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## STRUCTURAL ASPECTS OF SHRUBS IN MEDITERRANEAN-TYPE PLANT COMMUNITIES

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**Key words:** Adaptive value, crypt, bark structure, vasicentric tracheid, phenomorphology.

**Abstract:** It is the purpose of this contribution to discuss the adaptive value of a few morphological characteristics of shrubs of mediterranean-type ecosystems. Structural characters, such as the crypts in the leaf epidermis of some sclerophyllous shrub species, the smooth bark of many chaparral shrubs, which increases stem flow and thus adds water and fertilizer to the root crown area which is specially high in fine-root density, or the presence of vasicentric tracheids in the wood of drought supporting shrubs, seem ideally "designed" to improve shrub response to drought conditions. However, experimental evidence for the adaptive value of these structures is widely missing. The phenomorphological analysis of the plants of mediterranean-type ecosystems has the potential to improve the objectivity of scrub vegetation comparisons and to elucidate the adaptive value of these structural features. Overall, it is concluded that suites of anatomical features and not single characters decide upon the adaptive value of morphological properties.

### INTRODUCTION

The structure of mediterranean-type plant communities has been studied frequently (see recent reviews by Mooney 1977, Thrower and Bradbury 1977, Maragaris and Mooney 1981, Di Castri et al. 1981, Miller 1981, Kruger et al. 1983), and the accumulated wealth of information places these ecosystems among the best studied in the world. In the context of this contribution we will interpret the title "struc-

tural aspects in mediterranean-type plant communities" as referring to the specific architecture or morphology of shrubs because these represent the most characteristic plant form in mediterranean-type ecosystems. The fact that we do not pay attention to herbs in this contribution is justified only by the constraints imposed by space limitations.

We will discuss morphological structures which are considered conventionally to have adaptive

value although newer results make this dubious (Kummerow and Ellis 1988). Special attention will be paid to the below-ground organs because knowledge of roots and root systems is lagging behind that of the shoot systems. Fine-root growth dynamics shall be related to shoot growth activity. Likewise, lignotubers merit attention because they are very characteristic and appear to play an important role in the resilience of the shrub vegetation.

Finally, we will focus on a few phenological observations. Specific rates of plant development under variable environmental conditions may shed more light on the relationship between plant growth, reproduction, and specific environmental conditions. However, prediction of the timing of phenological events is difficult considering the unpredictability of rainfall events. Nevertheless, the analysis of timing of flower differentiation provides new insights into ecosystems biology. In conclusion, we will discuss briefly phenomorphological observations a method with the potential to provide more objectivity to ecosystems comparisons.

#### Leaves

Perhaps the most typical organ of the mediterranean-type vegetation is the sclerophyll a leathery, hard and stiff leaf which lasts generally more than one growth period. Commonly reported characteristics of the sclerophyll are a strong cuticle which may be as thick as the entire epidermis, stomates sunk beneath the epidermis and sometimes hidden in crypts (invaginations of the epidermis), frequent formation of a hypodermis, abundant sclereids, lignification of the epidermis cell walls and vascular bundle sheaths, and also dense hair are commonly reported characteristics (Napp-Zinn 1984). A relatively small stomatal pore area of 0.2 - 0.5 % of the total leaf area vs. 0.5 - 1.5 % of plants from temperate climates has been discussed as a morphological feature providing an adaptive advantage to sclerophylls (Larcher 1975). However, the concept of "adaptive advantage" is not always clear. For example, in southern California the evergreen sclerophyllous shrubs *Ceanothus greggii* and *C. leucodermis* frequently grow side by side. The former species has the stomates hidden in deep crypts, a fact which is, according to prevalent dogma, an efficient protection against excessive transpiration. However, *C. leucodermis* leaves display their stomates flush with the lower epidermis. Both species appear to be well adapted to their environment although *C. leucodermis* loses up to 3/4 of its foliage in dry summers thus approaching a summer-deciduous character.

It might be wrong to analyze each of these morp-

hological features independently, because it is conceivable that only a suite of several of these sclerophyllous characters have adaptive value. The lack of crypts in *C. leucodermis* does not mean that they could not have adaptive value for *C. greggii*. It might well be, although experimental evidence is missing, that *C. leucodermis* compensates for the loss of a large part of its foliage by stem photosynthesis, a feature missing in *C. greggii*. Only rigorous experimentation might answer these questions.

#### Stems

Recent work regarding xylem anatomy of southern California shrubs focussed on vasicentric tracheids (Carlquist 1985). Vasicentric tracheids are defined as tracheids found adjacent to vessels in wood with libriform fibers or fiber tracheids as additional imperforate tracheary elements. The anatomical similarity among these three cell types explains why the presence of vasicentric tracheids in the wood of a species is diagnosed rather from a point of view of distribution in the xylem, i.e. being present throughout an entire growth ring or in the wood of a diffuse-porous species, than by specific structural characteristics. It is hypothesized that these vasicentric tracheids can supply stems and leaves with water when the vessels to which they are adjacent lose their function because of air embolisms (Carlquist 1985). The fact that vasicentric tracheids have been found in 86 plant families of dryland shrubs and trees, insinuates an adaptive advantage of this anatomical feature. However, quantitative analysis and experimental data to support the hypothesis are not yet available.

An important question regarding stem morphology is that of the significance of bark structure. According to Hamilton and Rowe (1949) the smooth stem surface of many shrubs of mediterranean-type ecosystems enhances stemflow from precipitation. They found that tall shrubs with smooth bark yielded about 280 mm of stem flow out of an average annual rainfall of 965 mm, (i.e. 29%), whereas rough-barked and spreading shrub types yielded only 8%. Stemflow would indeed irrigate and fertilize the immediate area around the shrub root crowns which has a specially high fine-root density (Hoffmann and Kummerow 1978).

Although the difference in stemflow yield between rough- and smooth-barked chaparral shrubs is evident, more data and experimental research is needed to demonstrate the superiority of smooth-barked species under conditions of water stress.

Stem photosynthesis is a property of numerous

shrubs of mediterranean-type ecosystems. Up to 50% of the species of some central Chilean plant communities show stem photosynthesis (Rundel 1981). Stem photosynthesis is an important process. Shrub species such as the nearly leafless *Retanilla ephedra* in central Chile showed carbon uptake rates almost equivalent to those of evergreen sclerophylls (Oechel et al. 1981). It is noteworthy that these shrubs with stem photosynthesis are largely lacking in California chaparral and the Mediterranean area. A more general evaluation of this phenomenon in the context of carbon uptake efficiency in mediterranean-type ecosystems has yet to be made.

### Lignotubers

Mediterranean-type ecosystems are characterized by a large number of shrubs with resprouting capacity. This results from the numerous dormant buds in the cortex of lignotubers which develop into characteristic epicormic shoots after severe perturbations such as fire, grazing or cutting. However, the terminology for these underground organs is not completely clear. The outgrowths at the base of the stem(s) of shrubs, e.g. in many species of the genus *Eucalyptus*, have been named lignotubers because they are woody and are considered tubers (Kerr 1925), while burls have been defined as aggregations of short branchlets fused into masses of wood (Garland and Marion 1960). In any case, the similarities between lignotubers and burls in regard to function, physiological, and ecological significance appear to be great enough to name all these structures lignotubers. The term "burl" can be used to describe tissue swellings caused by pathological agents (James 1984). Genera such as *Eucalyptus* in Australia, *Quercus* in the Mediterranean area, *Arctostaphylos* in California, and *Lithraea* in the Chilean matorral are well known for containing shrub species with lignotubers.

The recently described underground structures of *Quercus gambelii* consisted of a massive system (6 Kg / m<sup>2</sup>) of lignotubers, interconnecting rhizomes, and roots which amounted to 72 % of the total belowground biomass (Tiedemann et al. 1987). These structures are very similar to those found in *Quercus dumosa* in California (Kummerow and Mangan 1981) and *Q. coccifera* in the French garrigue (Rambal 1984).

The importance of lignotubers as the site of the renovation buds is undisputed. However, there are in the same ecosystems shrub species that rely on seed germination for their propagation and renewal growth after fire. Considerable efforts have been spent to show the advantages and disadvantages

of lignotubers for the stability of a shrub species in the mediterranean-type environment (Keeley and Zedler 1978).

Little is known about the function of lignotubers and burls as storage organs. Water, mineral nutrients, and carbohydrates are accumulated in these structures, although storage capacity and immediate carbohydrate availability to other plant parts are not well studied. Lignotubers, rhizomes and larger roots in *Quercus coccifera* had average starch concentrations of 8% of dry weight in early spring and 4-5% at the onset of winter time. The standing crop of 5 - 6 Kg/m<sup>2</sup> of lignotubers and rhizomes allows us to estimate that about 400 g/m<sup>2</sup> of starch were stored belowground in a dense garrigue stand (Kummerow, unpubl.). This amount appears to be adequate to "pay" the cost of maintenance respiration and to provide the energy for the development of a new shoot system after a severe perturbation. However, these data and observations show also the need for a new analysis of lignotuber function in the context of ecosystems studies.

### Roots

Roots have been for many obvious reasons much less studied than aboveground shoot systems. Therefore, it is more difficult to find appropriate generalizations. Nevertheless, numerous specific topics have been addressed by a large number of investigators.

Important for any discussion is the definition of the different root categories. Roots generally thicker than 1 mm and mostly perennial have a vascular cambium and are thus comparable (analogous) to the branches and twigs of the shoot system. Roots with smaller diameters generally do not have a cambium cylinder, have a determinate growth pattern, and a limited longevity. Thus, fine-roots are analogous to leaves. Both these organs have absorbing functions and a life span that ranges in leaves from several weeks to a few years and in fine roots from a few days in the tropical rain forest (Kummerow et al. 1982) to several months or even longer in temperate climate zones (Reynolds 1975)

A major and still unresolved task of ecosystems research is the measurement of fine-root production. In mediterranean-type ecosystems. This task is especially difficult because the generally rocky substrate makes fine-root collecting a tedious and frustrating endeavor. Fine-root production and replacement costs can range from 8-67% of net primary production in forests (Santantonio and Grace 1987). For mediterranean-type ecosystems there

are only coarse estimates available (Kummerow et al. 1978).

In a mature mixed chaparral we found in midsummer a total amount of 108 g/m<sup>2</sup> of live and 266 g/m<sup>2</sup> of dead fine roots (Kummerow and Wright 1988). Early winter fine-root length under the canopy of *Adenostoma fasciculatum* was measured as 3.5 m/100 cm<sup>2</sup>, while the summer maximum reached 20.2 m/100 cm<sup>2</sup>. Thus, root length increased by a factor of 5.8 from winter to summer. However, this value underestimates production because the continuously ongoing replacement of fine roots is not taken into account.

A technique based on <sup>14</sup>C/<sup>12</sup>C dilution ratios allowed calculation of a seasonal fine-root turnover coefficient of 0.24 in cold desert *Atriplex confertifolia* communities (Caldwell and Camp 1974). Fine-root production and turnover was estimated recently for a 14-yr pine plantation in New Zealand (Santantonio and Grace 1987). A compartment flow model was developed for this purpose. The main component of this model is the fine-root decomposition as a function of soil temperature. Fine-root decomposition calculated by means of this model was not significantly different from an independent set of decomposition data. It would be attractive to re-parameterize this model for a mediterranean-type vegetation.

These data show clearly the difficulties of fine-root production measurements. However, one can safely assume that after dry summers the amount of living fine roots becomes so small that one may talk about root shedding as analogous to leaf shedding. Considering the typically low carbon content of the soils, fine-root litter then becomes a major component of carbon transfer to the soil. It has been estimated that the belowground litter production in mediterranean-type ecosystems is substantially higher than aboveground litter fall (Kummerow 1981).

#### *Balance of leaf and fine-root activity*

While allocation to roots and shoots has been studied in several herbaceous plants there is almost no information for woody plants. Previous analysis of partitioning often have been based on the theory of balanced root and shoot activity which states that the product of root biomass and root specific activity is proportional to the product of shoot biomass and shoot specific activity (Davidson 1969). However, there is only indirect evidence available that supports the applicability of this principle for woody plants. Resprouting chaparral shrubs which were repeatedly burned appear to

have the ability to rapidly re-establish a functional balance in above- and belowground activities (Tenhunen et al. 1988).

The typically synchronous flushing of shoots in cocoa (*Theobroma cacao*) in Bahia, Brazil was characterized by very low rates of fine-root growth. Once the shoots had finished their growth flush, fine root growth assumed the original rate (Kummerow et al. 1982). This observation is supported by data from Vogel (1975) who found direct observations of cocoa trees in containers with observation windows that periods of active shoot growth were preceded by intensive fine-root development. These data suggest a tendency toward balanced root and shoot growth in a tropical tree growing in an environment with little seasonality.

Experiments with chaparral shrubs in large redwood containers has shown that with increasing aridity of the growing conditions the fine-root to leaf biomass ratio increased (Kummerow 1981). This means that under drought conditions a relatively larger fraction of the available carbohydrates was allocated to the fine-root system. We may expect that more experimentation and deeper insight into the root:shoot relations will eventually allow us to predict the standing crop of fine-roots from an estimate of the standing leaf biomass. However, the special architecture of the sclerophyllous shrub has to be considered. A large storage capacity for water, minerals, and carbohydrates in lignotubers buffers these shrubs against rapid changes. Adjustments to new growth conditions caused by environmental perturbations may require time periods in the magnitude of several months.

#### *Phenology*

The pronounced seasonality of the mediterranean climate -- dry hot summers alternating with wet and cool winters -- is reflected by the patterns of growth and development of the vegetation. A considerable wealth of information on timing and sequence of phenophases has been accumulated (Pierce 1984, Kummerow 1983). In the present contribution only two phenological phenomena, both of them relating to phenology and morphology, will be discussed.

Timing of flower differentiation. -- Organisms adapt to environmental conditions according to their genetic constitution. Thus, an array of genetically determined responses will characterize the temporal sequences of phenophases in an ecosystem (Anderson 1974). This explains why, for example, not all the shrubs in a mediterranean ecosystem flower at the same time. The relationship bet-

ween actual flowering and flower bud differentiation in chaparral was studied recently by Steele (1985). In *Adenostoma fasciculatum* flowers develop at the distal ends of the current year's vegetative growth. Generally, at the beginning of May, perhaps triggered by seasonally decreasing soil moisture potential, apical meristems change from the vegetative to the generative mode. This is an irreversible process which proceeds without further delay towards anthesis in June-July. Since the vegetative bud has to change to a generative one during the spring, early blooming is impossible for this species.

This flowering pattern is in contrast to that of *Ceanothus greggii* and other *Ceanothus* species. These shrubs flower from axillary inflorescences in March-April (according to temperatures) even before vegetative growth has been initiated. The flower buds are differentiated in the axils of young leaves in May, about 11 months prior to the actual anthesis. Thus, flowering in this species is independent of vegetative growth. A consequence of this flowering mode is that the abundance of flowers in *Ceanothus* shrubs does not permit us to infer on the amount of precipitation in the winter that precedes the flowering. The flowers are the product of the weather conditions of the winter two years prior to actual flowering.

A third pattern can be seen in the California scrub oak, *Quercus dumosa*. The catkins (inflorescences of staminate flowers) are differentiated in September, in the midst of the summer drought period. However, the scrub oak is very deep rooted and rarely experiences soil water potentials too low to prevent catkin differentiation and development. By mid May, flower buds break and catkins appear but pollen is not yet shed. Simultaneously, vegetative buds break and new shoot development proceeds rapidly. In the axils of the first leaves of these new shoots carpellate flowers develop in rapid sequence. At this time the catkins begin to shed pollen. Thus, staminate flowers develop in the fall of the year preceding anthesis, while carpellate flowers are differentiated and developed to maturity during the same spring of their anthesis.

A comparative study of flowering and flower differentiation in different mediterranean-type ecosystems could shed light on the evolutionary history of the shrub species of these widely disjunct areas of the world.

Phenomorphology. -- The physiognomic similarity of plant forms in different mediterranean-type ecosystems has stimulated since long the development of growth-form systems with the explicit purpose of defining the degree of similarity between

ecosystems. Best known is Raunkiaer's (1904) system which is based on the single feature of the location of the perennating buds, e.g. the phanerophytes with their buds above ground or the cryptophytes with their bulbs below the soil surface.

Recently, a new system based on 36 morphological and functional characters was proposed by Orshan (1986). Since this system is based on a large number of characters such as plant height, width of photosynthetic organs, bark shedding, or depth of root systems, etc., it becomes possible to distinguish objectively between two sites which may not appear to be very different from each other. The idea is attractive because the subjectivity in the appraisal of similarity could be replaced by objective data. However, there are also some difficulties with this phenomorphological approach. Not all the listed characters are independent from each other, e.g. a plant taller than 30 m will most probably have a root system deeper than 10 cm. Some of the characters are difficult to obtain, e.g. depth and lateral spread of root systems or the longevity of assimilating stems. However, most of these difficulties might be overcome with a good working experience of the field sites in question. There remains the problem that the application of this system is very labor intensive.

## CONCLUSIONS

This short and necessarily selective review of structures characteristic for mediterranean-type plant communities has revealed a series of features which have generally been considered as of adaptive value. In some cases a reappraisal of the adaptive value may be due. However, a suite of belowground structures can be added to those already in use to explain the resilient nature of the mediterranean-type shrub vegetation. Energy and water storage in lignotubers and fine-root shedding should be further investigated. Soil improvement as a result of belowground litter production (fine-root turnover) has to be appraised. Results of phenological observations have the potential to integrate the effect of environmental conditions on the vegetation. Patterns of the timing of flower differentiation and actual flowering might provide a powerful tool for the comparison of disjunct mediterranean-type shrub vegetations and the analysis of their evolutionary history, and phenomorphological observations may increase the objectivity of comparative studies of mediterranean-type ecosystems. Overall it appears that not a specific feature but a suite of morphological characteristics make the species cope with the environmental requirements of the mediterranean-climate areas.

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