THE MEDITERRANEAN DWARF SHRUBS: ORIGIN AND ADAPTIVE RADIATION

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ABSTRACT - Basing on literature data, a synthesis on the morphologic, anatomic and physiologic adaptations of the Mediterranean dwarf shrubs is outlined. Three different functional types can be recognized: saltbushes, thermo-xerophilous fire-resistant dwarf shrubs and orophilous cushion-shrubs. The thermo-xerophilous fire-resistant dwarf shrubs mainly derive from the Mesogean flora and differentiated after the beginning of the Oligocene, and especially from the Pliocene, in the coastal regions around the Tethys Sea, as the result of a local adaptive radiation triggered by the shifting from subhumid to semiarid climatic conditions at the boundary between the tropical and the temperate zone. For the other two functional types, a Tethyan origin can be assumed. Both are probably originating from Irano-Turanian and Saharo-Arabian elements and came into the Mediterranean basin during the Messinian age. At the end of the Messinian age, the saltbushes didn't differentiate too much from their ancestors, while the orophilous cushion-shrubs, together with their "Polstergäste", passed through a new adaptive radiation, that gave rise to one of the richest systems of vicariant endemism.

KEYWORDS - Mediterranean Region, dwarf shrub, adaptation, endemism.

INTRODUCTION

In the Mediterranean region, three main kinds of dwarf shrubs are occurring: those dominating in the saltmarshes, those forming the thermoxerophilous vegetation locally named "tomillar", "garigue", "phrygana" or "bath'a", and those forming the oro-mediterranean thorny cushion-like vegetation, that was called by Pignatti (1978) "irano-nevadense". The name proposed by Pignatti emphasizes the pan-Mediterranean distribution of such vegetation, from Iran to Sierra Nevada (S-Spain), wherever the mountains are reaching the altitude of 1.600 m a.s.l.

Morphologic, anatomic and physiologic adaptations are featuring the three different typologies. Basing on relevant literature, the main differences of the three functional types are summarized in the following paragraphs.

Saltbushes

Saltbushes are represented in the Mediterranean region namely by *Chenopodiaceae*, such as *Arthrocnemum*, *Atriplex*, *Camphorosma*, *Cremnophyton*, *Halocnemum*, *Haloxylon*, *Kochia*, *Sarcocornia*, *Salsola*, *Suaeda*. All of them are found in coastal areas, on rocky or sandy substrates, periodically flooded of sprinkled by the seawater. In these environments, vegetation patterns are mainly driven by variation in the following parameters: salinity, waterlogging (soil saturation), inundation, soil texture and pH (Barbagallo *et al.*, 1991).

Most of the saltbushes have succulent leaves, with big vacuoles where large quantities of ions can be accumulated, in order to facilitate the water uptake from a soil solution that has a low water potential. The morpho-physiologic adaptations of saltbushes enable them to cope with the adverse effect of salts internally, or to excrete salts from cells and tissues (McKell, 1994). Cells of saltbushes are able to increase salt levels in the vacuoles by intracellular compartmentalization of ions and thus avoid high levels in the cytoplasm (Gorham, 1995). Although precise measurements are missing, it is likely that these plants need an intense solar radiation, because high levels of energy are required to keep efficient the ionic pump for the intracellular compartmentalization. Therefore, for these plants, an obligatory heliophily can be postulated. In TABLE 1, a synopsis of the main adaptations to environmental stresses of the Mediterranean saltbushes is reported.

Thermo-xerophilous fire-resistant dwarf shrubs

The thermo-xerophilous Mediterranean dwarf-shrubs developed several adaptations in order to tolerate the summer drought and heat stress, eventually ensuring a

TABLE 1 - Synopsis of the main adaptations to environmental stresses of the Mediterranean saltbushes.

Environmental stress	Adaptation	Functional consequence	Reference
Ionic imbalance/toxicity	Ion exclusion at the surface of the roots	Tolerance of salinity	Munns et al., 1983
	Cytoplasmatic compartmentalization	Tolerance of salinity	Marcum, 2001
	Salt extrusion through specialised glands or bladders	Tolerance of salinity	McKell, 1994
	Germination suspended during periods of high salinity	Tolerance of salinity	Ungar, 1978
Physiological drought	Highosmotic pressure in the tissues	Adequate water supply	Marcum, 2001
Summer drought	Reduced leaf area	Reduced water loss	(hypothesized)
Drought in general	High root/shoot ratio	Increased absorptive area	Maas, 1986
Summer heat	Succulence	Increased thermic inertia	(hypothesized)
	Reduced leaves	Reduced heat loading	(hypothesized)
	Open canopy architecture	Sensible heat removal	(hypothesized)
Wind	Reduced leaves	Reduced physical resistance and damage	(hypothesized)
	Low stature of plants	Reduced mechanical stress	(hypothesized)

vigorous post-fire regeneration. These adaptations include deep rooting, persistent seeds, flamable secondary compounds, epidermal trichomes, sunken stomata, reduced leaf area and seasonal leaf dimorphism.

In most cases, the adaptation to the summer environmental stresses includes a significant loss of the leaves. Several representatives of *Cistaceae*, *Rosaceae*, *Lamiaceae*, *Asteraceae*, *Scrophulariaceae*, Asparagaceae thin out the foliage during the dry season (Orshan, 1972; Pignatti, 1978; Margaris, 1981). Drought-deciduous plants often exhibit a seasonal dimorphism, with two sets of leaves: soft, drought-sensitive ones in winter and spring, replaced by smaller, more drought resistant ones in summer (Christodoulakis, 1989; Christodoulakis *et al.*, 1990; Kyparissias & Manetas, 1993; Gratani & Bombelli 1999; Aronne & De Micco, 2001).

Many Mediterranean thermo-xerophilous dwarf-shrubs are noted for the fragrance of their foliage. Aromatic oils have a threefold effect: they protect the plant against grazers, increase the speed of wildfires and diminish the loss of water vapour, as oils evaporate into the stomatal chambers (Margaris & Vokou, 1982; De Lillis, 1991).

TABLE 2 - Synopsis of the main adaptations to environmental stresses of the Mediterranean thermo-xerophilous fire-resistant dwarf-shrubs (after Richardson *et al.* (1986), modified).

Environmental stress	Adaptation	Functional consequence	Reference
Summer drought	Epidermal trichomes, waxes, thick cuticle	Reduced evapotranspiration	Orshan, 1972
	Sunken stomata	Increased boundary layer resistance	Orshan, 1972
	Reduced leaf area	Reduced water loss	Orshan, 1972
	Seasonal leaf dimorphism	Increased growth efficiency	see text
	Summer loss of the leaves	Reduced evapotranspiration	see text
	Aromatic oils in the stomatal chambers	Decreased evapotranspiration	De Lillis, 1991
	High root/shoot ratio	Increased absorptive area	(hypothesized)
	Deep rooting	Access to perennial water	Richardson et al., 1995
Summer heat	Rapid root growth of seedlings	Adequate water supply	Richardson et al., 1995
	Reduced or dissected leaves	Reduced heat loading	Orshan, 1972
	Open canopy architecture	Sensible heat removal	Orshan, 1972
	Epidermal trichomes, waxes, thick cuticle	Increased reflectance	Orshan, 1972
Wildfires	Serotiny	Fire avoidance	Mazzoleni, 1989
	Myrmechochory	Maintenance of viable populations	Aronne & Wilcock, 1994a
	Persistent seeds	Maintenance of viable populations	Mazzoleni, 1989
	Big rootstocks	Vigorous post-fire regeneration	Keeley, 1986
	Secundary flamable compounds	Limited fire damage	Richardson et al., 1995
Nutrient limitation	Bacterial symbioses	Facilitation of nutrient uptake	Lamont, 1983
	Fungal symbioses	Facilitation of nutrient uptake	Lamont, 1983
	Slow growth at maturity	Reduced nutrient requirements	Lamont, 1983
	Big rootstocks	Nutrient sequestration	Lamont, 1983
Predation	Secundary aromatic/toxic compounds	Unpalatability	Richardson et al., 1995
	Sclerophylly	Low nutrient content for herbivores	Richardson et al., 1995
	Low seed set	Minimization of predator resource base	Aronne & Wilcock, 1994b
	Prolific seed set	Predator satiation	Aronne & Wilcock, 1994b
	Myrmechochory	Avoidance of post-fire predation	Aronne & Wilcock, 1994b
Wind	Reduced leaves	Reduced physical resistance and damage	(hypothesized)
	Low stature of plants	Reduced mechanical stress	(hypothesized)

The root system, as well, helps these shrubs to cope with wildfires and summer drought: many species have a deep roots and young seedlings that typically germinate in autumn or late winter, have fast-growing taproots that ensure an early root development away from the soil surface, thus limiting the effects of the summer drought. Moreover, most of the Mediterranean thermo-xerophilous dwarf-shrubs developed several symbioses with fungi and bacteria, in order to increase the efficiency of nutrient-uptake (Kummerow, 1981; Puppi & Tartaglini, 1991).

In TABLE 2, a synopsis of the main adaptations to environmental stresses of the Mediterranean thermo-xerophilous fire-resistant dwarf shrubs is reported.

Orophilous cushion-shrubs

The oro-mediterranean dwarf-shrubs are often spiny, with a cushion-like growth form, that grants a remarkable resistance to intense solar radiation, persistent drought, wide-ranging temperatures and to the mechanical disturbance performed by strong winds (e.g. *Astragalus*, *Anthyllis*, *Armeria*, *Acantholimon*, *Erinacea*, *Plantago*). The oro-mediterranean seasonal drought is partially buffered by the moisture condensation that happens quite regularly in the early morning. The architecture of the thorny cushion-like shrubs is particularly efficient in filtering the moisty air: the point of the thorns constitutes the nucleus for the condensation of water droplets, that flow together along the branches and join the rootstock (Pignatti *et al.*, 1980). The spiny pulvinate growth form is so efficient in trapping the water and shielding from the harsh environmental conditions that many other plant species use to take shelter in the cushions. These plants have been defined "Polstergäste" by Rauh (1940).

An additional morphologic feature of these plants is a dual root system, with a thick, deep taproot and finer roots forming a mat near the soil surface, that

TABLE 3 - Synopsis of the main adaptations to environmental stresses of the Mediterranean orophilous cushion-shrubs.

Environmental stress	Adaptation	Functional consequence	Reference
Summer drought	Epidermal trichomes, waxes, thick cuticle	Reduced evapotranspiration	Steemann-Nielsen E., 1940
	Sunken stomata	Increased boundary layer resistance	Steemann-Nielsen E., 1940
	Reduced leaf area	Reduced water loss	Steemann-Nielsen E., 1940
	Thorny, hairy pulvinate architecture	Effective captation of the air moisture	Pignatti et al., 1980
	High root/shoot ratio	Increased absorptive area	Pignatti et al., 1980
	Dimorphic root system	Access to dew and deep water	Pignatti et al., 1980
Winter cold	Low stature of plants	Protection under the snow-deck	(hypothesized)
	Persistent dead leaves	Seasonal isolation of the buds	(hypothesized)
Nutrient limitation	Bacterial symbioses	Facilitation of nutrient uptake	Lamont, 1983
	Pulvinate architecture	More effective retention of the organic matter	Werner, 1978
	Slow growth at maturity	Reduced nutrient requirements	Pignatti et al., 1980
	Big rootstocks	Nutrient sequestration	Pignatti et al., 1980
Predation	Spines, secundary aromatic/toxic compounds	Unpalatability	Rikli, 1948
	Low seed set, prevalent anemochory	Minimization of predator resource base	(hypothesized)
Wind	Reduced leaves	Reduced physical resistance and damage	(hypothesized)
	Low stature of plants	Reduced mechanical stress	(hypothesized)
	Pulvinate architecture	More effective retention of finer soil particles	Werner, 1978

ensures an additional water uptake from the dew (Zederbauer, 1906; Pignatti *et al.*, 1980).

In TABLE 3, a synopsis of the main adaptations to environmental stresses of the Mediterranean orophilous cushion shrubs is reported.

Origin and Evolutionary trends

The thermo-xerophilous fire-resistant Mediterranean dwarf shrubs mainly derive from the so-called "Mesogean flora". They probably differentiated after the beginning of the Oligocene, and especially from the Pliocene, in the coastal regions around the Tethys Sea, as the result of a local adaptive radiation triggered by the shifting from subhumid to semiarid climatic conditions at the boundary between the tropical and the temperate zone. The Mesogean dwarf shrubs derive either from the humid Paleotropical Tertiary flora, coming from the African plate, and from the cool temperate Arcto-Tertiary flora, coming from Laurasia (Raven, 1973; Axelrod, 1975, Quezel 1995).

Some important evolutionary trends can be observed within this group (Pignatti, 1978; Herrera, 1984; Aronne & Wilcock, 1994b): from evergreen to drought-deciduous, from long to short life cycle, from dioecy to hermaphroditism, from fleshy few-seeded to dry many-seeded fruits. All these trends can be seen as the result of a local evolution triggered by a progressive increase of the summer drought and an increased probability of fire, under the selective pressure of limited soil nutrient and water availability. These trends are associated, as well, to remarkable year to year fluctuations of rainfalls and temperatures, that are featuring the Mediterranean climates more than any other climatic type in the world (Donley *et al.*, 1979, Hofrichter *et al.*, 2001). These factors may also explain the general evolutionary tendency of many Mediterranean plants towards therophytism (Mossa *et al.*, 2004), rewardless, species-speciion strategies (Dafni, 1987), and high investment in seed productivity (Wells, 1969). Obligate seeders have greater numbers of sexually produced generations, resulting in greater genetic recombination, which in turn contributes to more rapid speciation. This could explain why the Mediterranean region has such an high diversity of plant and insect species (Médail & Quézel, 1997).

The human exploitation of the environmental resources in the Mediterranean region increased everywhere the frequency and abundance of the thermo-xerophilous fire-resistant Mediterranean dwarf shrubs. The human activity created favourable conditions for the spreading of these plants and, perhaps, for a new adaptive radiation through hybridization and segregation of populations in different microhabitats related to the habitat fragmentation induced by man, whose activity exasperated the naturally fragmented habitat diversity of the Mediterranean lands.

For the other two types of Mediterranean dwarf shrubs, a Tethyan origin can be assumed: the saltbushes along the coasts of the inland sea and the orophilus cushion-shrubs in mountain deserts. Both are probably originating from Irano-Turanian and Saharo-Arabian elements and came into the Mediterranean basin during the Messinian Age (5.6 to 5.3 Myr. bp.). In that time, due to the periodical obstruction of the Gibraltar Strait, a large part of the Mediterranean Sea dried up and reflooded several times. In the most critical periods, the continental scarps were almost com-

FIGURE 1 - Hypothetical patterns of migration, during the Messinian age, of some representative genera of the Mediterranean cushion-shrubs, deriving from Saharo-Arabian (left) and Irano-Turanian (right) ancestors.

TABLE 4 - Synopsis of some orophilous vicariant species on the 5 biggest Mediterranean islands.

	Corsica	Sardinia			Sicily		Crete	Cyprus
	All massifs	Limbara	Gennargentu	Other massifs	Madonie	Etna	All massifs	Troodos
Silene	S. nodulosa	S. nodulosa	S. nodulosa	S. nodulosa	S. sicula	S. sicula	S. dictaea	S. longipetala
[illegible]	P. bicolor	P. bicolor	P. bicolor	P. bicolor	P. gasparrinii	P. gasparrinii	P. taygetea	P. kennedyae
Viola	V. corsica	V. limbarae	V. limbarae	V. limbarae	V. nebrodensis	V. aetnensis	V. fragrans	V. [illegible]
Galium	G. corsicum	G. corsicum	G. corsicum	G. corsicum	G. [illegible]	G. aetnense	G. creticum G. [illegible]	
Thymus	T. herba-barona	T. catharinae	T. catharinae	T. catharinae	T. spinulosus	–	T. leucotrichus	T. integer
Genista	G. salzmannii G. lobelioides	G. salzmannii	G. pichi-sermolliana	G. sulcitana G. desoleana	G. cupani	–	–	G. [illegible]
Cerastium	C. boissierianum C. soleirolii	C. boissierianum	C. boissierianum	C. supramontanum	C. columnae	C. columnae	–	–
Acinos	A. corsicus	–	–	A. sardous	A. nebrodensis	A. aetnensis	A. [illegible]	A. troodi
Saponaria	S. alsinoides		S. alsinoides	S. sicula	S. sicula	S. sicula	–	S. cypria
Euphorbia	E. corsica E. insularis		E. insularis	E. insularis	E. myrsinites	–	E. herniariifolia E. rechingeri	E. rigida E. veneris
Herniaria	H. litardierei	–	H. litardierei		H. nebrodensis	H. nebrodensis	H. cretica	H. [illegible]
Carlina	C. macrocephala	–	C. macrocephala		C. nebrodensis	C. nebrodensis	C. curetum	–
Thlaspi	T. brevistylum		T. brevistylum		T. rivale	–	T. creticum T. zaffranii	T. cyprium
Scleranthus	S. burnatii	–	–	–	S. marginatus	S. vulcanicus	S. verticillatus	S. verticillatus
Armeria	A. multiceps	A. sardoa	A. gennargentea	A. sardoa A. sulcitana	A. nebrodensis	–	–	–
Alyssum	A. robertianum		–	A. tavolarae	A. nebrodense	–	A. idaeum A. lassiticum	A. troodi A. cypricum
Astragalus	A. genargenteus	A. genargenteus	A. genargenteus	–	A. nebrodensis	A. siculus	A. angustifolius A. creticus A. dolichophyllus	A. [illegible]
Plantago	P. insularis		P. insularis	P. insularis	P. humilis	–	–	–
Scorzonera	–	–	–	S. callosa	S. villosa	–	S. idaea	S. troodea
Helianthemum			–	H. morisianum	H. nebrodense	–	H. hymettium	H. obtusifolium
Cynoglossum					C. nebrodense	–	C. sphacioticum	C. troodi
Sideritis		–	–	–	S. sicula	–	S. syriaca	S. cypria
Scutellaria	–	–	–		S. rubicunda		S. hirta	S. cypria
Onosma	–	–			O. canescens	–	O. erectum	O. troodi
Lepidium	L. [illegible]	–	–	–	L. nebrodense	–	L. hirtum	–
Peucedanum	P. paniculatum		–	–	P. nebrodense	–	P. alpinum	–
Erysimum	–		–	–	E. bonannianum	E. aetnense	E. mutabile E. raulinii	–

pletely emerged, and the bathyal floor turned into a patchy mosaic of sebkhas (i.e. salty deserts), saltmarshes and hypersalted, highly alkaline lakes, in depressions (Hsü, 1973). Erosion increased everywhere and diverse rocks were rapidly exposed. Moreover, the indirect uplift of the mountain ranges gave rise to huge rockfalls. The topographic diversity increased, and as mountain ranges were rapidly elevated, hundreds of new canyons and gorges were incised into them, steep slopes came into existence and divergent localised microhabitats developed everywhere. A lot of new ecological niches were ready to be colonised by pioneer plants with different adaptations (Bertolani-Marchetti & Cita, 1975; Bocquet *et al.*, 1978).

It is likely that saltmarshes and salty warps have been massively colonized by many halophilous Chenopodiaceae, coming from the southern- and eastern-rim of the Mediterranean basin, while screes, rockfall deposits and the continental scarps represented a suitable habitat for the ancestors of the thorny, cushion-like dwarf shrubs that are nowadays widely spread on the highest Mediterranean mountains (FIGURE 1). This kind of shrubs, originating from Irano-Turanian and Saharo-Arabian subdeserts, are still surviving next to the sea level in few, very isolated places of the Mediterranean region: for instance, in NW-Sardinia and S-Corsica (*Astragalus terraccianoi*, *Astragalus thermeum* and *Centaurea horrida*). Elsewhere, after the sea transgression that ended the Messinian age and a relative stability during late Pliocene, a new intensive speciation started in the Pleistocene (Pignatti, 1978), as a consequence of the early human impacts (fire). The progressively increasing competition with the Eu-Mediterranean thermo-xerophilous species cast the subdesertic ones out from the coastal garigues. But these strong, slow-growing plants have found an available ecological niche on the highest Mediterranean mountains, at the same altitudinal belt that, before the Messinian events, was chiefly colonised by the *Pino-Juniperetea* vegetation (Brullo *et al.*, 2001). The Mediterranean oro-echinophytes probably reached the high altitudes along huge rockfall screes.

After becoming isolated, at the end of the Messinian age, the saltbushes didn't differentiate too much from their ancestors, while the orophilous cushion-shrubs, together with their "Polstergäste", passed through a new adaptive radiation, giving rise to one of the richest system of vicariant endemism in the world. In TABLE 4, some orophilous vicariant species of the 5 biggest Mediterranean islands are listed, but similar examples of geographical vicariance can be observed on the North African mountains, on Sierra Nevada (S-Spain), on the Macedonian and Greek mountains, in Turkey and wherever, in the Mediterranean region, the mountains exceed the altitude of 1.600 m a.s.l.. The prevailing enthomophilous pollination probably contributed to the massive speciation of the Mediterranean oro-echinophytes, while the evolutionary torpidity of the Mediterranean saltbushes may be a result of the anemophilous pollination and the extreme physiologic adaptations characterizing this group of plants.

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