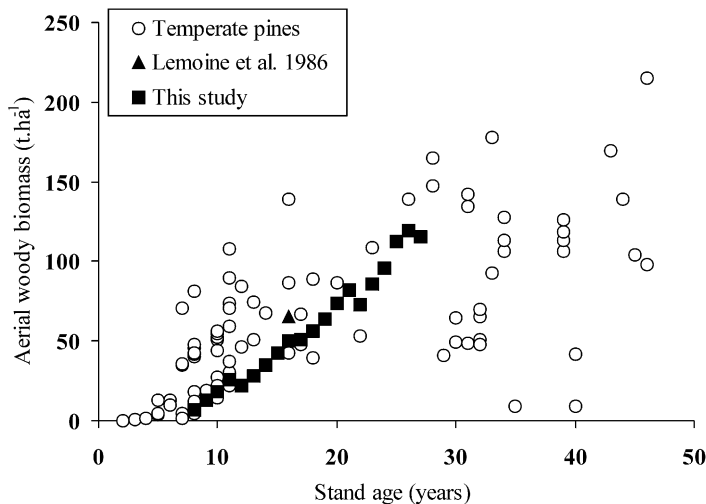


Fig. 5. Stand woody biomass (t ha^{-1}) as a function of stand age: (○) data measured on pine plantations from temperate regions (Gower et al., 1994); (●) biomass measurement done on Maritime pine (Lemoine et al., 1986); (■) the estimations we made in the present study.

layer between 80 and 100 cm, same climate, same forest management, etc.).

The tree level models should act as better extrapolating tools than the branch level model since they were valid on different stands. However, they are probably specific of the general growth conditions of humid Landes; another type of Landes, or human interventions such as fertilising or watering would probably result in different parameterisation (fertilisation effect observed on foliage allometry in *P. taeda* (Gillespie et al., 1994), in *P. mensiezii* (Kershaw and Maguire, 1995), stand density effect in *P. mensiezii* (Maguire and Bennett, 1996)). The estimations of stand biomass could not be tested against data. Their confrontation with literature data on stand woody biomass in pines of temperate regions (Gower et al., 1994) indicated that our models provided coherent stand biomass values. They were located in the lower part of the encountered range for younger stands (<20-year-old) and in the middle of the range for older stands (Fig. 5). The expansion factors that we calculated for the Maritime pine adult stands were consistent with the range of values (1.30–2.19) presented by Johnson and Sharpe (1982) for both hardwood and conifer stands in the United States. As a consequence, we can conclude that our models provide coherent biomass

estimations and accept them to be used to estimate Maritime pine biomass during the first 35 years of the stand, for diameters lower than 40 cm.

By using joint models from the branch level to the stand level, we introduced errors at each step of the calculation. We were not able to estimate these errors on the intermediate or the final results: it would consist in a purely statistical analysis that would require time and high skills. We could have avoided these multiple errors by working directly at the tree or stand level. However, the branch level was made necessary by the companion study on foliage biomass to determine the distribution inside the crown (Porté et al., 2000). Moreover, these biomass studies are part of a modelling project: the tree level models were a requirement to parameterise a tree level growth model (Porté, 1999).

5. Conclusion

We established allometric relationships that can be used to estimate biomass of the aerial woody compartments at the branch and tree levels. Tree models performed as efficient and simple modelling tools, requiring only DBH and tree age to be known. Although limited regarding the number of trees and

stands studied, this work required a lot of field work. However, more measurements would be required to check the field of validity of the relations (larger range of stand age, of tree dimensions, of environmental conditions, of silvicultural treatments, etc.). A large point has not been assessed in this study: coarse and fine roots biomasses were not determined. Architectural measurements were undertaken (Danjon et al., 1999) but we did not dispose so far of biomass or growth information. However, the allometric equations developed here, added to the equivalent ones regarding foliage (Porté et al., 2000) were successfully used to model carbon distribution between the main aerial tree compartments in a model developed by Porté (1999).

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References

- Baldwin Jr., V.C., Peterson, K.D., Burkhart, H.E., Amateis, R.L., Dougherty, P.M., 1997. Equations for estimating loblolly pine branch and foliage weight and surface area distributions. *Can. J. For. Res.* 27, 918–927.
- Bartelink, H.H., 1996. Allometric relationships on biomass and needle area of Douglas-fir. *For. Ecol. Mgmt.* 86, 193–203.
- Bartelink, H.H., 1997. Allometric relationships for biomass and leaf area of beech (*Fagus sylvatica* L.). *Ann. Sci. For.* 54, 39–50.
- Bartelink, H.H., 1998. A model of dry matter partitioning in trees. *Tree. Physiol.* 18, 91–101.
- Berbigier, P., Bonnefond, J.M., 1995. Measurements and modelling of radiation transmission within a stand of Maritime pine (*Pinus pinaster* Ait.). *Ann. Sci. For.* 52, 23–42.
- Berbigier, P., Diawara, A., Loustau, D., 1991. Etude microclimatique de l'effet de la sécheresse sur l'évaporation d'une plantation de pin Maritime à sous-bois de Molinie. *Ann. Sci. For.* 22, 157–177.
- Bosc, A., 1999. Etude expérimentale du fonctionnement hydrique et carboné des organes aériens du pin Maritime (*Pinus pinaster* Ait.): intégration dans un modèle structure-fonction appliqué à l'analyse de l'autonomie carbonée des branches de la couronne d'un arbre adulte. Thèse de l'Université de Bordeaux II, 192 pp.
- Brown, S., Gillespie, A.J.R., Lugo, A.E., 1989. Biomass estimation methods for tropical forests with applications to forest inventory data. *For. Sci.* 35, 881–902.
- Danjon, F., Bert, D., Godin, C., Trichet, P., 1999. Structural root architecture of 5-year-old *Pinus pinaster* measured by 3D digitising and analysed with AMAPmod. *Plant Soil.* 217, 49–69.
- Dewar, R.C., Ludlow, A.R., Dougherty, P.M., 1994. Environmental influences on carbon allocation in pines. *Ecol. Bull.* 43, 92–101.
- Gillespie, A.R., Allen, H.L., Vose, J.M., 1994. Amount and vertical distribution of foliage in young loblolly pine trees as affected by canopy position and silvicultural treatment. *Can. J. For. Res.* 24, 1337–1344.
- Gower, S.T., Gholz, H.L., Nakane, K., Baldwin, V.C., 1994. Production and carbon allocation patterns of pine forests. *Ecol. Bull.* 43, 115–135.
- Granier, A., Loustau, D., 1994. Measuring and modelling the transpiration of a Maritime pine canopy from sap-flow data. *Agric. For. Meteorol.* 71, 61–81.
- Johnson, W.C., Sharpe, D.M., 1982. The ratio of total to merchantable forest biomass and its application to the global carbon budget. *Can. J. For. Res.* 13, 372–383.
- Kershaw Jr., J.A., Maguire, D.A., 1995. Crown structure in western hemlock, Douglas-fir, and grand fir in western Washington: trends in branch-level mass and leaf area. *Can. J. For. Res.* 25, 1897–1912.
- Lemoine, B., 1969. Le pin Maritime dans les Landes de Gascogne. Etude des relations d'allométrie concernant le volume des peuplements, en liaison avec certaines caractéristiques de la station. *Ann. Sci. For.* 26 (4), 445–473.
- Lemoine, B., 1980. Densité de peuplement, concurrence et coopération chez le pin Maritime. II. Résultats à 5 et 10 ans d'une plantation à espacement variable. *Ann. Sci. For.* 37 (3), 217–237.
- Lemoine, B., 1982. Croissance et production du pin Maritime. I. Recherche d'un modèle et d'une méthode. *Ann. Sci. For.* 39 (4), 321–354.
- Lemoine, B., 1991. Growth and yield of Maritime pine (*Pinus pinaster* Ait.): the average dominant tree of the stand. *Ann. Sci. For.* 48, 593–611.
- Lemoine, B., Decourt, N., 1969. Tables de production pour le pin Maritime dans le sud-ouest de la France. *Rev. For. Fr.* XXI (1), 5–16.
- Lemoine, B., Sartolou, A., 1976. Les éclaircies dans les peuplements de pin Maritime d'âge moyen: résultats et interprétation d'une expérience. *Rev. For. Fr.* XXVIII (6), 447–457.

- Lemoine, B., Gelpe, J., Ranger, J., Nys, C., 1986. Biomasses et croissance du pin Maritime. Etude de la variabilité dans un peuplement de 16 ans. *Ann. Sci. For.* 43 (1), 67–84.
- Leonardi, S., Santa Regina, I., Rapp, M., Gallego, H.A., Rico, M., 1996. Biomass, litterfall and nutrient content in *Castanea sativa* coppice stands of southern Europe. *Ann. Sci. For.* 53, 1071–1081.
- Linder, S., McMurtrie, R.E., Lansberg, J.J., 1984. Growth of eucalypts: a mathematical model applied to *Eucalyptus globulus*. In: Tigerstedt, P.M.A., Puttonen, P., Koski, V. (Eds.), *Crop Physiology of Forest Trees. Proceedings of the International Conference on Managing Forest Trees as Cultivated Plants, Finland, July 23–28, 1984. University of Helsinki, Finland*, pp. 117–126.
- Loustau, D., Berbigier, P., Granier, A., 1992a. Interception, throughfall and stemflow in a Maritime pine stand. II. An application of the Gash's model. *J. Hydrol.* 138, 469–485.
- Loustau, D., Berbigier, P., Granier, A., El Hadj Moussa, F., 1992b. Interception, throughfall and stemflow in a Maritime pine stand. I. Variability of throughfall and stemflow. *J. Hydrol.* 138, 449–467.
- Loustau, D., Berbigier, P., Kramer, K., 1997. Sensitivity of the water balance of southwestern France Maritime pine forests to climate. In: Mohren, G.M.J., Kramer, K., Sabaté, S. (Eds.), *Impacts of Global Change on Tree Physiology and Forest*. Kluwer Academic Publishers, Dordrecht, pp. 193–207.
- Loustau, D., Domec, J.C., Bosc, A., 1998. Interpreting the variability of xylem sap flux density within the trunk of Maritime pine (*Pinus pinaster* Ait.): application for calculating the water flow at the tree and stand levels. *Ann. Sci. For.* 55, 29–46.
- Maguire, D.A., Bennett, W.S., 1996. Patterns in vertical distribution of foliage in young coastal Douglas-fir. *Can. J. For. Res.* 26, 1991–2005.
- Mäkelä, A., 1986. Implications of the pipe-model theory on dry matter partitioning and height growth in trees. *J. Theoret. Biol.* 123, 103–120.
- Mäkelä, A., Virtanen, K., Nikinmaa, E., 1995. The effect of ring width, stem position, and stand density on the relationship between foliage biomass and sapwood area in Scots pine (*Pinus sylvestris*). *Can. J. For. Res.* 25, 970–977.
- Margolis, H., Oren, R., Whitehead, D., Kaufmann, M.R., 1995. Leaf area dynamics of conifer forests. In: Smith, W.K., Hinckley, T.M. (Eds.), *Ecophysiology of Coniferous Forests*. Academic Press, San Diego, pp. 181–224.
- McMurtrie, R.E., Leuning, R., Thompson, W.A., Wheeler, A.M., 1992. A model of canopy photosynthesis and water use incorporating a mechanistic formulation of leaf CO₂ exchange. *For. Ecol. Mgmt.* 52, 261–278.
- Pardé, J., Bouchon, J., 1988. Dendrométrie. ENGREF, Nancy, pp. 1–328.
- Porté, A., 1999. Modélisation des effets du bilan hydrique sur la production primaire et la croissance d'un couvert de pin Maritime (*Pinus pinaster* Ait.) en Lande humide. Thèse de Docteur en Sciences No. XI. Option Ecologie Générale, de l'Université d'Orsay, Paris, pp. 172 + annexes.
- Porté, A., Loustau, D., 1998. Variability of the photosynthetic characteristics of mature needles within the crown of a 25-year-old *Pinus pinaster*. *Tree Physiol.* 18, 223–232.
- Porté, A., Bosc, A., Champion, I., Loustau, D., 2000. Estimating the foliage area of Maritime pine (*Pinus pinaster* Ait.) branches and crowns with application to modelling the foliage area distribution in the crown. *Ann. For. Sci.* 57 (1), 73–86.
- Salas-Gonzalez, R., 1995. Modélisation de l'évolution de la ressource du massif du pin Maritime (*Pinus pinaster*) des Landes de Gascogne. Doctorat "Sciences Forestières". ENGREF, Nancy, pp. 187 + annexes.
- Santa Regina, I., Tarazona, T., Calvo, R., 1997. Aboveground biomass in a beech forest and a Scots pine plantation in the Sierra de la Demanda area of northern Spain. *Ann. Sci. For.* 54, 261–269.
- Stokes, A., Berthier, S., Sacriste, S., Martin, F., 1998. Variations in maturation strains and root shape in root systems of Maritime pine (*Pinus pinaster* Ait.). *Trees* 12, 334–339.
- Thornley, J.H.M., 1991. A transport-resistance model of forest growth and partitioning. *Ann. Bot.* 68, 211–226.
- Valentine, H.T., 1985. Tree-growth models: derivations employing the pipe-model theory. *J. Theoret. Biol.* 117, 579–585.
- Valentine, H.T., 1990. A carbon-balance model of tree growth with a pipe-model framework. In: Dixon, R.K., Meldahl, R.S., Ruark, G.A., Warren, W.G. (Eds.), *Forest Growth: Process Modelling of Forest Growth Responses to Environmental Stress*. Timber Press, Portland, OE, pp. 33–40.
- Valentine, H.T., Baldwin Jr., V.C., Gregoire, T.G., Burkhardt, H.E., 1994. Surrogates for foliar dry matter in loblolly pine. *For. Sci.* 40 (3), 576–585.
- Vanninen, P., Ylitalo, H., Sievänen, R., Mäkelä, A., 1996. Effects of age site quality on the distribution of biomass in Scots pine (*Pinus sylvestris* L.). *Trees* 10, 231–238.
- Webb, W.L., Unga, M.J., 1993. Three-dimensional distribution of needle and stem surface area in a Douglas-fir. *Tree Physiol.* 13, 203–212.