

The contribution of two common shrub species to aboveground and belowground carbon pool in Iberian Dehesas

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Abstract

Shrubs play an important role in water-limited agro-silvo-pastoral systems by providing shelter and forage for livestock, for erosion control, to maintain biodiversity, diversifying the landscape, and above all, facilitating the regeneration of trees. Furthermore, the carbon sink capacity of shrubs could also help mitigate the effects of climate change since they constitute a high proportion of total plant biomass. The contribution of two common extensive native shrub species (*Cistus ladanifer* L. and *Retama sphaerocarpa* (L.) Boiss.) to the carbon pool of Iberian dehesas (Mediterranean agro-silvo-pastoral systems) is analyzed through biomass models developed at both individual (biovolume depending) and community level (height and cover depending).

The total amount of carbon stored in these shrubs, including above and belowground biomass, ranges from 1.8 to 11.2 Mg C ha⁻¹ (mean 6.8 Mg C ha⁻¹) for communities of *C. ladanifer* and from 2.6 to 8.6 Mg C ha⁻¹ (mean 4.5 Mg C ha⁻¹) for *R. sphaerocarpa*. These quantities account for over 20-30% of the total plant biomass in the system. The potential for carbon sequestration of these shrubs in the studied system ranges 0.10-1.32 Mg C ha⁻¹ year⁻¹ and 0.25-1.25 Mg C ha⁻¹ year⁻¹ for the *C. ladanifer* and *R. sphaerocarpa* communities' respectively.

Keywords: agro-silvo-pastoral system; biomass; carbon balance; *Cistus ladanifer*; *Quercus ilex*; *Retama sphaerocarpa*; root:shoot ratio

1. Introduction

Increasing our knowledge of the forest carbon cycle is key for the development of ecosystem management practices, particularly in complex systems such as agro-silvo-pastoral rangelands. These systems are of great ecological and socio-economical importance, providing a variety of products and services, including carbon sequestration, being the potential of the plant biomass for carbon-sequestration estimated between 0.29 and 15.21 Mg ha⁻¹ year⁻¹ (Nair et al., 2009), depending on the site and agro-silvo-pastoral type.

The term ‘agro-silvo-pastoral system’ refers to the practice of combining tree and crop production with livestock grazing in such a way that a variety of benefits and services are achieved (Nair et al., 2009). One of the best-known agro-silvo-pastoral systems in the Mediterranean area comprises open woodland (established and managed by humans), shrubs and native pastures or crops within the same land unit (Moreno et al., 2007). These multi-layered dryland systems are named ‘dehesas’ in Spain, where they cover an area of around 3.5 million hectares (MAPA, 2008), and ‘montados’ in Portugal, where 0.7 million hectares have this land use (Pereira et al., 2004). Evergreen oaks are the main species (especially *Quercus ilex* L. or *Q. suber* L.) and the predominant activity is extensive livestock rearing, alongside other marginal uses such as hunting and firewood production. These dryland systems provide an example of traditional yet sustainable land use which also contributes to the conservation of biodiversity (Canteiro et al., 2011). One of the potential ecosystem services of the dehesa, which needs to be considered in management planning, is carbon sequestration. Agro-silvo-pastoral systems have a great potential for carbon sequestration in plant biomass, both above and belowground as well as in the soil (Návar-Cháidez, 2008) and management practices should be aimed towards harnessing this potential.

In these seasonally water-limited ecosystems, the different length of biological activity cycles of different plant functional groups (Gitay and Noble, 1997) and the stratification of soil water and root systems (Silva and Rego, 2004; Haase et al., 1996) are key factors to ensure community composition (Lin et al., 1996). Indeed, the presence of a shrub layer reduces

significantly the water availability for both trees and pasture (Cubera and Moreno, 2007), and frequently shrubs species lower the productivity of trees and/or pasture, depending on the species combination (Rivest et al., 2011). On the other hand, shrubs as an additional vegetation layer in agro-silvo-pastoral systems can contribute to additional carbon sequestration, but the competition for such a limited resource (water) could prevent this positive role from happening. Maestre et al. (2012) have reported empirical data supporting that species richness in drylands significantly enhances the ability of ecosystems to maintain multiple functions, such as carbon storage. Drylands, restricted to arid, semi-arid and dry-subhumid ecosystems, defined as sites with an aridity index (precipitation/potential evapotranspiration) between 0.05 and 0.65 (Middleton and Thomas, 1997), cover 41% of Earth land surface and support over 38% of the human population (Maestre et al., 2012). In the Iberian Peninsula, dehesas are dryland systems as most shrublands are. For that reason, it is vital to increase our knowledge about their development and management in these water-limited areas.

Despite the economic importance and the variety of products and ecosystem services (including carbon sequestration) the dehesa provides, there are still many issues related to the functioning and dynamics of the ecosystem, which are poorly understood, mainly regarding the principal product and/or vegetation layer management priority (Moreno and Pulido, 2008). In the case of the trees, either wood or fruit production may be given priority; regarding the components of the system, the issue may be tree production vs pasture understory (Moreno et al., 2007), and shrub management should be very important to achieve the objectives. In this manner, the encroachment of shrubs as opposed to periodic removal to encourage pasture production, fire risk reduction and/or competition (Moreno and Pulido, 2008), could be considered a better option for recruitment of oak species (Pulido et al., 2010), livestock protection or increase carbon stock in biomass and soil (Castro and Freitas, 2009). Thus, the aim of shrub management would be to find a balance between these different objectives (functions and products) by all stakeholders (Moreno et al., 2007).

Cistus ladanifer L. (*Cl*) and *Retama sphaerocarpa* (L.) Boiss. (*Rs*) are two native representative shrub species in the Mediterranean agro-silvo-pastoral rangelands; they also

cover large areas as the dominant woody species. *Cl* shrub systems are widespread in Mediterranean areas, growing in dense populations and are associated with early successional stages and fire disturbance. Furthermore, the leaf exudate of this species has an allelopathic effect, which inhibits the germination of seeds of other species (Chaves and Escudero, 1997). *Rs* is a leguminous shrub, which plays an important role in the dynamics of the herbaceous layer facilitating their growth in its understory (Pugnaire et al., 1996) and tree regeneration as nurse plants (Plieninger et al., 2010). The effect of each of these species on the pasture component of dehesas is very different. *Cl* shrubs can significantly reduce pasture production and *Rs* shrubs increase pasture production and quality (Rivest et al., 2011). Similarly, each species has contrasted effects on the mature oaks functioning (Rolo and Moreno, 2011). Therefore, shrubs are of great ecological importance in habitat restoration due to its pioneer nature. Shrubs provide grazing for livestock as well as soil and watershed protection, biodiversity and carbon sequestration, among other non-marketable services.

Shrubs cover a surface area of almost 18 million hectares in Spain (about 36% of the total) both in the Atlantic and the Mediterranean areas, of which 11 million ha are associated with forested areas (3.2 million ha as areas of woodland and 7.8 million as areas of scattered trees or treeless) (San Miguel et al., 2008) and the figure is 1.9 million ha in Portugal, 22% of the total surface (AFN, 2010). In Spain, *Cl* communities cover 2.8 million ha and *Rs* communities 1.7 million ha (Ruiz de la Torre, 1990). In light of these figures, shrubs could play an important role in carbon sequestration because of the large surface area covered and because they are an intermediate stage of vegetation between pasture and woodland. Additionally, we can predict shrubs to usually have dense rooting systems and high root:shoot ratios in these water-limited communities (Schenk and Jackson, 2002a), which is an important fact for carbon sequestration.

In recent times there has been a marked worldwide increase in the density and cover of shrubs in former areas of open woodland (e.g., Barnes and Archer, 1999). A large number of causes are behind this global phenomenon, ranging from climate change to a reduction in both grazing and fire occurrence.

Shrub plants exhibit a wide variety of forms (both single and multiple stemmed). Hence, it is difficult to make accurate biomass estimations due to the mixture of species typically present in some shrublands. Indirect estimation methods have been developed to relate biomass weight to various dimensional variables (Murray and Jacobson, 1982) or to the shrub age (Paton et al., 1998) by fitting specific equations for individual plants or community models (Návar et al., 2004). In the case of Mediterranean shrub species in the Iberian Peninsula, there is some information available as regards to biomass estimation (e.g., Castro and Freitas, 2009; Navarro and Blanco, 2006), nevertheless, due to the large number of different communities and situations there is certainly a need for more knowledge. Therefore, in order to develop appropriate management strategies, we need to improve our understanding of these systems and quantify their contribution to the global carbon cycle more accurately. Despite the economic importance of agro-silvo-pastoral systems, research into their role as carbon sinks has only recently been undertaken (e.g., Howlett et al., 2011).

It is unusual to find data on individual shrubs or estimations of the number of shrubs per area in forest inventories, since data on the shrub layer is not generally included. Ideally, models need to be able to estimate biomass from data which are relatively simple to obtain such as canopy cover and/or mean height of the shrub layer (Flombaum and Sala, 2007). Vegetation maps or aerial photographs could then be used to quantify shrub biomass.

The objective of this study is to quantify the importance of the shrub layer in dehesa systems in relation to the carbon cycle and the extent to which its contribution as a carbon sink could help mitigate climate change. For this purpose, given the great variety of structural, morphological and functional types of shrubs present in Mediterranean woodlands, we have selected two widespread shrub species representative of two common plant functional types (sensu Gitay and Noble, 1997), one deep rooted resprouter (*R. sphaerocarpa* (L.) Boiss) and one shallow-rooted seeder (*C. ladanifer* L.), using both individual and community methods to estimate their biomass.

2. Methods

2.1. Study Area

The studied sites are located in the north of Extremadura, near the town of Plasencia, in the west of Spain (39° 54' – 40° 02'N, 05° 58' – 06° 15' W). Dehesas cover 30% of this region, around 1.23 million ha (MAPA, 2008), meaning 35% of the total area of Spanish dehesas. The climate is Mediterranean, with long, hot, dry summers and mild, wet winters. Mean temperature is approximately 16 °C, annual potential evapotranspiration averages 920 mm, and annual rainfall averages 560 mm (precipitation/potential evapotranspiration ~ 0.60) (MAGRAMA, 2011). Oak woodlands with an understory of *Cl* are found on fine-textured soils, whereas oak woodlands with an understory of *Rs* are found on coarse-textured soils, developed over schists, which are oligotrophic and acidic.

The landscape is mainly flat with low, rolling hills and the vegetation in the dehesas generally consists of open woodland of *Quercus ilex* L. (10-40 trees ha⁻¹), shrubs and natural pastures used for livestock breeding (mainly cattle, sheep and pigs). The main shrub species in the area are *Cl* and *Rs*, which are the dominant species covering large forested, as well as deforested areas. Other shrub species present in the study area, although in smaller proportions, include *Lavandula stoechas* L. (3% in *Cl* and 4% in *Rs* communities), *Daphne gnidium* L. (1% in both formations) and *Genista hirsuta* Vahl (1% only present in *Cl* communities). Where shrub layer encroaches on pastures, shrubs are periodically cleared in order to regain areas of natural pasture.

2.2. Sampling design

Sampling was carried out in six private dehesa farms, representative of the study area. *Cl* was the dominant shrub species in three of the sites, whereas *Rs* was the main species in the other three. In order to reduce the high degree of heterogeneity in the studied areas for the purposes of the study, within each dehesa, shrub-encroached areas were divided into three development stages: early, mid-stage and mature. The development stage of these shrubs

depends mostly on the length of time since pasture abandonment, although the fertility of the zone could also influence.

Biomass of the tree layer was estimated using the models of Montero et al. (2005) for above and belowground biomass, only depending on the diameter at breast height as an independent variable.

2.2.1. Individual shrub aboveground biomass data

In order to obtain individual estimations for aboveground biomass, a random sampling of individual plants was carried out for all the sites from early to mature stages (not sampling at seedling or sapling stages). A total of 58 *Cl* and 72 *Rs* shrubs were sampled, covering the whole range of sizes and development stages found on these farms. A larger sample of *Rs* shrubs was collected due to the greater variability found. Two basic measurements were recorded for each plant: height (*H*), defined as the maximum height of the shrub, and two perpendicular crown diameters (*CD*). Finally, plants were cut and weighed in the field to obtain fresh weight and representative samples of shrubs were taken to the laboratory and oven-dried to constant weight at 102 °C to determine moisture content and dry weight.

2.2.2. Shrub community biomass data.

We selected nine sampling plots (transects) in each dehesa farm, using three replicates for each development stage previously defined, in order to test the spatial variability. The total number of plots was 27 for *Cl* (3 farms x 3 development stages x 3 replications) and 25 for *Rs* (in this case out of the 27 possible combinations, two of them were not present). Sample plots were given a specific size depending on the different characteristics of the communities: 100 m² (2 m width x 50 m length) for *Cl* plots and 200 m² (4 m x 50 m) for *Rs* due to the high variability found for this species, with taller individuals and lower community canopy cover. Using the line intercept method, we estimated the shrub canopy cover (*CV*) (expressed as a percentage), the tree canopy cover in the plots (%) and the mean height of the shrub layer (*H*) (meters) calculated as the mean height of the plants measured at meter intervals on the

centerline over the length of the transect. All the plant biomass within the transect was cut at ground level and weighed in the field to obtain fresh weight. Dry weight was obtained by subtracting the mean moisture content calculated from the individual plants. Shrub age was estimated from the sampled plants in each plot through growth-ring analysis (Paton et al., 1998). Shrubs were cut at ground level and sections of 3-5 cm wide were collected from the stem base (root collar) 5-6 samples per plot. Damaged sections (by fungus or insects) were rejected in the field and other samples were chosen. As *Rs* is a resprouter plant and it presents more than a simple stem, following Keeley (1993), we chose the thickest and largest stem as the oldest one. In the laboratory, the sections were oven-dried and mechanically polished using different size sandpaper until the shrub growth-rings could easily be observed. Also, annual bands were more accentuated if we applied oil in the surface before identifying the rings with a measuring table using a binocular microscope. In order to confirm that these species formed growth-rings annually, some sampled sites of *Rs* and a small burned area of *Cl* were re-visited three growing seasons later (two and half years later), in which we cut some basal sections in young shrubs to identify annual growth-rings, confirming the assumption that a growth-ring was a one-year period. So, the annual carbon increment for each transect was calculated dividing the carbon stock found by the age (from counting growth-rings) of each transect (Návar, 2001).

2.2.3. Belowground biomass data.

In order to quantify the ratio relating to above and belowground biomass, 12 individuals of *Cl* and 14 of *Rs* were harvested and their root system excavated. Samples were chosen in such a way that the different development stages of the species were represented. Given the different regeneration strategies of the two species (Herrera, 1992) (*Cl* is a seeder and *Rs* is mainly a resprouter) precise carbon stock estimations can only be achieved if the biomass partitioning is determined. Root systems were excavated by using a small backhoe and then using spades to complete the job. For each plant, soil was excavated down to 100 cm depth, in a circular area of twice the mean crown diameter. Coarse roots (> 2 mm of diameter) were roughly cleaned on site with small brooms and then weighed in the field. Weighed subsamples

were then taken to the laboratory, cleaned carefully with water, dried and weighed. In this manner, the dry root biomass was calculated for whole samples weighed in the field.

With this procedure we acknowledge that part of the roots were lost. But, to get a reliable estimation of the belowground biomass, we made the following assumptions. First, roots going deeper than 1 m were very rare for *Cl* but frequent for *Rs*. Some authors have reported a very shallow rooting profile for *Cl* (e.g., Silva and Rego, 2004) and a very deep rooting profile for *Rs* (e.g., Haase et al., 1996); however, detailed empirical data on vertical distribution of roots is scarce for both species, noteworthy for *Rs*. Consequently, we assume that most root biomass was located in the first 100 cm of soil depth, although we accept that *Rs* could usually reach greater depths. Also, during the excavation, a few lateral roots of *Rs* went beyond the limits of excavation, responding to the dimorphic root system of this species (long lateral surface roots and deep roots; Haase et al., 1996), but this was rather rare in our study and they were considered as negligible in terms of biomass. *Cl* never prolonged (in our excavations) its roots beyond twice the length of the crown diameter. Secondly, our sampling procedure only accounted for coarse roots. In order to make more accurate estimations, we considered including fine roots using data from other similar studies to complete the root weight estimations. Rolo and Moreno (2012) studied the rooting profile in shrub-encroached dehesas and reported fine root values of 85-130 g m⁻² for *Cl* sites, sampling up to 1.5 m depth, and 75-95 g m⁻² for *Rs* sites up to 2.5 m depth. The total amount of fine roots was calculated applying these mean values to the excavated area for each sampled plant.

2.3. Carbon content data

No specific carbon content figures are available for the studied species, except for the general figure of 50% proposed in the literature. In order to estimate the carbon content of the shrub species studied, we randomly selected 12 wood samples of stem and branches from each species to be analyzed through the dry combustion procedure at 1050 °C using a LECO HCN 600 element analyzer.

2.4. Model Fitting

Individual biomass dry weight data was used to obtain species-specific biomass models for individual plants based on canopy volume (Murray and Jacobson, 1982) where the volume of the canopy is calculated by considering it a solid geometric form with a similar shape. This canopy volume is usually named 'biovolume' or volumetric index in the literature and is usually calculated for shrub species as a cone, cylinder or semi-spherical shape.

Initial attempts were made to relate shrub community data to age (Navarro and Blanco, 2006; Paton et al., 1998). However, shrub patches were frequently uneven-aged communities and an average age could not be assigned. Because of the difficulty involved in determining shrub age for large areas, other variables were tested in the models, such as mean height, shrub canopy cover or tree canopy cover.

Different equations used in biomass estimation, including linear and non-linear forms (allometric) with additive error term, were tested using the SAS software proc MODEL and proc NLIN (SAS Institute, 2004) to find out which one best related to individual biomass weight (kg) and community biomass weight (kg ha⁻¹). Each model was evaluated through graphical analysis of residuals and goodness of fit statistics (bias and precision), computing the mean residuals (*MRES*), root mean square error (*RMSE*) and model efficiency (*MEF*) (Soares et al., 1995). Heterocedasticity present in biomass data was taken into account by using weighted regression (Parresol, 1999). This technique was carried out in SAS software following the methodology explained in Balboa-Murias et al. (2006).

The root:shoot ratio was calculated as the ratio between the dry weight of the belowground biomass and the dry weight of the aboveground biomass of an individual plant.

To identify whether any significant differences existed between species a Mann-Whitney-Wilcoxon test ($\alpha = 0.05$) was applied to the root:shoot ratios, after non-normality were verified, and a Tukey Honestly Significant Difference test ($\alpha = 0.05$) was used to analyze the carbon content data, after normality was checked.

3. Results

Biomass weight for individual shrubs ranges between a minimum of 0.27 kg and a maximum of 6.25 kg (mean $\pm$ SE) (2.62 ± 1.41 kg) in the case of *Cl* and between 0.45 kg and 16.58 kg (mean 4.51 ± 3.86 kg) for *Rs*. The mean characteristics of the samples are shown in Table 1.

Aboveground biomass weighs for the studied communities ranged between 2305 and 14161 kg ha⁻¹ (8551 ± 3483 kg ha⁻¹) for *Cl* shrub understory and between 2063 and 6733 kg ha⁻¹ (3492 ± 1222 kg ha⁻¹) for *Rs* shrub layers. A high degree of variability was detected for shrub canopy cover in the sampled dehesas, being *Cl* communities generally denser (54%) than *Rs* communities (36%). The former reached almost 100% canopy cover while the latter presented a maximum canopy cover of approximately 60%. However, height was greater for *Rs* shrub layer than for *Cl*. A complete description of the data is presented in Table 2.

Growth-rings have been identified visually for the two studied species, being verified as real annual rings from the young samples collected (samples with known age). Therefore, the age plot was determined for all plots (Table 2). As the available growth samples were short (mean 12 and 9 years old for *Cl* and *Rs* respectively) it was not possible to use crossdating techniques.

3.1. Individual biomass models.

The models that best related biomass weight to plant size were allometric models using biovolume as an independent variable. Other variables and model forms were tested but none of them led to an improvement. The best fitting was achieved by using a cone shape in the biovolume calculation for both species, after testing the cylinder or semi-sphere shapes. The calculation was done using $VI = \pi/3 \cdot (CD_m/2)^2 \cdot H$; where *VI* is the volumetric index, *CD_m* is the mean crown diameter and *H* is the maximum height. The biomass models fitted for the studied species are presented in Table 3. Figure 1 shows the observed data used and the models fitted for the two species.

3.2. Biomass models for shrub understory communities.

Non-linear models were used to fit the *Cl* communities and linear models were employed in the case of *Rs*. Mean height and shrub cover were chosen as independent variables, giving a satisfactory goodness-of-fit rating (Table 4). Other variables such as tree canopy cover were not significant in the models. Age could not be included because an entire range of ages was not available from the sample due to the fact that only a portion of the age range was sampled.

3.3. Root:shoot ratios.

The above and belowground biomass partitioning (expressed as root:shoot ratio) found for these species ranged from 0.44 to 0.81 (0.56 ± 0.03) in the case of *Cl* and from 0.72 to 3.41 (1.46 ± 0.21) for *Rs*. Significant differences between species were found using a comparison test. When the root:shoot ratios estimated were applied to the aboveground biomass data for the studied communities, we obtained a figure for belowground biomass ranging from 1280 to 7861 kg ha⁻¹ for the *Cl* sites (mean 4956 kg ha⁻¹) and from 3009 to 9819 kg ha⁻¹ for the *Rs* communities (mean 5093 kg ha⁻¹).

3.4. Carbon stock of the shrub layer and carbon sequestration potential.

Cl carbon values ranged between 48.95 and 51.92, with a mean of 50.90 % (0.23). The mean carbon value for *Rs* was 52.11 % (0.47), with a maximum of 54.47% and a minimum value of 47.91 %. Statistical differences were detected in the carbon content for the two studied species through a comparison test.

With the sampled values for aboveground biomass, the calculated values for belowground biomass and the carbon content for these species, the estimated carbon stock in these shrub layers from dehesas ranged between 1.82 and 11.21 Mg C·ha⁻¹ (mean value 6.77 Mg C ha⁻¹) for *Cl* communities and between 2.64 and 8.63 Mg C·ha⁻¹ (mean value 4.47 Mg C ha⁻¹) for *Rs* shrublands.

Using the age of each site sampled, the current annual increment of these shrub communities for carbon sequestration ranged between 0.11 and 1.32 Mg C ha⁻¹ year⁻¹ in the case of *Cl* communities (mean value of 0.65 Mg C ha⁻¹ year⁻¹) and between 0.25 and 1.25 Mg C ha⁻¹ year⁻¹ (mean value of 0.54 Mg C ha⁻¹ year⁻¹) for *Rs* sites.

Carbon stocks and increments could be estimated for these shrub species in the dehesa systems of the Iberian Peninsula with the mean values of carbon stock, the mean annual carbon increments, the occupied areas by dehesas (MAPA, 2008; Pereira et al., 2004) and the information of the National Forest Inventory about dehesas with shrubs. Considering that 31% and 15% of the Iberian dehesa areas have *Cl* (1329000 ha) or *Rs* (633000 ha) respectively, as understory, the total carbon stock of the shrub layer (above and belowground biomass) of dehesas with *Cl* is 8.99 Tg C (7.62 Tg C in Spain and 1.37 Tg C in Portugal) and 2.83 Tg C for dehesas with *Rs* (2.40 Tg C and 0.43 Tg C in Spain and Portugal respectively). The estimated annual carbon increment for the shrub layer is 0.86 Tg C year⁻¹ for dehesas with *Cl* (0.73 Tg C year⁻¹ for Spain and 0.13 Tg C year⁻¹ for Portugal) and 0.37 Tg C year⁻¹ for dehesas with *Rs* (0.32 Tg C year⁻¹ and 0.05 Tg C year⁻¹ for Spain and Portugal respectively).

4. Discussion

The mean aboveground biomass found for *Cl* shrub understory in the dehesa system was 8551 kg ha⁻¹ and for *Rs* was 3492 kg ha⁻¹; these findings are similar to those obtained in other studies concerning shrub biomass. Navarro and Blanco (2006) reported a similar mean value (9820 kg ha⁻¹) for *Cl* shrublands in southern Spain, whereas the figure obtained by Castro and Freitas (2009) for *Cl* shrub layers in the Portuguese montados was higher (11650 kg ha⁻¹). Puigdefabregas et al. (1996) reported a mean value for *Rs* shrublands in the south-east of Spain of 1620 kg dry matter ha⁻¹, which is less than half the amount observed in this study. However, the study stands of Puigdefabregas et al. (1996) were of a lower density and they were situated in areas with annual rainfall of 300-350 mm.

If the results are expressed in terms of weight of carbon sequestered, the mean carbon stock in the aboveground biomass of these communities is 4.35 Mg C ha⁻¹ and 2.42 Mg C ha⁻¹ in the belowground biomass in the case of *Cl* shrub layer and 1.82 Mg C ha⁻¹ (aboveground) and 2.65 Mg C ha⁻¹ (belowground) for *Rs*. These results are aligned with those of other studies conducted at different locations. For example, Pérez-Quezada et al. (2011) reported mean aboveground values of 3.2 Mg C·ha⁻¹ for shrublands in Chile, and Cleary et al. (2010) recorded values of 3.1 Mg C·ha⁻¹ for the mature stages of sagebrush in semiarid shrublands in the USA and Návar-Cháidez (2008). Total shrub layer carbon stock, including both above and belowground biomass, ranged between 6.77 Mg C ha⁻¹ for *Cl* and 4.47 Mg C ha⁻¹ for *Rs*. These carbon stock values are also similar to those presented by Beier et al. (2009) for Spanish and Italian shrubland sites under Mediterranean conditions, with drought periods.

Using the models that have been developed in this study together with the equations proposed by Montero et al. (2005) for *Q. ilex* trees and the soil carbon stocks in Spanish dehesas (Howlett et al., 2011) it was possible to estimate the total carbon stored in the shrub as well as the tree strata and soil for the studied dehesas. In the case of *Cl* communities the ‘overall’ estimate for carbon stored in live biomass is 23.0 Mg C ha⁻¹ and for *Rs* communities the figure is 22.0 Mg C ha⁻¹ (with the mean characteristics shown in Table 2; open woodland with shrubs). The contribution of the shrub strata to the total biomass in each case is 29 % and 20 % for *Cl* and *Rs* respectively. If the figure of 29.9 Mg C ha⁻¹ is considered for soil carbon stock in Spanish dehesas (Howlett et al., 2011), the total carbon stock found in *Cl* communities were 52.9 Mg C ha⁻¹ and in *Rs* communities 51.9 Mg C ha⁻¹, being the contribution of the shrub layer between 13% (*Cl*) and 9 % (*Rs*) (Fig. 2). This case showed that soil carbon is the principal component (~55 %) in the dehesa systems, as it is the case in the arid and semi-arid landscapes (e.g., Návar-Cháidez, 2008).

The identification of growth-rings and age determination for these species was done without many problems, not finding double or missing growth-rings. Some problems with growth-rings identification in deeper roots species had been observed by Keeley (1993), tied to the continuation of cambial growth through summer. But in our samples, we found a clear

visible difference between growth-rings so the annual bands could be identified in age-known samples. Furthermore, the potential of this agro-silvo-pastoral system in tree and shrub strata for carbon sequestration, ranged between 0.41 and 1.62 Mg C ha⁻¹ year⁻¹ for *Cl* dehesas (0.11-1.32 potential for *Cl* shrub layer) and 0.56 and 1.56 Mg C ha⁻¹ year⁻¹ for *Rs* dehesas (0.25-1.25 for *Rs* shrub understory). These values fall into the lower part of the range reported by Nair et al. (2009) for agroforestry systems (0.29-15.21 Mg C ha⁻¹ year⁻¹), although we should specify that the studied dehesas are characterized by water-limited conditions, poor soils and the tree strata is usually composed of older trees (> 100 years). Also, the obtained figures are consistent with reported values (0.83 Mg C ha⁻¹ year⁻¹) by Návar et al. (2001) for Mexico's northeastern Tamaulipan thornscrub forests (subtropical, semi-arid plant community).

The root:shoot ratios identified in this study for both *Rs* and *Cl* fall within the range reported in other studies conducted in Mediterranean systems: Kummerow (1981) in a compilation reported a range of 0.3-0.9 for chaparral shrubs (California) and values for a Chilean matorral between 0.3 and 2.7; Martínez et al. (1998) found a higher value (2.7) in a sand dune community in Spain; Almagro et al. (2010) found a mean value for a Mediterranean shrubland with scattered trees in Spain of 0.84. In general, this ratio is linked to the different regeneration systems of the species. Resprouter species such as *Rs* usually have higher root:shoot ratios than seeders such as *Cl* because the former allocate more resources in belowground organs while seeders direct their resources towards developing aboveground growth (Kruger et al., 1997; Silva and Rego, 2004). Furthermore, seeders are shallow rooted whereas resprouters have deep root systems (Keeley and Zedler, 1978), reaching depths of more than 20 m in the case of *Rs* according to Haase et al. (1996). Although the two species grow in very similar habitats, cover large areas and are both influenced by the frequent disturbances associated with these agro-silvo-pastoral systems, as they use different regeneration strategies, they exhibit large differences in root:shoot ratio (0.56 for a seeder as *Cl* and 1.46 for a resprouter as *Rs*). Rolo and Moreno (2012) have confirmed that *Cl* plants present shallow roots while *Rs* plants have a deeper root system, showing the different water use and perpetuation strategy.

Considering both coarse and fine root biomass for the two species provides more accurate estimations. Although the sampling depth (1-m) could have some limitations to find some roots (particularly the fine roots for *Rs*), most of the coarse roots were collected. According to Schenk and Jackson (2002b), probably the proportion of coarse roots located in the first 100 cm is higher than the proportion reported for fine roots (90% and 65%). They showed that coarse woody roots, which have large effects in weight measurements, tend to be concentrated in shallower soil layers than fine roots. Besides, although deep taproots are essential for plant water economy, in terms of biomass they are of little relevance (Canadell et al., 1996). For the fine root fraction, Rolo and Moreno (2012) found that more than 90% of *Cl* fine roots are located in the first 100 cm depth, but only 65% of *Rs* fine roots can be found in the first 100 cm in the same studied dehesas. Since fine root proportions increase with depth and coarse roots tend to be concentrated in shallow and medium depth (Schenk and Jackson, 2002b), the sampled method could be used for biomass estimation.

Carbon content does not vary greatly between woody species and, if specific percentage of carbon for a given species is unknown, a figure of 50% is generally accepted to be approximately correct for woody biomass. However, the accuracy of the estimations could be increased if the exact carbon content of the different species were known, as we present in this study for *Cl* and *Rs*.

The individual biomass models presented for the studied species use biovolume as an independent variable in non-linear form. Other authors, such as Blanco and Navarro (2003), who developed models for *Cl* and *Rs* in Andalusia (Spain), reported similar relationships for these species. They fitted a power equation for *Cl* and a lineal model for *Rs*, using biovolume as an independent variable, in a similar range of biomass weights. Castro et al. (1996) also fitted linear and non-linear models for these species in Central Spain and found that biovolume in allometric models provided satisfactory goodness-of-fit in the biomass weight estimation. The model efficiency was slightly lower in our study due to the greater degree of variability associated with the private-own dehesas sampled, bearing in mind the three development stages sampled, the wide range of livestock and diverse management history.

The models developed in this study for biomass community estimations use mean height and shrub layer canopy cover as independent variables since they can be measured in forest inventories with relatively little effort or economic cost. Despite the fact that some authors developed biomass age-depending models (e.g., Navarro and Blanco 2006; Paton et al. 1998), shrub layer age could not be used to fit these models because samples did not cover all the age range for these communities and moreover, shrub plots at different development stages were often found to have a similar mean age, in spite of having a different visual appearance, and other times the sampled plots were in uneven-aged communities. This may be due to the occurrence of different disturbance events in the dehesas such as shrub clearance (vegetation management), livestock management, fires or natural development, which creates a landscape with a multitude of vegetation patches. Nevertheless, the absence of age in the models permits a greater applicability of the developed models and avoids problems related to shrub layer age-determination in large areas.

The shrub understory biomass estimations undertaken in this study contribute towards completing our understanding of carbon storage in agro-silvo-pastoral systems (in this case, dehesas), being essential for the application of appropriate management practices. Vegetation management can play an important role in increasing soil fertility by trees (Moreno and Obrador, 2007) or, in addition, appropriate shrub management can lead to an increase the opportunities for tree layer regeneration (Pulido et al., 2010) and reinforce the carbon sink capacity of dehesa systems. On the other hand, the enlargement of shrub cover causes a reduction in both fodder production and nutrient value (Rivest et al., 2011) as in water availability, which is very significant for drylands plus it leads to a higher risk of forest fire. Therefore, in order to design the most appropriate production and conservation strategies, managers and owners need to analyze the interactions between the components of the system and the activities carried out in the dehesa and similar silvopastoral systems and, then, prioritize and select the compatible objectives and functions of the ecosystem.

The models developed in this study are for shrub understory in open woodlands (agro-silvo-pastoral systems), where the influence of the trees on the shrubs is low, even though the

tree component is important in the system as a whole. However, the models developed are also applicable to treeless shrublands because when tree canopy cover was tested as an independent variable in community models it was found not to be statistically significant. The use of these models could prove particularly interesting given the fact that the two studied shrub communities (*Cl* and *Rs*) cover a large part of the western Mediterranean Basin as the dominant species in cleared systems.

Conclusions

The models developed to estimate shrub carbon stock, use mean height and canopy cover as independent variables, which gives them greater applicability and makes them more practical to apply, since the inclusion of these variables in forest inventories requires relatively little effort or economic cost. In Spain, as in many other countries, the National Forest Inventory already provides information on shrub height and cover in forest areas; hence the shrub biomass and carbon content models could be applied to obtain accurate estimations for extensive regions.

Developed models can be applied to treeless rangelands in order to estimate the carbon stock without the inclusion of other auxiliary variables. This gives more relevance to the models to be applied where trees have also been replaced by shrub due to clearance or fires.

The contribution of shrub layer to the carbon stock of the dehesa ranges between 29% and 20%) if we are only considering the tree and shrub layers (plant biomass) and between 13% and 9% if the soil compartment is also considered (for *Cl* and *Rs* communities, respectively).

Closely related to shrub layer management and carbon sequestration is the potential use of shrubs in biomass energy as a new output of the already multifunctional agro-silvo-pastoral systems. Periodical removal of the shrub vegetation in order to obtain natural pastures plus shrub encroachment with the objective of natural oak regeneration should be combined for the perseverance of these important dryland systems of the Iberian Peninsula.

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TABLES

Table 1. Maximum, mean and minimum values for crown diameter, volumetric index and above and belowground (coarse and fine roots) biomass for the individual sample plants of the studied species.

Species	Aboveground biomass										Belowground biomass						
	n	Crown diameter			Volumetric			Biomass			n	Coarse biomass			Fine root		
					index												
		Max	Mean	Min	Max	Mean	Min	Max	Mean	Min		Max	Mean	Min	Max	Mean	Min
<i>Cl</i>	58	2.30	1.28	0.32	2.36	0.82	0.03	6.25	2.62	0.27	12	1.22	0.55	0.16	2.13	1.50	0.50
<i>Rs</i>	72	3.50	1.78	0.75	7.00	2.08	0.13	16.58	4.51	0.45	14	18.34	6.01	0.75	3.95	2.18	0.68
<i>n</i> : number of samples; Units: <i>Crown diameter</i> in meters, <i>Volumetric index</i> in cubic meters, <i>Biomass</i> , <i>Coarse biomass</i> and <i>Fine root</i> in kg dry matter plant ⁻¹ .																	

Table 2. Maximum, mean and minimum values found for the communities sampled (values from transects).

Type	n	Tree layer							Shrub layer														
		Cover			Trees				Diameter			Height			Cover			Aboveground biomass			Age		
		Max	Mean	Min	Mean	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean	Min
<i>Cl</i>	27	54	20	0	25	54.7	40.1	12.7	1.8	1.3	0.5	99	54	23	14161	8551	2305	17	12	6			
<i>Rs</i>	25	29	10	0	25	65.9	41.5	11.8	2.9	1.8	1.2	58	36	11	6733	3492	2063	22	9	4			

n: number of transects; Units: *Cover* in percentage, *Trees* in number ha⁻¹, *Diameter* (at the breast height) in centimeters, *Height* in meters, *Aboveground biomass* in kg-dry matter ha⁻¹ and *Age* in years.

Table 3. Individual biomass models and goodness of fit indices for the studied species.

Species	Individual Model	MRES	RMSE	MEF
<i>C. ladanifer</i>	$W = 3.120 (0.150) \cdot VT^{0.563 (0.0640)}$	0.0002	0.896	0.61
<i>R. sphaerocarpa</i>	$W = 2.154 (0.237) \cdot VT^{1.008 (0.0774)}$	0.0115	1.857	0.85

MRES: mean residuals; *RMSE*: root mean square error; *MEF*: model efficiency; *W*: biomass dry weight; *VT*: volumetric index (biovolume) of the individual shrub calculated as an inverted cone.

Standard deviation is showed in brackets. Units: *MRES* and *RMSE* in kg plant⁻¹, *MEF* is dimensionless, *W* in kg plant⁻¹, *VT* in m³.

Table 4. Community biomass models for the studied species and goodness of fit indices.

Type	Model	MRES	RMSE	MEF
<i>Cl</i>	$W = 0.576 (0.202) \cdot H^{0.731 (0.1585)} \cdot SC^{0.632 (0.0891)}$	71.27	1527	0.82
<i>Rs</i>	$W = 0.651 (0.0652) \cdot H^2 + 0.000544 (0.0000770) SC^2 \cdot H$	52.36	738	0.65

MRES: mean residuals; *RMSE*: root mean square error; *MEF*: model efficiency *W*: biomass weight; *H*: mean height of the shrubland (m); *SC*: canopy cover for the shrubland. Standard deviation is showed in the brackets. Units: *MRES* and *RMSE* in Mg dry matter·ha⁻¹, *MEF* is dimensionless, *W* in Mg dry matter·ha⁻¹, *H* in meters and *SC* in percentage.

FIGURES

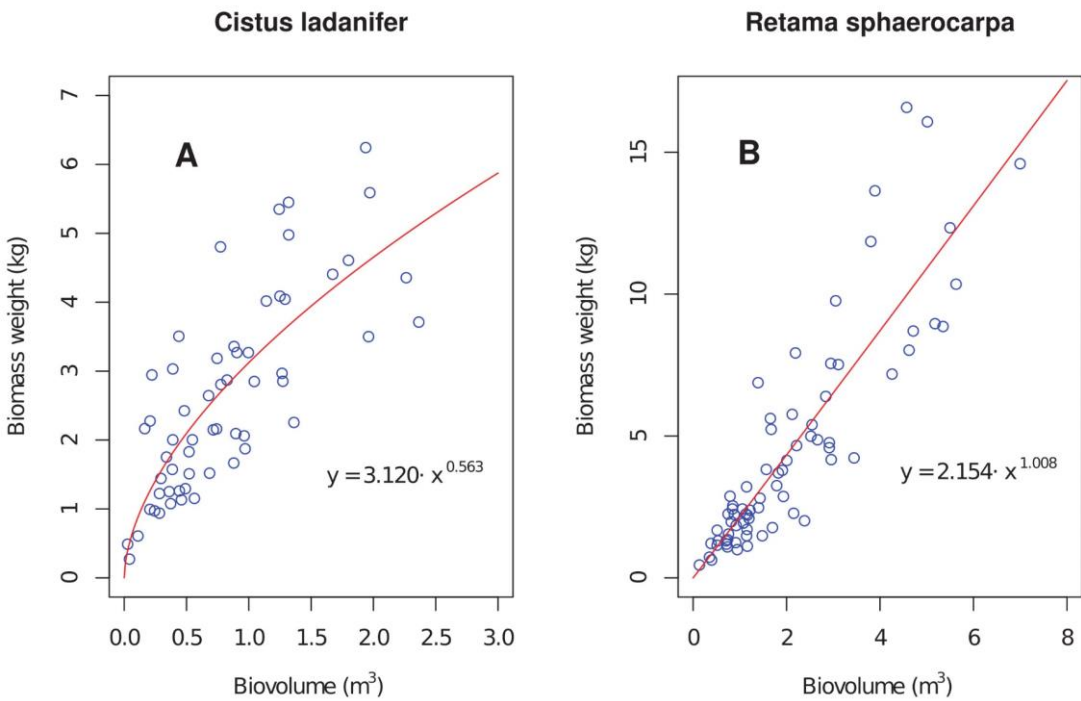


Figure 1. Scatterplot of the observed values and the selected models for *Cl* (A) and *Rs* (B) individual plants.

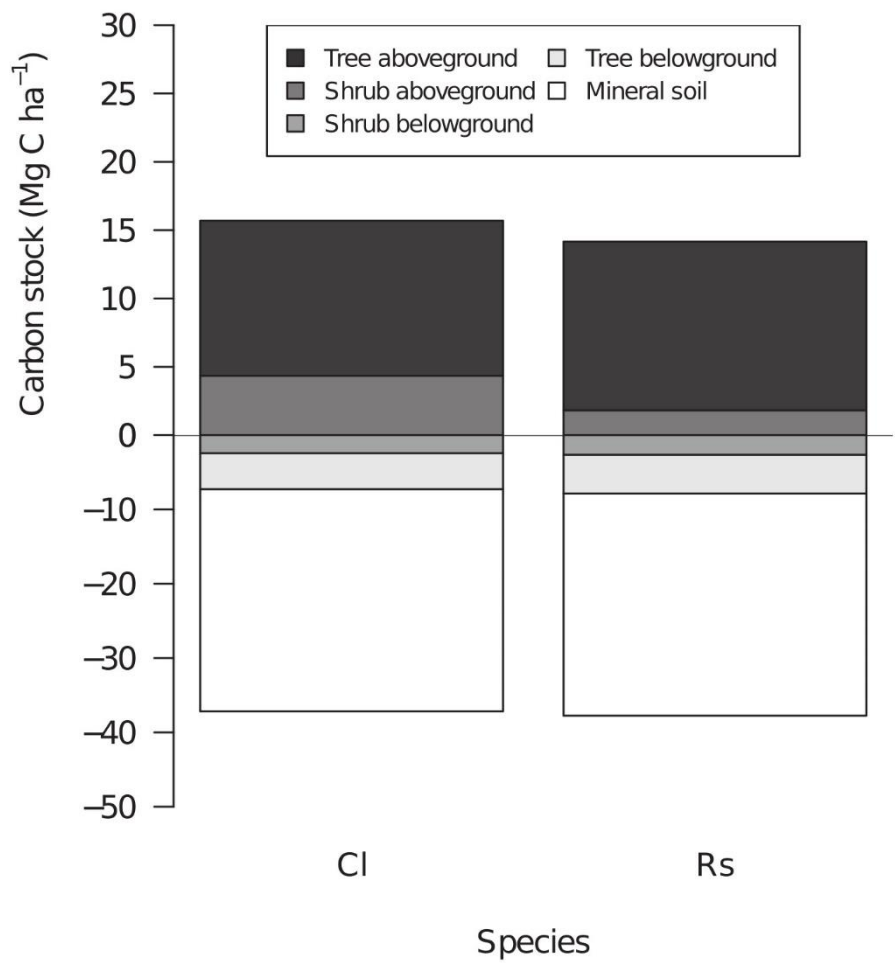


Figure 2.

Above and belowground carbon stock (Mg C ha⁻¹) of the shrub layer (present study), tree (Montero et al., 2005) and soil (Howlett et al., 2011) in the dehesa system, for the two communities studied.