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Variation in shrub structure and species co-occurrence in the Mediterranean maquis

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Abstract

The structure of the Mediterranean maquis developing inside the Presidential Estate of Castelporziano (S-SW of Rome) was due to mixture of different evergreen species. On an average six species co-occurred in shrub formation, the highest frequency being of *Cistus incanus* (80%), *Erica multiflora* (73%), *Smilax aspera* (53%) and *Quercus ilex* (50%). Discriminant analysis indicated that shrub volume was the most discriminating trait among the analysed shrub traits (height, volume, crown height, crown depth, major axis and minor axis of the crown, crown projection at soil, crown volume, leaf area index). On the base of shrub volume, three different sizes of shrubs were defined by cluster analysis: small (S), medium (M) and large (L) shrubs and they were characterised by a volume of 1.9±1.5m^3, 13.1±4.8 m^3 and 34.9±8.8 m^3 respectively. The considered maquis stand was constituted by 1050±300 shrubs ha^{-1}, corresponding to a total shrub volume of 7793±1401 m^3 ha^{-1}; the frequency of S, M and L shrubs was 63%, 31% and 6% respectively. Number of species increased from S to L shrubs: S were constituted by 4.8±1.7 species, M by 7.4±1.6 and L shrubs by 8.3±0.8. *Cistus incanus*, *Daphne gnidium*, *Erica multiflora*, *Pistacia lentiscus* and *Rosmarinus officinalis* of small height (< 1 m) occurred mainly in S shrubs, while *Arbutus unedo*, *Erica arborea*, *Phillyrea latifolia* and *Quercus ilex* (height = 1.4±0.3 m) in medium and large shrubs. The impact of shrub size on the Mediterranean maquis resulted in a patchiness of microclimatic variations showing the buffering effect of the shrub size: 78% of the study area was covered by shrubs having 4% and 94% reduction of air temperature and light transmittance respectively, and 10% and 165% increase of air humidity and soil water content respectively. The remaining 22% of the study area was uncovered and directly subjected to the climate of the zone.

Introduction

Mediterranean maquis is largely distributed in areas around the Mediterranean Basin, and its structure is strongly influenced by water and light availability (Sala, 1999; Vilà and Sardans, 1999). Soil moisture permitting, sites with high radiation often support nearly monospecific closed canopy stands of large-stature shrub species (Schlesinger *et al*., 1982) and high leaf area index (LAI) values (Diaz Barradas and Garcia Novo, 1987). Where canopy closure is prohibited, due to insufficient soil moisture, shrub species exploit canopy opening due to their drought tolerance (Kirkpatrick and Hutchinson, 1980; Shmida and Whittaker, 1981; Schlesinger *et al*., 1982). In coastal shrubs, certain species and species-assemblages are distributed in accordance with gradient in environmental conditions (Mooney and Harrison, 1972; Kirkpatrick and Hutchinson, 1980; Steward and Webber, 1981; Westman, 1981; Franklin, 1998). The canopy structure of shrub species modifies the microclimate beneath and around them by shading, and it influences the amount of soil moisture available to plants (Miller *et al*., 1981; Sala *et al*., 1994; Breshears *et al*., 1998). Depending on their structure, individuals occupy their areas exclusively that is fill them completely or share with individuals of other species leading to plant aggregation in which neighbours buffer one another from potentially limiting physical stresses (Franco and Nobel, 1989; Bertness and Callaway, 1994; Franco-Pizaña *et al*., 1995). Shrub structure may affect plant production under variable water availability; in arid and semi-arid areas, different spatial distribution patterns of the same numbers of shrubs have different effects on plant water use, evaporation and hydrology (Shuttleworth and Wallace, 1985).

Global change is considered to affect various ecosystems in the world, and monitoring their response to global change has been identified as a crucial component of global research programs (Merino *et al.*, 1995; Saxe *et al.*, 2001). Predictions of future climate include an expectation that changes in the average values of climatic variables may modify the intensity and interactions of environmental stress on vegetation, particularly in the areas like the Mediterranean Basin where aridity is an actual problem. Most major responses of shrub species on the long-term to global change seem to be variation in plant structure, productivity and species distribution (Haase *et al.*, 2000; Saxe *et al.*, 2001). A lower productivity and a reduced total leaf area accelerate soil degradation and erosion leading to mass movement and landscape instability (Haase *et al.*, 2000). The shrub relatively complex structure makes them excellent models to determine and understand the impact of global change on ecosystem functioning (Moreno and Oechel, 1995).

In the present study, we analysed shrub structure in the Mediterranean maquis developing along the coast near Rome. We would analyse: 1) if the size of shrubs depended on the co-occurrence of different species, 2) the role of shrub size in affecting microclimate. A better understanding of shrub structure and species co-occurrence in Mediterranean ecosystems may provide useful information on the resource dynamics of the communities. Furthermore, this type of data is important for map-making, remote sensing and regional estimation of primary productivity in Mediterranean areas (Sternberg and Shoshany, 2001).

Methods

Study area

The study area was located in the Mediterranean maquis developing inside the Presidential Estate of Castelporziano, near Rome (Italy) (41°45’ N; 12°26’ E). The climate was of Mediterranean type (Fig. 1): the average annual total rainfall was of 701 mm, most of which (68%)

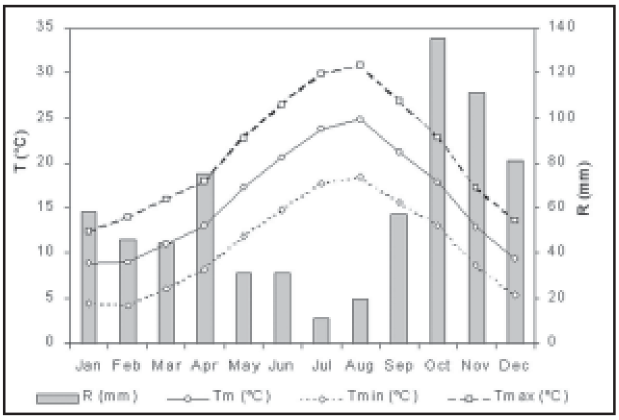

Fig. 1. Annual trend of total monthly rainfall (R), monthly average minimum air temperature (Tmin), monthly average air temperature (Tm) and monthly average maximum air temperature (Tmax). Data by the Castelporziano Meteorological Station for the period 1987-2001.

distributed in autumn and winter. The average minimum air temperature of the coldest month (February) was 4.1°C, and the average maximum air temperature of the hottest month (August) was 30.9°C. Dry period was from the middle of May to the end of August (77 mm, total rainfall of the period) (data by the Castelporziano Meteorological Station for the period 1987-2001). The considered maquis stand was in a good conservation state.

Measurements were carried out during the year 2001 on five sample areas (100 m^2 each) randomly distributed over an area of 10.000 m^2.

Variation in structural traits among species

The considered species were characterised by one or more shoots. Measurements of species structure included: height (h_s, defined as the maximum vertical distance from the ground level to the highest point of the plant, Acosta *et al.*, 1997) and length (l_s) for the liane species (*Lonicera implexa* Aiton and *Smilax aspera* L.) and *Asparagus acutifolius* L. The crown projection area on the soil (p_s) was calculated by the orthogonal axes assigning a simple geometric plane such as circle or ellipse.

Variation in structural traits among shrubs

Measurements of shrub structure were carried out on fifty shrubs randomly distributed in the sample areas, and including: total height (h, defined as the maximum vertical distance from the soil level to the highest point of the shrub), height of the shrub crown (Ch, defined as the vertical distance from the lowest leaf insertion to the highest point of the shrub), depth of the shrub crown (CD, excluding the central non-foliated branch portion, according to Schulze *et al.*, 1977), major axis (A) and minor axis (a, orthogonal to A) of the shrub crown, the shrub crown projection area on the soil (CP, calculated from A and a by assigning simple geometric planes, such as circle or ellipse). Shrub volume (V) was derived from the measured traits, by assigning simple geometric solids to shrub form, such as cone, semisphere and ellipsoid; the volume of the shrub crown (CV) was calculated excluding the central non-foliated branch portion of shrub. Number of species per shrub and shrub density (number of shrubs ha^{-1}) were recorded.

Leaf area index (LAI, total leaf area per unit of ground area) of shrubs was estimated by the “LAI 2000 Plant Canopy Analizer” (LI-COR Inc., Lincon, Nebrasca, USA), according to Morales *et al.* (1996). The LAI of the maquis was calculated as the mean value of 100 measurements carried out randomly in the considered stand.

Microclimate within shrubs

Microclimate measurements were carried out on twenty shrubs randomly distributed in the selected sample areas. All measurements (ten measurements per shrub) were carried out outside and inside (at the base) shrubs, during the drought period (July-August).

Photosynthetic active radiation (PAR) was measured by a Radiometer (LI-185B with a 190SB Quantum Sensor, LI-COR, U.S.A.), according to Hartz–Rubin and De Lucia (2001); air temperature (T) and air humidity (H) were measured by a Thermo-Hygrometer (HD8901, Delta Ohm, It), soil water content (SWC) by three soil samples taken at 30 cm depth, soil dry weight after drying at 105°C until constant weight (Rundel and Jarrell, 1989). The ratio between PAR ($PAR_{i/o}$), air temperature ($T_{i/o}$), air humidity ($H_{i/o}$) and soil water content ($SWC_{i/o}$) measured inside and outside (at the base) shrubs was calculated.

Statistical analysis

All statistical tests were performed using a statistical software package (Statistica, Statsoft, USA). Differences in mean shrub traits were determined by analysis of variance (ANOVA) and Tukey test for multiple comparisons. Box and whisker plots were used to compare the distribution of shrub volume.

A test of the best predictors of the shrub traits was conducted by stepwise multiple regression analysis employing microclimatic data as dependent variables and structural measured traits as independent variables (Nevo *et al.*, 2000).

Cluster analysis, using Euclidean distance and unweighted pair-group average method (UPGMA), and dendrograms were used to analyse similarity among shrubs and to define shrub clusters (Sneath and Sokal, 1973; Scudeller *et al.*, 2001; Smith and Steenkamp, 2001).

Stepwise discriminant analysis was conducted on shrub traits to determine the most discriminant traits among clusters; at each step all traits were reviewed in order to evaluate which one contributed most to the discrimination between clusters (Nevo *et al.*, 2000; Menalled and Kelty, 2001).

Results

Variation in structural traits among species

The Mediterranean maquis of Castelporziano was characterised by the following evergreen woody species: *Arbutus unedo* L., *Asparagus acutifolius* L., *Cistus incanus* L., *Daphne gnidium* L., *Erica arborea* L., *Erica multiflora* L., *Lonicera implexa* Aiton, *Pistacia lentiscus* L., *Phillyrea latifolia* L., *Quercus ilex* L., *Rosmarinus officinalis* L. and *Smilax aspera* L. All the considered species were characterised by one or more shoots.

Table 1. Structural traits of the considered species: h_S = species height; p_S = species crown projection area on the soil. * = species length.

Species	h_S (m)	p_S (m^2)
A. unedo	1.2±0.2	5.3±2.0
C. incanus	0.8±0.1	1.2±0.7
D. gnidium	0.8±0.3	0.2±0.1
E. arborea	1.8±0.2	2.8±0.2
E. multiflora	0.9±0.1	2.0±1.0
P. latifolia	1.2±0.2	1.9±0.7
P. lentiscus	0.9±0.2	0.8±0.4
Q. ilex	1.5±0.3	6.4±2.9
R. officinalis	0.9±0.2	2.4±1.5
A. acutifolius	1.08±0.26*	-
L. implexa	0.53±0.22*	-
S. aspera	1.23±0.17*	-

Significant ($p < 0.01$) variations were observed in species height, ranging from 0.8±0.1 (*C. incanus* and *D. gnidium*) to 1.8±0.2 m (*E. arborea*), and crown projection on the soil, from 0.2±0.1 (*D. gnidium*) to 6.4±2.9 m^2 (*Q. ilex*); length ranged from 0.53±0.22 (*L. implexa*) to 1.23±0.17 m (*S. aspera*) (Table 1).

Variation in structural traits among shrubs

Shrubs did not overlapped, though the crown of adjacent shrubs sometimes just touched. On an average, 86% of shrubs was formed by several species (up to a maximum of ten) the highest frequency of occurrence being of *C. incanus* (80%), *E. multiflora* (73%), *S. aspera* (53%) and *Q. ilex* (50%) (Table 2). 14% of shrubs was formed by one species of which 6 % by *C. incanus*, 3 % by *D. gnidium,* 2 % by *R. officinalis* and 1 % by *Q. ilex*.

Table 2. Frequency of occurrence (%) of species in shrubs.

C. incanus	*E. multiflora*	*S. aspera*	*Q. ilex*
80	73	53	50
P. latifolia	*A. acutifolius*	*A. unedo*	*D. gnidium*
45	42	41	41
R. officinalis	*L. implexa*	*P. lentiscus*	*E. arborea*
31	14	11	6

Significant differences ($p < 0.01$) were observed in shrub structural traits: h (from 0.5 to 2.7 m), Ch (from 0.2 to 2.4 m), CP (from 0.5 to 28.3 m^2), CD (from 0.1 to 0.4 m), CV (from 0.1 to 11.6 m^3), V (from 0.2 to 47.6 m^3) and LAI (from 1.3 to 4.0). The highest shrub LAI values (3.5-4.0) were mainly related to the occurrence of *Q. ilex* and *A. unedo*, and the lowest to *C. incanus* and *E. multiflora*.

Shrub traits were subjected to cluster analysis in order to define the affinity among shrubs by statistical linkage: the dendrogram obtained using the nine considered traits showed three clusters (Fig. 2). Discriminant analysis was used to indicate the most discriminant traits among clu-

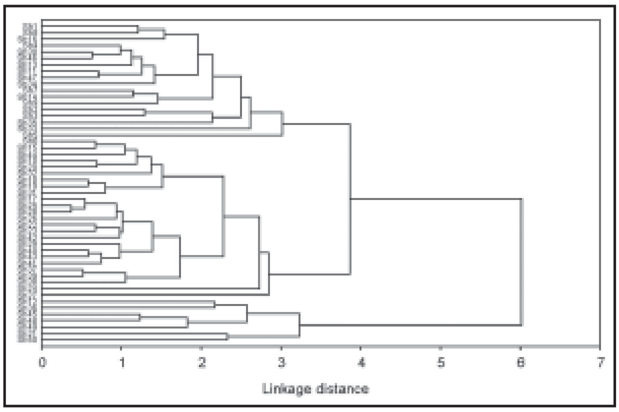

Fig. 2. Dendrogram based on Euclidean distance and unweighted pair-group average method using nine structural shrub traits (A = major axis of the shrub crown, a = minor axis of the shrub crown, CD = shrub crown depth, Ch = shrub crown height, CP = shrub crown projection area on the soil, CV = shrub crown volume, h = shrub height, LAI = leaf area index, V = shrub volume) for fifty shrubs randomly distributed in the sample areas.

Table 3. Summary table obtained by stepwise discriminant analysis based on the shrub structural traits. A = major axis of the shrub crown, a = minor axis of the shrub crown, CD = shrub crown depth, Ch = shrub crown height, CP = shrub crown projection area on the soil, h = shrub height, LAI = leaf area index, V = shrub volume.

Traits	N	Wilk's lambda	R2	F statistic
V	1	0.13073	0.9432	156.3
A	2	0.08319	0.9205	13.1
h	3	0.05571	0.9087	11.1
CP	4	0.04225	0.9810	7.0
Ch	5	0.03842	0.9129	2.1
a	6	0.03409	0.8677	2.7
CD	7	0.03155	0.2552	1.7
LAI	8	0.02933	0.2101	1.5

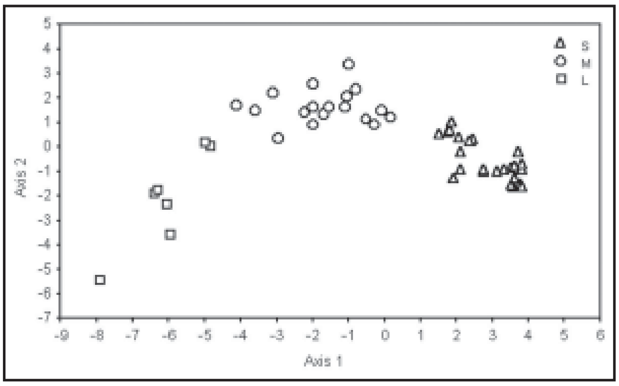

Fig. 3. Plot of canonical discriminant functions 1 and 2 based on eight differentiating traits (A = major axis of the shrub crown, a = minor axis of the shrub crown, CD = shrub crown depth, Ch = shrub crown height, CP = shrub crown projection area on the soil, h = shrub height, LAI = leaf area index, V = shrub volume). Three shrub clusters were distinguished: small (S), medium (M) and large (L) shrubs. The proportion of discriminatory power attributed to the first and second functions was 85.5% and 15.5%, respectively. Values in brackets were correlations with axis 1 and correlation with axis 2, respectively: V (-0.76, -0.41); A (-0.46, 0.22); h (-0.63, 0.09); CP (-0.70, -0.12); Ch (-0.61, 0.02); a (-0.58, -0.12); CD (-0.20, 0.14); LAI (-0.26, -0.07). Each point represented the value of a shrub.

sters, and stepwise procedure (Table 3) showed that shrub volume was the most discriminant trait (Fig. 3). Thus, on the base of the volume it was possible to define the size of the three clusters: the first cluster (small shrub = S) was characterised by 1.9±1.5 m^3 V, the second cluster (medium shrub = M) by 13.1±4.8 m^3 V, and the third cluster (large shrub = L) by 34.9±8.8 m^3 V (Table 4). Box and whisker plots confirmed the different distribution of V values in the three shrub clusters (Fig. 4). The increase of the shrub crown volume was not directly proportional to the increase of total shrub volume, and the ratio of CV to V decreased from S (0.30±0.09) to L (0.21±0.04) shrubs.

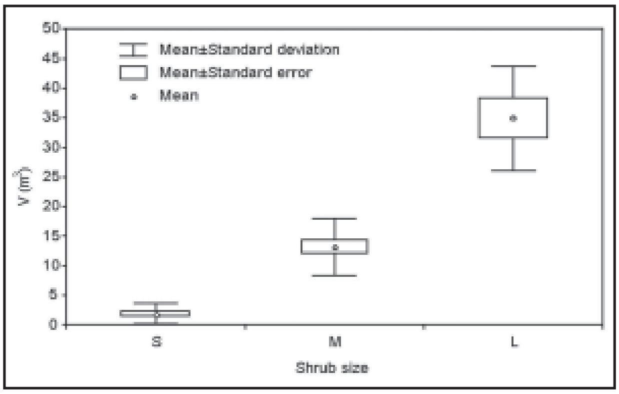

Fig. 4. Box and whisker plots showing the different distribution of shrub volume (V) in the three shrub clusters: small (S), medium (M) and large (L) clusters. Mean volume values were significantly different among shrub clusters ($p < 0.01$). Solid dot indicated the mean, box gave ± standard error, and bar showed ± standard deviation.

The number of species increased from S to L shrubs: on an average S shrubs were constituted by 4.8±1.7, M by 7.4±1.6 and L shrubs by 8.3±0.8 species. In particular, *C. incanus* (100% of frequency), *E. multiflora* (96%), *A. acutifolius* (60%) and *R. officinalis* (38%) occurred mainly in S shrubs, C. *incanus* and *S. aspera* (94%), *Q. ilex* and *E. multiflora* (89%) in M shrubs, and *A. unedo, P. latifolia* and *Q. ilex* (100%) in L shrubs (Table 5).

The density of the considered Mediterranean maquis stand was 1050±300 shrubs ha^{-1} corresponding to a total shrub volume of 7793±1401 m^3 ha^{-1}, the frequency of occurrence of S, M and L shrubs in the stand was 63%, 31% and 6% respectively. The total surface area covered by shrubs (calculated by the shrub crown projection on the soil) was 7807±938 m^2 ha^{-1}, of which 29%, 52% and 19% were of S, M and L shrubs respectively.

Microclimate within shrubs

$H_{i/o}$ and $SWC_{i/o}$ significantly ($p < 0.05$) increased from S (1.02±0.04 and 1.70±0.71 respectively) to L shrubs (1.18±0.05 and 4.44±0.38 respectively), while $PAR_{i/o}$ and $T_{i/o}$ significantly ($p < 0.05$) decreased from S (0.07±0.04 and 0.99±0.02 respectively) to L (0.04±0.02 and 0.92±0.02 respectively) ones (Table 6).

Multiple regression analysis between microclimatic variables ($T_{i/o}$, $H_{i/o}$, $PAR_{i/o}$, $SWC_{i/o}$) and the measured shrub structural traits (A, a, h, Ch, CD, LAI) was highly significant ($p < 0.01$); h, Ch and CD were the most significant traits contributing to changes in PAR, air temperature, air humidity and soil water content within shrubs (Table 7).

Table 4. Structural traits of S (small), M (medium) and L (large) shrub clusters: A = major axis of the shrub crown, a = minor axis of the shrub crown, CD = shrub crown depth, Ch = shrub crown height, CP = shrub crown projection area on the soil, CV = shrub crown volume, h = shrub height, LAI = leaf area index, V = shrub volume. Means of S, M, L shrubs with the same letter are not significantly different (p > 0.05).

Shrubs	h (m)	A (m)	a (m)	Ch (m)	CD (m)	CP (m2)	CV (m3)	V (m3)	LAI
S	0.72±0.18	2.36±1.00	1.57±0.52	0.49±0.15	0.21±0.08	3.39±2.22	0.53±0.41	1.92±1.54	2.36±0.53
M	1.50±0.29	4.89±1.06a	3.01±0.60	1.21±0.30	0.30±0.06	12.53±3.79	3.12±0.90	13.12±4.81	2.98±0.56
L	2.13±0.39	6.11±0.71a	4.86±0.91	1.88±0.41	0.32±0.06	23.80±4.17	7.44±2.32	34.89±8.77	3.82±0.20
Mean	1.20±0.58	3.80±1.79	2.55±1.30	0.94±0.56	0.26±0.09	9.54±7.82	2.43±2.58	10.57±11.99	2.81±0.71

Table 5. Frequency of occurrence (%) of species in small (S), medium (M) and large (L) shrub types.

Shrubs	*A. acutifolius*	*A. unedo*	*C. incanus*	*D. gnidium*	*E. arborea*	*E. multiflora*	*L. implexa*	*P. latifolia*	*P. lentiscus*	*Q. ilex*	*R. officinalis*	*S. aspera*
S	60	32	100	32	0	96	16	36	8	24	38	36
M	67	72	94	83	17	89	28	61	17	89	44	94
L	71	100	86	43	29	71	29	100	29	100	14	86

Table 6. Microclimate changes within S (small), M (medium) and L (large) shrub clusters: $PAR_{i/o}$ = ratio between photosynthetic active radiation measured inside and outside shrub, $T_{i/o}$ = ratio between air temperature measured inside and outside shrub, $H_{i/o}$ = ratio between air humidity measured inside and outside shrub, $SWC_{i/o}$ = ratio between soil water content measured inside and outside shrub. Means of S, M, L shrubs with the same letter are not significantly different ($p > 0.05$).

Shrubs	$PAR_{i/o}$	$T_{i/o}$	$H_{i/o}$	$SWC_{i/o}$
S	0.07±0.04[a]	0.99±0.02	1.02±0.04	1.70±0.71
M	0.05±0.02[ab]	0.95±0.02	1.12±0.06[a]	2.47±0.28
L	0.04±0.02[b]	0.92±0.02	1.18±0.05[a]	4.44±0.38
Mean	0.06±0.03	0.96±0.04	1.10±0.08	2.65±1.21

Table 7. Coefficients of multiple regression (r) for the microclimatic variables, as the dependent variables, and six shrub structural traits (only the non-derived structural traits) as the independent variables. A = major axis of the shrub crown; a = minor axis of the shrub crown; CD = shrub crown depth; Ch = shrub crown height; h = shrub height; LAI = leaf area index; $H_{i/o}$ = ratio between air humidity measured inside and outside shrub, $PAR_{i/o}$ = ratio between photosynthetic active radiation measured inside and outside shrub; $SWC_{i/o}$ = ratio between soil water content measured inside and outside shrub; $T_{i/o}$ = ratio between air temperature measured inside and outside shrub. All the correlations were significant at $p < 0.01$.

Microclimatic variables	Stepwise model	by structural traits
$PAR_{i/o}$	CD	CD
	$r = 0.62$	$r = 0.62$
$T_{i/o}$	h	h, a
	$r = 0.89$	$r = 0.90$
$H_{i/o}$	h	h
	$r = 0.86$	$r = 0.86$
$SWC_{i/o}$	Ch	Ch, A, a, h
	$r = 0.88$	$r = 0.91$

On the base of these results it was possible to evaluate the microclimatic patchiness of the study area: 78% of the study area was covered by shrubs and this area had a microclimate characterised by 4% and 94% reduction of air temperature and light transmittance respectively, and 10% and 165% increase of air humidity and soil water content respectively. The remaining 22% of the study area was uncovered and directly subjected to the climate of the zone.

Discussion

The results on the whole underline that the maquis stand at Castelporziano is characterised by twelve evergreen woody species occurring in shrub composition. A number of factors including the distribution of resources in habitats, morphological traits and competition processes may contribute to species individuals being aggregated (Falster *et al.*, 2001). On an average six species co-occur in shrub formation, the highest frequency (50%) being of *C. incanus*, *E. multiflora*, *S. aspera* and *Q. ilex*.

As regard as the size, three types of shrubs are identified and the number of species increases from small to large shrubs. *C. incanus*, *D. gnidium*, *E. multiflora*, *P. lentiscus* and *R. officinalis*, characterised by a small height (< 1m) and 1.3±0.8 m^2 mean crown projection area on the soil, occur frequently in small size shrubs or at the edge of medium and large size shrubs. *A. unedo*, *E. arborea*, *P. latifolia* and *Q. ilex*, characterised by 1.4±0.3 m mean height and 4.1±2.1 m^2 mean crown projection area on the soil, occur frequently in medium and large size shrubs. *A. acutifolius*, *L. implexa* and *S. aspera* seem to be not in relationship with the shrub size.

The climate of the studied area, characterised by 701 mm of the total annual rainfall and a drought period of three-four months, makes possible the presence of an aspect of the Mediterranean maquis characterised by a density of 1050±300 shrubs ha^{-1} corresponding to a total covered area of 7807±938 m^2 ha^{-1}, of which 29% of small, 52% of medium and 19% of large shrubs, and a mean LAI of 2.8. *E. multiflora* (17.1%), *Q. ilex* (15.5%), *C. incanus* (14.0%) and *A. unedo* (12.4%) contribute to 60% of the total covered area. The LAI of the vegetation in Mediterranean region commonly is in the range 1-2 increasing to 3-4 as rainfall increases or the site water balance becomes more favourable (Lossaint, 1973; Cody and Mooney, 1978; Miller *et al.*, 1981; Diaz Barradas and Garcia Novo, 1987; Rambal and Leterme, 1987), the highest values corresponding to *Quercus ilex* evergreen forests (Gratani, 1997; Gratani and Crescente, 2000).

Shrub volume modifies the microclimate beneath and around shrubs, in accordance to the results of Cernusca and Seeber (1981) and Breshears *et al.* (1998). Microclimate within shrubs varies according to shrub size defining patterns of light-capturing areas (94% light extinction, mean value), and the air temperature buffering effect of the canopy (4% temperature reduction, mean value). Shrubs of medium size contribute the most to the microclimatic patchiness of the maquis: i.e. 41% of the stand has a PAR reduction of 95%, associated to 5% air temperature reduction, 12% air humidity increase and 147% soil water content increase. The inter-shrub patches directly exposed to the local climate are 22% of the total area. This structural arrangement of shrubs in the space seems to be an optimisation strategy creating favourable microenvironmental conditions which are advantageous to limit canopy evaporation of the considered species during drought (Gratani, 1995; Gratani and Bombelli, 1999).

Climate-induced increases in disturbance could, in turn, significantly alter the species composition and the structural arrangement of the plant species in the space (Overpeck *et al*., 1990). The realised inventory of shrub structural traits, representative of 54 ha of Mediterranean maquis in a good conservation state, may provide a critical foundation for understanding seasonal and spatial pattern in shrub canopy water use efficiency over time under the impact of global change. Moreover, this type of data may be used to realise ecosystem inventories giving information on the status, the resource use, and the possible time-scale of responses to perturbations (Halvorson and Maender, 1994; Halvorson, 1998).

Acknowledgments

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