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# MEDITERRANEAN WOODY PLANT GROWTH-FORMS, BIOMASS AND PRODUCTION IN THE EASTERN PART OF THE IBERIAN PENINSULA

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## SUMMARY

The major physiognomic features of Mediterranean vegetation in the eastern part of the Iberian Peninsula are described considering a coastal and a continental gradient and oro-Mediterranean formations. The main communities include broadleaved evergreen forest, maquis, pine woodlands, "garigue", matorral, thorn-scrub and dwarf-shrub steppes along mesic-xeric gradients, and pine-juniper woodlands and xeroacanthic cushion-like formations as altitudinal stages. We discuss some morphologico- functional traits of dominant plants from these different formations as related to environmental conditions, and their corresponding energy use strategies. Even though there are relatively few data on biomass and production, a broad synthetic approach is given, with some reference values.

KEY WORDS : Mediterranean vegetation, growth-forms, biomass, production, energy use strategy

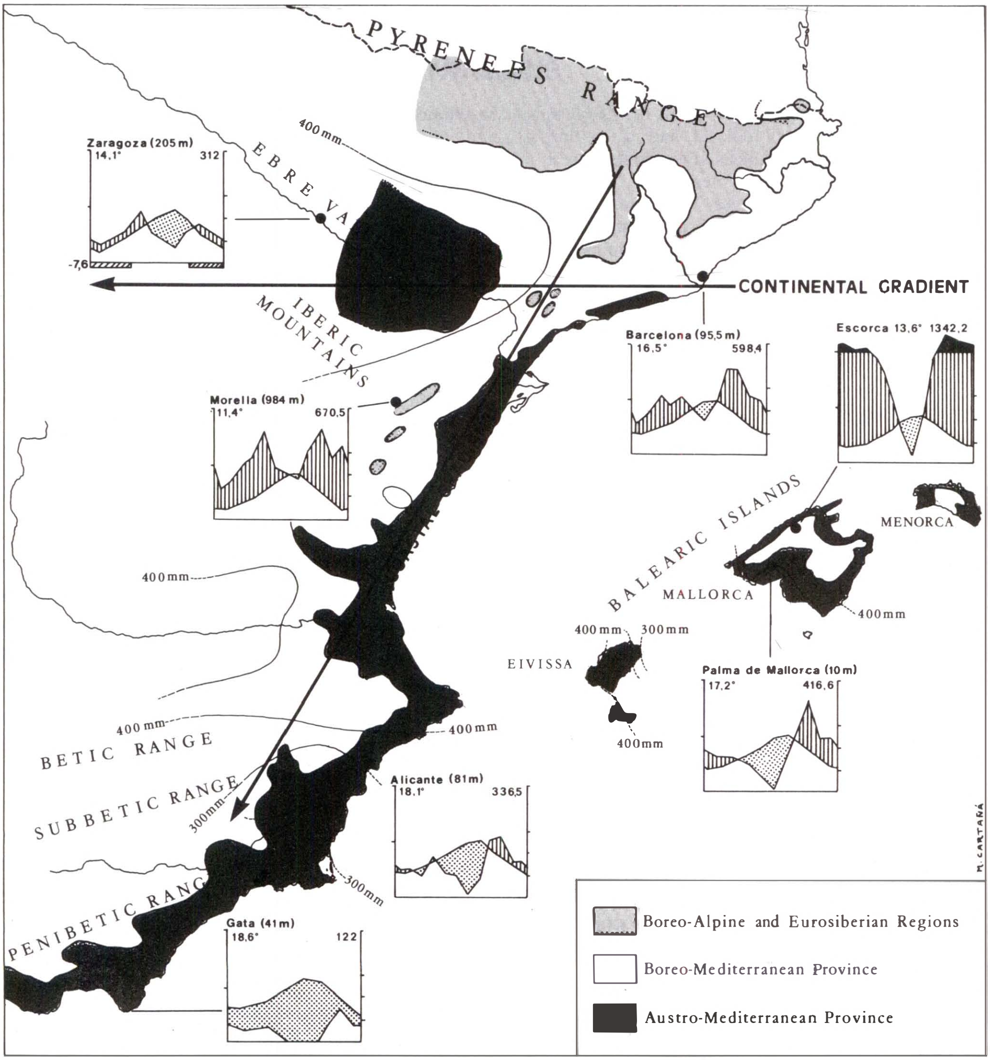
## INTRODUCTION

Two major mesic-xeric gradients are observed in the eastern part of the Iberian Peninsula (Fig. 1). One runs from the Pyrenees to the south, from areas with 700-1000 mm annual rainfall to areas with 190-350 mm. The second runs from the northeast coast to continental areas, and its annual rainfall ranges from 600-700 mm to 300-400. In what follows we refer to them as coastal gradient and continental gradient. Different temperature changes occur along both gradients. Along the coastal gradient, there is an increase in summer length, average temperature and winter minima. Along the continental gradient, both winter length and thermic amplitude increase, whereas winter minima decrease.

Different shifts could thus be expected in vegetation structure and plant-growth forms following each gradient. Other factors, such as wind, soil, etc., can also affect plant fitness and modify adaptation features. Moreover, there are local deviations from climatic general patterns due to local climatic circumstances that will not be considered here.

Mediterranean climax ecosystems have been discussed on phytosociological grounds by BOLÒS (1985) for most of the area (Catalan countries), RIVAS (1974) for the southern part, and RIVAS (1987) for all Spain. BOLÒS (1985) distinguishes between a boreo-Mediterranean province, with climax communities corresponding to *Quercion ilicis* alliance, an austro-Mediterranean province, with climax communities corresponding to *Rhamno-Quercion cocciferae* and *Oleo-Ceratonion* alliances, and a western oro-Mediterranean province, corresponding to high and moderately high Mediterranean mountains, with *Pino-Juniperion sabinae*, *Xeracantho-Erinaceion* and *Hypericion balearici* climax communities, the last one found only in Majorca.

In the southern end of the area, RIVAS (1974) identifies mature communities as included in *Asparago-Rhamnion oleoidis* and *Periplocion angustifoliae* alliances. Ebro river valley vegetation is puzzling, and a *Rhamno-Quercion cocciferae* climax has been classically assumed (BRAUN-BLANQUET & BOLÒS 1957), but this might be an incomplete view (TERRADAS, 1986).



▨ Boreo-Alpine and Eurosiberian Regions

☐ Boreo-Mediterranean Province

■ Austro-Mediterranean Province

FIGURE 1. The eastern Iberian Peninsula and major features referred to in the text.

## A PHYSIOGNOMIC DESCRIPTION OF VEGETATION

From a morphological point of view, mature vegetation along the coastal gradient changes from the broadleaved evergreen forest to tall thicket matorral and maquis (*Oleo-Ceratonion*), and thorn-scrub communities (*Oleo-Ceratonion* and *Asparago-Rhamnion*). Broadleaved evergreen forests are dominated by *Quercus ilex* ssp. *ilex* or, on sandy soils in the northern part of the area, by *Quercus suber*. These forests are often replaced by pine-oak mixed forests, by *Quercion-ilicis* maquis with *Arbutus unedo* and *Erica scoparia*, or by matorral: *Cistion mediomediterraneum* on siliceous soils and *Quercus coccifera* "garigues" or *Rosmarino-Ericion* scrub on limestone, all of them often with pines. Forests, maquis and "garigues" are communities with phanerophytes with plane leaves, often coriaceous or sclerophyllous and entire, as the dominant plants, whereas matorral communities are richer in nanophanerophytes or chamaephytes with soft (malacophyllous) leaves, sometimes plane (like in *Cistus* species) but in other cases leptophyllous (*Erica*) or linear.

The austro-Mediterranean *Oleo-Ceratonion* maquis is also dominated by phanerophytes with coriaceous or sclerophyllous leaves, mostly medium or small sized or divided (as in *Ceratonia siliqua* or *Pistacia lentiscus*). But this sclerophyllous vegetation has very often been replaced by *Cistion* or *Rosmarino-Ericion* communities. Malacophyllous plants become more frequent and diverse in this area.

In the southern part of the territory, maquis broadleaved evergreen phanerophytes like *Olea europaea*, *Quercus coccifera* and *Pistacia lentiscus* are progressively replaced in mature communities by a thorn-scrub. These communities are at first dominated by *Rhamnus lycioides*, a malacophyllous phanerophyte with long shoots and short shoots (dolichoblasts and brachiblasts) and marked seasonal heteromorphism, and the dwarf palm *Chamaerops humilis*. Floristically, they are similar to maquis and so they are included by phytosociologists in the *Rhamno-Quercion* alliance, but the physiognomy has shifted. We are near the tree border (which is found somewhere between 350 and 400 mm of annual rainfall). Also replacing communities after disturbance are clearly different: large surfaces are covered by chamaephytes, i. e. "tomillares" (*Thymo-Siderition leucanthae*), or halophytic, nitrophilous or gypsophylous communities, and by dry therophytic grasslands. The typical thorny shrub growth-form diversifies to the south, when climate becomes drier, with plants like *Maytenus europaeus*, *Periploca angustifolia*, *Ziziphus lotus*, *Asparagus albus* or *Lycium intricatum* added to *Rhamnus lycioides* (*Asparago-Rhamnion* and *Periplocion* alliances).

The continental gradient begins at the northeast edge with the broadleaved sclerophyllous forest or maquis near the coast, which is soon replaced by an impoverished *Quercus ilex* ssp. *rotundifolia* forest with *Quercus coccifera* "garigues", *Rosmarino-Ericion* matorral or pine woodlands as successional stages. At

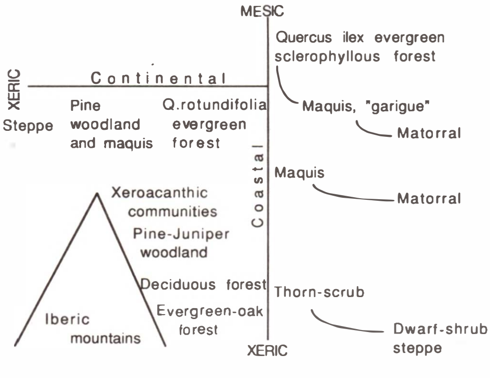


FIGURE 2. Major plant formations along the two mesic-xeric gradients and on Mediterranean mountains. For the coastal gradient, degradation series are shown.

the Ebro valley, rainfall decreases fast and broadleaved trees disappear, and are replaced by a pine woodland with a shrub understory also classified phytosociologically as *Rhamno-Quercion cocciferae*. Thermophyllous species of this community, including the pine itself, are gradually disappearing to the centre of the Ebro valley, where the winter climate becomes colder. There, on gypsic ground, slopes and shallow soils are mostly covered by a nitrophilous or gypsophilous chamaephyte semidesert or steppe (*Salsolo-Peganion, Gypsophylion*), whereas fine-textured loams are occupied by hemicryptophytic or rhizomatous geophytic perennial grasses (*Agropyro-Lygeion*). In this landscape, a high diversity of therophytes covers the free spaces between perennial grasses or shrubs during the short wet periods. Halophytic chamaephytes or nanophanerophytes appear on saline soils, near the bottom of undrained valleys.

Further up the mountains in the northern part of the territory, extra-Mediterranean conditions are soon found, which correspond to the Euro-Siberian or Boreo-Alpine regions. But in the Iberian and southern (sub-Betic, Betic and Penibetic) mountains, some features of Mediterranean climates reach higher altitudes. According to BOLÒS (1985), oro-Mediterranean vegetation covers a very limited area in some scattered isolated patches, occurring above *Quercus rotundifolia* and deciduous sub-Mediterranean forests. *Pino-Juniperion sabinae* communities of Iberian mountains are made up of large carpet-like patches of *Juniperus sabina* or *J. communis* ssp. *hemisphaerica*, with isolated individuals or clumps of *Pinus sylvestris* or *Juniperus thurifera* emerging from shrub cover and a therophytic grassland as a background. In more exposed environments this seems to be very dynamic vegetation, because pine growth overshadows *Juniperus* carpets and can suppress them, but pines germinate only under the carpet protection.

A dense forest is rarely obtained. Summits of Iberian mountains and southern "sierras" are occupied by spiny cushion-like *Xeracantho-Erinaceion* communities, in a poor form if compared with Sierra Nevada and Atlas equivalents.

Spiny cushion-like shrubs are also present above 1100 m in Majorca (*Hypericion balearici*), with a different floristic composition. Xeroacanthic shrubs can be considered as an interesting case of evolutionary convergence in oro-Mediterranean climates: different families are represented by species with similar morphology in these highly fluctuating windy environments. Similar forms are also found on the coasts of the Balearic islands, in windy environments too.

## DOMINANT WOODY GROWTH FORM

We will now try to summarize the major woody plant growth forms that dominate Mediterranean landscapes in our territory. MARGARIS (1981) has suggested two main adaptation syndromes for Mediterranean environments: maquis plants, corresponding to typical sclerophyllous woody plants, and phrygana plants (equivalents are said to be Israeli "botha", Iberian "tomillares", Portuguese "barocales", Italian "gariga" and some other formations). Similar views have been discussed by ORSHAN (1983).

Maquis plants are called isomorphic because they maintain the same kind of leaves all through the year. The average life span of the leaf is usually between 1-2 years, but can be shorter in some species like *Pistacia lentiscus* (7.9-15.7 months according to DIAMANTOGLOU & MITRAKOS, 1981). Leaf fall peaks tend to be advanced in early summer. Leaves are rich in structural components (lignine, hemicelluloses) that make them rigid and have low nutrient contents. This last condition also means that nutrient requirements are low. In *Quercus ilex* we have found accumulation of nutrient reserves in branches (ESCARRÉ *et al,* 1987) and these reserves are used to build new leaves. Sclerophyllous plants may use wood reserves as a way to deaden the effects of environmental fluctuations. In any case, plant function is usually based on a conservative nutrient economy. Canopy structure is shaped by light availability acting as a key factor (GRACIA, 1983).

Phrygana strategy consists in a marked seasonal heteromorphism, with large leaves during the wet-season, appearing on dolicoblasts just with the first autumn rains, and showing high photosynthetic rates (almost twice the rates of the sclerophyllous leaves of maquis plants). During the spring, phrygana plants have their maximal growth rates. Then wet-season leaves are shed, and they are replaced by drought-season leaves. Meanwhile, dolicoblasts elongate and lignify. Before leaf fall, there is a retranslocation of most leaf nitrogen stocks to other plant organs (data on *Timbra capitata*, *Phlomis fruticosa*, *Cistus* spp. and *Sarcopoterium spinosum* are given by MARGARIS, 1981). The morphological traits of summer leaves differ from those of wet-season leaves (palissade parenchyma thickness, stomata distribution, etc.) and they are more xeromorphic. Dimorphism seems to be controlled by day length. Soft leaves can fold, which reduces their exposed area in transpiration. Light is not a major factor for canopy organization. A shallow root system enables these plants to respond faster than maquis plants to early autumn rains.

ORSHAN (1989) has pointed out that heteromorphic plants have much larger fluctuations of transpiratory rates during the year than isomorphic plants. In fact, isomorphic plants are regulated by deep water use at the end of summer (higher rates are thus possible in this period); moreover, the properties of sclerophyllous leaves impose some limitations on spring transpiration. These authors assume that isomorphic plants use soil water gradually by developing roots to deeper soil levels when surface horizons become dry. This process can help to control activity rates, thus allowing the plants to reach the end of summer with predawn water potentials that are not too negative : -5 MP has been measured in *Arbutus unedo* (TENHUNEN *et al*., 1985), less stable than other sclerophylls like *Quercus coccifera*, whereas in the malacophyllous *Rosmarinus officinalis* MERINO (1988) measured -7 MP. Gas exchange can be controlled by a high number of stomata in isomorphic plants; stomata number in heteromorphic plants is usually lower. The ecophysiology of maquis plants has been studied by authors like LARCHER (1972) and BRECKLE (1966); recent important advances in that subject have been reported by Lange and co-workers in several papers on *Arbutus unedo, Ceratonia siliqua, Quercus suber, Phyllirea,* etc. (LANGE *et al.,* 1982; TENHUNEN *et al*., 1987). Daily and seasonal cycles clearly show effective stomatal control of transpiratory and photosynthetic rates. Nevertheless, considerable differences are found between species: *Arbutus unedo* has larger decreases in both maximal photosynthetic rates and xylem potential than *Quercus coccifera*; this seems to be related to much shallower roots in *Arbutus* (TENHUNEN *et al*., 1985). *Pistacia lentiscus*, which has low gas exchange control and short leaf span, can be considered as a maquis plant with some transition characters to the malacophyllous strategy, enabling it to live in rather xeric environments.

To these two morphologico-functional types, we must add some others. One is constituted by pines, with only a few species, but dominant over large areas. Pine growth-form is clearly not a specifically Mediterranean adaptation pattern. In fact, it is found in many other climates. Besides, it does not represent specific adaptations to any Mediterranean environment because it is found in most conditions. But we should not forget the success of the pine form in Mediterranean countries. Mediterranean pines have relatively shallow root systems. Nevertheless, *Pinus halepensis* can endure rather xeric conditions. In that case, morphological changes appear both in the canopy form and in leaf size. GINDEL (1973) found that leaf length was closely dependent on annual rainfall, both in *P. halepensis* and *P. pinea.* An interesting case to be studied is *Chamaerops humilis,* the only native European palm, which is a dominant plant in a large variety of maquis, matorral, "garigue" and thorn-scrub formations. It represents an atypical successful growth-form in Mediterranean environments, with very large sclerophyllous leaves. However, very scarce data exist on its ecophysiological characteristics, underground parts and other relevant features. Other morphologico-functional types are related to more local conditions. Let us discuss these conditions briefly.

With increasing water stress and unpredictability of water resources, woody plants can follow different strategies. One is that of nanophanerophytes and phanerophytes with both long and short shoots. These plants respond to rainfall by producing either leaves from axillary buds or from short shoots dispersed along the branches (SHMIDA & BURGESS, 1988). These leaves, generally small, are produced quickly after episodic rains because few resources are invested in short internodal growth, whereas during long wet periods long shoots elongate. So, leaf area can show pronounced changes (some plants with these characteristics grow in relatively dry habitats of temperate areas, such as *Berberis vulgaris*). In extreme cases, summer deciduous plants are found (for instance, *Asparagus albus*, *Withania frutescens*). Individual canopy structure is very open and leaves are arranged in a diffuse way, making convective exchange and cooling easy. Transpiration rates per leaf surface unit are relatively high; however, they are low on a soil surface basis. Also photosynthetic rates are high during periods of leaf growth. But during long periods, the carbon budget must be negative, because maintenance costs are high. Spines are probably an adaptation to reduce herbivory and maintain positive total carbon budgets. In a *Thymo-Siderition* community, we have observed *Rhamnus lycioides* roots passing through the petrocalcic layer, whereas chamaephyte dwarf-shrubs had only shallow roots branching within the top 15-30 cm of soil. The biomass of thorny shrubs can be greater underground than aboveground, as shown by MARTÍN (1984) in *Withania frutescens* and *Rhamnus lycioides.* If compared with other thorny shrubs, *Rhamnus lycioides* has some characteristics, such as high chlorophyll content, low nitrogen content and high specific leaf density, which are more similar to those of sclerophyllous plants. This might be related to the fact that its larger distribution range extends further to the north than most other thorn-shrub species.

In *Quercus ilex* forests evapotranspiration can amount to about 500 mm in the course of a year: by using water budgets in small catchments, 469 mm have been measured at La Castanya (Montseny) by ÀVILA (1989) and 495 mm at l'Avic (Prades) by ESCARRÉ *et al.* (1984). Under higher rainfall inputs, near Montpellier, RAMBAL (1986) calculates, from a water relationships model, a 529-665 mm $yr^{-1}$ evapotranspiration for a *Quercus coccifera* "garigue". Values can certainly be reduced along mesic-xeric gradients, but closed woody sclerophyllic canopies (forest, maquis, garigues) do not seem to be able to develop below 350-400 mm of annual water supplies (from rain or lateral flow).

Below 300 mm of annual rainfall, or even above this value on slopes with shallow and eroded soils, nanophanerophytes are replaced by chamaephytes or hemicryptophytic and rhizomatous grasses. Differences between chamaephytes and grasses have recently been discussed by SHMIDA & BURGESS (1988). A high diversity of chamaephytic dwarf shrubs exists in our territory. Small microphyllous or nanophyllous leaves are largely dominant. Roots are often scarce and relatively long; so, they can exploit localized wet sites. Nevertheless, when a chalk crust exists they cannot usually pass through it and deep water resources are unavailable to these plants. An opportunistic strategy is the response to unpredictable and scarce water availability, either at the individual (leaf production and growth bursts) or community (fast population dynamics) level. High maintenance costs and short productive periods, as well as terminal shoot growth, would made chamaephytes vulnerable to strong herbivory. As a result, chemical defence and unpalatability are frequent.

Some woody plants can exploit more permanent, local water resources, such as rock crevices or soil under rock protection, by developing a system of long roots. This permits more conservative strategies of energy use, thus allowing plants of the maquis type, chamaephytes or thorny shrubs to survive under climates drier than expected.

Other stress causes besides drought are present in Mediterranean countries. MITRAKOS (1980) has noted the double stress, summer drought and winter cold, to which Mediterranean plants are subject. Winter cold depresses metabolism and can also provoke frost-drought injury, thus reducing production, as we have shown for *Quercus ilex* along an altitudinal gradient (SAVÉ *et al.*, 1986). Further inland or at higher altitudes, the Mediterranean flora becomes clearly impoverished in our territory, as indicated before. The vegetative period can be reduced either by increasing summer duration along the coastal gradient or by colder and longer winters as one proceeds into the continent or up onto the mountains. Along the continental gradient, the shift to colder and longer winters comes along with a change from mesic to xeric conditions, while the vegetational change shows analogies with the change along the coastal gradient. On the mountains, the effects of colder conditions could be expected to lead to different morphological types of plants. Nevertheless, carpet-like forms are also found in extra-Mediterranean climates and xeroacanthic communities are present in warmer Mediterranean climates on the Balearic coast. Pines and junipers dominate cold oro-Mediterranean climates and xeroacanthic communities seem to be more associated with strong wind exposure than with temperature values or fluctuations.

Obviously, there is also a variety of conditions linked to soil differences, and we can especially distinguish rocks, sands, marshes and saline soils. Sandy, waterlogged or saline environments sustain similar vegetation forms under very different climates, with only a few minor adaptations to local conditions. To some extent, the same is true for rocky environments, although they are often isolated refuges with a high level of endemism. Perhaps the only fact worth mentioning here is the increase in saline mainland habitats along the mesic-xeric gradients.

Both succulent leaves and stems are mostly restricted to rocks, saline soils and salt-sprayed coastal environments. Some succulent plants from xeric habitats have expanded after successful introductions (*Agave*, *Opuntia*). On gypsic soils we can find some species with succulent leaves (i.e. *Helianthemum squamatum*, *Ononis tridentata*). The thorny shrub *Lycium intricatum* also has succulent leaves. Only one species, the rhizomatous herb *Caralluma europaea*, can be considered a spontaneous stem succulent linked to xeric conditions, but it has a very restricted distribution in the southern end of the territory. No desert succulent formations exist directly related to increasing aridity.

The xeroacanthic cushion-like growth-form needs perhaps more comment. A general characteristic of this type of plants is the fact that they undergo not only the seasonal double stress, very marked in mountain plants, but also a continuous loss due to sprout mortality by wind mechanical effects or other associated physiological factors.

So, this form is a result of heavy exploitation by the physical environment, which adds to herbivorism, making it difficult to sustain a positive carbon budget. Spines, as well as very closed canopies, reduce losses due to herbivory. Individual canopies have an extreme monolayer leaf arrangement: leaves are densely packed in a 0.5-2 cm thick layer. Malacophyllous leaves are common, with some transition forms to sclerophylly, in true cushion-like plants. In coastal habitats under salt spray influence, succulent leaves sometimes occur. So, leaf overheating would be expected under high irradiance, due to low convective cooling, except under strong wind regimes that cause efficient eddy transfers. Another factor to be taken into account with these plants is their nutrient cycling.

Nutrient losses by both litter wind carrying and soil erosion are very high, but the closed structure of these plants tends to minimize them. For instance, under summit cushions in the Aytana Sierra we have measured litter stocks of 0.125 g $cm^{-2}$, a quantity similar to that found in developed forests with much larger aboveground biomass. An external but growth-form controlled nutrient reserve is thus obtained. We have measured underground biomass in some mountain and coastal cushion-like Balearic plants. *Astragalus balearica* has slightly more than 20 % of its total biomass under ground and this rate is 26 % in *Launaea cervicornis* individuals; these are not high values, if compared with many woody plants from arid zones.

Cushion forms are often found on mountains and coasts under other climates, but all the xeroacanthic Mediterranean cushions have a very closed and spiny canopy, which gives a characteristic physiognomy to their formations. Although cushions can be merely morphogenic structures, this is not always the case. Sometimes this morphology has a genetic basis (BRAUN-BLANQUET, 1962). We have tried to distinguish these two different origins in some cushion-like Balearic coastal plants (TERRADAS *et al.*, 1989). So, branching angles ranging from 10° to 15° in cushion shrubs are assumed to depend on genetic determinism, whereas branching angles ranging from 45° to 90°, or even more, are found in morphogenic cushions (M. Riba, pers. comm.).

## GROWTH-FORMS AND ENERGY USE STRATEGIES

SHMIDA & BURGESS (1988) recognize different strategies of desert plants using a two axis space. The first axis is oriented from poor to rich resources, while the second axis goes from episodic to stable resources. This seems to us a useful approach. Along a mesic-xeric gradient, rich resource availability becomes more episodic, then unreliable, whereas reliable resources become lower in concentration or quality. Near the mesic end of our gradients, most dominant plants use relatively (for this area) stable and rich resources in a competitive strategy (GRIME, 1979). Maquis-type isomorphic plants in mature communities are *K* strategists, with slow energy use. Pioneer stages in disturbed sites can follow *r* strategies. When approaching the xeric end of the gradient, resource patchiness increases over time and space. As a result, *K* and *r* strategists (or competitive, ruderal and stress resistants if Grime's classification is preferred), find opportunities, and *r*-strategists are eventually more favoured. Resource availability fluctuations have effects similar to disturbance, promoting high energy strategies (in the sense of SHMIDA & BURGESS, 1988): short active periods with high production per time of activity. Transpiration and photosynthetic rates can be high, but leaf area is low and variable. For instance, *Rhamnus lycioides* leaves have on average much larger transpiration rates and water content changes than *Quercus coccifera*, *Pinus halepensis* or *Juniperus thurifera*. The leaves, however, have a diffuse arrangement and small coverage, and leaf area can decrease during drought periods (TERRADAS, 1973). So, *Rhamnus lycioides* has a higher energy strategy than *Quercus coccifera* and is adapted to fast responses to rich episodic resources, whereas *Q. coccifera* relies more on continuous use of poorer but stable resources.

All along the gradients, man's use of the landscape can promote pioneer and less mature communities. As a result, we can expect *r*-strategists to increase in importance. But other associated changes take place as well, thus reducing plant cover and modifying soil conditions. This can open spaces to species adapted to more xeric environments, and benefit the northwards advance of southern xerophytic *r*-strategists. A good example of this might be *Inula viscosa*. Original habitats of this Asteraceae deciduous shrub are the south-Mediterranean "ramblas" (dry bed watercourses), an environment under a high disturbance regime by episodic waterflows. A ruderal strategist, this plant has expanded its area to the north, colonizing old fields and waste lands. During the earlier years after field abandonment, it behaves like a chamaephyte, but as soil becomes compacted it shifts to a hemicryptophytic mode (SORIA, 1980).

True xeroacanthic cushion-like plants use stable and poor resources, with a high control of the external steps of nutrient cycles. But they cannot easily be classified as *K*-strategists, because they are under heavy exploitation by the physical environment. Photosynthetic rates have not been measured, but they are likely to be relatively high to balance losses and long inactive periods. Growth rate can be higher than expected from poor cover, after observations on *Centaurea balearica* colonizing disturbed sites on the coast of the island of Minorca. On the same, *Anthyllis hermanniae* and *Launaea cervicornis* are found on disturbed sites, being replaced by *Erica multiflora*, *Phillyrea media* var. *rodriguesii*, *Pistacia lentiscus* and *Pinus halepensis* scrubs and woodlands in the succession to more mature stages.

First growth is probably fast in cushions, but it must slow down and take place as short bursts after a certain size (ruled by local wind conditions) is reached. Studies in population dynamics could also be very useful in order to understand fully the energy strategy of these plants.

When considering energy use, different levels must be taken into account. Individual survival is important to phanerophytes and nanophanerophytes, because construction costs are high, but investment in structure assures either aerial or subterranean space control. But certain parts of the plants, such as leaves or fine roots, can be used in a way which is more or less economical in terms of energy. A certain degree of opportunism is always present. In an adult tree canopy, leaf morphology, leaf size, leaf behaviour and leaf span change along a vertical axis. We can consider woody plants as complex systems or populations of organs including hierarchically organized structures, some of them with high turnover rates protecting the others from external fluctuations or exploiting episodic resources. Under appropriate conditions, *Quercus* species can have more than one shoot growth period. The very high capacity of resprouting and increasing production rates after disturbance in *Q. coccifera* and other *K*-strategists (as a result of use of internalized resource stocks) allows them to conserve space control and dominance, succeeding each other as if there was a shift in energy use strategy within the same genetical individuals. Leaves of young resprouts show morphological and physiological differences from adult normal leaves (PERY *et al.*, 1989): higher Chl a/Chl b, transpiration rates, and osmotic potential, lower specific weight, cuticle and leaf thickness, proline and starch grain content. In fact, resprout leaves have many more available resources than adult normal leaves because they can use stocks. Besides, the rate between leaf area and fine root biomass is much higher in resprouts. So, in the same individual low energy use is dominant, but periods of high energy use occur seasonally or as a result of disturbances, when high quantities of resources are freely available. In phrygana and thorny shrub types, leaves conserve and always maintain the high energy pattern. Woody structure is also maintained, but leaf "populations" can fluctuate greatly, as can individual leaf area (by folding). Moreover, thorny shrubs have a similar leaf strategy but higher investment in woody parts: they use deeper soil resources and have longer individual life than phrygana-type plants or dwarf-shrubs. In very poor dry sites, as well as in heavily exploited and fluctuating environments, site conservation can become less important or not feasible, and individual turnover increase (steppe chamaephytes, therophytes), giving a classical *r*-strategy gradually adapted to the use of more episodic energy pulses.

To sum up, some plants tend to conserve space control by means of large investments in woody structures (which means a long individual life). We found a shift in these plants from slow gradual to fast pulsed changes both in leaf area and leaf activity as a response to increasingly episodic and unpredictable resource availability in the environment.

Other plants sacrifice space control and long individual life, invest relatively more in photosynthetic organs and show a higher turnover at population levels. But in all kinds of plants, when large resources by leaf area unit are either available in the environment or are mobilized as a result of disturbance, a pattern of high energy is developed. Relatively stable forest as well as maquis, no matter how rich they are in resources, usually show closed canopies and low resource availability by leaf unit; thus, they behave in a low energy manner. However, in transient conditions after canopy removal due to disturbance, large resource stocks are mobilized and root systems are always present. So, new leaves have much higher resource availability by leaf unit and they behave in a high energy manner. Other less stable communities limit their activity to episodic periods of high resource availability, and always have open

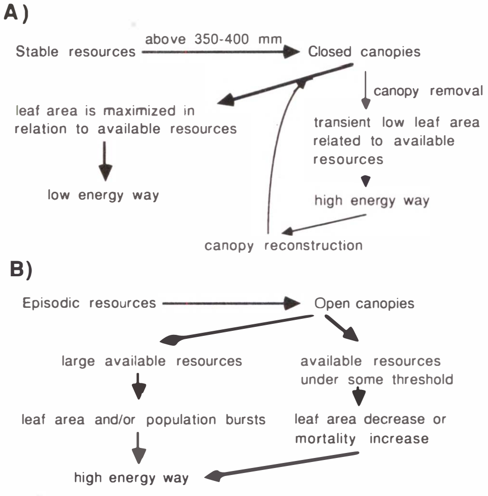


FIGURE 3. Two main ways of energy use are present along our mesic-xeric gradients. Sclerophyllous forest and maquis plants use a low energy strategy: they have low nutrient requirements, maintain long continuous periods of activity, and show some regulation due both to their internal stocks and their good stomatal control. Other plants, such as mallacophyllous phrygana and some thorn-scrub plants, have episodic pulses of high energy use due to their high dependence on external patched reserves; they show high nutrient requirements, discontinuous growth bursts and regulation of gas exchanges by leaf area changes.

canopies working in a pulsed high energy manner (Fig. 3).

## BIOMASS AND PRODUCTION

There are few data on biomass and production for the area considered, except for forests. A number of evaluations have been made in the last few years, mostly unpublished, on different types of natural communities. They allow us a general overview.

As far as broadleaved forests are concerned, accurate studies on Montseny and Prades holm-oak forests have been carried out. Aboveground biomass of a high quality 60-90 years old stand from La Castanya (Montseny) is 165 t $ha^{-1}$ (dry weight) for trees and 4.7 for understory, while root biomass is 65 t $ha^{-1}$. At Prades, a lower and denser holm-oak coppice has 100 t $ha^{-1}$ aerial tree biomass and a 15 t $ha^{-1}$ understory (ESCARRÉ *et al*., 1984). Aboveground biomass values from 40 to 270 t $ha^{-1}$ have been measured in different holm-oak forests in the Mediterranean region, and these values probably give us a range estimation for this type of forest in our territory. Values for cork-oak forests are probably a little lower, because these forests usually have more open canopies. *Arbutus unedo* and *Erica arborea* maquis or heaths lie somewhere between 10 and 60 t $ha^{-1}$, and *Quercus coccifera* "garigue" in the 10-50 t $ha^{-1}$ range, probably with a lower average than maquis.

*Oleo-Ceratonion* mature maquis are hardly found as a continuous cover, and there are no good estimates of their biomass. A Balearic community with *Olea europaea* and *Pistacia lentiscus* in patches covering 40 % of the soil surface has a biomass of only 9 t $ha^{-1}$. Mediterranean pine forests and woodlands include very diverse communities, often rather open. A *Pinus halepensis* woodland at Sierra Espunya gave 61 t $ha^{-1}$ of aboveground biomass. Average *P. halepensis* woodland biomass is almost certainly between 50 and 80 t $ha^{-1}$ in most areas. RAPP (1978) has measured 151 t $ha^{-1}$ near Montpellier for the same species. Under much wetter conditions, 146 t $ha^{-1}$ was found in a *Pinus pinea* forest studied by CABANETTES & RAPP (1978) in southern France. Aboveground biomass in most *Rosmarino-Ericion* and *Cistion* matorral communities is less than 25 t $ha^{-1}$. *Thymo-Siderition* dwarf shrub formations are clearly under 10 t $ha^{-1}$ (we have measured 4.3 t $ha^{-1}$ in such a community near Alicante; see also FISHER *et al*., 1987), with underground biomass lower than aboveground biomass; similar low values are found in most *Salsolo-Peganion* communities. There are no evaluations of thorn-scrub community biomass in southern Spain, and in fact it is difficult to find well preserved representative formations. Isolated thorny shrub individuals usually appear in dwarf-shrubs communities.

Xeroacanthic formations usually have less than 30% plant cover and corresponding low biomass: we have measured 1 t $ha^{-1}$ with 15-20 % cover in *Launaeetum cervicornis* from the Balearic coastal (much higher values can be expected in *Aro-Phillyreetum* communities, but these are constituted by morphogenic cushions of maquis species); in the *Hypericion balearici* from the Balearic mountains, with a 60% cover we have found 4.2-4.8 t $ha^{-1}$ biomass; on the summit of Aytana sierra, cover, is 10-15 % and biomass is 3.3 t $ha^{-1}$.

Available data on primary production are very scarce. Moreover, spatial and temporal variations can be very large. Whereas in the high quality Montseny holm-oak stand production reaches a noticeable 9.7 t $ha^{-1}$ $y^{-1}$, similar to the values found for most mid-European forests, many mature holm-oak forests do not exceed 4-5 t $ha^{-1}$ $yr^{-1}$ (3 of them being leaves). Pine forests can show higher figures: the Sierra Espunya forest, in the south of this area, reaches 8-9.5 t $ha^{-1}$ $yr^{-1}$. Obviously, there is a marked north-south decreasing gradient of forest production associated with the climatic gradient. GRACIA (in TERRADAS *et al*., 1989) gives a range of stem wood production between 12.2 and 0.64 t $ha^{-1}$ $yr^{-1}$ (provincial averages for any kind of forest, evergreen oaks excluded), following the same decreasing pattern.

In maquis the aboveground production is usually below 4 t $ha^{-1}$ $yr^{-1}$, even though during the first year after disturbance (fire, for instance) it can be higher. In *Quercus coccifera* "garigue" we find 2-3 t $ha^{-1}$ $yr^{-1}$ one year after fire and 0.5-1.25 in most other cases. Higher productions can be found in old field scrub of *Inula viscosa* (SORIA, 1984), where 5-6 t $ha^{-1}$ $yr^{-1}$ has been measured in the early years after field culture abandonment, but these values decline rapidly. *Rosmarinus* matorral and dwarf shrub communities are probably below 1 t $ha^{-1}$ $yr^{-1}$, and the same must be true for xeroacanthic communities, but we lack direct measurements.

The patterns of change in productivity along mesic-xeric gradients remain obscure because belowground productions are unknown. Leaf production decreases clearly from a maximum around 3 t $ha^{-1}$ $yr^{-1}$ in broadleaved, pine forests and tall shrub formations with complete soil cover to chamaephyte steppes, whereas the rate of photosynthetic organ production to total aboveground production increases. In general, increasing aridity implies more energy being invested in belowground and photosynthetic parts, as well as higher costs of maintenance.

Biomass and production are not simple responses to rainfall gradients. Man has exploited the Iberian Peninsula resources for thousands of years. As a result, we cannot know to what degree soil degradation and nutrient losses have been increased and water-holding capacity has decreased by overgrazing, fire and agriculture. A consequence of man's exploitation of the land could be a northwards shift of plant communities adapted to more xeric environments, especially along the coastal gradient.

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