

Legumes in the Fire-Prone Mediterranean Regions: an Example From Greece*

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Abstract. Mediterranean climate ecosystems of the Mediterranean rim are rich in legumes, both as woody shrubs of the late successional stages and as short-lived, pioneer herbaceous plants. In a survey of the floras of numerous geographic regions of Greece, legumes in Mediterranean parts are found to contribute considerably more (11-16% of the total number of species) than in non-Mediterranean regions (6-8%). Legume presence is also notable in other Mediterranean-type ecosystems of the world; nevertheless most leguminous taxa of the Mediterranean basin are herbs in contrast to a significant contribution of shrubs in California and Chile. Due to their long-lived soil banks of hard coated seeds herbaceous legumes are usually among the early post-fire colonizers in the Mediterranean and may play a significant role in the succession of fire-prone communities.

Keywords: Mediterranean ecosystems; Greece; Leguminosae; Ecological success

Introduction

The legume family is considered an ecologically successful family of flowering plants worldwide (Rundel 1989). Legumes occur almost in every terrestrial biome, ranging from 80 m tall giants in the forests of South East Asia, to small desert ephemerals with a life span of a few months. The legume family comprises more than 17000 species which correspond to approximately 7% of the currently described vascular plants of the world. It is the third family in absolute number of taxa, exceeded only by Compositae and Orchidaceae (Mabberley 1987).

In the Mediterranean rim and in Greece it is the first in the number of taxa it has (Tutin et al 1964-1980), while it is high in the rank in other Mediterranean climate areas of the world, as for example, in the Cape Floristic Region, where it is the fourth (Cowling and Holmes 1992).

Ecological Success of Legumes

The legume taxa are ecologically very successful in terms of dominance and productivity. The morphological and physiological adaptations utilized by legumes are not unique. Other plant families demonstrate similar adaptive flexibility for one or several traits, but none exhibits the tremendous range of adaptations shown by legumes. These traits are expressed through remarkable levels of adaptive variation in morphological characters such as growth form, canopy architecture, root architecture, leaf morphology, pod and seed structure and in physiological features such as phenological controls, solar tracking, water relations, hard seed coats, nitrogen fixation and mycorrhizal associations (Rundel 1989).

In more detail, leguminous plants turn the leaves so that to have their surface perpendicular to the sun rays in the morning and the afternoon in order to maximize the incident radiation, while they keep them parallel to the sun rays at midday, in order to reduce the excessive heat load. They employ stem photosynthesis, which in certain cases may amount to about one third of the leaf tissue photosynthesis, with high water use efficiency of the fixed carbon (Rundel 1989). A similar high water use efficiency is presented by the phyllodes which are often developed as a sclerophyllous substitute of leaf tissue (Rundel 1989). An efficient water economy is also enhanced by adaptations such as nyctinastic closure of leaves and the phreatophytic habit in many desert legumes e.g. as the *Prosopis glandulosa* (Nilsen et al 1981). As far as it concerns nutrition, the adaptive mechanisms they have are related to nitrogen fixation through the development of nitrogen fixing root nodules in soils with limited nitrogen availability and the formation of mycorrhizal associations which enhance phosphorus uptake. Finally, they adopt various dispersal modes (endozoochory, autochory etc); in addition, the almost ubiquitous presence of hard seed coats ensures maximum seed survival (when fruits are consumed by animals) and contributes to the formation of permanent, long-lived soil seed banks.

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Distribution of Legumes

Legumes are abundant and frequently dominant in diverse terrestrial biomes, which cover a broad range of precipitation regime and length of dry periods.

In the dipterocarp forests of South East Asia legumes comprise only 3-5% of the total tree flora, while in the Neotropics the frequency of legumes in the tree flora is much higher, with typical values ranging between 11-13%. In the tropical forests of Africa legumes comprise 10% of the total flora (cited by Rundel 1989).

In the dry forests of the west coast of Mexico, 16% of the total flora are legumes, while in the subtropical forests of Brazil and Africa their participation ranges between 15 and 19% in ascending order (Eiten 1972, Malaisse 1978). In Africa and Australia, species of *Acacia* are overwhelmingly dominant in these communities (Palgrave 1977, Hopper and Maslin 1978, Whibley 1980, Ullmann 1985), while in North and South America woody legumes may make up to 90% or more of the woody plant cover in thornscrub, most notably with species of *Prosopis* and *Acacia* (Gentry 1942).

Deep Canyon in the Sonoran Desert of California has a legume flora of 11-13% of the total flora (Zabriskie 1979). The Sonoran Desert has 11.6% legume flora, while in the deserts of Central Australia legumes comprise 13% of the flora (Jessop 1981). The floristic diversity of legumes in the Sahara Desert is similarly high (Ozenda 1958).

The cold temperate environments typically have a relatively low diversity of legumes. In the cold and dry White Mountains of California only 4.3% of the flora are legumes (Loyd and Mitchell 1973). The flora of Alaska includes a similar 4.4% legume percentage (Hulten 1968).

Mediterranean climate ecosystems of the world have legume diversities ranging from very low values of 3.8% of the Chilean matorral (Rundel 1981) to relatively high, 13.3% for the sclerophyll forests of South Australia (Specht 1972), (Table 1).

Estimations based on the legumes listed in the Med-Checklist (Greuter et al. 1984-1989, Greuter 1991) give for the legume flora of the entire Mediterranean Basin an overall value of 7.6%. However, this is an underestimation, since countries, which do not have a Mediterranean-type climate, (like Libya and Bulgaria) are included in the list, simply because they are located around the Mediterranean Sea. In addition, larger or smaller parts of the circum-Mediterranean countries are not truly Mediterranean (e.g. northern and Atlantic France, southern parts of North African countries, tall mountain ranges in all countries), although they are considered as such.

When gradients in legume growth form and phenology are viewed from the wet tropical forest to dry deserts and Mediterranean climate ecosystems, there are clear patterns of change (Rundel 1989). One hundred per cent (100%) of the legume flora in the tropics of SE Asia are

trees, while only herbaceous forms of legumes can be found in Alaskan flora. At more mesic sites (seasonal tropical forest) legumes are predominately trees and woody lianas, with evergreen and semi-evergreen leaf phenology, while with increasing drought interactions the dominant growth forms become reduced in stature and leaves become reduced in size and have lower longevity. Growth forms change first to lower stature trees and shrubs and finally to domination by low shrubs and herbs. In more temperate environments, herbaceous perennials become the dominant growth form (Rundel 1989).

Legumes in the Mediterranean plant communities

According to estimations the total flora of Greece is composed of 4700 species; in the Med - Checklist, 416 legume species are recorded for Greece (Greuter et al. 1984-1989). One hundred and eighteen of these species (24.5%) belong to the mountain flora (Strid 1989), in altitudes higher than 1800 meters. Considering that the mountainous flora represents 42.1% of the total flora of Greece, it is evident that the legume flora is considerably underrepresented in the mountain flora of the country. Approximately 23% of the 1833 species of Leguminosae listed in the Med-Checklist (Greuter et al. 1984-1989) are found in Greece. Similarly, almost 49% of the species belonging to the Leguminosae family and referred in Flora Europaea are found in Greece (Tutin et al. 1964-1980), (Table 2).

In a survey of the floras of numerous (30 in total), typically Mediterranean regions of Greece (Figure 1, grey bars numbered 14-43) it is shown that legume percentage contribution in the total flora ranges from 11 to nearly 16% and in the majority of the cases between 12-14%, much higher than the overall values of Greece (or Cyprus). Mountainous areas (dotted bars 1-4) have a significantly lower contribution (6-7.5%). The existence of tall mountains is also considered to be the reason for the rather low percentage values of several areas with overall Mediterranean climates (5-13, stiped bars). Regions 5 and 11 are not mountainous but legume contribution is presumably decreased by the halophytic vegetation present (which is generally underrepresented in legumes); region 5,

Table 1. Contribution of leguminous taxa to the floras of several Mediterranean climate regions of the world; (1-5: Thomas 1961, Hoover 1970, Lathrop and Thorne 1978, Davis et al. 1988, Mooney 1977, 6: Rundel 1981, 7-9: Levyns 1966, Boucher 1977, Bond and Goldblatt 1984, 10: Specht 1972).

Region (Reference)	Legumes % of the total flora
CALIFORNIA (1-5)	3.9-6.9
CHILE (6)	3.8
SOUTH AFRICA (7-9)	7.3-10.9
AUSTRALIA (10)	8.8-13.3

Table 2. Contribution of legumes in the floras of selected floristic regions.

Floristic region	Total number of species	Number of legume species	Legume contribution (%)
Europe	11557	844	7.3
Mediterranean			
Countries	24000	1833	7.6
Greece	4700	416	8.8
Mountains of			
Greece	1980*	118*	6.0
Crete	1586	157	9.9
Cyprus	1800	168	9.3

* Numbers refer to species plus subspecies

Psathoura, is a small rocky island, seasonally covered in part by sea waves, while region 11, Strofilia coastal wetland, is mainly a marshland. Region 25 is a mountainous area with a climate between those of Mediterranean and Central Europe. The high legume contribution though is attributed to the human intervention and particularly the overgrazing pressure which is postulated to favour legumes. This same argument is used in the case of Oinousses islands (region 46) to explain the dramatically high percentage, 18.3% (Panitsa et al. 1994). As far as it concerns regions 44 and 45, the extreme values may be the artifact of the plant list compilation, which was performed during spring-time, thus favouring legumes and not including several autumn and winter flowering plants (geophytes, in particular).

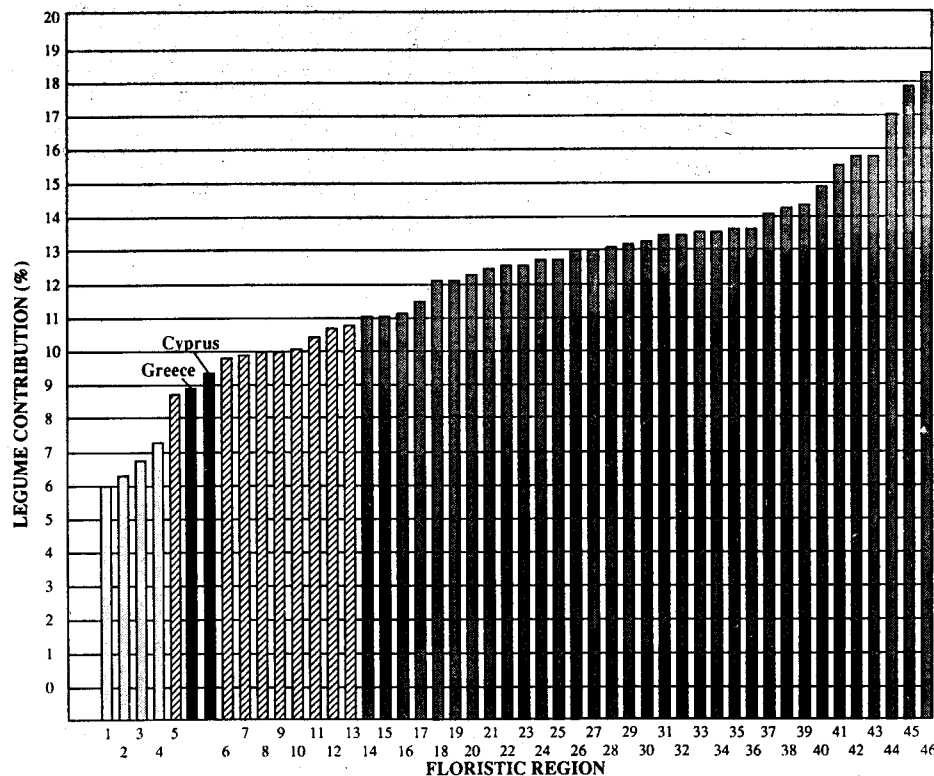


Figure 1. Contribution of legumes to the total flora of various geographic regions of Greece (in the cases marked with * the contribution has been estimated on a species plus subspecies basis). 1 Mountains of Greece * (Strid 1991) 2 Lailias Mt. (Voliotis 1977) 3 Macedonian Mts (Quezel and Contandriopoulos 1968) 4 Prespas Lakes Nat. Park (Pavlidis 1985) 5 Psathura Isl. (Snogerup et al. 1980) 6 Cholomon Mt. (Voliotis 1967) 7 Crete Isl. (Barclay 1986) 8 Lesbos Isl. (Cantargy 1889) 9 Euboea Isl. (Rechinger 1961) 10 Vertiscos Mt. range (Pavlidis 1982) 11 Strofilia hydrobiotope (Georgiadis et al. 1990) 12 Cephallonia Isl. (Phitos and Damboldt 1985) 13 Central Euboea Isl. (Phitos 1960) 14 Yioura Isl. (Kamari et al. 1988) 15 Armathia Isl. and 15 islets (Raus 1989) 16 Corfu Isl. (Georgiou 1988) 17 Syros Isl. (Sarlis 1994) 18 Skopelos Isl. (Economidou 1973) 19 Hymettus Mt. (Zerlendis 1973) 20 Ag. Evstratios Isl. (Snogerup 1991) 21 Schinias pine forest (Brofas and Karetos 1991) 22 Yiaros Isl. (Tzanoudakis 1981) 23 Skiathos Isl. (Economidou 1969) 24 Cythera Isl. (Yannitsaros 1969) 25 Mt. Paikon grazelands (Drossos and Athanassiadis 1989) 26 Kira Panagia Isl. (Snogerup et al. 1991) 27 Aetoloacarnanian lakes (Koumpli-Sovantzi 1983) 28 Cassandra Peninsula (Lavrentiadis 1961) 29 Dionysades Isls (Christodoulakis et al. 1990) 30 Chios Isl. * (Meikle 1954) 31 Santorini Isls (Hansen 1971) 32 Sithonia Peninsula (Pavlidis 1976) 33 Samos Isl. (Christodoulakis 1986) 34 Kos-Kalymnos-Pserimos-Telendos Isls (Hansen 1980) 35 Spetses Isl. (Nikolaidou and Yannitsaros 1992) 36 S. Euboeic Gulf islands (Sarlis 1981) 37 Elaphonesos Isl. (Yannitsaros 1971) 38 Piperi Isl. (Tsimburla and Yannitsaros 1992) 39 Skantzoura Isl. (Gustaffson and Snogerup 1974) 40 Nisyros Isl. (Papatsou 1975) 41 Paxi Isl. (Georgiadis et al. 1986) 42 Kassandra pine forests* (Tsitsoni and Karagiannakidou 1987) 43 Seven islets of N. Dodecanesus (Panitsa and Tzanoudakis 1991) 44 Kastellorizo Isl. (Greuter 1979) 45 Psara Isl. (Greuter 1976) 46 Oinousses Isls (Panitsa et al. 1994).

According to Flora Europaea (Tutin et al. 1964-1980), out of 844 legume species native in Europe, only 3 (0.4%) belong to Caesalpinioideae subfamily and 10 (1.8%) to Mimosoideae in contrast to the 831 species (98.5%) of the Papilionoideae (Lotoideae) subfamily. All 13 species belonging to Caesalpinioideae and Mimosoideae are trees. On the contrary, in the Papilionoideae subfamily, all growth forms are represented, but, the herbaceous elements dominate. Overall, in the leguminous flora of Europe only 2.1% are trees, while 75.6% are herbaceous plants (Table 3).

There is strong evidence that the majority of the legume plants of the floras of several Mediterranean regions of Greece are annual, biennial or perennial herbs: 85.9% of the legume flora of Kythira island (mostly phryganic vegetation, mature stage), (Yannitsaros 1969), 76.5% of the legume flora of Samos island (*Pinus brutia* forest and maquis), (Christodoulakis 1986), approximately 90% of the relevant flora of *Pinus halepensis* forests of Attica, recently burned, (Kazanis and Arianoutsou 1994). This habit might be related to their most common adaptation towards fire, which is seed germination. Most herbaceous legumes overcome fire occurrence through seed germination, while woody ones may also be resprouters (pers. observ.).

The vegetation of the Mediterranean communities is extremely flammable during summer months, because of the accumulation of great amounts of dead material (standing and fallen as litter) and the prevailing climatic conditions (high temperatures, shortage of available water), (Naveh 1967, 1973). Although fire is considered as a climate related hazard, it is also an environmental element itself. It is not surprising therefore that the plant species of the fire-prone environments of the Mediterranean ecosystems display many adaptations to fire (Naveh 1973, Rundel 1981, Arianoutsou-Faraggitaki and Margaris 1981). One of the most potentially adaptive traits of these plants is increased post-fire seed germination. The characteristics of this recruitment are strongly selected for at "normal" fire intervals.

It is well known that seeds of legumes possess a hard, water impermeable seed coat, which does not only permit the survival of seeds during a wildfire, but also requires the high temperatures developed by fire for the induction of germination (Doussi and Thanos 1993, Doussi and Thanos 1994). Legumes have been referred as an important component of post-fire successional communities of Mediterranean climate regions (Naveh 1967,

Arianoutsou-Faraggitaki and Margaris 1981, Thanos et al. 1989, Papavassiliou and Arianoutsou 1993, Kazanis and Arianoutsou 1994, Papavassiliou et al 1994, Thanos et al 1996). Although detailed data about the floristics and the dynamics of this succession are scarce there are certain evidences that an enrichment of the local floras in leguminous elements occurs. This enrichment may be slight, as in the case of a Californian chaparral (Armstrong 1977), to really impressive, as in the case of a *Pinus halepensis* forest in Attica, Greece, where legume taxa constituting approximately 9% of the flora of a mature stand more than doubled immediately after fire (Kazanis and Arianoutsou 1994).

The prolific appearance of the leguminous plants in the burned areas lasts for only the very early successional post-fire stages (Kazanis and Arianoutsou 1994). Most of these plants are annual or biennial herbs (op.c), which gradually become restricted both in species represented as well as in cover.

Up to the present, the work published cannot answer the questions why legumes are so abundant after fire and why legumes are so dominant in the burned places during only the early post-fire successional stages. On the other hand, their prolific presence in the regenerating post-fire communities has been attributed to their ability to fix atmospheric nitrogen, thus competing with other non-leguminous plants in the early post-fire environment. Papavassiliou and Arianoutsou (1993) have found that post-fire legumes do appear to have nodulation capacities, however, the actual effectiveness of this nodulation still remains to be studied.

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Table 3. Growth forms in the European legumes.

Subfamily	% Trees	% Shrubs	% Herbs
Caesalpinioideae	100 (3 spp.)	—	—
Mimosoideae	100(10 spp.)	—	—
Lotoideae	0.6 (5 spp.)	22.6 (188 spp.)	76.8 (638 spp.)
LEGUMINOSAE	2.1 (18 spp.)	22.3 (188 spp.)	75.6 (638 spp.)

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