

Mediterranean shrublands carbon sequestration: environmental and economic benefits

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Abstract To date, only a few attempts have been done to estimate the contribution of Mediterranean ecosystems to the global carbon cycle. Within this context, shrub species, composition and structure of the Mediterranean shrublands developing along the *Latium* coast (Italy) were analyzed in order to evaluate their contribution to carbon (C) sequestration, also taking into consideration the economic benefits at a national level. The considered shrublands had a shrub density of $1,200 \pm 500$ shrubs ha^{-1} . Shrubs were classified into small (S), medium (M) and large (L), according to their volume (V) and leaf area index (LAI). The total yearly carbon dioxide (CO_2) sequestration per species (SC_y) was calculated multiplying the total photosynthetic leaf surface area (spt) of each species by the mean yearly photosynthetic rate and the total yearly photosynthetic activity time (in hours). *Q. ilex* and *A. unedo* had the highest SC_y (46.2 ± 15.8 kg CO_2 year^{-1} , mean value), followed by *P. latifolia* (17.5 ± 6.2 kg CO_2 year^{-1}), *E. arborea*, *E. multiflora*, *C. incanus*, *P. lentiscus*, *R. officinalis*, and *S. aspera* (6.8 ± 4.2 kg CO_2 year^{-1} , mean value). The total yearly CO_2 sequestration per shrub (SC_{shy}) was 149 ± 5 kg CO_2 year^{-1} in L, decreasing 30 % in M and 80 % in S shrubs. Taking into account the frequency of S, M and L and their SC_{shy} , the total CO_2 sequestration of the Mediterranean maquis was quantified in $80 \text{ Mg } \text{CO}_2 \text{ ha}^{-1} \text{ year}^{-1}$, corresponding to $22 \text{ Mg C ha}^{-1} \text{ year}^{-1}$. From a monetary viewpoint, this quantity could be valued to more than $500 \text{ US\$ ha}^{-1} \text{ year}^{-1}$. Extending this benefit to the Mediterranean shrublands throughout the whole country, we obtained a nationwide estimated annual benefit in the order of \$500 million.

Keywords Carbon sequestration · Evergreen species · Economic benefit · Global change · Mediterranean shrublands

1 Introduction

The increase in greenhouse gases is projected to lead to $1.0\text{--}3.5$ °C in the global mean surface temperature by 2100 (IPCC 1996). The major objective of the United Nations Framework Convention on Climate Change (UNFCCC) is to develop national inventories

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of greenhouse gas emissions and sinks, and reducing the emissions of greenhouse gases (FAO 2001). Moreover, a fundamental point in the UNFCCC Kyoto Protocol (UNFCCC 1997) is the acceptance of carbon (C) sequestration through the biosphere in forest biomass, as an offset mechanism for emissions from burning fossil fuels (Knoke and Weber 2006). C sequestered is the difference between C gained by photosynthesis and C lost or released by respiration of all components of the ecosystem, and this overall gain or loss of C is usually represented by net ecosystem productivity (Montagnini and Nair 2004). C is stored in plant tissues at different quantities depending on factors such as species, growth rate and leaf life span (Nowak et al. 2002; Gratani and Varone 2006a, 2007). Trees with a large crown tend to sequester and store more C than trees with a small one (Brack 2002; Gratani and Varone 2006a). Studies on vegetation and climate show a positive relationship between water availability and the increase in carbon (C) storage (Woomer et al. 2004; Dauber et al. 2008; Cifuentes Jara 2008). Moreover, warming can contribute to CO₂ fixation in temperate and high latitude ecosystems during the growing season (Keeling et al. 1996), while it can limit CO₂ assimilation in Mediterranean ecosystems (Sardans et al. 2008; Gratani et al. 2011), with a possible decrease in plant productivity and consequent changes in vegetation in the long term (Ciais et al. 2005; Pereira et al. 2007; Granier et al. 2007; De Boeck et al. 2007). Accounting for C sequestration requires adequate knowledge of variations in the ecosystems C exchange with the atmosphere (Pereira et al. 2007), and drought is one of the main sources of inter-annual C sequestration variations (Granier et al. 2007). Moreover, differences in the photosynthetic capacity among ecosystems contribute to the importance of land cover and use changes on potential C sequestration (Metting et al. 2001).

Among Mediterranean ecosystems, shrublands are largely distributed in areas around the Mediterranean region (Boix-Fayos et al. 2009), covering large areas in Europe (Gorissen et al. 2004). It has been shown that shrublands are nurse species for tree seedlings, especially in the Mediterranean region (Martínez 2003; Castro et al. 2004; Padilla and Pugnaire 2006). Shrubs can protect and improve water and light regime, allowing the germination of seeds and the establishment of late-successional species (de Dato et al. 2009). Moreover, planting shrubs improves physical and chemical soil properties through the increase of soil microbes (García et al. 2002; Pariente 2002; Goberna et al. 2007).

Climate projections in the Mediterranean region point to a potential acceleration of climatic trends, with rising air temperatures (1–6 °C) in the 21st century (García-Ruiz et al. 2011) and a precipitation amount decrease by 22 % from April to September (Giorgi 2006). Climate change could significantly affect C acquisition in Mediterranean areas considering that spring rainfall is more important than total annual rainfall (Gratani and Crescente 1997; Ma et al. 2007; Pereira et al. 2007; Allard et al. 2008). Climate change could make these ecosystems even more vulnerable because in contrast to forest ecosystems growing on comparable soils, shrubs are less capable of exploring deeper soil layers for water (Gorissen et al. 2004; Wessel et al. 2004). Moreover, the decrease of Mediterranean shrublands cover might accelerate soil degradation and erosion leading to mass movements and landscape instability (Haase et al. 2000). The contribution of Mediterranean ecosystems to the global carbon cycle has received low attention in the past (Evrendilek et al. 2006) and few estimates have been carried out to date (Del Galdo et al. 2003). How climate change could affect ecosystem functioning and how that could trigger a positive feedback on climate by modifying C sequestration in different ecosystems is a key question for comprehending atmospheric changes in the on-going century (Allard et al. 2008). Moreover, it is important to develop the economic aspects of carbon sequestration in the forest sector, with a framework of ecological and social functions, as well as the sustainable demand of the forests (Knoke and Weber 2006). Nevertheless, with regards to the economic aspect, the use

of different methods, concepts and terms when calculating carbon sequestration has complicated the comparison of estimates from different studies (Richards and Stokes 2004; Torres et al. 2010). Enhancing C sequestration by increasing forested land areas has been suggested as an effective measure to lower atmospheric carbon dioxide (CO₂) concentration contributing towards the prevention of global warming (Watson 2000). Nevertheless, conservation of forests having large amounts of C stocks is also a valuable way to reduce CO₂ emissions which is more beneficial than reforestation in the short run (Sharma et al. 2010). Therefore, it is imperative to improve understanding of the processes regulating C sequestration in order to manage landscapes, maximizing their potential to store C in the future (Jones and Donnelly 2004) and plan policies to mitigate desertification, especially in arid and semiarid lands (Iglesias et al. 2012).

The main objective of this research was to analyze shrub species composition in the Mediterranean shrubland developing along the *Latium* coast in central Italy, considering their contribution to C sequestration and the correspondent economic value. The Mediterranean forests and shrublands are heavily utilized by man (Boix-Fayos et al. 2009) with a possible increase in the near future of degraded areas due to coastal urbanization, landscape fragmentation, overgrazing and excessive wildfires (Wessel et al. 2004; Boix-Fayos et al. 2009). Thus, a better knowledge of the Mediterranean shrublands C sequestration capability is also important for improving targeted protection actions of coastal vegetation, and reinforces arguments in forest conservation as well as in contributing to global sustainability (Padilla et al. 2010).

2 Materials and methods

2.1 Study area and plant species

The study was carried out in the Mediterranean shrubland developing along the *Latium* coast (Capocotta, Italy, 5 m a.s.l., 41°40'23"N; 12°23'38"E), in the period January–December 2011. The area under study was representative of the Mediterranean evergreen shrublands (Gratani and Crescente 2000; Fioretto et al. 2001; Francaviglia et al. 2004) and it was characterized by the presence of the following dominant species: *Arbutus unedo* L., *Phillyrea latifolia* L., *Pistacia lentiscus* L., *Quercus ilex* L., *Cistus incanus* L., *Erica arborea* L., *Erica multiflora* L., *Rosmarinus officinalis* L., and *Smilax aspera* L. (Gratani et al. 2003).

The climate of the area was of Mediterranean type: the mean minimum air temperature (T_{\min}) of the coldest month (January) was 5.2 ± 1.6 °C (mean value \pm SD), the mean maximum air temperature (T_{\max}) of the hottest months (July and August) 30.8 ± 0.1 °C, and the mean yearly air temperature (T_m) 16.8 ± 6.5 °C. Total annual rainfall was 689 mm, most of it occurring in autumn and winter. Dry period was from the middle of May to the beginning of September (with 67 mm total rainfall) (Data from the Collegio Romano Meteorological Station for the years from 1995 to 2011). In 2011 T_{\min} of the coldest month (February) was 4.2 ± 1.2 °C, T_{\max} of the hottest month (August) 31.4 ± 1.3 °C, and total rainfall 610 mm (Data from the Collegio Romano Meteorological Station for the year 2011). The soil was a regosol (Gisotti and Collamarini 1982) and its morphology was mainly flat with sandy materials (Francaviglia et al. 2004). Soil water content was 0.5–8 % during the year, the minimum values occurring in August and the maximum ones in December (Gratani and Crescente 1997). The maximum water availability was from April to the end of May while water deficit occurred from June to September (Gratani and Varone 2004a).

The species structural and physiological leaf traits were analyzed on sixty shrubs randomly distributed in five square sample areas (100 m² each) within a larger area (1 ha), according to Gratani et al. (2003).

2.2 Shrub structural traits

Measurements of shrub structure was carried out in October–November and included: total height (H, m), defined as the maximum vertical distance from the soil level to the highest point of the shrub; major axis (A, m) and minor axis (a, m, orthogonal to A) of the shrub crown; shrub volume (V , m^3), derived from the measured traits (A, a, and H) by assigning a simple geometric solid to the shrub's form, according to Karlik and Winer (2001); leaf area index (LAI, i.e. total leaf area per unit of ground area) of shrubs, measured by the “LAI 2000 Plant Canopy Analyzer” (LI-COR Inc., Lincoln, Nebraska, USA), according to Morales et al. (1996). Shrub structural traits were used to group the considered shrubs in class sizes. For each shrub, the number of species was counted; shrub density in the sample areas (SD) was calculated as number of shrubs ha^{-1} .

The total leaf number per species in each sampled shrubs was counted, and the total photosynthetic leaf surface area (spt, m^2) per species was calculated multiplying the total number of leaves by the mean leaf surface area (Crescente et al. 2000) using the Image Analysis System (Delta-T Devices, UK) ($n=20$ leaves per species).

2.3 Gas exchange

Measurements of gas exchange for all the species were carried out using the infrared gas analyzer (ADC LCA4, UK), equipped with a conifer leaf chamber (PLC, *Parkinson Leaf Chamber*) for *E. arborea*, *E. multiflora* and *R. officinalis*, and with a broad leaf chamber (PLC, *Parkinson Leaf Chamber*) for *Q. ilex*, *A. unedo*, *C. incanus*, *P. latifolia*, *P. lentiscus* and *S. aspera*.

Measurements were taken on attached fully expanded sun leaves ($n=5$ in each sampling occasion for *A. unedo*, *C. incanus*, *P. latifolia*, *P. lentiscus*, *Q. ilex*, and *S. aspera*) and on fully expanded sun apical shoots ($n=5$ in each sampling occasion for *E. arborea*, *E. multiflora* and *R. officinalis*).

Net photosynthesis (P_N , $\mu mol CO_2 m^{-2} s^{-1}$) and photosynthetically active radiation (PAR, $\mu mol photons m^{-2} s^{-1}$) were measured from 9.00 a.m. to 11.00 a.m under natural conditions on cloud-free days ($PAR \geq 1,000 \mu mol m^{-2} s^{-1}$, saturating level), periodically, during the study period, and in particular in spring, summer and winter.

2.4 CO₂ sequestration capacity

The total yearly CO₂ sequestration capacity per species (SC_y) was calculated by multiplying spt of each species by the mean yearly P_N and the total yearly photosynthetic activity time (in hours), according to Gratani and Varone (2006a). Likewise, spring, drought and winter CO₂ sequestration were calculated by multiplying spt of each species by the mean P_N rate and the total photosynthetic activity time in April and May (SC_s , spring), July and August (SC_d , drought) and January and December (SC_w , winter), respectively.

The total yearly CO₂ sequestration capacity per shrub (SC_{shy}) was calculated for S, M and L by adding the SC_y of all the species in each shrub. The CO₂ sequestration capacity per shrub in spring, drought and winter (SC_{shs} , SC_{shd} , SC_{shw} , respectively) was also determined in the same way, by adding SC_s , SC_d , SC_w of all the species in each shrub. The total yearly CO₂ sequestration of the shrubland was estimated taking into account the number of shrubs (S, M, L) per ha. Moreover, the total CO₂ sequestration of the shrubland in spring, drought and winter was estimated considering SC_{shs} , SC_{shd} and SC_{shw} . The coefficient of $CO_2/C=3.67$ was used to convert the amount of sequestered CO₂ in equivalent C amounts, according to Evrendilek et al. (2006).

2.5 Statistical analysis

Differences of the means for the considered traits were tested by one-way ANOVA, and *Tukey* test for multiple comparisons, and linear regression analysis was used to evaluate the correlation between LAI and V, and between SC_{shy} and LAI.

Two Principal Component Analyses were carried out in order to highlight the physiological relationships among species sampled. Specifically, the first ordination (PCA1) was performed on the set of variables related to the species net photosynthetic activity P_{Nys} , P_{Nss} , P_{Nd} and P_{Nw} while the second ordination (PCA2) was performed on the variables summarizing the CO_2 sequestration SC_y , SC_s , SC_d and SC_w .

A species co-occurrence analysis was performed to identify species pairs that occurred together within single shrubs more or less often than expected by chance irrespective of shrub size. The actual co-occurrences of all species pairs in the real species-per-shrub matrix were checked against the co-occurrence distribution in a set of randomized null matrices to identify the species pairs showing significant deviation, either at the lower part of the distribution (less co-occurrence than expected by chance, or negative species association) or at the upper part of the distribution (higher than random co-occurrence, meaning positive species association), according to Sfenthourakis et al. (2004). The identification of the significant species co-occurrences was carried out with the program COOC (Sfenthourakis et al. 2004), while all randomized matrices were generated with the program ‘EcoSim 2004’, using the independent swap algorithm to keep species richness within shrubs and the frequency of species occurrences across shrubs unchanged with respect to the real matrix (Gotelli and Entsminger 2001).

3 Results

3.1 Structural shrub traits

Shrub density was $1,200 \pm 500$ shrubs ha^{-1} , 17 % of them were constituted by one species and 83 % were multispecies. According to V and LAI, the shrubs were classified in three classes: small (S), medium (M) and large (L) shrubs: V and LAI were 1.4 ± 0.9 m³ and 2.0 ± 0.4 ; 12.6 ± 1.5 m³ and 3.1 ± 0.4 ; 35.5 ± 2.5 m³ and 3.9 ± 0.1 in S, M and L shrubs, respectively. The regression analysis showed that 63 % of variance in LAI depended on V (Fig. 1a). The frequency of occurrence of S, M and L shrubs in the sample areas was 57, 32 and 11 %, respectively.

The number of species increased from S to L: S shrubs were constituted by 3 ± 2 species, M by 6 ± 2 species, and L by 6.0 ± 0.4 species. The frequency of monospecies shrubs was 26 and 5 % in S and M shrubs, respectively, while L shrubs were always multispecies. *C. incanus* (91 %), *E. multiflora* (71 %) and *R. officinalis* (38 %) were the most frequent species in S shrubs, while *E. arborea* was always absent. *Q. ilex*, *C. incanus* and *S. aspera* (89 %) were the most frequent species in M shrubs, followed by *E. multiflora* (84 %), *A. unedo* (68 %), *P. latifolia* (58 %), *R. officinalis* (42 %), *E. arborea* and *P. lentiscus* (16 %). *A. unedo*, *P. latifolia* and *Q. ilex* were always present in all L shrubs, followed by *C. incanus* and *S. aspera* (86 %), *E. multiflora* (71 %), *E. arborea* and *P. lentiscus* (29 %) and *R. officinalis* (14 %). Sixty percent of the monospecies shrubs were constituted by *C. incanus*, 30 % by *R. officinalis* and 10 % by *Q. ilex*.

The analysis of the species co-occurrences identified 12 pairs of species out of 36 possible ones that occurred together more (or less) often than that expected by chance within single shrubs, meaning that Mediterranean shrubs are not assembled at random from the

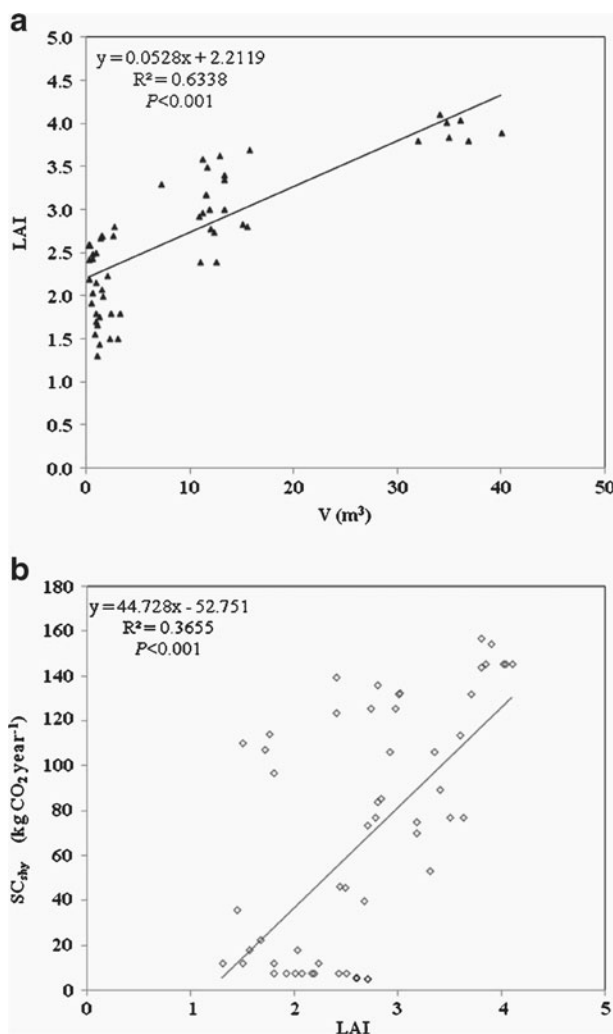


Fig. 1 Regression analysis between leaf area index (LAI) and volume (V) (a), and between total yearly carbon sequestration (SC_{shy}) and LAI (b) for the considered shrubs. Regression equation, determination's coefficient (R^2) and P -level are shown

available species pool - (two-tailed test, $p=0.05$, 999 randomizations). Among them the species pairs showing significantly negative association were: *A. unedo* – *E. multiflora*; *A. unedo* – *R. officinalis*; *E. arborea* – *E. multiflora*; *E. multiflora* – *P. lentiscus*; *E. multiflora* – *S. aspera*; *P. latifolia* – *R. officinalis*. The species pairs showing significantly positive association were: *A. unedo* – *P. latifolia*; *A. unedo* – *P. lentiscus*; *A. unedo* – *Q. ilex*; *A. unedo* – *S. aspera*; *P. latifolia* – *P. lentiscus*; *Q. ilex* – *S. aspera*.

3.2 Physiological leaf traits

The P_N rates of the same species measured in different shrubs did not vary significantly meaning that shrub size does not influence the photosynthetic performance of a single species.

During the study period, P_N rates of the considered species peaked in the months April–May ($T_m=17.4\pm2.3$ °C) and *C. incanus* had the highest P_N (20.4 ± 1.1 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) while *E. multiflora* and *R. officinalis* the lowest ones (7.8 ± 0.1 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, mean value). P_N decreased, on an average, 73 % of the maximum in August and 47 % in December. The mean yearly photosynthetic rate (P_{Ny}) was the highest in *C. incanus* (11.9 ± 0.4 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and the lowest in *E. multiflora* and *R. officinalis* (5.4 ± 0.1 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, mean value).

3.3 CO₂ sequestration capacity

At species level, *Q. ilex* had the highest SC_y (57.4 ± 5.8 $\text{kg CO}_2 \text{ year}^{-1}$), SC_s , SC_d and SC_w (10.1 ± 1.0 ; 3.8 ± 0.4 ; 4.4 ± 0.6 $\text{kg CO}_2 \text{ month}^{-1}$, respectively) while *S. aspera* the lowest ones ($SC_y=0.07\pm0.03$ $\text{kg CO}_2 \text{ year}^{-1}$; SC_s , SC_d and $SC_w=0.014\pm0.005$, 0.002 ± 0.001 and 0.004 ± 0.001 $\text{kg CO}_2 \text{ month}^{-1}$, respectively) (Table 1).

At shrub level, L shrubs had the highest SC_{shy} (149 ± 5 $\text{kg CO}_2 \text{ year}^{-1}$) decreasing 80 % in S and 30 % in M shrubs (Table 2). In spring, during the favorable period, SC_{shs} was 5.3 ± 6.1 in S, 19.1 ± 4.8 in M and 27.4 ± 1.1 $\text{kg CO}_2 \text{ month}^{-1}$ in L shrubs, decreasing, 70 %, 66 % and 67 % in drought in S, M and L shrubs, respectively. SC_{shw} decreased 62 % in S, 64 % in M and 66 % in L shrubs in winter (Table 2).

The regression analysis showed that 36 % of SC_{shy} variance depended on LAI (Fig. 1b). The total yearly CO₂ sequestration capability of the Mediterranean shrublands was 80 $\text{Mg CO}_2 \text{ ha}^{-1} \text{ year}^{-1}$, corresponding to 22 Mg of C year^{-1} . S, M and L shrubs contributed by 24 %, 50 % and 26 %, respectively, to the overall C sequestration of the Mediterranean shrublands. The highest CO₂ sequestration capacity of the shrublands happened in spring (14 $\text{Mg CO}_2 \text{ month}^{-1}$), decreasing 64 % in winter and 67 % in drought.

3.4 Principal component analysis

The PCA1 highlighted a clear non-linear gradient among the considered species as concerned their net photosynthetic activity with the first two principal components accounting for 96 % of the system variance (PC1=78.5 % and PC2=17.5 %) (Fig. 2). In particular,

Table 1 Mean values \pm standard deviation of total yearly, spring, drought and winter CO₂ sequestration for the considered species

Species	SC_y $\text{kg CO}_2 \text{ year}^{-1}$	SC_s $\text{kg CO}_2 \text{ month}^{-1}$	SC_d $\text{kg CO}_2 \text{ month}^{-1}$	SC_w $\text{kg CO}_2 \text{ month}^{-1}$
<i>A. unedo</i>	35.0 ± 6.6 a	6.0 ± 1.4 a	2.2 ± 0.4 a	1.9 ± 0.3 a
<i>C. incanus</i>	9.7 ± 4.9 bc	2.3 ± 0.9 b	0.3 ± 0.2 b	0.6 ± 0.3 bc
<i>E. arborea</i>	12.4 ± 1.5 c	2.6 ± 0.2 b	0.9 ± 0.1 bc	0.9 ± 0.1 b
<i>E. multiflora</i>	6.8 ± 2.7 b	1.3 ± 0.5 c	0.3 ± 0.1 c	0.4 ± 0.1 bc
<i>P. latifolia</i>	17.5 ± 6.2 c	3.2 ± 1.2 b	1.4 ± 0.6 b	1.1 ± 0.3 b
<i>P. lentiscus</i>	5.4 ± 2.5 b	0.9 ± 0.4 c	0.3 ± 0.2 b	0.3 ± 0.1 bc
<i>Q. ilex</i>	57.4 ± 5.8 d	10.1 ± 1.0 d	3.8 ± 0.4 d	4.4 ± 0.6 d
<i>R. officinalis</i>	6.7 ± 2.1 b	1.4 ± 0.4 c	0.2 ± 0.1 b	0.4 ± 0.1 bc
<i>S. aspera</i>	0.07 ± 0.03 e	0.014 ± 0.005 e	0.002 ± 0.001 e	0.004 ± 0.001 e

Values in the columns followed by the same letter are not significantly different ($P<0.05$), according to Tukey test; \pm denotes standard deviation; SC_y =total yearly carbon sequestration; SC_s =spring carbon sequestration; SC_d =drought carbon sequestration; SC_w =winter carbon sequestration

Table 2 Mean values±standard deviation of the total yearly, spring, drought and winter CO₂ sequestration, for the different shrubs size

Shrub size	SC _{shy} kg CO ₂ year ⁻¹	SC _{shs} kg CO ₂ month ⁻¹	SC _{shd} kg CO ₂ month ⁻¹	SC _{shw} kg CO ₂ month ⁻¹
S	29±35 a	5.3±6.1 a	1.6±2.3 a	2.0±2.6 a
M	104±27 b	19.1±4.8 b	6.5±1.9 b	6.9±1.6 b
L	149±5 c	27.4±1.1 c	9.0±0.4 b	9.4±0.3 b

Values in the columns followed by the same letter are not significantly different ($P<0.05$), according to Tukey test; ± denotes standard deviation. S=small shrubs; M=medium shrubs; L=large shrubs; SC_{shy}=total yearly carbon sequestration; SC_{shs}=spring carbon sequestration; SC_{shd}=drought carbon sequestration; SC_{shw}=winter carbon sequestration

P. latifolia, *Q. ilex* and *A. unedo* showed the highest P_{Nd} and relatively high P_{Nw} , P_{Ny} and P_{Ns} , followed by *P. lentiscus* and *E. arborea*, which had relatively high P_{Nd} , P_{Ns} , P_{Ny} and P_{Nw} , and by *E. multiflora*, *R. officinalis* and *S. aspera*: among these species *E. multiflora* and *R. officinalis* had a lower P_{Ny} and P_{Ns} and relatively low P_{Nw} and P_{Nd} , while *S. aspera* higher P_{Ny} , P_{Ns} and P_{Nw} and the lowest P_{Nd} . *C. incanus* was at the opposite end of the gradient showing the highest P_{Ns} and P_{Ny} , relatively high P_{Nw} and low P_{Nd} .

To the contrary, PCA2 highlighted an almost univariate linear gradient in the species CO₂ sequestration capability with 98.7 % of explained variance associated to the first factor 1 (Fig. 3). Along the species gradient, *Q. ilex* and *A. unedo* showed the highest SC_y, SC_s, SC_d and SC_w, followed by *P. latifolia* showing a relatively high SC_y, SC_s, SC_d and SC_w, and by the others species, showing the lowest SC_y, SC_s, SC_d and SC_w.

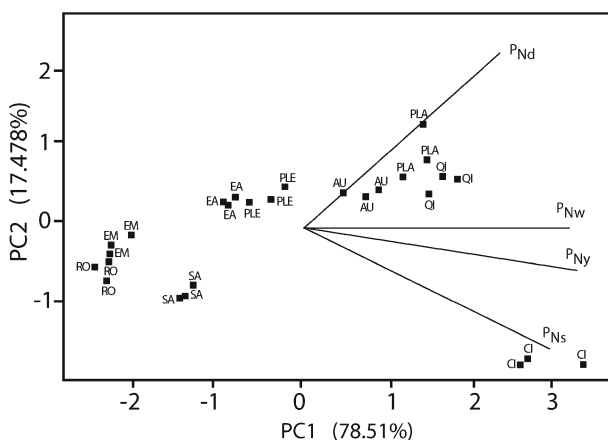


Fig. 2 Ordination plot of the first two axes of a principal component analysis (PCA) on the set of standardized variables related to the species net photosynthetic activity during spring (P_{Ns}), winter (P_{Nw}), drought (P_{Nd}), and mean yearly value (P_{Ny}), respectively. Numbers in brackets are the percentage of variance associated with each principal component. Vectors represent the direction and the strength of the correlation between explanatory variables and the first two ordination axes. AU=*Arbutus unedo*, CI=*Cistus incanus*, EA=*Erica arborea*, EM=*Erica multiflora*, PLA=*Phillyrea latifolia*, PLE=*Pistacia lentiscus*, QI=*Quercus ilex*, RO=*Rosmarinus officinalis*, SA=*Smilax aspera*

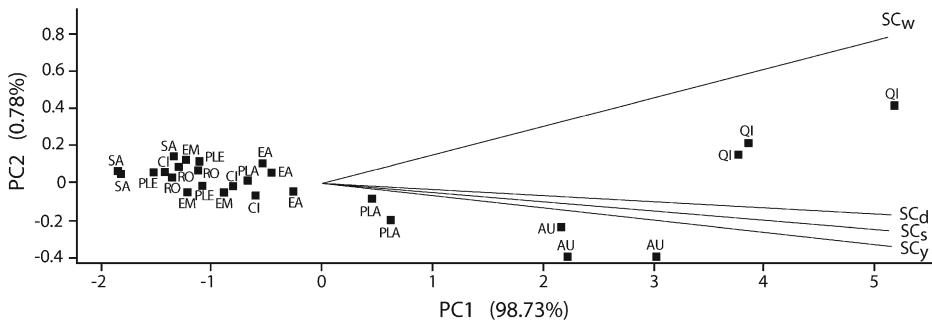


Fig. 3 Ordination plot of the first two axes of a principal component analysis (PCA) on the set of standardized variables related to the species CO₂ sequestration in spring (SC_s), winter (SC_w), drought (SC_d), and the total yearly carbon sequestration (SC_y), respectively. Numbers in brackets are the percentage of variance associated with each principal component. Vectors represent the direction and the strength of the correlation between explanatory variables and the first two ordination axes. AU=*Arbutus unedo*, CI=*Cistus incanus*, EA=*Erica arborea*, EM=*Erica multiflora*, PLA=*Phillyrea latifolia*, PLE=*Pistacia lentiscus*, QI=*Quercus ilex*, RO=*Rosmarinus officinalis*, SA=*Smilax aspera*

4 Discussion

There is a strong need for studies to increasing our understanding of the ecosystems function and C storage (Beier et al. 2009). The major long-term effects of global change on Mediterranean shrublands seem to be related to variations of their structure and productivity (Haase et al. 2000; Saxe et al. 2001) with possible changes in C sequestration capability (Evrendilek et al. 2006; Pan et al. 2009; Gratani et al. 2011). Thus, knowledge of structural traits of shrubs, their composition and functioning in favorable as well as in drought conditions could be used to monitor their response to global change and perturbations. Our results underline a significant correlation between LAI and V, and between SC_{shy} and LAI of shrubs. For instance, leaf area index is an important variable for characterizing vegetation structure and function including estimation of plant productivity and canopy cover density (Whittaker and Marks 1975; Kaufmann and Troendle 1981; Garrigues et al. 2008). LAI constitutes the interface between plants and the atmosphere, and it is therefore a key trait for quantifying and monitoring carbon exchange (Gower and Norman 1991; Gratani and Crescente 2000). The analysis of species co-occurrence carried out on the shrublands shows a significantly negative association between some species, depending on their size. In fact, plant interaction strongly influences community structure and dynamics, and is responsible for the species presence or absence in the community (Padilla and Pugnaire 2006). Moreover, competition for light may be important in plant species association, as indicated by Vilà (1997). Accordingly, species characterized by a small size (i.e. low V and LAI) co-occur rarely with large size species, because of large plants can shade and reduce the growth of small plants (Weiner 1990). The negative co-occurrence of *E. multiflora* and *R. officinalis* with *A. unedo*, *E. arborea*, *P. latifolia* and *P. lentiscus* may be explained by their need to grow in full sun. In fact, both species grow exclusively in shrublands while they are absent in Mediterranean evergreen forests where total irradiance is decreased by 94 % with respect to the open space (Gratani 1997; Gratani et al. 2006). The analysis of co-occurrence underlines that *C. incanus* does not form preferential pairs with the others species, also attested by its presence in all shrub sizes (90 %), and its contribution to 60 % of the monospecies shrubs. *C. incanus* always occupies a position outside the shrub sizes (L, M and S) since it is a *helifilous* species (Gratani and Amadori 1991; Civeyrel et al.

2011). On the contrary, the co-occurrence of *S. aspera* with *A. unedo* and *Q. ilex*, can be explained by the species ability to grow in full sun as well as in shade, as suggested by Sack et al. (2003). Moreover, *S. aspera* is a non-self-supporting plant species that gains advantage by directing biomass into extension growth and stem length rather than stem stiffness (Niklas 1994; Isnard et al. 2003). *S. aspera* naturally grows in the understory of the Mediterranean evergreen forests and it is a component of the shrub vegetation (Gratani 1997).

The PCA1 underlines differences in the photosynthetic rates of the considered species. In particular, the sclerophyllous species (*Q. ilex*, *P. latifolia* and *A. unedo*) have a relatively high P_{Ny} rates ($9.3 \pm 0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$, mean value) and the highest P_{Nd} ($4.7 \pm 0.6 \mu\text{mol m}^{-2} \text{s}^{-1}$, mean value). The latter being justified by a large and deep root system that accesses water stored deeply in the soil (Meinzer et al. 1999; Gratani and Bombelli 2001; Gratani and Varone 2004a) and a high leaf consistency (i.e. high LMA, Gratani and Varone 2006b) which increases drought resistance. *E. arborea* and *P. lentiscus* show a lower P_{Nd} ($3.3 \pm 0.2 \mu\text{mol m}^{-2} \text{s}^{-1}$, mean value) compared to the above mentioned sclerophyllous species. The presence of *E. arborea* (a narrow-leaved species) in the same position of *P. lentiscus* along the separation gradient is justified by its deep root system (Aubert 1978). On the contrary, the other narrow-leaved species (*R. officinalis* and *E. multiflora*) and *S. aspera* are characterized by the lowest P_{Nd} ($1.3 \pm 0.3 \mu\text{mol m}^{-2} \text{s}^{-1}$, mean value), because of their narrow root system (Gratani and Varone 2004b). *C. incanus* (the semi-deciduous species) has the highest P_{Ny} ($11.9 \pm 0.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$) and a low P_{Nd} ($2.8 \pm 0.3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$), the first resulting from the larger light-capture area deployed per leaf mass (Gratani and Bombelli 2001), and the second by its shallow root system (Gratani and Varone 2004a) and the low leaf consistency (Gratani and Bombelli 2001), which decreases drought resistance (Werner et al. 1999; Gratani and Varone 2006b). The allocation of a greater amount of photosynthates during the favorable period seems to justify the large *C. incanus* vegetative regeneration capability, emphasizing its ecological role in the first reconstitution stages of the Mediterranean maquis after fire (Gratani and Amadori 1991).

The PCA2 shows a different physiological gradient among the considered species underlining that spt is a key factor in CO_2 sequestration. In particular, *Q. ilex* and *A. unedo* are very close to each other in the ordination plot, with the highest SC_y ($46.2 \pm 15.8 \text{ kg CO}_2 \text{ year}^{-1}$) while *P. latifolia* occupies a different position because of its lower SC_y ($17.5 \pm 6.2 \text{ kg CO}_2 \text{ year}^{-1}$). *E. arborea*, *E. multiflora*, *C. incanus*, *P. lentiscus*, *R. officinalis* and *S. aspera* are characterized by the lowest SC_y ($6.8 \pm 4.2 \text{ kg CO}_2 \text{ year}^{-1}$, mean value). Nevertheless, *S. aspera*, despite a low SC_y ($0.07 \pm 0.03 \text{ kg CO}_2 \text{ year}^{-1}$), plays an important role in many aspects of forest dynamics (Schnitzer and Bongers 2002) which should be taken into consideration. At the shrub level, the non-random co-occurrences among species determines the shrub SC_{shy} which is $149 \pm 5 \text{ kg CO}_2 \text{ year}^{-1}$ in L decreasing 30 % in M and 80 % in S shrubs. Considering the frequency of S, M and L shrubs in the study area and their SC_{shy} , the CO_2 sequestration capacity of the Mediterranean shrublands is calculated by $80 \text{ Mg CO}_2 \text{ ha}^{-1} \text{ year}^{-1}$, corresponding to $22 \text{ Mg of C ha}^{-1} \text{ year}^{-1}$. Our results concerning C sequestration are comparable to those shown by Padilla et al. (2010) for *Q. ilex* and for *Adenostoma fasciculatum* shrublands. In particular, our results on *Q. ilex* shrubs are lower than those obtained by Padilla et al. (2010) for *Q. ilex* trees measured in the forest, considering that shrubs have a lower biomass and LAI than trees (Bruno et al. 1976; Gratani and Crescente 2000). On the contrary, our C sequestration estimations are higher than those of *A. fasciculatum* shrublands due to the more xeric conditions where the species grows.

Although in recent years large areas in the Mediterranean region have suffered degradation and habitat loss by human activities (Rotondi et al. 2003; Tzatzanis et al. 2003; Evrendilek et al. 2006; Peñas et al. 2011), we can assume a monetary value for sequestered

CO₂ of 0.00334 \$/lb (i.e. 0.00736 \$/kg; Peper et al. 2007) obtaining an economic benefit of 589,64 \$ ha⁻¹year⁻¹ for the Mediterranean shrublands. Extending this benefit to the Mediterranean shrublands of the whole country, which cover an area of roughly 10,000 km² (ISPRA 2010), we obtain a nationwide estimated annual benefit in the order of \$500 million. This means on one hand that, besides forests, Mediterranean shrublands contribute to a relevant amount of carbon sequestration. On the other hand, in the wake of increasing human pressure on natural resources caused by population growth in the coastal regions of the southern Mediterranean Basin (García-Ruiz et al. 2011), it is mandatory to protect the Mediterranean shrublands in order to preserve their carbon sequestration capacity. Nonetheless, global climate change could alter the species growth leading to a shift in species composition of the Mediterranean shrublands, according to their tolerance to drought. For instance, the competitive ability and fitness of *C. incanus*, *R. officinalis* and *E. multiflora*, which are characterized by a lower drought resistance, could be reduced with respect to the other Mediterranean species. In turn, variations in species composition might determine changes in the long-term CO₂ sequestration capacity of the Mediterranean shrublands. Negative changes in global climate (rising temperatures, higher frequency of drought and flood) are often the most consequential processes associated with an increased CO₂ concentration in the atmosphere (USDA NRCS 2000). The storage of higher C in these Mediterranean shrublands emphasizes the importance of maintaining or increasing the number of protected areas, according to Sharma et al. (2010). Accordingly, for correctly managing the effects of climate change, in particular in the more degraded or dryer areas of the Mediterranean region, the effects on the species capacity of sequestering carbon need to be taken into account.

From a methodological viewpoint, some considerations can be made on the method we used to monitor C sequestration capability in Mediterranean shrublands. On one hand, one possible drawback of the selected method could be that C sequestration in forests and shrublands is strongly age dependent. Moreover, C stored in soils is not considered here, while it may be important for carbon balance, as suggested by Padilla et al. (2010). Nevertheless, considering that Mediterranean shrublands characterized by sclerophyllous species usually have a low relative grow rate (Gratani and Crescente 1997), thus maintaining their biomass more or less constant over time (Gratani and Amadori 1991; Gratani and Crescente 2000), neglecting the age-dependency of C sequestration will not result in a serious source of error. Overall, the proposed method can facilitate monitoring of C sequestration over large areas with a low monetary cost and with the possibility to change the management practices where C sequestration estimates will result in decreases over time. In this framework, it would be interesting to promote an international data bank on C sequestration per vegetation type and according to different management practices. Overall, the results underline the value of the ecosystem services provided by the Mediterranean shrublands throughout their contribution to decrease carbon emissions. Considering that forest management practices, which were successful in the past may not guarantee future success (Bravo et al. 2009), C sequestration may become an additional output that land-owners might consider in their management decisions (Montagnini and Nair 2004).

5 Conclusions

The generalized pressure increase on natural resources caused by population growth in the southern Mediterranean Basin has affected plant cover, in particular, in the Mediterranean forests and shrublands (Padilla et al. 2010; García-Ruiz et al. 2011). To reverse the land

degradation processes, restoration in the Mediterranean Basin has been frequently obtained by planting indigenous and exotic conifers (Pausas et al. 2004), because of their rapid growth and aridity resistance. Nevertheless, the introduction of exotic species altered the original landscape (Bianchi et al. 2005). Several studies reported that planting indigenous shrubs is more efficient than using allochthonous species for restoring degraded soils (Olukoye et al. 2003; Caravaca et al. 2003; Rey Benayas and Camacho-Cruz 2004; Harris et al. 2006). Our results emphasize that the association of native shrub species is important for keeping the shrublands efficient in C sequestration. Moreover, our results also show that volume, LAI and spt are the key traits characterizing the CO₂ sequestration capability of the main Mediterranean shrublands species. Increasing drought stress could lead to a shift in the species composition, in particular, *C. incanus*, *R. officinalis* and *E. multiflora* which are characterized by a lower drought resistance could be at a disadvantage with respect to the other species. This disadvantage in the long-term could be followed by changes in species distribution conferred by the capacity of the species to survive under the new climatic constraints, and consequently by changes in C acquisition of the Mediterranean shrublands. Thus, a central goal of comparative ecology is the understanding of functional strategies among Mediterranean species to cope with increasing drought in order to monitor carbon sequestration capacity over time. One of the current challenges of forest management is to promote regeneration of tree species to preserve the genetic variability at the community level (Muscolo et al. 2010). Overall, Mediterranean shrublands are able to remove significant quantities of C from the atmosphere (22 Mg C ha⁻¹ year⁻¹). Therefore, a better understanding of the carbon sequestration at the species level could be useful for improving restoration projects and reintroduction actions of native species, in particular, in more degraded or dryer areas in the Mediterranean region.

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