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# LEGUMES IN THE FIRE-PRONE MEDITERRANEAN ENVIRONMENT

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## SUMMARY

Mediterranean climate ecosystems of the Mediterranean rim are impressively rich in legumes, both as woody shrubs of the mature stages and as short-lived, pioneer herbaceous taxa. In a wide survey of the floras of various geographic regions with Mediterranean climate in Greece, legumes are found to contribute with a high number of species in contrast to their lower representation in non-Mediterranean regions of Greece. Legume presence, although not impressive, is also notable for other Mediterranean type ecosystems of the world. Most leguminous taxa of the Mediterranean Basin are herbs, which is not the case for the other Mediterranean climate regions. The herbaceous legume taxa are among the early post-fire colonizers, thus assigning themselves an eminent role in the succession of the community.

## INTRODUCTION

The legume family might be considered as the most ecologically successful family of flowering plants in the world. Legumes occur almost in every terrestrial biome, ranging from 80 m 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. In the Mediterranean rim and in Greece it is the first in the number of taxa it has, while it is high in the ordination 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 do 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, seed hardcoatness, nitrogen fixation and mycorrhizal associations.

Table 1. Ecophysiological traits of legumes

**A. Photosynthesis**

1. Leaf orientation

Leaves track the sun in order to maximise the incident radiation (leaf surface perpendicular to the sun rays in the morning and afternoon) and reduce the excessive heat load (leaves parallel to the sun rays at midday).

2. Stem photosynthesis

It is only about one third of leaf tissue photosynthesis, however the water use efficiency of this fixed carbon is high.

3. Development of phyllodes

They provide a sclerophyllous substitute of leaf tissue, low in photosynthetic capacity but with high water use efficiency of the fixed carbon.

4. Fruit photosynthesis

The developing pods remain green for relatively long periods.

**B. Water relations**

- Many legumes are phreatophytes: e.g. the desert legumes (*Prosopis glandulosa*).
- Nyctinastic closure of leaves.

**C. Nutrient relations**

1. Development of nitrogen-fixing root nodules in soils with limited availability.
2. Development of mycorrhizal associations for increasing phosphorus uptake.

**D. Reproduction**

1. Hard seed coats

- Maximization of seed survival when fruits are consumed by animals.
- Formation of permanent soil seed banks.
- Development of fire resistance and successful post-fire colonization.

2. Modes of dispersal

Various.

**E. Chemical defence**

Formation of secondary compounds (e.g. alkaloids) as chemical defence substances against herbivory.

## 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 consist 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 Chilean matorral (Rundel, 1981) to rather high ones of 13.3% to the sclerophyll forest of South Australia (Specht, 1972). Table 2 presents data on the contribution of legumes to the floras of several locales having Mediterranean climate.

Table 2. Percentage contribution of leguminous taxa to the floras of several Mediterranean climate regions of the world. 1: Thomas, 1961; 2: Hower, 1970; 3: Lathrop and Thorne, 1978; 4: Davis et al 1988; 5: Keeley, unpub. data; 6: Munz and Keck, 1959; 7: Rundel, 1981; 8: Levyns, 1966; 9: Boucher, 1977; 10: Bond and Goldblat, 1984; 11: Specht, 1972; 12: Greuter et al 1984-1986

| LEGUMES IN THE MEDITERRANEAN CLIMATE ECOSYSTEMS | | |
|---|---|---|
| LOCALE | | LEGUMES % of the total flora |
| CALIFORNIA | | |
| chaparral | Santa Cruz[1] | 6.5 |
| | San Luis Obispo[2] | 6.5 |
| | Santa Ana[3] | 6.9 |
| | Santa Barbara[4] | 5.3 |
| coastal sage | Camp Pendleton[5] | 3.9 |
| | Sierra Pedro Martir[6] | 3.9 |
| CHILE | | |
| matorral | Overall[7] | 3.8 |
| SOUTH AFRICA | | |
| fynbos | Cape Peninsula[8] | 7.3 |
| | Cape Hangklip[9] | 7.3 |
| | Overall[10] | 10.9 |
| AUSTRALIA | | |
| sclerophyll forest | South Australia[11] | 13.3 |
| mallee | South Australia[11] | 12.4 |
| "arid land" | South Australia[11] | 11.9 |
| savanna | South Australia[11] | 8.8 |
| MEDITERRANEAN BASIN | Overall[12] | 7.6 |

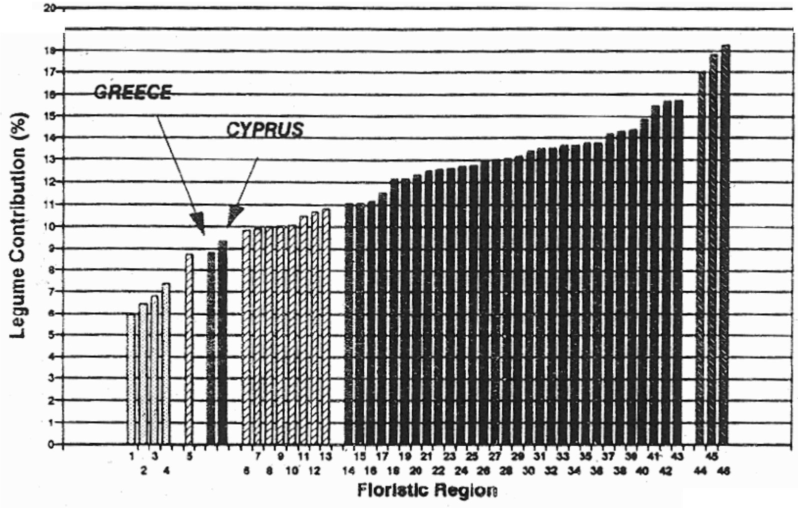
Data obtained from the Med-Checklist (Greuter et al 1984-1989) give for the legume flora of the Mediterranean Basin an average value of 7.6%. The real value is underestimated, since countries, which do not have a Mediterranean-type climate, like Libya, Bulgaria are included in the list, simply because they are located around the Mediterranean Sea. Also, larger or smaller parts of the circum Mediterranean countries have not a true Mediterranean climate, e.g. northern and Atlantic France, southern parts of North African countries, tall mountain ranges in all countries.

In a broad survey of the flora of numerous (30) Mediterranean regions of Greece (Figure

1, grey bars) it is shown that legumes percentage 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 and Cyprus. Mountainous areas (1-4, dotted bars) have a significant lower contribution (6-7%). The exixtence of tall mountains is considered to be the reason for the intermediate percentage values of several areas with overall Mediterranean climates (5-13, slash-lined bars). Regions 5 and 11 are not mountainous but legume contribution is decreased by the halophytic vegetation present (which is generally underrepresented by legumes). Region 5, Psathoura, is a small rocky island, covered seasonally in part by sea waves. 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 inervention and particularly the overgrazing pressure which favours legumes. This same argument is used in the case of Oinousses islands (# 46) to explain the dramatically high percentage. 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).

Total flora of Greece constitutes of 4700 species, 416 of which are legumes (Greuter et al, 1984-1989). One hundred and eighteen (24.5%) of these species belong to the mountain flora (Strid, 1989), while the remaining 75.5% is found in altitudes lower than 1800 meters (Table 3). Considering that the mountainous flora represents the 42.12% of the total flora of Greece, it reasonable to claim that legume flora is rather underrepresented in the mountain flora of the country. Of the 1833 species of Leguminosae enlisted in the Med-Checklist (Greuter et al 1984-1989), 416 are found in Greece, a percentage of 22.7%. According to data from Flora Europaea (Tutin et al 1969-1980), 844 species belonging to the Leguminosae family are found in Europe and 49.20% of them in Greece.

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).




| | | |
|---|---|---|
| 1 | Mountains of Greece* | (Strid, 1991) |
| 2 | Lailias Mt. | (Voliotis, 1977) |
| 3 | Macedonian Mts | (Quezel-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-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-Karetsos, 1991) |
| 22 | Yiaros Isl. | (Tzanoudakis, 1981) |
| 23 | Skiathos Isl. | (Economidou, 1969) |
| 24 | Cythera Isl. | (Yannitsaros, 1969) |
| 25 | Mt. Paikon grazelands | (Drossos-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-Yannitsaros, 1990) |
| 36 | S. Euboeic Gulf islands | (Sarlis, 1981) |
| 37 | Elaphonesos Isl. | (Yannitsaros, 1971) |
| 38 | Piperi Isl. | (Tsimbourla-Yannitsaros, 1990) |
| 39 | Skantzoura Isl. | (Gustaffson-Snogerup, 1974) |
| 40 | Nisyros Isl. | (Papatsou, 1975) |
| 41 | Paxi Isl. | (Georgiadis et al., 1986) |
| 42 | Kassandra pine forests* | (Tsitsoni-Karagiannakidou, 1987) |
| 43 | 7 islets of N. Dodecanesus | (Panitsa-Tzanoudakis, 1991) |
| 44 | Kastellorizo Isl. | (Greuter, 1979) |
| 45 | Psara Isl. | (Greuter, 1976) |
| 46 | Oinousses Isls | (Panitsa et al., 1994) |

Figure 1. Contribution of legume species (* species and subspecies) to the total flora of various geographic regions of Greece.

Table 3. Contribution of legumes in the floras of selected floristic regions.

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

According to Flora Europaea (Tutin et al 1964-1980), out of 844 legume species native in Europe, only 4 (0.35%) belong to Caesalpinioideae subfamily, 9 (1.18%) to Mimosoideae and 831 species (98.46%) to the Papilionidae (Lotoideae) subfamily. All 13 species belonging to the Caesalpinioideae and Mimosoideae subfamilies are trees. On the contrary, in the Papilionideae subfamily, all growth forms are represented, however, the herbaceous elements dominate. Overall, in the leguminous flora of Europe only 2.5% are trees, while 75.35% are herbaceous plants (Table 4).

Data from the floras of several regions in Greece show that the majority of the legume plants are annual, biennial or perennial herbs: 85.9% of the legume flora of Kythira island (mostly phryganic vegetation), (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 (Kazanis and Arianoutsou, in the same volume).

Table 4. Growth forms of the European legumes

| Taxon | % Trees | % Shrubs | % Herbs |
|---|---|---|---|
| Caesalpinioideae | 100 (4 spp.) | | |
| Mimosoideae | 100 (9 spp.) | - | - |
| Lotoideae | 0.96 (8 spp.) | 22.5 (187 spp.) | 76.5 (636 spp.) |
| LEGUMINOSAE | 2.5 (21 spp.) | 22.5 (187 spp.) | 75.3 (636 spp.) |

## LEGUMES IN THE POST-FIRE MEDITERRANEAN COMMUNITIES

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). 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. 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). 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, in the same volume). Although detailed data about the floristics and the dynamics of this succession are scarse it is evident that an enrichment of the local floras in leguminous elements occurs (Table 5). This enrichment may be slight, as in the case of a Californian chaparral (Armstong, 1977), where the native leguminous flora increased by 7.3% only, 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 icreased over a 100% immediatelt after fire (Kazanis and Arianoutsou, in the same volume).

The prolific appearance of the leguminous plants in the burned areas lasts for only the very early successional post-fire stages (Kazanis and Arianoutsou, in the same volume). 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 other non-leguminous plants in the early post-fire environment. Papavassiliou and Arianoutsou (1993) have found that post-fire legumes do appear nodulation capacities, however, the actual effectiveness of this nodulation still remains to be studied.

Table 5. Legumes in post-fire Mediterranean plant communities. 1: Hanes, 1977; 2: Armstrong, 1977; 3: Trabaud, 1980; 4: Thanos et al (in prep.), 5: Kazanis and Arianoutsou, in the same volume.

| LOCALE | TOTAL FLORA (TF) | LEGUME FLORA (LF) | LF/TF (%) |
|---|---|---|---|
| North California Chaparral[1] | 159 | 12 | 7.5 |
| South California Chaparral[2] | 261 | 16 | 6.1 |
| South France Garrigue[3] | 30 | 4 | 13.3 |
| South France *Pinus halepensis* forest[3] | 50 | 6 | 12.0 |
| Central Greece *P. halepensis* forest[4] | 80 | 11 | 13.8 |
| Central Greece *P. halepensis* forest[5] | 72 | 19 | 26.4 |

As an overall conclusion, we could claim that all the above mentioned features of legume plants give them, reasonably enough, the character of the most ecologically successful family among the flowering plants.

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