

New models for estimating the carbon sink capacity of Spanish softwood species

R. Ruiz-Peinado^{1,2*}, M. del Río^{1,2} and G. Montero^{1,2}

¹ Departamento de Selvicultura y Gestión de Sistemas Forestales. CIFOR-INIA.
Ctra. A Coruña, km 7,5. 28040 Madrid. Spain

² Instituto Universitario de Investigación en Gestión Forestal Sostenible. Universidad de Valladolid-INIA

Abstract

Quantifying the carbon balance in forests is one of the main challenges in forest management. Forest carbon stocks are usually estimated indirectly through biomass equations applied to forest inventories, frequently considering different tree biomass components. The aim of this study is to develop systems of equations for predicting tree biomass components for the main forest softwood species in Spain: *Abies alba* Mill., *A. pinsapo* Boiss., *Juniperus thurifera* L., *Pinus canariensis* Sweet ex Spreng., *P. halepensis* Mill., *P. nigra* Arn., *P. pinaster* Ait., *P. pinea* L., *P. sylvestris* L., *P. uncinata* Mill. For each species, a system of additive biomass models was fitted using seemingly unrelated regression. Diameter at the breast height and total height were used as independent variables. Diameter appears in all component models, while tree height was included in the stem component model of all species and in some branch component equations. Total height was included in order to improve biomass estimations at different sites. These biomass models were compared to previously available equations in order to test their accuracy and it was found that they yielded better fitting statistics in all cases. Moreover, the models fulfil the additivity property.

We also developed root:shoot ratios in order to determine the partitioning into aboveground and belowground biomass. A number of differences were found between species, with a minimum of 0.183 for *A. alba* and a maximum of 0.385 for *P. uncinata*. The mean value for the softwood species studied was 0.265.

Since the Spanish National Forest Inventory (NFI) records species, tree diameter and height of sample trees, these biomass models and ratios can be used to accurately estimate carbon stocks from NFI data.

Key words: aboveground biomass; belowground biomass; carbon sequestration; root:shoot ratio; softwood species.

Resumen

Nuevos modelos para estimar la capacidad de fijación de carbono de las coníferas españolas

Conocer el balance de carbono en los bosques es uno de los principales retos dentro de la gestión forestal. Habitualmente, la estimación de carbono en los bosques se realiza de manera indirecta, mediante la aplicación de modelos de diferentes fracciones de biomasa a los datos de inventario forestal. Para ello, en este estudio se han desarrollado sistemas de ecuaciones para estimar la biomasa forestal de las principales coníferas de los bosques de España: *Abies alba* Mill., *A. pinsapo* Boiss., *Juniperus thurifera* L., *Pinus canariensis* Sweet ex Spreng., *P. halepensis* Mill., *P. nigra* Arn., *P. pinaster* Ait., *P. pinea* L., *P. sylvestris* L., *P. uncinata* Mill. Se ha usado la metodología de mínimos cuadrados generalizados conjuntos, para el cumplimiento de la aditividad entre componentes. Como variables independientes se utilizaron el diámetro normal y la altura total del árbol. El diámetro aparece en todas las ecuaciones como variable significativa, mientras que la altura aparece también en todos los modelos para la biomasa de fuste y en algunos modelos para las ramas. Con la inclusión de la altura total se mejoran las estimaciones de los modelos en diferentes sitios. Los modelos ajustados fueron comparados con otras ecuaciones publicadas para comprobar la precisión, presentando mejores estadísticos en todos los casos. Mediante el uso de esta metodología, las ecuaciones cumplen la propiedad aditiva.

Además, se han desarrollado relaciones específicas entre la parte radical y parte aérea, para conocer como se realiza el reparto de biomasa. Se han encontrado diferencias entre especies, alcanzándose un mínimo de 0,183 para *A. alba* y un máximo de 0,385 para *P. uncinata*, siendo el valor medio para estas especies de coníferas estudiadas de 0,265.

* Corresponding author: ruizpein@inia.es

Received: 09-11-10; Accepted: 14-02-11.

Como el Inventario Forestal Nacional (IFN) identifica para todas las especies medidas el diámetro normal y la altura total de todos los árboles inventariados, estos modelos y relaciones ajustadas pueden ser aplicados con precisión en la estimación de cantidades de carbono a partir de aquellos datos.

Palabras clave: biomasa aérea; biomasa radical; fijación de carbono; relación parte aérea y parte radical; coníferas.

Introduction

Southern European forests are characterised by a distinctive set of features. They support high levels of biological diversity (both plant and animal) as a result of the survival of many species in southern European refuges during the glacial periods. Furthermore, they have a harsh, unpredictable climate, difficult socio-economic conditions and have suffered a long history of over-exploitation accompanied by landscape transformations since ancient times. In these forests, the non-marketable products and services they provide are usually more valuable than their direct yields, especially timber production (Scarascia-Mugnozza *et al.*, 2000). Soil and watershed protection, biodiversity, scenic beauty and, increasingly, recreational use, are the main functions covered by these stands, to which carbon sequestration has recently been added in accordance with international agreements on climatic change mitigation (Kyoto Protocol, UNFCCC, EU Forestry Strategy, Ministerial Conference on the Protection of Forests in Europe).

Hence, in the context of this function as mitigators of the effects of climate change, it is important to estimate the quantity of biomass present in forests, to understand the way in which the biomass accumulates and how it is distributed among the different fractions of the tree. This information will provide a basis for further nutrient studies and facilitate research on the use of biomass in energy production (Schlamadinger and Marland, 1996; Clark *et al.*, 2001). The use of forest inventories as a data source allows us to estimate the quantity of carbon fixed in living vegetation. However, depending on the quality and the amount of information provided by the forest inventory, the accuracy of these estimations will vary. National Forest Inventories have provided the basis for several regional and national-level carbon budgets (Dixon *et al.*, 1994; Goodale *et al.*, 2002).

Indirect approaches such as biomass expansion factors (BEF's) or biomass equations applied to forest inventory data (Brown, 2002) are usually used to quantify carbon sequestration in forests. BEF's convert stem volume or stand volume directly into biomass weight estimates,

although they vary depending on growth conditions and stand development, particularly on stand age (Lehtonen *et al.*, 2004, 2007), stand timber volume (Fang *et al.*, 2001) or tree height (Levy *et al.*, 2004). Therefore, more complex biomass models can provide more accurate estimations than BEF's, hence, are more commonly used to obtain forest biomass estimations (IPCC, 2003). Biomass models are built using destructive, highly costly sampling procedures and relate the dry weight of biomass to dendrometric characteristics; in most cases, the diameter at breast height (d) and/or the total height (h) of the tree (Crow and Laidly, 1980; Pardé, 1980).

Softwood species play an important role in the Mediterranean Basin forests due to their widespread distribution and their ecological and socio-economic value. The most important softwood species in Spain include: *Abies alba* Mill. (silver fir), *A. pinsapo* Boiss. (pinsapo fir), *Juniperus thurifera* L. (Spanish juniper), *Pinus canariensis* Sweet ex Spreng. (Canary Islands pine), *P. halepensis* Mill. (Aleppo pine), *P. nigra* Arn. (black pine), *P. pinaster* Ait. (maritime pine), *P. pinea* L. (stone pine), *P. sylvestris* L. (Scots pine) and *P. uncinata* Mill. (mountain pine). These softwood species occupy more than 9.9 million ha in Spain, of which 6.4 million are pure forests (MARM, 2008).

The information available for estimating forest biomass varies from one species to another. A number of studies have dealt with biomass estimation in *P. sylvestris* and *P. pinaster*, although much of this relates to Northern Europe in the case of the former (Marklund, 1988; Lehtonen *et al.*, 2004; Muukkonen, 2007) or to the Atlantic range of the species in the case of *Pinus pinaster* (Lemoine *et al.*, 1986; Montero *et al.*, 1999; Porte *et al.*, 2002; Balboa-Murias *et al.*, 2006). However, less research has been undertaken with regard to *P. nigra* (Neiryneck *et al.*, 1998; Fattorini *et al.*, 2004), *P. pinea* (Cabanettes and Rapp, 1978; Correia *et al.*, 2010) or *P. halepensis* (Grunzweig *et al.*, 2007). *J. thurifera* was studied in Morocco for biomass production using non-destructive methods due to its ecological importance (Montes *et al.*, 2000, 2002). As far as the other softwood species are concerned (*A. alba*, *A. pinsapo*, *P. canariensis* and *P. uncinata*), biomass production has not been studied in any depth

due to their limited distribution, so scarce information exists in this regard. Recently, Montero *et al.* (2005) fitted a set of biomass models for the main forest species in Spain (including those mentioned above), which allow us to quantify the biomass and carbon sequestration in forest ecosystems. These allometric biomass equations relate different tree biomass components (stem, different size branches, foliage, total above-ground biomass and root system) to tree diameter, although additivity among the component equations was not considered and each component was independently fitted.

Although allometric equations based on dbh provide one of the easiest and most accurate ways to estimate root biomass from forest measurements (Drexhage and Colin, 2001; Le Goff and Ottorini, 2001), it can be useful to determine the root:shoot partitioning of biomass for the purposes of ecological studies or carbon accounting. These ratios can be applied to individual plants or stands at local, regional or landscape level (Mokany *et al.*, 2006). Moreover, National Greenhouse Gas Inventories under the IPCC, generally employ root:shoot ratios to estimate root biomass and specific values are often unavailable.

In order to improve the existing biomass estimations and to offer more precise information on carbon accumulation in Spanish forests, new biomass equations for conifer species have been developed in this study. The use of methods that guarantee the additivity property among tree biomass components provides consistency between total tree and tree component biomass and also ensures greater statistical efficiency (Parresol, 1999, 2001). Furthermore, the inclusion of tree height in biomass equations as an additional predictor variable, could improve the accuracy of the biomass estimations (Ketterings *et al.*, 2001). The objectives of this study were: i) to determine the extent to which the use of additive methods and the inclusion of tree height as an independent variable improve biomass estimations in the studied species; and ii) to analyse the root:shoot partitioning of biomass for the main softwood species in Spain.

Material and methods

Study area

Individual tree biomass data were collected in representative regions across the natural range of the studied

species in Spain. Data for *Abies alba* were collected in the Pyrenean Mountain Range; for *A. pinsapo* in the Sierra de Grazalema and Sierra de las Nieves (Southern Spain); for *Juniperus thurifera* in Guadalajara (Central Spain); *Pinus canariensis* on the island of Tenerife (Canary Islands); *P. halepensis* was sampled in the Segura Mountain Range (South East Spain); *P. nigra* in the Iberian Mountain Range; *P. pinaster* in the Central Mountain Range (Guadalajara, Central Spain) and the Sierra Morena Mountain Range (Ciudad Real, Southern Spain); *P. pinea* in the Northern Plateau (Central Spain) and Huelva (South-West Spain); *P. sylvestris* in the Central Range (Madrid and Segovia, Central Spain) and *P. uncinata* in the Pyrenean Mountain Range (Fig. 1).

Data

For each species, stands were selected in medium quality sites (medium site index) distributed according to age classes. Average trees and growing conditions were chosen for the destructive sample. Because *A. pinsapo* is a protected species, the sample trees were not as representative as those of other species and it was not possible to collect belowground samples. Trees were sampled by 5 cm diameter classes, starting at 7.5 cm up to the maximum diameter found in the area. The number of sample trees varied from a minimum of 21 trees in the case of *J. thurifera* and *P. uncinata* to a maximum of 305 trees for *P. sylvestris*. For each sample tree, diameter at breast height (1.30 m) (*d*), total height (*h*) and crown height (*hc*) were measured. The minimum diameters sampled were between 6.2 for *P. sylvestris* and 10.0 for *P. canariensis* and *P. nigra*. The maximum diameters ranged from 41.0 cm for *P. uncinata* to 77.3 cm for *P. nigra* (Table 1).

Sampled trees were felled and separated into biomass components in the field. The biomass components considered were: stem with bark (commercial volume, up to a top diameter of 7 cm), thick branches (diameter larger than 7 cm), medium branches (diameter between 2 and 7 cm), thin branches (branches with a diameter smaller than 2 cm) and needles (Montero *et al.*, 1999). Estimation of root biomass was only undertaken on a few trees per species and diameter class due to the complexity and cost of the work involved (Table 1). The root component was collected using a backhoe, by digging a trench around the stump and extracting all the roots inside this hole. Using this approach, most

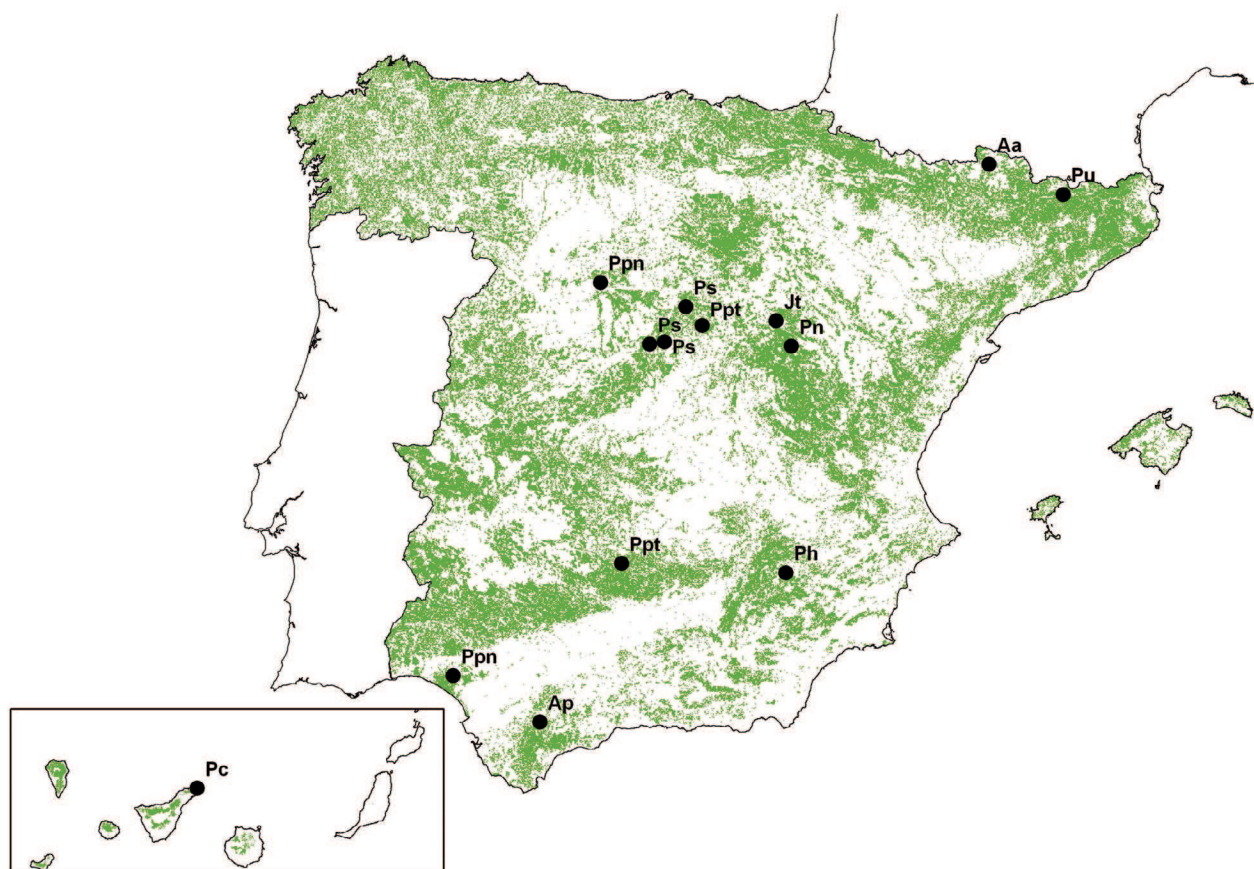


Figure 1. Distribution of the sample zones in Spain for the studied species. Aa: *Abies alba*. Ap: *A. pinsapo*. Jt: *Juniperus thurifera*. Pc: *Pinus canariensis*. Ph: *P. halepensis*. Pn: *P. nigra*. Ppt: *P. pinaster*. Ppn: *P. pinea*. Ps: *P. sylvestris*. Pu: *P. uncinata*.

of the root system was extracted. Fine roots were not captured by this method.

Each component was weighed in the field (fresh weight) and a representative sample (10 kg) of each of them was taken to the laboratory to be oven-dried at

102°C to constant weight. Thus, it was possible to determine moisture content and estimate dry matter. In those cases where the stem could not be weighed in the field, the diameter was measured at meter intervals up the stem in order to determine the log volumes using

Table 1. Minimum, maximum and mean values for diameter, height and biomass sample weight for the studied species

Species	dbh			height			Aboveground biomass				Root biomass			
	Min	Max	Mean	Min	Max	Mean	n	Min	Max	Mean	n	Min	Max	Mean
<i>A. alba</i>	9.0	57.5	30.4	8.0	29.0	18.5	29	27	2,503	661	10	8	394	132
<i>A. pinsapo</i>	7.0	51.0	27.3	4.0	21.5	11.3	29	7	624	200	—	—	—	—
<i>J. thurifera</i>	9.5	49.8	25.7	3.5	8.9	5.8	21	23	539	205	8	12	130	69
<i>P. canariensis</i>	10.0	53.0	29.8	9.0	27.6	18.0	27	22	2,292	595	13	7	428	177
<i>P. halepensis</i>	8.0	44.0	23.2	4.6	12.5	9.1	54	13	703	171	9	3	190	64
<i>P. nigra</i>	10.0	77.3	35.4	5.2	22.6	12.9	50	23	3,274	791	13	8	811	234
<i>P. pinaster</i>	7.0	64.0	19.7	6.1	20.7	11.6	199	5	1,521	116	10	6	325	115
<i>P. pinea</i>	9.0	63.0	29.2	4.3	21.2	10.3	54	16	2,225	426	13	6	777	235
<i>P. sylvestris</i>	6.2	76.0	18.1	4.6	27.7	10.9	305	8	3,368	175	14	4	1,193	125
<i>P. uncinata</i>	8.0	41.0	25.6	7.3	20.1	15.6	21	16	868	346	7	3	401	146

dbh: diameter at breast height (cm). height: total height (m). Abov. biomass: aboveground biomass weight (kg). Root biomass: root biomass weight (kg). Min: minimum. Max: maximum. Mean: mean. n: number of samples.

Smalian's formula. Dry weight was calculated by applying the basic wood density for the different species (Gutiérrez Oliva and Plaza Pulgar, 1967). Needles were totally separated and weighed in the case of small trees, while a subsample of thin branches with foliage was taken to estimate foliage mass in larger trees.

Maximum and minimum aboveground biomass for the conifer species sampled ranged from 5 kg for *P. pinaster* to 3,368 kg for *P. sylvestris* and belowground biomass ranged from 3 kg (*P. halepensis* and *P. uncinata*) to 1,193 kg (*P. sylvestris*).

Biomass equations

Different linear and non-linear equations found in biomass literature (Table 2) were tested for relating the weight of the biomass components to tree variables for each species using diameter at breast height (d) and tree height (h) as independent variables.

In a first step, the best model for each component and species was chosen, based on graphical analysis of residuals and fitting statistics (bias and precision), computing the mean residuals ($MRES$), root mean square error ($RMSE$), model efficiency (MEF) (equations 1-3) (Gadow *et al.*, 2001) and the Akaike information criterion (AIC) (Akaike, 1974). The biological behaviour of the model was also evaluated in order to choose the best equations.

Table 2. Biomass models evaluated for the different tree components

Model tested
$W = \alpha + \beta \cdot d$
$W = \alpha + \beta \cdot d^2$
$W = \alpha + \beta \cdot d \cdot h$
$W = \alpha + \beta \cdot d^2 \cdot h$
$W = \alpha + \beta \cdot d + \lambda \cdot d^2$
$W = \alpha + \beta \cdot d + \lambda \cdot d^2 + \theta \cdot d^2 \cdot h$
$W = \alpha + \beta \cdot d + \lambda \cdot h$
$W = \alpha + \beta \cdot d^2 + \lambda \cdot d^2 \cdot h$
$W = \alpha + \beta \cdot d^2 + \lambda \cdot h$
$W = \alpha + \beta \cdot d^2 + \lambda \cdot h + \theta \cdot d^2 \cdot h$
$W = \alpha + \beta \cdot d^2 + \lambda \cdot d \cdot h$
$W = \alpha + \beta \cdot d^2 \cdot h + \lambda \cdot d \cdot h$
$W = \alpha + \beta \cdot d^{\lambda} \cdot h^{\theta}$
$W = \alpha + \beta \cdot d^{\lambda}$
$W = \alpha + \beta \cdot (d^2 \cdot h)^{\lambda}$

W : Biomass weight (kg). d : dbh (cm). h : tree height (m). α , β , λ , θ : parameters of the models.

$$MRES = \frac{\sum_{i=1}^n (y_i - \hat{y}_i)}{n} \quad [1]$$

$$RMSE = \frac{\sqrt{\sum_{i=1}^n (y_i - \hat{y}_i)^2}}{n - p} \quad [2]$$

$$MEF = 1 - \frac{\sum_{i=1}^n (y_i - \hat{y}_i)^2}{\sum_{i=1}^n (y_i - \bar{y})^2} \quad [3]$$

where y_i is the observed value, $\hat{y}_i$ is the estimated value, $\bar{y}$ is the mean observed value, n is the number of observations and p is the number of parameters in the model.

Afterwards, the best models selected were simultaneously fitted using joint generalized regression (known as *Seemingly Unrelated Regressions*, SUR) (Zellner, 1962) to make consistent estimates of the different components with non-linear systems (Parresol, 2001; Bi *et al.*, 2004) (system of equations 4). This method takes into account cross-equation error correlation in order to come up with the sum of total aerial biomass components (additivity property). The employment of this technique guarantees that total aboveground biomass will be the sum of the tree component estimations.

$$\begin{aligned} W_1 &= f_1(\alpha_1, \beta_1) + \varepsilon_1 \\ W_2 &= f_2(\alpha_2, \beta_2) + \varepsilon_2 \\ &\dots \\ W_k &= f_k(\alpha_k, \beta_k) + \varepsilon_k \\ W_{total} &= f_{total}(\alpha_1, \beta_1, \dots, \alpha_k, \beta_k) + \varepsilon_{total} \end{aligned} \quad [4]$$

Weighted regression was used to avoid heteroscedasticity, frequently present in biomass data. Each observation was weighted by the inverse of its variance to homogenize the variance of residuals. This weighting factor was estimated through a power function of an independent variable as explained by Parresol (2001) and Balboa-Murias *et al.* (2006).

The possible presence of multicollinearity was verified through the condition number (Myers, 1990). Model fits were performed using the MODEL procedure in the SAS/ETS software (SAS Institute Inc., 2004).

In order to evaluate the predictive accuracy of the system of equations, they were compared with the equations previously proposed by Montero (2005) for these Mediterranean species whose models were fitted separately for each biomass component using log transformed data and OLS regression. The RMSE and MEF ratios (equations 5 and 6) obtained using both systems

of equations were used in the comparison (Bi *et al.*, 2004).

$$RMSE_{ratio} = \frac{RMSE (this study)}{RMSE (Montero et al., 2005)} \quad [5]$$

$$MEF_{ratio} = \frac{MEF (this study)}{MEF (Montero et al., 2005)} \quad [6]$$

Root:shoot ratios

Root:shoot ratios were calculated as the dry mass relationship between belowground and aboveground

biomass of a tree. Honestly Significant Difference tests (HDS) suitable for multiple comparisons were applied to the relationships in order to identify differences between species.

Results

Best models, independently fitted for each component and specie, were later included in the SUR fitting (Table 3). Tree diameter was the variable that showed the best correlation with biomass weight for all tree components. Tree height was also included in all stem

Table 3. Selected biomass models from SUR fitting statistics for softwood species

Species/components	Model	MRES	RMSE	MEF
<i>Abies alba</i> Mill.				
Stem	$W_s = 0.0189 \cdot d^2 \cdot h$	19.24	73.27	0.97
Thick + Medium branches	$W_{b7+} = 0.0584 \cdot d^2$	2.62	37.42	0.75
Thin branches + needles	$W_{b2+n} = 0.0371 \cdot d^2 + 0.968 \cdot h$	3.12	21.64	0.77
Roots	$W_r = 0.101 \cdot d^2$	1.98	121.79	0.89
<i>Abies pinsapo</i> Boiss.				
Stem	$W_s = 0.00960 \cdot d^2 \cdot h$	-10.09	36.82	0.85
Thick branches	If $d \leq 32.5$ cm then $Z = 0$; If $d > 32.5$ cm then $Z = 1$; $W_{b7} = [1.637 \cdot (d-32.5)^2 - 0.0719 \cdot (d-32.5)^2 \cdot h] \cdot Z$	6.23	15.32	0.69
Medium branches	$W_{b2-7} = 0.00344 \cdot d^2 \cdot h$	2.25	23.84	0.70
Thin branches + needles	$W_{b2+n} = 0.131 \cdot d \cdot h$	-0.17	25.30	0.47
<i>Juniperus thurifera</i> L.				
Stem	$W_s = 0.0132 \cdot d^2 \cdot h + 0.217 \cdot d \cdot h$	-1.96	14.34	0.98
Thick branches	If $d \leq 22.5$ cm then $Z = 0$; If $d > 22.5$ cm then $Z = 1$; $W_{b7} = [0.107 \cdot (d-22.5)^2] \cdot Z$	2.37	8.87	0.82
Medium branches	$W_{b2-7} = 0.00792 \cdot d^2 \cdot h$	0.41	11.90	0.92
Thin branches + needles	$W_{b2+n} = 0.273 \cdot d \cdot h$	3.03	16.59	0.79
Roots	$W_r = 0.0767 \cdot d^2$	-0.82	24.97	0.69
<i>Pinus canariensis</i> Sweet ex Spreng.				
Stem	$W_s = 0.0249 \cdot (d^2 \cdot h)^{0.975}$	2.39	51.84	0.98
Thick branches	If $d \leq 32.5$ cm then $Z = 0$; If $d > 32.5$ cm then $Z = 1$; $W_{b7} = [0.634 \cdot (d-32.5)^2] \cdot Z$	16.85	30.09	0.79
Medium branches	$W_{b2-7} = 0.00162 \cdot d^2 \cdot h$	2.44	20.93	0.71
Thin branches + needles	$W_{b2+n} = 0.0844 \cdot d^2 - 0.0731 \cdot h^2$	2.12	28.02	0.77
Roots	$W_r = 0.155 \cdot d^2$	-2.02	54.27	0.89
<i>Pinus halepensis</i> Mill.				
Stem	$W_s = 0.0139 \cdot d^2 \cdot h$	-4.13	21.43	0.93
Thick branches	If $d \leq 27.5$ cm then $Z = 0$; If $d > 27.5$ cm then $Z = 1$; $W_{b7} = [3.926 \cdot (d-27.5)] \cdot Z$	1.54	14.75	0.61
Medium branches	$W_{b2-7} = 4.257 + 0.00506 \cdot d^2 \cdot h - 0.0722 \cdot d \cdot h$	-0.19	7.54	0.91
Thin branches + needles	$W_{b2+n} = 6.197 + 0.00932 \cdot d^2 \cdot h - 0.0686 \cdot d \cdot h$	-1.14	13.79	0.93
Roots	$W_r = 0.0785 \cdot d^2$	0.40	23.46	0.87

Table 3 (cont.). Selected biomass models from SUR fitting statistics for softwood species

Species/components	Model	MRES	RMSE	MEF
<i>Pinus nigra</i> Arn.				
Stem	$W_s = 0.0403 \cdot d^{1.838} \cdot h^{0.945}$	-2.73	71.13	0.99
Thick branches	If $d \leq 32.5$ cm then $Z = 0$; If $d > 32.5$ cm then $Z = 1$; $W_{b7} = [0.228 \cdot (d-32.5)^2] \cdot Z$	18.89	25.33	0.85
Medium branches	$W_{b2-7} = 0.0521 \cdot d^2$	-1.31	31.48	0.89
Thin branches + needles	$W_{b2+n} = 0.0720 \cdot d^2$	-1.44	26.86	0.95
Roots	$W_r = 0.0189 \cdot d^{2.445}$	0.80	30.14	0.98
<i>Pinus pinaster</i> Ait.				
Stem	$W_s = 0.0278 \cdot d^{2.115} \cdot h^{0.618}$	-0.42	14.47	0.99
Thick + Medium branches	$W_{b7} + W_{b27} = 0.000381 \cdot d^{3.141}$	0.21	7.04	0.89
Thin branches + needles	$W_{b2+n} = 0.0129 \cdot d^{2.320}$	-0.03	7.67	0.89
Roots	$W_r = 0.00444 \cdot d^{2.804}$	-6.65	20.29	0.99
<i>Pinus pinea</i> L.				
Stem	$W_s = 0.0224 \cdot d^{1.923} \cdot h^{1.0193}$	-6.70	36.76	0.99
Thick branches	If $d \leq 22.5$ cm then $Z = 0$; If $d > 22.5$ cm then $Z = 1$; $W_{b7} = [0.247 \cdot (d-22.5)^2] \cdot Z$	8.76	46.17	0.86
Medium branches	$W_{b2-7} = 0.0525 \cdot d^2$	2.88	29.46	0.80
Thin branches + needles	$W_{b2+n} = 21.927 + 0.0707 \cdot d^2 - 2.827 \cdot h$	1.95	19.65	0.90
Roots	$W_r = 0.117 \cdot d^2$	1.38	14.86	0.98
<i>Pinus sylvestris</i> L.				
Stem	$W_s = 0.0154 \cdot d^2 \cdot h$	2.23	34.01	0.99
Thick branches	If $d \leq 37.5$ cm then $Z = 0$; If $d > 37.5$ cm then $Z = 1$; $W_{b7} = [0.540 \cdot (d-37.5)^2 - 0.0119 \cdot (d-37.5)^2 \cdot h] \cdot Z$	0.14	12.63	0.86
Medium branches	$W_{b2-7} = 0.0295 \cdot d^{2.742} \cdot h^{-0.899}$	-0.24	10.83	0.87
Thin branches + needles	$W_{b2+n} = 0.530 \cdot d^{2.199} \cdot h^{-1.153}$	0.73	11.41	0.87
Roots	$W_r = 0.130 \cdot d^2$	1.55	110.17	0.98
<i>Pinus uncinata</i> Mill.				
Stem	$W_s = 0.0203 \cdot d^2 \cdot h$	7.56	70.81	0.90
Thick + Medium branches	$W_{b7} + W_{b27} = 0.0379 \cdot d^2$	1.41	15.86	0.64
Thin branches + needles	$W_{b2+n} = 2.740 \cdot d - 2.641 \cdot h$	1.27	14.86	0.66
Roots	$W_r = 0.193 \cdot d^2$	8.17	81.86	0.68

W_s : Biomass weight of the stem fraction (kg). W_{b7} : Biomass weight of the thick branch fraction (diameter larger than 7 cm) (kg). W_{b2-7} : Biomass weight of medium branch fraction (diameter between 2 and 7 cm) (kg). W_{b2+n} : Biomass weight of thin branch fraction (diameter smaller than 2 cm) with needles (kg). W_r : Biomass weight of the belowground fraction (kg); d : dbh (cm). h : tree height (m).

fraction models, although it did not always appear in the models for the other biomass components. Furthermore, most of the stem fraction models had the standard allometric form:

$$W_s = a \cdot d^b \cdot h^c \quad [7]$$

where W_s is the weight of stem biomass, d is the dbh, h is the total height, a , b and c are parameters of the model.

For all species, the belowground biomass fraction depended exclusively on the diameter variable.

Parameters of the models from SUR fitting and statistics for bias and precision ($MRES$, $RMSE$ and MEF) are shown in Table 3. Every parameter was significant at the 95% confidence level. Predicted values *versus* observed values for total aboveground biomass did not show presence of bias in the models fitted (Fig. 2). Due to multicollinearity problem, it was not possible to include an individual model for needles in any species, this latter fraction being included in the thin branch component.

Stem models had good MEF values, being higher than 0.87 for these softwood species. Branch models

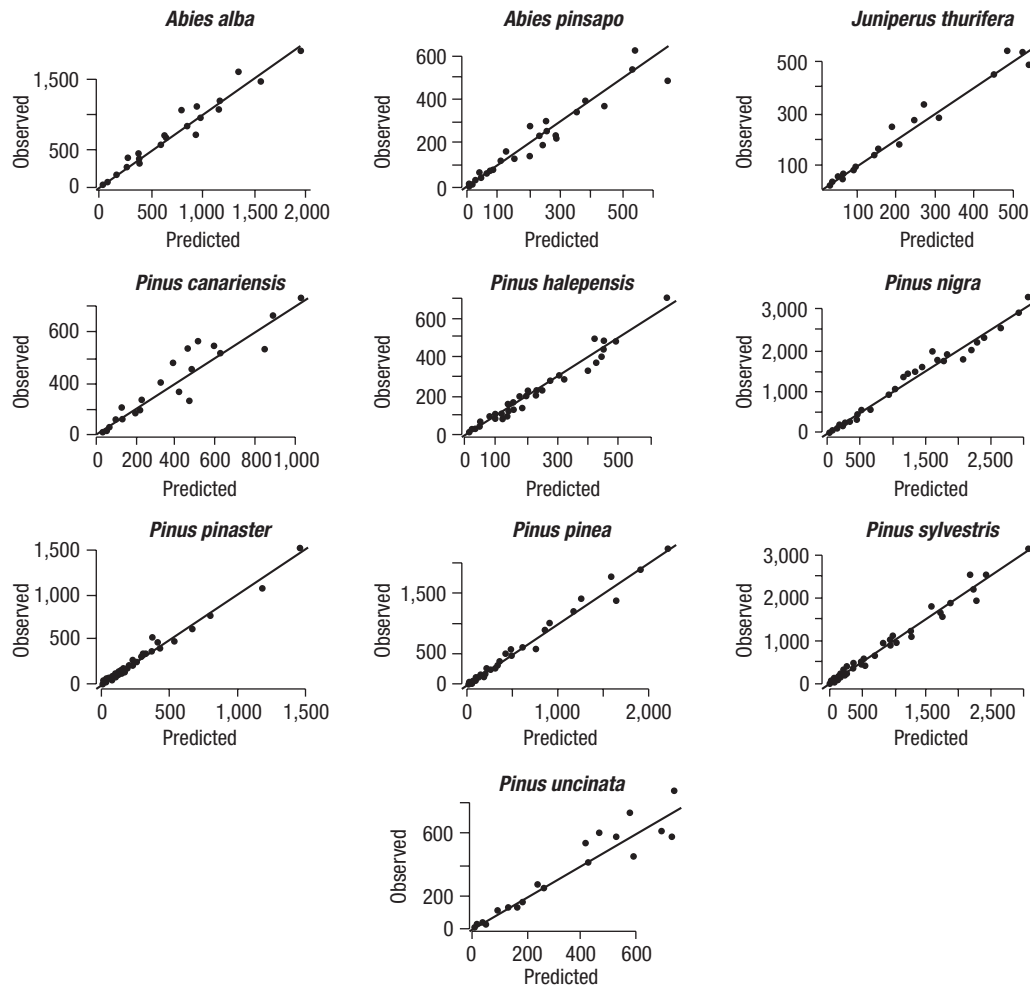


Figure 2. Observed and predicted values for aboveground biomass of the studied species.

showed more variability, presenting smaller *MEF* values for *A. alba* and *P. uncinata*. Thick branch models for *P. canariensis* and *P. nigra* also yielded high bias values (*MRES*). Regarding root biomass, the model efficiency was always greater than 0.85 except in the cases of *J. thurifera* and *P. uncinata*. The bias of the root models was also higher in these species than in the rest.

In some cases, the thick branch component was absent in smaller trees as this fraction only appears when trees reach a certain size. Therefore, the available sample size for this component was smaller than for the rest of components and the equation was only suitable for trees with a larger threshold diameter. For this reason, models for the thick branch component presented a restriction based on a threshold diameter, which varied from 22.5 cm for *P. pinea* and *J. thurifera* to 37.5 cm for *P. sylvestris*. In the cases of *A. alba*, *P. pinaster* and

P. uncinata, which do not normally have a large number of thick branches, the sample size for this component was so limited that it was included in the medium branch component.

Comparison with previous models developed by Montero *et al.* (2005) through *RMSE* and *MEF* ratios, showed that *RMSE ratio* values are equal to or less than 1.0 in all cases (the *RMSE* values for the newer models were lower than those for the previous equations) (Table 4). Large differences in *RMSE* were revealed when this ratio was small, as in the thick branch fraction in *P. pinea* or the stem fraction ratio in *P. pinaster* and *P. sylvestris*, which all exhibited values below 0.5. *MEF* ratios presented values equal to or higher than 1.0 (the *MEF* values for the newer models were equal to or higher than those of the previous ones). The improvement in model efficiency was particularly notable for the thick branch component and the thin branch

Table 4. Root mean square error (RMSE) and model efficiency (MEF) ratios to compare additive equations fitted in this study and Montero *et al.* (2005) equations (fitted separately for each biomass component using log transformed data)

	RMSE ratio					MEF ratio				
	Above	Stem	Branches			Above	Stem	Branches		
			Thick	Medium	Thin + needles			Thick	Medium	Thin + needles
<i>A. alba</i>	0.76	0.57	0.98	0.98	0.99	1.03	1.07	1.01	1.01	1.00
<i>A. pinsapo</i>	0.89	0.81	0.92	1.00	1.00	1.03	1.11	1.09	1.00	1.00
<i>J. thurifera</i>	0.88	0.66	0.98	0.91	0.99	1.01	1.05	1.00	1.02	1.01
<i>P. canariensis</i>	0.95	0.67	0.94	0.84	0.89	1.00	1.02	1.08	1.02	1.05
<i>P. halepensis</i>	0.61	0.74	0.81	0.83	0.78	1.04	1.06	1.50	1.05	1.05
<i>P. nigra</i>	0.78	0.66	0.84	0.53	0.99	1.01	1.01	1.08	1.47	1.00
<i>P. pinaster</i>	0.83	0.43	0.81	0.81	0.96	1.01	1.06	1.07	1.07	1.01
<i>P. pinea</i>	0.77	0.57	0.41	0.69	0.31	1.19	1.03	1.48	1.16	1.49
<i>P. sylvestris</i>	0.87	0.47	0.70	0.97	0.95	1.00	1.04	1.21	1.01	1.02
<i>P. uncinata</i>	0.95	0.74	0.96	0.96	0.97	1.01	1.09	1.05	1.05	1.03

(with needle) component in *P. pinea*, as well as for the thick branch fraction in *P. halepensis* and the medium branch component in *P. nigra*.

The partitioning of tree biomass into stem, crown (branches + foliage) and belowground components is shown in Figure 3, using the models developed for an average tree with a dbh of 35 cm and height calculated from the sample. The stem was the biggest fraction in all cases for these conifer species. The contribution of the stem to total tree biomass varied from 39.9% for

P. halepensis or 40.0% for *J. thurifera*, to 65.7% for *A. alba* and 61.6% for *P. pinaster*. Crown fraction was also an important biomass component, with maximum values of 38.7% and 36.6% for *P. halepensis* and *J. thurifera* respectively, and minimum values of 11.4% in the case of *P. uncinata* and 14.9% for *P. canariensis*. Root biomass accounted for between a third and a fifth of the total tree biomass, with maximum values of 29.3% and 28.8% for *P. uncinata* and *P. sylvestris* respectively and minimum values of 16.2% for *A. alba* and 18.6% for *P. nigra*.

The root:shoot ratios for the species analysed in this study are reported in Table 5. The mean ratios between belowground and aboveground biomass varied from 0.18 (*A. alba*) to 0.38 (*P. uncinata*), with a mean value

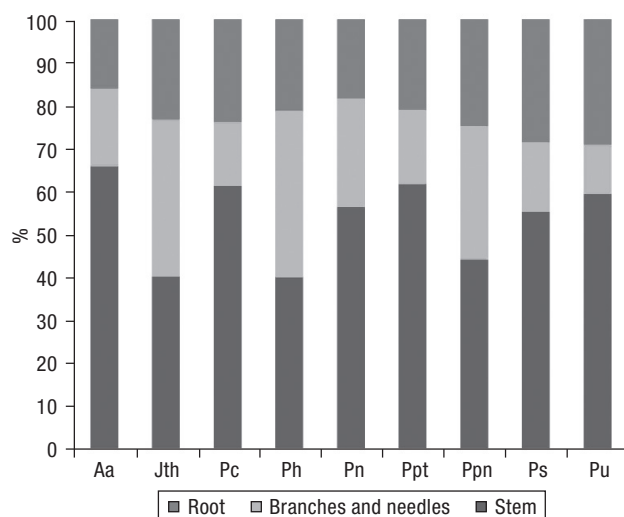


Figure 3. Comparison of biomass partitioning between softwood species for a mean tree with a dbh of 35 cm (mean height to this diameter was calculated from the original data). Aa: *Abies alba*. Jth: *Juniperus thurifera*. Pc: *Pinus canariensis*. Ph: *P. halepensis*. Pn: *P. nigra*. Ppt: *P. pinaster*. Ppn: *P. pinea*. Ps: *P. sylvestris*. Pu: *P. uncinata*.

Table 5. Root:shoot ratios for the studied species, standard error and multiple comparisons

	Root:shoot ratio	Groups	Std. error
<i>A. alba</i>	0.183	d	0.0164
<i>J. thurifera</i>	0.343	a, b	0.0356
<i>P. canariensis</i>	0.259	c, d	0.0261
<i>P. halepensis</i>	0.229	c, d	0.0146
<i>P. nigra</i>	0.240	c, d	0.0116
<i>P. pinaster</i>	0.285	b, c	0.0132
<i>P. pinea</i>	0.243	c, d	0.0143
<i>P. sylvestris</i>	0.279	b, c	0.0217
<i>P. uncinata</i>	0.385	a	0.0426
Softwoods	0.265	—	0.0274

Significant differences are shown by different letters (HSD test; $\alpha = 0.05$; $p < 0.001$).

of 0.27 for the softwood species studied. Statistical differences were found between species: *A. alba* presented the lowest value different from the rest of species; the *Pinus* species showed similar values between them and *J. thurifera* and *P. uncinata* exhibited a large variability and presented similar values.

Discussion

The estimation of forest carbon stocks from forest inventories requires the use of accurate and unbiased biomass models. In this study, new biomass estimation models for the main forest species in Spain have been developed in order to improve on the performance of previous models which did not consider the additivity property (Montero *et al.*, 2005); the latter being a desirable attribute for a system of biomass component equations. The use of the nonlinear seemingly unrelated regressions (NSUR) method to fit the system of equations guarantees this property, giving consistency (Kozak, 1970) and reducing the confidence and prediction intervals of the biomass estimations (Parresol, 1999, 2001).

The new models included tree height as an independent variable in some components, resulting in improved model fit statistics. Other authors have also reported improvements in biomass estimations where height and diameter (rather than just diameter) dependent models are used (Lambert *et al.*, 2005; Cienciala *et al.*, 2006). By including tree height, information regarding the competitive environment (stand age, site index, density...) is indirectly considered in the model (Wirth *et al.*, 2004). This fact makes the model more general and permits the use of the equation for different sites (Ketterings *et al.*, 2001). Other independent variables like crown length have been tested in other studies for crown biomass estimation (Carvalho and Parresol, 2003; Antonio *et al.*, 2007). However, in order to assure the applicability of the models, we have not considered this variable because it is not available in the Spanish National Forest Inventory and is not usually measured in forest inventories.

As a consequence of considering simultaneous fitting and the use of tree height as a predictor variable, the additive biomass equations presented in this study represent a considerable improvement on those proposed by Montero *et al.* (2005) for the studied species. The latter were fitted to the same data, but log transformed data were used and each biomass component was

fitted separately, using ordinary least squares regression. The improvement in model efficiency reached around 50% for the thick branch component of *P. halepensis* and *P. pinea* as well as for the thin branch (with needles) component of *P. pinea* (Table 4). For total aboveground biomass, the greatest improvements were found for *P. pinea*.

In the case of the stem biomass component, all the models fitted were non-linear with an allometric expression including dbh and total height. This expression is very similar to those used for volume estimations, yielding high model efficiency values. Many authors have highlighted the suitability of this combination of variables for stem biomass predictions (Bi *et al.*, 2004; Antonio *et al.*, 2007). For the other tree components (branches of different diameter sizes), models could be either linear or non-linear, with dbh and/or tree height appearing by themselves with different parameters or together in various different combinations. The coefficients related to dbh were in most cases positive numbers, showing that biomass increases with diameter. Conversely, coefficients related to tree height were sometimes negative, particularly for crown fractions, indicating that for the same diameter size, taller trees allocate less biomass to the crown due to the processes involved in competition for light (Lambert *et al.*, 2005).

The ability of the model to predict biomass is lower for branch components than for the stem (Table 3). Branch and foliage biomass are more dependent than bole biomass on tree competition and stand density, hence they present greater variability (Cole and Ewel, 2006; Návar, 2009). The high variability in crown biomass displayed by *P. pinea* trees is due to frequent pruning for fruit and firewood production.

A number of authors have proposed the use of general equations to estimate aboveground biomass per genus or group of species (Pastor *et al.*, 1983/1984) (Schroeder *et al.*, 1997). However, the variability found in allometric ratios and in biomass component equations among the studied species, suggests that separate equations for each species are essential to accurately estimate biomass per fraction of the tree. This information is required to estimate nutrient stocks, biomass amounts for firewood after treatment or to consider different management options in relation to the nutrient cycle and carbon stocks (Balboa-Murias *et al.*, 2006; Cole and Ewel, 2006; Bravo *et al.*, 2008).

Belowground biomass is not generally considered in biomass studies because of the high-cost and difficulty involved in sampling, even though it makes up a

significant part of the total tree biomass. In the case of the species studied, the root weight model depends exclusively on tree diameter, as determined by Drexhage and Colin (2001) or Le Goff and Ottorini (2001).

As regards the relationship between belowground and aboveground biomass (stem, branches and needles), Kurz *et al.* (1996) found differences in the relationships between softwood and hardwood species. However, Cannell (1982) and Cairns *et al.* (1997) found no significant differences between species groups and reported general root:shoot ratio figures of 0.26 for conifers and 0.25 for deciduous. The figure for conifers in the present study is in accordance with this general value. Levy *et al.* (2004) found a mean root:shoot ratio for conifers in Great Britain of 0.359. This mean value differs from our result, although the figures they present for *P. sylvestris* (0.301) and *P. nigra* (0.224) are similar to our figures for these species. Correia *et al.* (2010) reported a root:shoot ratio for *P. pinea* of 0.30 for trees at low densities. This value is slightly higher than ours, although our samples were collected at higher densities so there may have been greater competition between trees. Although the root:shoot ratio can vary depending on tree size and stand characteristics, these high observed values highlight the importance of the root fraction in Mediterranean forests.

Although we took samples from a broad range of diameters, only a small number of root samples were taken to evaluate belowground biomass and soil types were not checked as part of this study. Therefore, further research into belowground biomass in Mediterranean forests may be necessary.

Conclusions

The use of seemingly unrelated regression and the large sample size employed to fit the models, result in accurate additive biomass equations for the main Spanish Mediterranean forest species and provide a considerable improvement on the existing equations. Given that the Spanish National Forest Inventory (NFI) identifies the forest species and records tree diameter and height of all sample trees per plot, the models developed could be applied to NFI data, allowing ecosystem-wide, regional and national carbon accounts.

Belowground biomass accounts for a significant proportion of total biomass in Mediterranean ecosystems, which must be considered and quantified in order to obtain complete biomass and carbon estimations.

In Mediterranean forests, where wood production is not the main function, these biomass estimates by component are highly useful to define the best forest management practices to be followed and to identify the role of the forest as a carbon sink.

Acknowledgments

We would like to thank all those who participated in the field work, especially M. Muñoz and E. Garriga, as well as S. Mutke for his comments on the manuscript. This study was partially financed by projects OT-03-002 and PSS-310000-2009-22.

References

- AKAIKE H., 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19, 716-723.
- ANTONIO N., TOMÉ M., TOMÉ J., SOARES P., FONTES L., 2007. Effect of the tree, stand and site variables of the allometry of *Eucalyptus globulus* tree biomass. *Can J For Res* 37, 895-906.
- BALBOA-MURIAS M.A., RODRÍGUEZ-SOALLEIRO R., MERINO A., ÁLVAREZ-GONZÁLEZ J.G., 2006. Temporal variations and distribution of carbon stocks in aboveground biomass of radiata pine and maritime pine pure stands under different silvicultural alternatives. *For Ecol Manage* 237, 29-38.
- BI H.Q., TURNER J., LAMBERT M.J., 2004. Additive biomass equations for native eucalypt forest trees of temperate Australia. *Trees-Struct Funct* 18, 467-479.
- BRAVO F., BRAVO-OVIEDO A., DÍAZ BALTEIRO L., 2008. Carbon sequestration in Spanish Mediterranean forest under two management alternatives: a modeling approach. *Eur J Forest Res* 127, 225-234.
- BROWN S., 2002. Measuring carbon in forests: current status and future challenges. *Environmental Pollution* 116, 363-372.
- CABANETTES A., RAPP M., 1978. Biomass, nutrient distribution and productivity in a *Pinus pinea* forest. I. Biomass. *Oecologia Plantarum* 13, 271-286.
- CAIRNS M.A., BROWN S., HELMER E.H., BAUMGARDNER G.A., 1997. Root biomass allocation in the world's upland forests. *Oecologia* 111, 1-11.
- CANNELL M.G.R., 1982. World forest biomass and primary production data. Academic Press, London. 391 pp.
- CARVALHO J.P., PARRESOL B.R., 2003. Additivity in tree biomass components of Pyrenean oak (*Quercus pyrenaica* Willd.). *For Ecol Manage* 179, 269-276.
- CIENCIALA E., CERNY M., TATARINOV F., APLTAUER J., EXNEROVA Z., 2006. Biomass functions applicable to Scots pine. *Trees-Struct Funct* 20, 483-495.

- CLARK D.A., BROWN S., KICKLIGHTER D.W., CHAMBERS J.Q., THOMLINSON J.R., NI J., 2001. Measuring net primary production in forests: concepts and field methods. *Ecological Applications* 11, 356-370.
- COLE T.G., EWEL J.J., 2006. Allometric equations for four valuable tropical tree species. *For Ecol Manage* 229, 351-360.
- CORREIA A.C., TOMÉ M., PACHECO C.A., FAIAS S., DIAS A.C., FREIRE J., CARVALHO P.O., PEREIRA J.S., 2010. Biomass allometry and carbon factors for a Mediterranean pine (*Pinus pinea* L.) in Portugal. *Forest Systems* 19, 418-433.
- CROW T.R., LAIDLAY P.R., 1980. Alternative models for estimating woody plant biomass. *Can J For Res* 10, 367-370.
- DIXON R.K., BROWN S., HOUGHTON R.A., SOLOMON A.M., TREXLER M.C., WISNIEWSKI J., 1994. Carbon pools and flux of global forest ecosystem. *Science* 263, 185-190.
- DREXHAGE M., COLIN F., 2001. Estimating root system biomass from breast-height diameters. *Forestry* 74, 491-497.
- FANG J.Y., CHEN A.P., PENG C.H., ZHAO S.Q., CI L., 2001. Changes in forest biomass carbon storage in China between 1949 and 1998. *Science* 292, 2320-2322.
- FATTORINI L., GASPARINI P., NOCETTI M., TABACCHI G., TO V., 2004. Above-ground tree phytomass prediction and preliminary shrub phytomass assessment in the forest stands of Trentino. *Studi Trent. Sci Nat, Acta Biol* 81, 75-121.
- GADOW K.V., REAL P., ÁLVAREZ GONZÁLEZ J.G. (eds), 2001. Modelización del crecimiento y la evolución de bosques. IUFRO, Vienna.
- GOODALE C.L., APPS M.J., BIRDSEY R.A., FIELD C.B., HEATH L.S., HOUGHTON R.A., JENKINS J.C., KOHLMAIER G.H., KURZ W., LIU S.R., NABUURS G.J., NILSSON S., SHVIDENKO A.Z., 2002. Forest carbon sinks in the Northern Hemisphere. *Ecological Applications* 12, 891-899.
- GRUNZWEIG J.M., GELFAND I., FRIED Y., YAKIR D., 2007. Biogeochemical factors contributing to enhanced carbon storage following afforestation of a semi-arid shrubland. *Biogeosciences* 4, 891-904.
- GUTIÉRREZ OLIVA A., PLAZA PULGAR F., 1967. Características físico-mecánicas de las maderas españolas. Ministerio de Agricultura, Madrid. 103 pp.
- IPCC, 2003. Good practice guidance for land use, land-use change and forestry. Institute for Global Environmental Strategies, Kanagawa, Japan.
- KETTERINGS Q.M., COE R., VAN NOORDWIJK V., AMBAGAU Y., PALM C.A., 2001. Reducing uncertainty in the use of allometric biomass equations for predicting above-ground tree biomass in mixed secondary forests. *For Ecol Manage* 146, 199-209.
- KOZAK A., 1970. Methods for ensuring additivity of biomass components by regression analysis. *Forestry Chronicle* 46, 402-404.
- KURZ W., BEUKEMA S., APPS M., 1996. Estimation of root biomass and dynamics for the carbon budget model of the Canadian forest sector. *Can J For Res* 26, 1973-1979.
- LAMBERT M.C., UNG C.H., RAULIER F., 2005. Canadian national tree aboveground biomass equations. *Can J For Res* 35, 1996-2018.
- LE GOFF N., OTTORINI J.M., 2001. Root biomass and biomass increment in a beech (*Fagus sylvatica* L.) stand in North-East France. *Ann For Sci* 58, 1-13.
- LEHTONEN A., CIENCIALA E., TATARINOV F., MAKIPAA R., 2007. Uncertainty estimation of biomass expansion factors for Norway spruce in the Czech Republic. *Ann For Sci* 64, 133-140.
- LEHTONEN A., MAKIPAA R., HEIKKINEN J., SIEVANEN R., LISKI J., 2004. Biomass expansion factors (BEFs) for Scots pine, Norway spruce and birch according to stand age for boreal forests. *For Ecol Manage* 188, 211-224.
- LEMOINE B., GELPE J., RANGER J., NYS C., 1986. Biomass and growth of maritime pine - a study of variability in a 16 years old stand. *Ann Sci For* 43, 67-84.
- LEVY P.E., HALE S.E., NICOLL B.C., 2004. Biomass expansion factors and root:shoot ratios for coniferous tree species in Great Britain. *Forestry* 77, 421-430.
- MARKLUND L.G., 1988. Biomass functions for pine, spruce and birch in Sweden. Rapport-Sveriges Lantbruksuniversitet, Institutionen foer Skogstaxering (Sweden).
- MARM, 2008. Anuario de Estadísticas Forestales 2007 [online]. Ministerio de Medio Ambiente y Medio Rural y Marino). Available in http://www.mma.es/portal/secciones/biodiversidad/montes_politica_forestal [15 July, 2010].
- MOKANY K., RAISON R.J., PROKUSHKIN A.S., 2006. Critical analysis of root:shoot ratios in terrestrial biomes. *Glob Change Biol* 12, 84-96.
- MONTERO G., ORTEGA C., CAÑELLAS I., BACHILLER A., 1999. Productividad aérea y dinámica de nutrientes en una población de *Pinus pinaster* Ait. sometida a distintos regímenes de claras. *Invest Agrar: Sist Recur For Fuera de Serie*, 175-206.
- MONTERO G., RUIZ-PEINADO R., MUÑOZ M., 2005. Producción de biomasa y fijación de CO₂ por los bosques españoles. Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria, Ministerio de Educación y Ciencia, Madrid. 270 pp.
- MONTES N., BERTAUDIERE-MONTES V., BADRI W., ZAOUI E.H., GAUQUELIN T., 2002. Biomass and nutrient content of a semi-arid mountain ecosystem: the *Juniperus thurifera* L. woodland of Azzaden Valley (Morocco). *For Ecol Manage* 166, 35-43.
- MONTES N., GAUQUELIN T., BADRI W., BERTAUDIERE V., ZAOUI E.H., 2000. A non-destructive method for estimating aboveground forest biomass in threatened woodlands. *For Ecol Manage* 130, 37-46.
- MUUKKONEN P., 2007. Generalized allometric volume and biomass equations for some tree species in Europe. *Eur J Forest Res* 126, 157-166.
- MYERS R.H., 1990. Classical and modern regression with applications. Duxbury Press Belmont, Calif. 488 pp.

- NÁVAR J., 2009. Allometric equations for tree species and carbon stocks for forests of northwestern Mexico. For Ecol Manage. 257, 427-434.
- NEIRYNCK J., MADDELEIN D., KEERSMAEKER L.D., LUST N., MUYS B., 1998. Biomass and nutrient cycling of a highly productive Corsican pine stand on former heathland in northern Belgium. Ann For Sci 55, 389-405.
- PARDÉ J., 1980. Forest biomass. Forestry Abstracts 41, 343-363.
- PARRESOL B.R., 1999. Assessing tree and stand biomass: a review with examples and critical comparisons. For Sci 45, 573-593.
- PARRESOL B.R., 2001. Additivity of nonlinear biomass equations. Can J For Res 31, 865-878.
- PASTOR J., ABER J.D., MELILLO J.M., 1983/1984. Biomass prediction using generalized allometric regressions for some northeast tree species. For Ecol Manage 7, 265-274.
- PORTE A., TRICHET P., BERT D., LOUSTAU D., 2002. Allometric relationships for branch and tree woody biomass of Maritime pine (*Pinus pinaster* Ait.). For Ecol Manage 158, 71-83.
- SAS INSTITUTE INC, 2004. SAS/ETS(R) 9.1 User's guide. In SAS Institute Inc, Cary, NC.
- SCARASCIA-MUGNOZZA G., OSWALD H., PIUSSI P., RADOGLU K., 2000. Forests of the Mediterranean region: gaps in knowledge and research needs. For Ecol Manage 132, 97-109.
- SCHLAMADINGER B., MARLAND G., 1996. The role of forest and bioenergy strategies in the global carbon cycle. Biomass & Bioenergy 10, 275-300.
- SCHROEDER P.E., BROWN S., MO J., BIRDSEY R.A., CIESZEWSKI C., 1997. Biomass estimation for temperate broadleaf forest of the United States using inventory data. For Sci 43, 424-434.
- WIRTH C., SCHUMACHER J., SCHULZE E.D., 2004. Generic biomass functions for Norway spruce in Central Europe - a meta-analysis approach toward prediction and uncertainty estimation. Tree Physiol 24, 121-139.
- ZELLNER A., 1962. An efficient method of estimating seemingly unrelated regressions and tests for aggregation bias. J Am Stat Assoc, 348-368.