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Estimation of above-ground biomass in shrubland ecosystems of southern Spain

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Abstract

Although forest biomass estimates are vital for estimating carbon fluxes, the database for estimating the biomass or carbon pool in Mediterranean shrub ecosystems is lacking. This paper reports the above-ground phytomass estimates obtained for shrub ecosystems in Southern Spain. The phytomass values obtained were 1143 g m^{-2} for heath, 447 g m^{-2} for rock rose thicket-heath, 788 g m^{-2} for rock rose thicket and 1404 g m^{-2} for gorse thicket formations; the corresponding values for bushes were 695 g m^{-2} for *mancha* phytomass and 1966 g m^{-2} for *Pistacia lentiscus* formations. The photosynthetic-to-total phytomass ratio ranged from 0.156 for *mancha* highbush to 0.213 in rock rose thickets, with a mean value of 0.187 for the study ecosystems as a whole. The estimates of sequestered carbon differed between the shrub-type ecosystems in the interval between 2.23 t ha^{-1} for *Cistus ladanifer* to 9.83 t ha^{-1} for *Pistacia lentiscus.* A better understanding of biomass in Mediterranean shrub communities will provide useful information on the growth pattern of these species, biomass mapping, remote sensing and regional estimations of primary productivity in these areas.

Key words: above-ground phytomass, Mediterranean shrub, photosynthetic phytomass, sequestered carbon.

Resumen

Estimación de la biomasa área de ecosistemas de matorral en el sur de España

La estimación de biomasa en ecosistemas forestales es un parámetro crucial para el cálculo del ciclo de carbono. Sin embargo, la información disponible para estos ecosistemas sigue siendo insuficiente. En este artículo se presentan los resultados del cálculo de biomasa aérea de algunos ecosistemas de matorral en el sur de España (Montes de Propios-Jerez de la Frontera, Cadiz). Los valores de biomasa aérea obtenidos han sido de 1143 g m^{-2} en brezales, 447 g m^{-2} en jarales-brezales, 788 g m^{-2} en jarales puros, 1404 g m^{-2} en aulagares, 695 g m^{-2} para *mancha,* y 1966 g m^{-2} para lentiscales. El valor de la relación biomasa fotosintética-biomasa área total vario entre 0,156 para mancha y 0,213 para jarales, con un valor medio de 0,187 para el conjunto de formaciones estudiadas. El carbono retenido en estos ecosistemas oscila en el intervalo entre 2,23 t ha^{-1} para *Cistus ladanifer* y 9,83 t ha^{-1} para lentiscares. Una información mas precisa sobre la biomasa de los ecosistemas de matorral puede suponer una ayuda muy importante para la interpretación de la dinámica de estos ecosistemas y la aplicación de nuevas herramientas para su estimación en grandes superficies.

Palabras clave: biomasa aérea, biomasa fotosintética, Matorrales mediterráneos, secuestro de carbono.

Introduction

All ecosystems whose dominant branching from the major species are more or less woody and are not the size of a tree are identified as shrubland ecosystems. Under the Mediterranean climate, the definition and characteristics of shrubland ecosystems are slightly more complex, as demonstrated in previous works, with regard to their definition and physiognomic and also ecological classification (Di Castri *et al.,* 1981; Ruiz de la Torre, 1990). These non-tree, woody formations are of great importance in the biophysics of Mediterranean ecosystems (Di Castri *et al.,* 1981), both for their significance in ecosystem dynamics and function, and for the great surface areas of land that they cover.

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Like other vegetal formations, biomass or phytomass is a key structural variable in the investigations of the dynamics of these ecosystems, the level of biodiversity they sustain, their role in the carbon cycle, and their sustainability (Waring and Running, 1996). In addition, the quantification of aboveground biomass resources constitutes necessary information for numerous studies, including the analysis of fixed-emission of CO_2 (Nabuurs and Mohren, 1995). There is an increasing need to improve the accuracy of biomass estimates as they determine the actual amount of carbon reaching the atmosphere (IPCC, 1996). In view of the agreement at UNFCC, biomass C densities for different forest types per country are important components for these assessments. Although forest biomass estimates are vital for estimating carbon fluxes, the database for estimating the biomass or carbon pool in Mediterranean shrub ecosystems is deficient. Further, shrub biomass density varies considerably because of climatic, edaphic and topographic differences, and also with the history of land use and human disturbance.

Traditionally, biomass estimation in forest ecosystems has been obtained through direct methods (destructive or extractive) or indirect methods (dimensional analysis) (Etienne, 1995; Wharton and Griffith, 1993). The first methods are based on harvesting and weiging all the plants in the sample plots. They give very accurate estimates, but the extraction of a large number of samples is very laborious and costly (Uresk *et al.,* 1977). Indirect methods are based on the measuring of different morphological variables used in mathematic models to estimate vegetal biomass. These methods give estimates that can reach prediction levels of the former methods, and in addition permit a large number of observations at a relatively low cost (Castro *et al.,* 1996; Uso *et al.,* 1997; Montes *et al.,* 2000). Among these, the proposal of Whittaker and Woodwell (1968), with some variations, has been the one most successfully adopted. It is a mixed method, in which the biomass of a species is estimated using a destructive method on a relatively reduced number of samples. These are used to construct prediction functions that relate a characteristic parameter of the vegetal structure (or a group of biometric variables) to the phytomass production per plant, making a later analysis possible.

In view of the importance of biomass estimates in the global C cycle, the present study aimed to estimate the above-ground phytomass and sequestered carbon of six shrub ecosystems in southern Spain and to propose regression equations to calculate the temporal evolution of dry phytomass.

Materials and methods

Investigation Area

The study area is located in the Andalusia region (southern Spain, Montes de Propios-Jerez de la Frontera, Cadiz), UTM, X: 267291.81, Y: 4059603.83 (Figure 1). The topography is not very pronounced (10-30% slopes), with elevations ranging from 450 m to 798 m above sea level. The climate is Mediterranean, with a mean annual temperature of 19.8°C and mean annual precipitation exceeding 500 mm. The dominant soils on the steep slopes are Entisols (suborder Orthent, group Xerorthent), with inclusion of Inceptisols and Entic chromoxererts and Typic chromoxererts.

The vegetation in this area ranges form maquis (evergreen sclerophyllous and semi-deciduous shrubs with herb associations) to dwarf shrublands. The study area was stratified into six major shrub types in terms of the dominant plant communities (species nomenclature and communities according to Ruiz de la Torre, 1990). The vegetation types selected were accurately delineated on aerial photos and maps and the resulting map was used to calculate the area occupied by each formation. The number of plots selected to represent each stratum was established as a function of the size of the stratum (Table 1):

(a) Heaths. Mid-slope cork oak on evolved soil exhibit high heather with dominant species *Erica scoparia* L. *Erica australis* L, *Erica umbelata* L. and *Calluna vulgaris* (L.) Hull.

(b) Rock rose thickets. When these fairly thick acid soils are decapitated, the previous heaths and shrubs are transformed into cyclic formations of *Cistus ladanifer* L. Sunny, drier zones exhibit *Cistus ladanifer* L forming mosaics with *Erica scoparia* L*, Lavandula stoechas* Boiss., *Genista hirsuta* Vahl.*, Cistus salvifolius* L.*, Cistus crispus* L.

(c) Gorse thickets. These are gorse clusters, a generic term used to designate *Ulex* spp and related genera; these are always ligneous, very thorny plants. The most frequent species are *Ulex baeticus* Boiss and *Genista triacanthos* Brot.

Figure 1. Location map of the study area.

(d) Wild olive grove. The wild olive grove is a sclerophilic, thermophilic formation of variable density, structure and composition where the wild olive (*Olea europaea* L. var. *sylvestris* (Miller) Lehr) prevails in the upper stratum including Kermes oaks (*Quercus coccifera* L.), mastic trees (*Pistacia lenstiscus* L.), savin junipers (*Juniperus phoenicea* L.), common junipers (*J. oxycedrus* L.), dwarf palms (*Chamaerops humilis* L.) and thorny species (*Rhamnus lycioides* L. subsp. *oleoides, Ulex baeticus* Boiss. subsp. *scaber, U. parviflorus* Pourret., *Asparagus albus* L).

(e) Mancha. The *mancha* is a dense, single-stratum consisting of an uneven combination of shrub species with different —particularly sclerophilic— life forms including Kermes oak (*Quercus coccifera* L), flatpod (*Adenocarpus telonensis* (Loissel.) D.C), hawthorn (*Calycotome spinosa* (L.) Link), midland hawthorn (*Crataegus monogyna* Jacq), myrtle (*Myrtus communis* L), turpentine tree (*Pistacia terebinthus* L), Italian buckthorn (*Rhamnus alaternus* L.), black buckthorn (*Rhamnus lyciodes* L. subsp. *oleoides)*, laurustinus (*Viburnum tinus* L.) and briar root (*Erica arborea* L. and *E. lusitanica* Rudolphi), among others.

Table 1. Shrub types studied and number of plots used per type

Types of vegetation	Dominant species	Average Height (cm)	Number of transects
Heath	*Erica* spp.	104	5
Heath-Rose thicket	*Erica* spp. and *Cistus ladanifer.*	133	5
Rose thicket	*Cistus ladanifer.*	120	9
Gorse thicket	Ulex *sp., and* Genista *sp.*	83	3
Mancha	*Pistacia lentiscus, Quercus coccifera* and others	101	7
Mastic tree	*Pistacia lentiscus*	164	5

(f) Mastic shrub and dwarf palm groves. These are continuous stands of mastic shrub (*Pistacia lentiscus* L.) or grassland formations including mastic shrub and dwarf palms (*Chamaerops humilis* L), with no other ligneous elements in the lower stratum. Mastic trees are accompanied by wild olive trees in formations involving a wide variety of shrubs or shrub species.

Evaluation of phytomass

A number of authors have determined phytomass from the phytovolume-to-phytomass ratio (Uresk *et al.,* 1977, Wharton and Griffith, 1993; Robles and Passera, 1995). The procedure used in this work was developed from Robles and Passera (1995) for species in the southeast of the Iberian Peninsula. Thus, we determined phytomass by using transects in combination with the distance method in its closest individual mode which permits the calculation of *density, coverage, phytovolume* and *phytomass* in a relatively expeditious manner (Wharton and Griffith, 1993). A combination of these variables is the best choice for obtaining an accurate description of a plant formation. The operational procedure was as follows:

a) Two transects were established from a randomly selected starting point in the chosen plot that was preferably located in the central region of each sampled zone. Plot centres were located in the field using GPS. Transects were 50 m in length; the first run in the direction of the slope gradient and the second normal to the first at its mid-point. An overall 100 observations per plot were made (Wharton and Griffith, 1993) in order to encompass as high a variety of shrubs as possible; as a result, the observation points were all 1 m apart in each transect. From each observation point, the distance to the nearest plant was measured, and the species of the plant recorded.

b) Four morphological variables [*viz.* plant height (*h,* cm), largest crown diameter ($Ø^m$, cm), smallest diameter ($Ø_m$, cm) and diameter at the bottom ($Ø_B$, cm)] were measured for each specimen using a measuring tape (reading range 0-5 m, precision 1 cm, observation error, 0.5 cm). These data were used to calculate the mean crown diameter ($Ø_M$, cm) and the phytovolume of each individual (Etienne, 1989; Blanco and Navarro, 2003).

c) After prior measurements were made in all plots, a representative sample of eight plants of each key species were cut at ground level. The samples thus obtained were weighed *in situ,* without separating the stem and leaves, using an electric balance *(PHILLIPS ESSENCE HR2388-0)* (maximum weighing capacity 5000 g, minimum weighing capacity 0 g, reading unit 1 g, observation error 0.5 g). Whole individuals were transferred to the laboratory for drying in a P Selecta forced-air stove at 70°C for 72 h until constant weight. The dried material was then weighed on the same balance in order to determine the dry weight of each fraction (ligneous and photosynthetic phytomass).

d) The plant density per unit surface, *D,* was calculated from

$$D = S / (\delta * d)^2 \qquad (1)$$

where *S* is the estimated area (10 000 m^2 in our case), *d* the average distance between individual plants and points in a sampling, and δ a correction factor depending on the particular method used and equal to 2 in the closest individual method (Wharton and Griffith, 1993). The density of each species was calculated from

$$D_{(sp\,i)} = (\text{no. plants sp } i/\text{total no. plants}) \bullet D \qquad (2)$$

The mean diameter, $Ø_M$, was used to obtain the coverage *C* of each plant associated with the ideal circle area:

$$C = \pi\,(Ø_M / 2)^2 \qquad (3)$$

where the total coverage for species *i* was obtained from

$$C_i = D_i \bullet C_{sp\,i} \qquad (4)$$

e) The phytomass per hectare for each species was calculated from the density values obtained in the samplings:

$$phytomass/ha = D_{(sp\,i)} \bullet dry\ weight_{(sp\,i)} \qquad (5)$$

the total phytomass B_T for each type of shrub or bush being

$$B_T/ha = \Sigma\,(D_{(sp\,i)} \bullet dry\ weight_{(sp\,i)}) \qquad (6)$$

f) The photosynthetic-to-total phytomass ratio for each type of shrub was determined from the ratio obtained for each individual species in the determination of its dry weight.

Once the mean phytomass per hectare for each ecosystem was calculated, the results were generalized by using spatial analysis to estimate the shrub phytomass provided by each type of vegetation.

Estimation of temporal changes in phytomass

Temporal changes in phytomass in the shrub types studied were determined by single regression analysis between the *phytomass* of each plot and its *age.* The age of each plot was determined from the information obtained by a Montes de Propios worker who provided the last clearing date of each shrub plot.

The analysis involved the calculation and interpretation of linear, exponential, logarithmic, quadratic and cubic models. In selecting the best predictive model for temporal changes in above-ground phytomass for each type of shrub, we conducted *a priori* and *a posteriori* analyses of the population sample in order to identify accurate explicative models (Sokal and Rohlf, 1995):

a) Relative measurements of goodness of fit based on the determination coefficient (R^2) and standard error of the estimate *(SE)*.

b) Goodness-of-fit tests based on an analysis of variance were used to compare the significance of R^2 by calculating the statistic F and its significance level *(p)*.

Data were stored and processed by using *Microsoft Excel 2000,* and the descriptive statistical analysis of the data was done with *SPSS v. 8.0.*

Shrub type carbon sequestration

As described previously, total phytomass for each shrub type was estimated in a stratified random sample of plots. For each of those shrubland types, the total amount of carbon sequestered in the biomass of the shrubs was determined as follow. First, the above-ground estimated biomass of each shrub type was predicted from its allometric model as discussed previously. The amount of carbon sequestered in the above-ground phytomass of each ecosystem was then assumed to be 50% of the predicted biomass. These proportions of carbon have been found to be appropriate for applying in a general manner in forests species (Gifford, 2000), with little differences between different taxa.

Results

Total phytomass

The shrubs present in the study area exhibited high total above-ground phytomasses that were maximal for the mastic tree formation (1966 g m^{-2}) and minimal for the rock rose thicket–heath mixed formations, with a value of 447 g m^{-2}.

The typical shrubs for the cork oak woodland exhibited substantial differences in their structural variables. Thus, the dominant species in the heath were *Erica arborea* (20.2% of overall plants), *Erica scoparia* (17.2% of overall plants), and *Ulex baeticus* (15.1% of overall plants). The ligneous plant coverage ranged from 44.5% to 144.3%, the average shrub density being 13,962 plants ha^{-1}, and the coverage 76.60%. The phytomass contributed by this type of shrub was 1143 g m^{-2}, but varied greatly (from 105 g m^{-2} to 4035 g m^{-2}) (Table 2). On the other hand, the dominant species in rock rose thicket-heath formations were *Cistus ladanifer* (22.8% of overall plants), *Stauracanthus boivinii* (30.9% of overall plants), and *Ulex baeticus* (19.3% of overall plants). The coverage of ligneous species ranged from 34.8% to 81.7%; however, the mean coverage was slightly above 50% and the density 57,940 plants ha^{-1}. The mean above-ground phytomass for this type of shrub was 447 g m^{-2} and also varied widely (from 71 g m^{-2} to 812 g m^{-2}) (Table 2). Rock rose thickets were clearly dominated by *Cistus ladanifer* (61.9% of overall plants), which was in clear dominance over other species. The coverage of ligneous species was high (16.4% to 188.7%); the mean coverage was slightly less than 100% and the density 23,008 plants ha^{-1}. The mean total above-ground phytomass for this type of shrub was 788 g m^{-2}, and ranged from 113 g m^{-2} to 1965 g m^{-2} (Table 2).

Table 2. Descriptive variables for the shrub type ecosystems. Mean value for each shrub type (± standard error of the mean)

Types of vegetation	Dominant Height (cm)	Density (plants/ha)	Coverage (%/ha)	Phytovolume (m^3/ha)	Above-ground phytomass (g m^{-2})
Erica sp.	104 ± 8	13,962 ± 5676	76 ± 17	59,509 ± 20519	1143 ± 736
Cistus ladanifer L. and *Erica* sp.	133 ± 14	27940 ± 16373	53 ± 7	24,640 ± 6955	447 ± 135
Cistus ladanifer L.	120 ± 10	23,008 ± 6701	97 ± 18	40,995 ± 14212	788 ± 232
Genista and *Ulex*	83 ± 4	33555 ± 19315	92 ± 27	10,054 ± 2917	1404 ± 215
Mancha	101 ± 10	14,257 ± 2943	56 ± 13	53,172 ± 15561	695 ± 248
Pistacia lentiscus L.	164 ± 14	21,068 ± 10887	42 ± 14	89,547 ± 27560	1966 ± 617

The phytomass values obtained for the plants associated with mastic trees were also widely variable. The dominant species in *mancha* formations were *Pistacia lentiscus* (55.7% of overall plants), and *Cistus ladanifer* (7.9% of overall plants), however, they were accompanied by substantial numbers of shrubs such as *Olea europaea* (2.2% of overall plants), *Quercus coccifera* (2.9% of overall plants) and *Phillyrea latifolia* (1.2% of overall plants). The coverage of ligneous species ranged from 5.9% to 101.6%, although the mean coverage was slightly higher than 50% and the density 14,257 plants ha^{-1}. The phytomass contributed by this type of shrub was 695 g m^{-2}, but varied over a wide range (98 g m^{-2} to 1782 g m^{-2}) (Table 2). The dominant species in mastic tree thickets, which are very similar to *mancha* formations, was also *Pistacia lentiscus* (67.5% of overall plants) (with an increased presence of *Quercus coccifera* 14.2%). The coverage of ligneous species was higher than in such formations (average slightly above 40%) and the density was 21,068 plants ha^{-1}. The phytomass contributed by this type of shrub was very high (mean 1966 g m^{-2}) and ranged from 1035 to 4403 g m^{-2}, depending on each plot (Table 3). In the replacement shrubs for these two formations (gorse thickets), the species typical of high shrubs were present in considerably smaller numbers, i.e. there was a clear dominance of *Ulex baeticus* (39.9% of overall plants) and a residual presence of *Pistacia lentiscus* (1.9% of overall plants). The coverage of ligneous species was quite high (slightly above 90%) and the density 33,555 plants ha^{-1}. The phytomass contributed by this type of shrub was also high (mean 1404 g m^{-2}) (Table 2).

Photosynthetic-to-total phytomass ratio

The mean photosynthetic-to-total phytomass ratio for the shrub types studied as a whole was 0.18, ranging from 0.16 for *Pistacia lentiscus* shrubs to 0.21 for *Cistus ladanifer* shrubs (Table 3). These ratios were calculated by weighing the values for shrub species in order to avoid variations due to the differential specific composition and relative significance of each one in the different shrub types studied.

Table 3. Total above-ground phytomass, photosynthetic-to-total above-ground phytomass ratio (B_p/B_t) and total photosynthetic biomass for the different types of shrubs studied

Type of vegetation	Phytomass g m^{-2}	B_f/B_t	Photosynthetic phytomass g m^{-2}
Erica sp.	1143 ± 736	0.18	211 ± 136
Cistus ladanifer L. and *Erica* sp.	447 ± 135	0.20	83 ± 25
Cistus ladanifer L.	982 ± 250	0.21	211 ± 53
Genista and *Ulex*	1012 ± 439	0.15	217 ± 94
Mancha	695 ± 248	0.19	122 ± 43
Pistacia lentiscus L.	1966 ± 617	0.16	363 ± 114

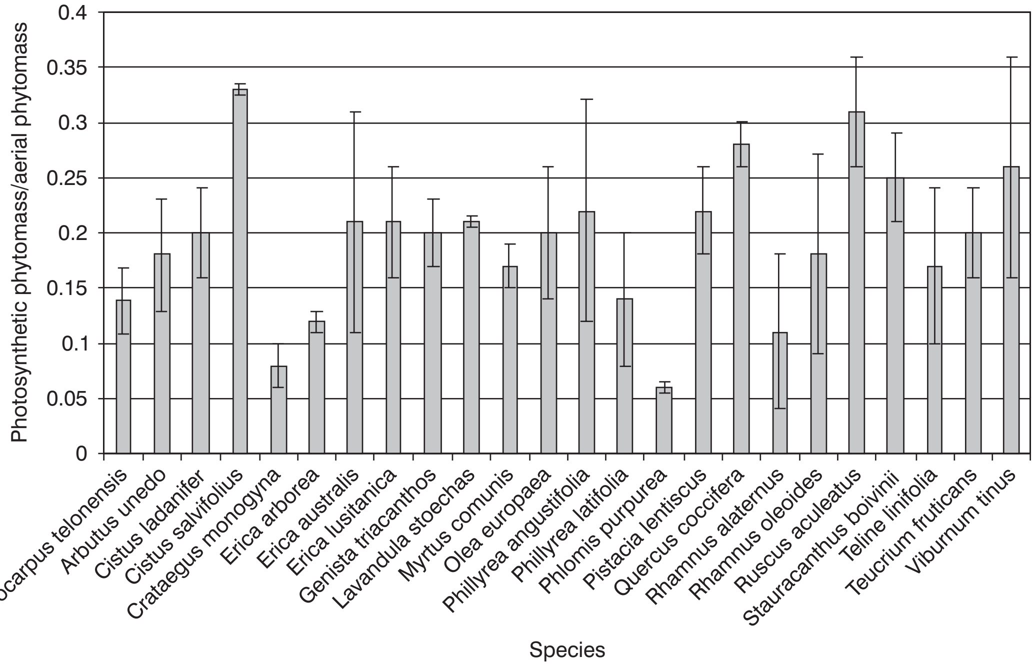

Figura 2. Photosynthetic-to-total aerial phytomass ratio (B_p/B_t) for the dominant species of shrub types studied. Mean value for each species (± standard error of the mean)

Figure 2 shows the photosynthetic-to-total phytomass ratio for the species present in all plots and, as can be seen, there were large differences between them. Thus, some shrub species exhibited very high B_p/B_t ratios (*e.g. Cistus salvifolius* 0.33, *Ruscus aculeatus* 0.31, *Quercus coccifera* 0.28) and, also, most ratios ranged from 0.15 to 0.25 (*e.g. Cistus ladanifer* 0.20, *Erica australis* 0.21, *Lavandula stoechas* 0.21, *Pistacia lentiscus* 0.22, *Teucrium fruticans* 0.20). Only a small number of species (*e.g. Crataegus monogyna* 0.08, *Rhamnus alaternus* 0.11) had ratios below 0.15.

Models for estimating temporal changes in phytomass

The models used to estimate temporal changes in phytomass for each type of shrub fitted polynomial regression equations for heather and rock rose. The results for the other types of shrub fitted a potential equation (gorse thicket and *mancha)* or an untransformed exponential one (mastic tree thicket). As can be seen from Table 4, the regression equations for all types of shrub met goodness-of-fit criteria: R^2 values were high in all instances, and ranged from 0.804 for

Table 4. Regression equation and the determination coefficients for the function fitted to biomass (W in g m^{-2}) and age (A in years ranging between 1 to 12) observations (N=sample size)

Type of vegetation	Equation	R^2	SE	*P*	N
Erica sp.	$W = 9.43\ A^2 - 184.11\ A + 1034.2$	0.99	202.62	0.0076	5
Cistus ladanifer L. and *Erica* sp.	$W = 27.54\ A^{1.202}$	0.71	0.59	0.0697	5
Cistus ladanifer L.	$W = 0.064\ A^2 + 79.39\ A - 76.42$	0.97	196.54	0.0000	9
Genista and *Ulex*	$W = 1.58\ A^{2.0714}$	0.80	0.17	0.2914	3
Mancha	$W = 28.06\ A^{1.3868}$	0.86	0.41	0.0025	7
Pistacia lentiscus L.	$W= 1.58\ e^{0.088\ A}$	0.94	0.14	0.0053	5

Table 5. Sequestered carbon estimation for the different types of shrubs studied

Type of vegetation	Phytomass g m^{-2}	Stored C tC ha^{-1}
Erica sp.	1143 ± 736	5.7 ± 0.3
Cistus ladanifer L. and *Erica* sp.	447 ± 135	2.2 ± 0.0
Cistus ladanifer L.	982 ± 250	4.9 ± 0.1
Genista and *Ulex*	1012 ± 439	5.0 ± 0.2
Mancha	695 ± 248	3.4 ± 0.1
Pistacia lentiscus L.	1966 ± 617	9.8 ± 0.3

the *Ulex baeticus* to 0.992 for the *Erica* sp.; all models exhibited a coefficient of determination of above 0.8. The ANOVA revealed significant differences ($p < 0.05$) for all the models with one exception, the *Ulex* shrub exhibited non-significant differences.

Shrub type carbon sequestration

The estimates of sequestered carbon differ between the shrub type ecosystems in the interval of 2.23 t ha^{-1} for *Cistus ladanifer* to 9.83 t ha^{-1} for *Pistacia lentiscus* (Table 5).

Discussion

The results of this work allowed us to estimate the dry above-ground phytomass for the typical ecosystems of various Mediterranean shrubs in the study area using indirect methods that provided values similar to those of other previous studies performed in the area (Basanta, 1982; García-Ple *et al.,* 1989; Blanco and Navarro, 2003). Overall, indirect methods appear to be effective choices for estimating above-ground phytomass. However, they can lead to major errors in very thick shrubs encompassing large numbers of species and have not yet been validated (Blanco and Navarro, 2003).

A scan of available literature on total above-ground phytomass for Mediterranean shrub formations revealed wide oscillations (Table 6). Our above-ground phytomass results for *Erica* shrubs falls within the range reported by Terradas (2001), *viz.* 1000 and 6000 g m^{-2}, and are close to the 1143 g m^{-2} obtained by Basanta (1982) for an acidophilic rock rose thicket including *Erica umbellata* specimens 0.5-1.5 m high (*i.e.* very similar to the mean height for our area, 1 m). Also, Fernández *et al.* (1995) obtained a value of 6680 g m^{-2} for unmanaged shrubs of over 40 years of age in Sierra de Cádiz, although this type of shrub is higher than those studied here and hence difficult to compare with the heath formations associated with the cork oak sublevel. Our values for rock rose-heather and rock rose (447 and 788 g m^{-2}, respectively) —two types of shrub which are more difficult to isolate on account of their species composition— fall within the range reported by Terradas (2001) (< 2500 g m^{-2}). However, they differ from the 2726 g m^{-2} obtained by Basanta (1982) in Sierra Morena, which correspond to much higher shrubs (1.5-2.5 m *versus* about 1.3 m in our study), and from those reported by Fernández *et al.* (1995) for Sierra de Cádiz (1730-303 g m^{-2}). The origin of this difference may be shrub age, which cannot be accurately represented by the mean height of the dominant stratum as the phytomass estimate for 30-year-old shrubs provided by the models developed in this work was 2353 g m^{-2} and hence very close to the stated values. The above-ground phytomass for the gorse thickets studied was high (1404 g m^{-2}) and very close to the 1328 g m^{-2} obtained by Fernández *et al.* (1995) for *Genista* in Sierra Nevada and the 1514-1689 g m^{-2} found by the same authors for *Asparagus albus* in Majorca (García-Ple *et al.,* 1989). On the other hand, the above-ground phytomass for the *mancha* shrub obtained in this work, 695 g m^{-2}, was low with respect to the 1000-6000 g m^{-2} reported for similar shrubs in Catalonia or the 2895 m g^{-2} obtained by Basanta (1982). Again, however, there were substantial differences in shrub height (1 m in our plots and 2-4.5 m in those of Sierra Morena). Finally, the above-ground phytomass for *Pistacia lentiscus* was high for a shrub

Table 6. Height *(H)*, total phytomass *(B)* and photosynthetic-to-total phytomass ratio (B_p/B_t) values reported by other authors for various types of Mediterranean shrubs

Vegetation types	Species	Height (m)	B_t (g m^{-2})	B_f/B_t	References
Heath	*Erica umbellata*	0.5-1.5	1248	0.26	Basanta. 1982
Sierra Morena	*Halimium ocymoides*				
	Chamaespartium tridentatum				
Garriga	*Quercus coccifera*	1	2350	0.17	Loissant. 1973
France					
Rose thicket	*Erica australis*	1.5-2.5	2482		Basanta. 1982
Sierra Morena	*Cistus ladanifer*				
	Phyllirea angustifolia				
	Genista hirsuta				
	Lavandula stoechas				
	Helychrisum stoechas				
Mancha	*Arbutus unedo*	2-4.5	2895	0.12	Basanta. 1982
Sierra Morena	*Viburnum tinus*				
	Pistacia lentiscus				
	Erica arborea				
	Rhamnus alaternus				
	Cistus salvifolius				
	Phyllirea latifolia				
	Lavandula viridis				
Mancha	*Erica scoparia*		1520		Fernández *et al.* 1995
Sierra Morena	*Arbutus unedo*				
Mancha	*Erica arborea*		6680		Fernández *et al.*. 1995
Sierra Cadiz	*Viburnum timus*				
Rose thicket	*Cistus ladanifer*		3030		Fernández *et al.*. 1995
Sierra de Cadiz					
Holm oak	*Quercus ilex*	2	2802-2580	0.16-0.18	García Plé *et al.*. 1989
Mallorca	*Arbutus unedo*				
	Calicotome spinosa				
	Cistus salvifolius				
	Rhamnus alternus				
Gorse thicket	*Ganista lucida*		3106-2142	0.19	García Plé *et al.* 1989
Mallorca	*Erica multiflora*				
	Dorycnium pentaphyllum				
Rose thicket	*Asparagus albus*		1514-1689	0.27-0.25	García Plé *et al.*. 1989
Mallorca	*Cistus albidus*				
	Chamaerops humilis				
Mancha	*Arbutus unedo*		1000-6000		Terradas. 2001
	Erica arborea				
Kermes oak			1000-5000		Terradas. 2001
Wild olive			1000		Terradas. 2001
Cistus shrubs			< 2500		Terradas. 2001

height of 1.6 m and closer to the 2895 m g^{-2} obtained for high *mancha* shrubs accompanied by abundant mastic trees in Sierra Morena (Basanta, 1982).

The phytovolumes obtained for the studied shrubs are quite high although there are few reported data with which they can be compared. For gorse thickets in semi-arid zones, Robles *et al.* (2002) obtained a phytovolume of 2577-8236 m^3 ha^{-1}, which is lower than the 10,540 m^3 ha^{-1} found in this work. However, the coverage was 49-52% in the former study and

92.8% in our case. Heather also exhibited high phytovolumes, which, however, were similar to those for the same type of shrub in Catalonia (Navarro, 2004). The other types of shrub exhibited lower phytovolumes. Although direct comparisons are unfeasible, phytovolume appears to be closely related to plant density and phytomass, as well as, to a lesser extent, the dominant height.

The mean photosynthetic-to-total phytomass ratio (B_p/B_t) for the different species and shrub types was 0.18 and very similar to the 0.17 obtained for garriga in France (Lossiant, 1973), the 0.16 for hygrophytic shrubs in southern Spain (Martin de Agar, 1979), the 0.19 for *frigana* in Greece (Margaris, 1982) and the 0.19 for *Globularia* (García-Ple *et al.,* 1991). The individual ratio for each species was also very close to the results presented by García-Plé *et al.* (1991). However, any comparisons of B_p/B_t will be strongly affected by the age of the individuals and community concerned — at least, on the species level, as shown, for example, for *Lavandula stoechas* (Diaz *et al.,* 1990). Also, the photosynthetic fraction for an individual species must be much lower as the underground parts of plants account for a very high fraction of total phytomass. However, the difficulty of examining root phytomass has to date resulted in a shortage of data for Mediterranean species.

The temporal evolution models constructed in this work are consistent with reported polynomial and exponential models (Robles and Passera, 1995). The values of the fitting parameters fall within reported ranges for shrub species or are slightly higher than those found for common shrub types. The standard errors of estimate obtained reflect a great heterogeneity. Despite this variability, efforts have been made to generalize models able to predict above-ground phytomass as age function without having to apply the time-consuming destructive phase separately for each new stand. Examples of such generalizations are infrequent in Mediterranean shrub communities. These models could be a support for management decisions and a standardized protocol could be developed to measure the biomass of shrub types. In any case, the models suggest that above-ground phytomass and age are very closely related but cannot be generalized to the estimation of phytomass from actual or age-estimated data for the most typical Andalusian shrubs.

The C storage capacity of above-ground shrub biomass ranges from 2.23 t ha^{-1} to 9.83 t ha^{-1}, showing a similar C storage capacity for other shrubland ecosystems (Specht and West, 2003).

Conclusions

A better understanding of biomass in Mediterranean shrub communities will provide useful information on the growth pattern of these species and on the resource dynamics of their communities. Furthermore, this information is importance for biomass mapping, remote sensing and regional estimations of primary productivity in these areas. The data obtained in this work allowed us to estimate the total above-ground phytomass for six dominant shrub communities in southern Spain. The indirect methods used proved accurate enough for large areas as well as for communities with specific compositions and complex structures. Phytomass data allowed us to determine the photosynthetic-to-total above-ground phytomass ratio, as well as to develop models for estimating temporal changes in phytomass as a function of plant age.

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