

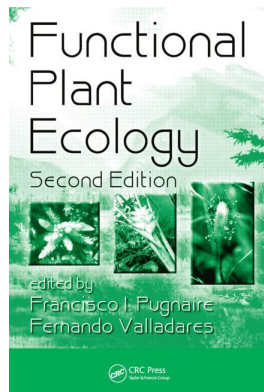
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9 Functional Attributes in Mediterranean-Type Ecosystems

Richard Joffre, Serge Rambal, and Claire Damesin

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INTRODUCTION

Mediterranean-type environments share unique climatic pattern with a cool wet winter and a hot dry summer (Köppen 1900), constituting the core of what we call the Mediterranean climate. These climatic conditions can be coarsely considered as a transition between dry tropical and temperate climates, with an occurrence of a distinct summer drought. These conditions occur on the west coasts of all continents between latitudes 30° and 45°, because of very general reasons of air circulation as the dry subtropical high pressure cells move poleward in the warm season blocking the entry of midlatitude storm. One of the main corollary of this approach is to clearly define Mediterranean regions as zonal ones and to exclude limited geographical definitions considering only the Mediterranean Sea (Joffre and Rambal 2002). It is important to note that the Mediterranean climate is very recent in geological terms and first appeared approximately 3.2 million years ago during the Pliocene. Mediterranean climates have attained their greatest extent at present.

Since the beginning of the century, numerous studies have highlighted structural and functional affinities of vegetation communities in Mediterranean-type climate regions throughout the world, that is, the Mediterranean Basin itself, California, central Chile, the Cape region of south Africa, and parts of southwestern and southern Australia (see Specht 1969a for a summary of early works of Schimper 1903 and Warming 1909). In the 1970s, comparisons of physiological and structural properties of Mediterranean-type ecosystem (MTE) (Naveh 1967, Specht 1969a,b, Mooney and Dunn 1970) have shown that, in some cases, similarities of these plants extend to patterns of growth, morphology, and physiology. In contrast to similarities that explained invoking an evolutionary convergence driven by climate and perturbation (periodic fire), Herrera (1992) introduced a critical distinction in the analyses of Mediterranean flora between taxa present before the Pliocene versus those that have immigrated into the regions since the onset of the Mediterranean-type climate and showed that the two groups exhibit distinctive traits, the former dominated by sclerophylly, large vertebrate-dispersed fruits and seeds, and the latter by nonsclerophyllous leaves, anemochory, dry fruits, and small seeds. Analyzing convergent traits of Mediterranean woody plants belonging to pre-Mediterranean lineages, Verdú et al. (2003) supported the view that common morphological and life-history traits are due to phylogenetical inertia and cannot be merely interpreted as a pure consequence of adaptive processes.

Understanding the diversity of physiological and functional strategies among co-occurring species as evergreen and deciduous in MTE could be done through identifying major axes of ecological and life-history strategies (Ackerly 2004a,b) and the underlying adaptive trade-offs between the traits (Westoby et al. 2002). In MTE, perennial species have to cope with the high temporal variability of resources and perturbations. Studying the trade-offs between phenology, relative growth rate, life form, and seed mass among Mediterranean woody species, Castro-Diez et al. (2003) pointed out that Mediterranean woody plants exhibit a wide phenological diversity that cannot be explained just on the basis of climatic constraints. They suggested that duration of primary shoot growth allow to sort out the species between two extreme growth strategies: a conservative strategy characterized by a concentration of the primary shoot growth into a short period, free of frosts and droughts, and an opportunistic strategy defined by the allocation of resources to current growth whenever they are available. These strategies should have been selected for in environments of predictable and unpredictable resource availability, respectively.

The aim of this chapter is to discuss some aspects of the functioning of perennial woody species by (1) briefly reviewing the main features of MTE resources, (2) illustrating how individual and ecosystem cope with variability in water resource and control water loss, (3) presenting the assimilation characteristics in relation to constraints, and (4) evaluating the role of nutrients at plant and community levels.

MTEs CHARACTERISTICS

Human occupation as well as past and present land use differ strongly between the five MTEs regions of the world. This obvious fact has evident and important consequences on biodiversity, landscape structure, and ecosystem functioning and have been extensively reviewed recently (Blondel and Aronson 1995, Hobbs et al. 1995, Davis et al. 1996). For instance, the high resistance of the Mediterranean Basin ecosystems to invaders could be a result of the long history of close interactions between humans and ecosystems (Butzer 2005, Thompson 2005, Blondel 2006). Probably no other part of the world than the Mediterranean Basin has played a more fundamental role in the history of mankind with the development of numerous civilizations. Their legacy concerns the transformation and shaping of primitive ecosystems to the present man-made landscapes but also cultural attitudes such as our present position and perception vis-à-vis nature. Agriculture and animal husbandry began more than 10,000 BP in the Eastern Mediterranean, and around 8000 BP in Greece and western Mediterranean. It is important to highlight in agreement with Butzer (2003) and Blondel (2006) that the long-lasting management of Mediterranean ecosystems has not always resulted in a decrease in biodiversity but has been in fact beneficial for many components of biological diversity. In reshaping natural forest toward more diversified landscapes, Mediterranean civilizations have created in many regions land-use models whose aim was to achieve sustainable long-term ecosystem management (Joffre et al. 1999, Blondel 2006).

CLIMATE DEFINITION AND VARIABILITY

The most distinctive feature of the Mediterranean climate involves the seasonality in air temperature and precipitation that lead to a hot drought period in summer and a cool wet period in winter (Köppen 1931, Bagnouls and Gaussen 1953, Aschmann 1973). This peculiarity of the Mediterranean climate has important implications for vegetation functioning and limits the most favorable season for growth to brief periods in spring and fall. As quoted by Rundel (1995), “dry summer conditions limit water availability and thus growth, while cool winter conditions limit growth during the season when water availability is generally highest.” Based on the total amount of annual precipitation and a combination of averaged maximum temperature of the hottest month and the averaged minimum temperature for the coldest month, the Emberger pluviometric quotient allows a classification of climates from arid to super-humid and from cold to hot (Daget 1977, Le Houérou 1990).

From an ecological point of view, the variability or unpredictability of precipitation imposes strong constraints on plants that could be more important for the survival of individuals than the mean values. An extreme event is here defined as an event where a climate variable had a low relative frequency of occurrence or was lower than (or exceeded) a given critical threshold. This concern arises naturally, since the impacts of climate are realized largely through the incidence of variation about normal conditions or extreme events (Wigley 1985). Examining annual precipitation at 360 stations scattered over the earth, Conrad (1941) long ago found a relationship between interannual variability and mean precipitation. For 73 stations located in a 100 km × 100 km area around Montpellier, Rambal and Debussche (1995) found a linear relationship ($r=0.87$, $P<0.01$) between mean and standard deviation. Table 9.1 presents some estimations of the coefficient of variation for a 1000 mm mean. The values range between 0.16 and 0.29. The lowest values (0.16–0.18) are proposed by Le Houérou (1992) for a large set of locations in Africa and in the near East. Conrad (1941), identifying variability more than the rule or positive anomalies in some dry areas, showed in his paper that positive anomalies of 3%, 7%, and 10% were observed in Marseille (Southern France), San Diego (California, USA), and Alicante (Southern Spain), respectively. These findings agreed with those of Waggoner (1989) who observed

TABLE 9.1
Coefficient of Variations for Mean Annual Rainfall Amounts

References	Source	Number of Stations	Coefficient of Variation
Conrad (1941)	World	360	0.21
Waggoner (1989)	USA	55	0.20
Le Houérou (1992)	North Africa, Near East	407	0.18
	Sahel, Soudan	228	0.17
	East Africa	300	0.16
Rambal and Debussche (1995)	Languedoc (France)	73	0.29

that “frequency distributions with much larger variance than expected are in the Mediterranean climates” of California.

Identifying the responsiveness of several regions of the world to climate change, Giorgi and Bi (2005) and Giorgi (2006) showed that the Mediterranean Basin emerges among the primary climate change hot spots in Northern hemisphere. According to projections by 20 global climate models, a very pronounced increase in variability of summer temperature and precipitation as well as a strong decrease of summer precipitations (−22%) characterize the Mediterranean Basin climate at the end of twenty-first century.

SUBSTRATE

Different parent rocks and geological histories of the five Mediterranean climate regions have given rise to very distinct soils and fertility levels. Table 9.2 summarizes the more frequent lithological substratum in each region and the associated nutrient status dependent on leaching and water-driven erosion. We modify the original table first published by Groves et al. (1983) to take into account the presence of siliceous parent rock in large areas of the Mediterranean Basin (part of Iberian Peninsula, Corsica, part of Provence). South Africa and southern Australia comprise older landscapes, consisting of an inland mass of geologically old material, surrounded by discontinuous strip of more recent marine deposits (Hobbs et al. 1995). Soils of the upland of the Cape Mountains as well as southwestern Australia have been exposed to weathering since Paleozoic. In contrast, soils of the Mediterranean Basin, California, and Chile are much younger, and reflect Tertiary and Quaternary orogenic events. Analyzing mineral nutrient relations among MTE, Lamont (1994) concluded that “among Mediterranean regions, the soils in Chile are more fertile than those in California, which in turn are more fertile than soils in south-eastern Australia, which in turn are more fertile than those of southwestern Australia.” It has been generally assessed that nutrient availability of soils in Mediterranean Basin and Chile is equivalent to that of South Africa and Australia (Groves et al. 1983).

VEGETATION TYPES

In the five MT regions, evergreen species are more abundant than deciduous ones and the vegetation formations are characterized by the dominance of trees and woody shrubs with small, sclerophyllous leaves. Nevertheless, although the woody shrub sclerophyllous growth-form is the dominant element, they never represent the majority of the total floras. The main vegetation formations are usually called garrigue or maquis in France depending on the nature of the soil substrate calcareous or siliceous, chaparral in California, heath and mallee in Australia, matorral in Chile, and fynbos in South Africa. These formations are fairly similar in their physiognomy and have provided the ideal testing ground for the theory of ecological convergence from evolutionary, morphological, and physiological points of view.

TABLE 9.2
Main Lithological Substratum and Associated Nutrient Status from Soils of Mediterranean Climate Regions

Substratum	Nutrient Status	South Australia	Southwest Australia	South Africa	California	Chile	Mediterranean Basin
Siliceous rocks	Strongly leached nutrient-poor soils	•••	•••	•••	•	—	••
Argillaceous rocks	Strongly leached nutrient-poor soils and moderately leached nutrient-rich soils	••	Trace	••	•••	•••	Trace
Calcareous rocks	Moderately leached nutrient-rich soils and shallow, high pH soils	•••	Trace	•	Trace	—	•••
Ultramafic rocks (serpentines)	Mg-rich, Ca-poor soils	—	—	—	•	—	Trace

Source: Data from Groves, R.H., Beard, J.S., Deacon, H.J., Lambrechts, J.J.N., Rabinovitch-Vin, A., Specht, R.L., and Stock, W.D. in *Mineral Nutrients in Mediterranean Ecosystems*, J.A. Day, ed., Council for Scientific and Industrial Research, Pretoria, South Africa, 1983, 1–17. With permission.

•••, common.

••, frequent.

•, present but not widespread.

Trace, found in restricted localities.

—, not recorded.

Physiologically based models were presented to explain the distribution of broad-leaved evergreen species, and a number of ecological paradigms have been developed explaining the nature of plant adaptation to MT climates (for a comprehensive account see Keeley 1989). Nevertheless, strict climatic control of sclerophyll leaf morphologies is questioned by the presence of sclerophyllous vegetation types in non-Mediterranean environments, for example, chaparral in Arizona, heathland communities in eastern Australia (Specht 1979), fynbos-like vegetation in the Afromontane region of Africa (Killick 1979), and tropical zone of Mexico (Verdú et al. 2003). Moreover, the majority of ecophysiological works dealing with drought resistance of plants in Mediterranean ambient have been conducted on genera existing before the Pliocene, that is, the establishment of true Mediterranean climate conditions (e.g., *Ceratonia*, *Hedera*, *Olea*, *Phillyrea*, *Pinus*, *Quercus*, *Vitis*). It is therefore difficult to interpret the physiological and anatomical properties of these species as adaptive responses to Mediterranean ambient. The character syndromes in Mediterranean plants may largely be explained in relation to the age of the lineage (Tertiary pre-Mediterranean vs. Quaternary true Mediterranean) and thus do not represent convergent evolution. The role of nutrients in species and ecosystem convergence was questioned in the 1980s (Kruger et al. 1983) based on observations of the contrasting conditions between the oligotrophic soil conditions of South Africa and Western and South Australia, and the relatively richer soil conditions of the other three MTEs. The role of fire in convergence of traits was recently questioned by Lloret et al. (2005), Pausas and Verdú (2005), Keeley et al. (2006) and Pausas et al. (2006).

INDIVIDUAL AND ECOSYSTEM RESPONSES TO VARIABILITY IN WATER RESOURCE

Among the numerous mechanisms for drought resistance, Mediterranean plant species have three responses that act together to dampen the effects of variability in water resource (Figure 9.1). Change in the leaf area allows the plants to cope with low-frequency oscillations such as a decrease in the annual rainfall amount. The response of the root system dampens the medium-sized oscillations, for example, changes in seasonal distribution of a given annual rainfall distribution. Finally, the stomatal activity allows quasioptimization of water use at a daily timescale. Any change in the leaf area induces change in the root system. The new

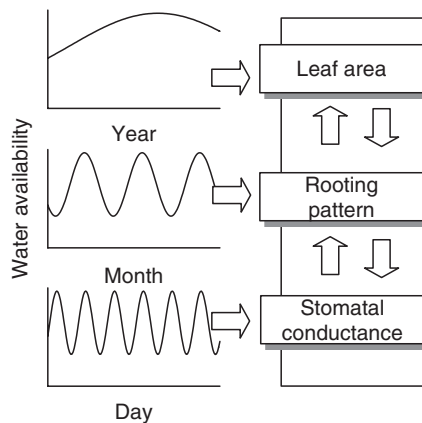


FIGURE 9.1 Conceptual diagram in which we proposed to associate the main mechanisms of drought resistance for Mediterranean plant species to the timescale of variations of the water availability from day to year. Vertical up and down arrows suggest that the mechanisms do not act independently.

functional equilibrium of the plant is controlled by carbohydrates and nitrogen or is hormonally mediated. Any change in the soil water deficit produces a change in the stomatal closure. The plant water status or a counterbalancing effect of phytohormones can act as indicators of the root stress. So, each mechanism is linked with the one immediately preceding it, providing an integrated strategy of the plant to improve its water balance under any given set of conditions (Rambal 1993, 1995).

WATER UPTAKE

Rooting Depth

Studies on the root distribution of several Californian chaparral shrub species established that deep root systems are characteristic for the dominant component of the Mediterranean-type vegetation (Hellmers et al. 1955). However, when examined in detail, these species have been shown to exhibit a great diversity in rooting depth (Kummerow et al. 1977) and consequently, in response to drought stress (Poole and Miller 1975). Based on these results, Mediterranean plant species can be roughly divided into two categories: deep-rooted species with root depth greater than 2 m, and shallow-rooted species with rooting depths less than 2 m. Mediterranean oaks are among the deepest-rooted plant species. For California oaks, Stone and Kalisz (1991) and Canadell et al. (1996) reported roots deeper than 8.5 m for the evergreen *Quercus agrifolia* (10.7 m), *Q. dumosa* (8.5 m), *Q. turbinella* (>9 m), *Q. wislizenii* (24.2 m), and the deciduous *Q. douglasii* (24.2 m). Similar or higher values have been estimated for species of the Chilean matorral (*Lithrea caustica* 5 m, *Quillaja saponaria* 8 m) and of the chaparral (*Adenostoma fasciculatum* 7.6 m). Lower values are found for dominant species of the Mediterranean Basin (*Pinus halepensis* 4.5 m, *Arbutus unedo* 3.5 m) or of the Australian mallee (*Casuarina* spp. >2.4 m, *Banksia* spp. 5 m). However, rooting depth is not the only functional trait helping the plant to access soil water. Root cover that is the maximum horizontal area colonized by the roots appears to be largely greater than the plant cover. This trait is particularly crucial in interpreting tree densities in savanna-like ecosystems, such as the ones we observed in dehesas of the Iberia peninsula (Moreno et al. 2005).

Soil Water Uptake Patterns

Deep root system as those presented earlier easily coped with low water availability. Rambal (1984) distinguished in *Q. coccifera* four patterns of water uptake throughout a drying cycle of 3 months (Figure 9.2). Late spring, water loss occurred exclusively from the top 0–50 soil layer, which lost about 4% of store water per day. The upper meter supplied three-quarter of the total. Early summer, root water uptake decreased in the upper layer, which then presents a daily loss of 1.2% of its reserve. Peak of water uptake was between 2 and 2.5 m depth. This layer supplied 0.62 mm day⁻¹ of 2.64 mm day⁻¹ of transpired water. Late summer was characterized by unevenness of water loss. All the upper layers were depleted and only the lower layers are able to supply water. During these two late periods, the deepest soil layers were contributing as much water as the top. Early fall, at the end of the dry period, all the layers were depleted. The flat profile did not allow the uptake of water at a rate greater than 0.62 mm day⁻¹. During the first three stages, the daily rates of transpiration were 2.84, 2.64, and 2.35 mm, respectively. Talsma and Gardner (1986) for various *Eucalyptus* observed the same patterning.

Rooting Patterns

In wet conditions, the major resistance to water uptake appears to be inside the root. Consequently, there is a good correlation between water uptake and rooting density.

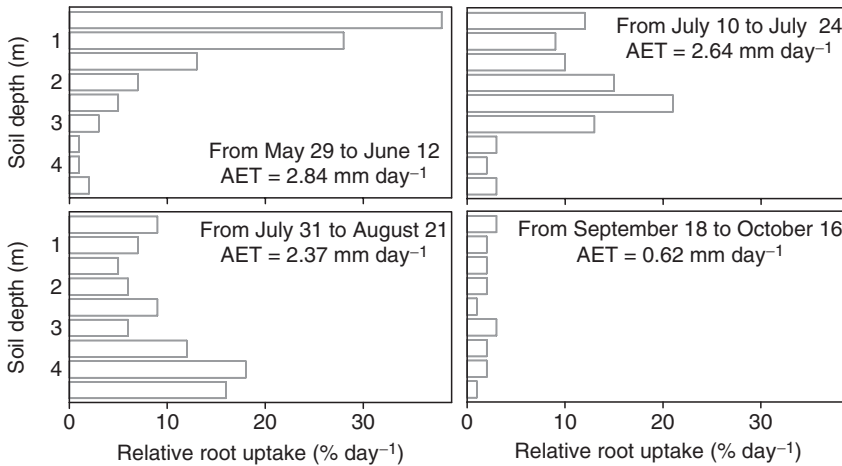


FIGURE 9.2 Patterns of water uptake with soil depth within four periods across a severe summer drought. For each 50 cm thick soil layer, the water uptake is expressed in percent of the extractable water used daily.

Hence, the late spring profile of water uptake we observed with *Q. coccifera* can be considered as a picture of its root density profile. The greatest accumulation of root mass was in the top meter. Below 1 m root mass decreased gradually with depth. The theoretical profile proposed by Jackson et al. (1996) for the sclerophyllous shrub group does not take into account the deep-rooted species we identified earlier. This sclerophyllous shrub group values included values from some chaparral, fynbos, heath, garrigue, and matorral stands. The root distribution with depth is described by the equation of Gale and Grigal (1987) $y = 1 - \beta^z$, where y is the cumulative root fraction from the soil surface to depth z (cm) and β is an extinction coefficient. For this largely Mediterranean group $\beta = 0.964$. This means that 67% of the root biomass are in the first 30 cm of soil and 90% in the 0–60 cm layer. These surprisingly high values are far to our estimates for *Q. coccifera* (48% for the 0–50 cm horizon, Rambal 1984) or values for *Q. turbinella* (53% for the 0–60 cm horizon). In the two species, the percent of roots deeper than 2 m were important (20% and 12%, respectively). Deep roots play a very important role during the summer period. As the soil dries, the layers below 2 m contribute an increasing fraction of the total water uptake, reaching between 12% and 23% of the total uptake depending of the severity of the drought (Rambal 1984).

WATER LOSS

Stomatal Regulation

Together with rooting pattern and leaf area, stomatal activity helps regulate water loss. According to their phenology, species may avoid or cope with water constraint. For instance, drought-deciduous species of the coastal sage community of California are drought evaders and chaparral species drought tolerators. Nevertheless, as stressed by Mooney (1989) “some coastal sage species that lose most of their leaves during the drought have been shown to tolerate very high water stress, whereas others somehow control stress while maintaining many of their leaves.” Phenological variations among individuals could also be very high. Ne’eman (1993) found in *Q. ithaburensis*, a deciduous oak of Israel, that some trees were clearly deciduous, while others had only a short duration of leaflessness and, as a consequence, could be considered as evergreen. By analogy, there appears to be a continuum of stomatal behavior in response to water stress: no stomata closure, progressive closure of

stomata (see Acherar et al. 1991 for Mediterranean oaks) and threshold effect leading to an early complete closure (see Aussenac and Valette 1982 for *Pinus* sp. pl.). With a rapid rate of drying, for example, with a shallow-rooted system, an early response of stomata closure was observed in some cases whereas a delayed response was observed when a slower rate of drying, for example, with a deep-rooted system, was imposed. Studies such as those of Poole and Miller (1975, 1981) showed that some chaparral species are more sensitive to water stress than others, as indicated by their water potential after stomata closure. These authors assume that the degree of drought tolerance is linked to rooting depth. Thus, shallow-rooted species tend to close their stomata at high water potential and to bear tissues with the greatest drought tolerance.

Stomatal closing is considered to be under the control of leaf turgor pressure or leaf water potential. Recently, however, some authors showed that leaf conductance is not always closely coupled with leaf water potential or leaf turgor pressure. There is now some evidence that soil water deficit can also induce stomatal closure even when the leaf water status remains unchanged. These results suggest that leaf conductance is not only affected by leaf water potential, but also, more directly, by soil or root water potential. One much-discussed possibility is that the counterbalancing effects of two phytohormones, cytokinin and abscissic acid, might provide information on the water status of the roots and induce stomatal closing or opening, as the case may be (Zhang et al. 1987). But, for modeling purposes, the leaf water status still remains the main control variable of the leaf stomatal conductance (Tardieu and Davies 1993).

Daily curves of stomatal conductance in MTE species can be coarsely classified according to three patterns following Hinckley et al. (1983) (Figure 9.3). Type 1 curves are bell-shaped and represent situations in which soil water potential, leaf water potential, and vapor pressure deficit do not limit stomatal conductance. Type 2 curves have two maxima, one at the start of the day and the other in the afternoon, both separated by a depression at midday. They correspond to situations where one or more of the previously mentioned factors limit stomatal conductance. In type 3, the curves have a high point only at the start of the day as

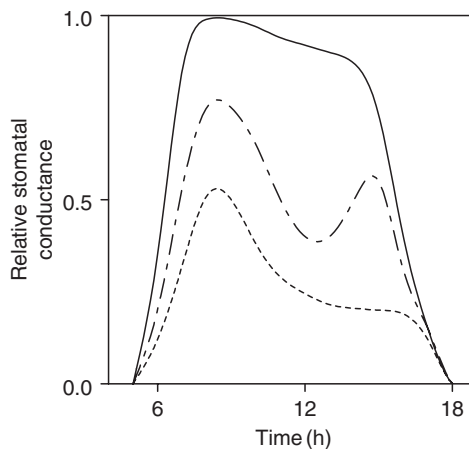


FIGURE 9.3 Typical patterns describing the daily courses of relative stomatal conductance during a drought period. Type 1 curve is bell-shaped and represents optimal situations in which soil water potential, leaf water potential, and vapor pressure deficit do not constraint transpiration. Curve of type 2 has two maximums, one early in the morning and the other in midafternoon, both separated by the so-called midday depression. They correspond to situations where water status and air dryness limit stomatal conductance. In type 3, the curve shows only a maximum early in the morning. Leaf water potential is at or below the turgor loss point for most part of the daylight period.

the leaf water potential of the plants, according to Hinckley, at or below the turgor loss point for part of the day. The midday stomatal closure was reported by Tenhunen et al. (1987) for many Mediterranean species. This drop in stomatal conductance has been interpreted as a feature, which allows Mediterranean species to limit water loss when the atmospheric evaporation is at its maximum. These authors suggested that midday stomatal closure is determined by the leaf-to-air vapor pressure deficit, whereas for Hinckley et al. (1983), this depends on the interaction among several factors, in particular the instantaneous water potential of the plant. Cowan and Farquhar (1977) showed theoretically how stomatal activity helps optimize water use on a daily timescale. This optimization pattern has been validated for few Mediterranean species (William 1983, see also Xu and Baldocchi 2003).

Leaf Area Index

The importance of adjustment in leaf area is emphasized by Passioura (1976): “It is the control of leaf area index and morphology which is often the most powerful means a mesophytic plant has for influencing its fate when subject to long term water stress in the field.” Over a large range of climates, changes in leaf area indices have been studied at both individual and ecosystem scale along gradients from higher to lower rainfall amounts or from more moisture to drier habitats in broad- or needle-leaf tree or shrub communities (Ladiges and Ashton 1974, Specht and Specht 1989). In Southern Australia, *Eucalyptus viminalis* trees occur over a wide range of rainfall conditions and soil types. Ladiges and Ashton (1974) observed that at moist sites mature trees are tall and produce large leaves and, at drier sites, trees are shorter and tend to produce smaller leaves. Poole and Miller (1981) hold a similar view for Mediterranean shrub species of the California chaparral: “the main response of the shrubs to different precipitation regimes in the chaparral range is to change leaf-area index, not physiological parameters.” The importance of this adjustment is largely species-dependent. The ranges of leaf-area index of some mature frequent MTE are summarized in Table 9.3. Understanding how the leaf-area index of a site comes into a predictable, dynamic equilibrium with the amount of water available is the target of researches in ecohydrology (Eagleson 2002, Eamus et al. 2006).

WATER TRANSFER

Soil–Plant Resistance to Water Flow

A simple application of Ohm’s Law analogy relating water potential difference from soil-to-leaf ($\Delta\Psi$) and transpiration rate (T) has been widely used to estimate total flow resistance (R)

TABLE 9.3
Leaf Area Index Ranges of Mature Stands of Some Frequent Vegetation Types

Vegetation Type	Dominant Species	LAI Range	References
Woodland	<i>Quercus ilex</i> (evergreen)	2.9–6.0	Damesin et al. (1998a)
Woodland	<i>Quercus pubescens</i> (deciduous)	2.0–4.2	Damesin et al. (1998a)
Shrubland	<i>Quercus coccifera</i> (evergreen)	1.5–4.0	Rambal and Leterme (1987)
Chaparral	<i>Adenostoma fasciculatum</i>	2.2–3.4	Rambal (2001)
	<i>Ceanothus megacarpus</i>	1.5–1.6	Rambal (2001)
Warm-temperate mallee	<i>Eucalyptus</i> spp.	1.5–6.0	Specht and Specht (1989)
Heathland south Australia	<i>Eucalyptus</i> spp.	2.5–4.0	Rambal (2001)

LAI, leaf area index.

expressed on a leaf-area basis: $\Delta\Psi = T R$ assuming firstly, little capacitance effect in the plant, and secondly, steady-state transpiration conditions. The pathway of water movement in soil and plant can be considered as comprising two main resistances in series, the soil-to-root resistance and the plant resistance. Partitioning soil and plant resistance is difficult. Generally, the plant resistance was assumed to be constant within a range of Ψ and so, the relative contribution of the soil resistance was estimated. For this, we applied Gardner (1964) who had showed that soil resistance is inversely proportional to the hydraulic conductance of the soil. As a consequence, the soil resistance is small at high water content and any observed difference in resistance should be largely attributable to differences in plant resistance. Under conditions of maximal transpiration (T_{\max}) in well-watered conditions: $\Delta\Psi_{\max} = T_{\max} R_{\min}$. Studying a large range of evergreen oak communities, we deduced a hierarchy of soil-to-leaf resistance from the highest R_{\min} in xeric sites to the lowest in mesic sites (Rambal 1992). Thus, for *Q. ilex* alone the ratio of xeric/mesic R_{\min} is 1.7. The presence and magnitude of differences in resistance suggest that this attribute could be an important component in drought tolerance. In the same way, Rambal and Leterme (1987) associated a decrease of leaf area index from 2.5 to 1.5 in the Mediterranean evergreen oak *Q. coccifera* growing across a rainfall gradient with changes in canopy structure and plant resistance. The role of the hydraulic resistance in the relative sensing of soil water deficit by roots has been emphasized. At a given rate of transpiration and soil water deficit, a plant with high hydraulic resistance lowers its leaf water potential to a greater degree than a plant with low resistance. This plant may further be more sensitive to maintain its rate of photosynthesis and growth. On the other hand, with a limited volume of water in the soil, an increase in hydraulic resistance saves water during the wetter periods for use during the drier ones.

Patterns of Changes in $\Delta\Psi$ with Increasing Water Stress

Richter (1976) observed that plant species “from sites with pronounced drought periods” did not undergo Ψ lower than that of desert plants. His analysis, for the first mentioned group, is largely based on works of Duhme (1974) conducted on 26 species of MTEs. In this study, Duhme measured Ψ of -4.4 MPa for *Q. coccifera*, a similar value of those we reported in a synthesis on Mediterranean evergreen oaks (Rambal and Debussche 1995). In this synthesis, whatever the study site and the amount of rain fallen during the measurement periods, minimum and predawn leaf water potentials were always higher than -4.4 and -3.8 MPa. Other examples well illustrated this assumption of lower bound of water stress even during a very dry year. Griffin (1973) observed at the end of the driest in 32 year period predawn potentials of the evergreen *Q. agrifolia*, in the more xeric location, between -2.5 and -3.1 MPa. These potentials remained also limited with the deciduous *Q. douglasii* and *Q. lobata*, -3.7 and -2.0 MPa, respectively (see also Damesin and Rambal 1995 for *Q. pubescens* values).

Nevertheless, the trajectories followed by minimum and predawn leaf water potentials to reach their limits were very different according to locations and species. This was particularly true for *Q. ilex* (Figure 9.4). $\Delta\Psi$ decreased to zero with decreasing soil water availability and predawn potential. As proposed by Ritchie and Hinckley (1975) “it is tempting to compare species based on these curves (. . .) as indicators of species differences.” Waring and Cleary (1967) on Douglas fir first observed this pattern. But it was initially considered as marginal. Indeed, Hickman (1970), from measurements done on 44 species, concluded that the opposite pattern in which $\Delta\Psi$ increases with the water stress is the most common pattern. It corresponds to species characterized as conformers. Species with the same pattern as our observations was named regulators. Hickman (1970) suggested “this pattern is probably typical of most plant species in areas with modified (?) Mediterranean climates.” It was also described by Aussenac and Valette (1982) for some trees (*Cedrus atlantica*, *Pinus* sp pl., *Q. pubescens*, and *Q. ilex*) and for the shrub *Buxus sempervirens*.

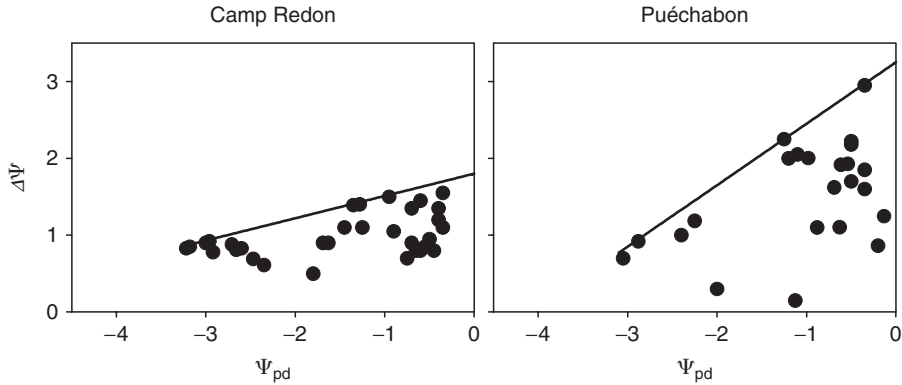


FIGURE 9.4 Scatter plots relating predawn leaf water potential Ψ_{pd} , MPa, and $\Delta\Psi$, that is predawn minus minimum potential from the same day, MPa. The boundary solid line gives information on how $\Delta\Psi$ declines with the drought. The data from Camp Redon (southern France) correspond to data from mature *Quercus ilex* trees growing in mesic conditions on a deep soil; those from Puéchabon (southern France) have been obtained on the same oak species growing in dry xeric conditions on karstic soil. In this location, *Q. ilex* functions as an isohydric plant (slope of $\Delta\Psi$ vs. $\Psi_{pd} \approx 1$) that can maintain nearly constant leaf water potential throughout the year despite changes in soil conditions.

An important question is asked by Reich and Hinckley (1989): “Does soil-to-leaf hydraulic conductance decrease with decreasing soil moisture due only to increased resistance in the soil, or is there a plant component as well?” (see also Bucci et al. 2005 for a substantial account). Changes in plant resistance under water limitation are attributable to effects on both roots and stems. As the soil dries, decreased permeability by root suberization and increased fine root mortality can reduce the balance between extraction capacity and transpiring leaf area. Xylem loss of vascular transport by cavitation might also cause an increase in plant resistance. There was evidence of embolism formation in Temperate and Mediterranean *Quercus*, one of the most common genera with ring-porous xylem anatomy (Cochard and Tyree 1990). For 1 year old twig segment of *Q. ilex*, the loss of conductivity began at -1.8 MPa and linearly increased to reach a total xylem cavitation at -4.35 MPa (Lo Gullo and Salleo 1993). When catastrophic xylem dysfunction occurs, Tyree and Sperry (1988) showed that minor branches begin to die, leading to a loss of leaf area and a reduction in the water flow, which improved water balance of the remaining living stems. Anatomical resistance to the formation and spread of air embolisms in the xylem may be of critical importance. There are a variety of features of xylem anatomy, which can increase the safety of water-conducting systems in Mediterranean species (Carlquist 1989). Vascentric tracheids adjacent to many vessels act as subsidiary conducting system and occur in numerous Mediterranean genera such as *Quercus*, *Arctostaphylos*, *Phyllirea*, *Rhus*, and *Banksia*. Vascular tracheids also provide conductive tissues at high stress and are present in drought-deciduous and ericoid evergreen species such as *Cistus*, *Erica*.

Hydraulic Architecture

Zimmermann (1983) introduced the principle of plant segmentation stating that embolism should develop first in the terminal part of the trees (i.e., leaves and little branches), thus preserving the other parts of the crown from embolism damage. The risk of xylem dysfunction especially in the petioles may determine the ability to resist to drought. Are Mediterranean species less vulnerable than other species? Cochard et al. (1992) and Higgs and Wood (1995) compared drought susceptibility by examining hydraulic dysfunction of the xylem

vessels in petioles of different oak species. The Mediterranean species (*Q. pubescens*, *Q. cerris*) did not show the lowest vulnerability (nor the highest) to embolism formation in comparison to the temperate ones (*Q. petraea*, *Q. robur*, *Q. rubra*). Early leaf senescence was also observed near -4 MPa on the Californian deciduous oak *Q. douglasii* (Griffin 1973); whereas all leaves of the deciduous *Q. pubescens* were yellowing at about -4.5 MPa in the Languedoc (Damesin and Rambal 1995). There is also some difference between Mediterranean species for their vulnerability to cavitation—partly explained by the distribution of xylem conduit diameter—which can be related to their different distribution within the Mediterranean Basin (Salleo et al. 1997, Cavender-Bares et al. 2005). As quoted by Preston et al. (2006), wood density and vessel characteristics are functionally interrelated but wood density was most strongly associated with soil water, and vessel traits showed contrasting relationships with plant height.

Maherali et al. (2004) compiled a database of 167 species and examined relationships among resistance to xylem cavitation and water transport capacity measured by the specific conductivity per unit of xylem area. For the Mediterranean woody species of this meta-analysis (Figure 9.5), we found mostly chaparral shrub species (*Ceanothus* and *Adenostoma* spp.) and some dominant trees growing around the Mediterranean Sea (*Quercus* spp.). Medians of Ψ_{50} for species occurring in the more arid environments were 6–7 times more negative than those growing in tropical rain forest. The Ψ_{50} medians are -5.3 , -4.5 , -2.8 , -2.4 , and -0.8 MPa for Mediterranean, desert, temperate forest, tropical dry forest, and tropical rain forest, respectively. Resistance increased significantly with decreasing precipitation and with the ratio of precipitation to potential evapotranspiration in evergreen angiosperms. The adaptive significance of increased resistance to cavitation with decreased precipitation as a mechanism of drought tolerance is of primary importance in such species because they need to preserve a water-conducting pathway for leaves year around. In contrast, Maherali et al. (2004) did not find association between water transport capacity and water availability suggesting that the evolutionary basis for a trade-off between cavitation resistance and water transport capacity is rather weak.

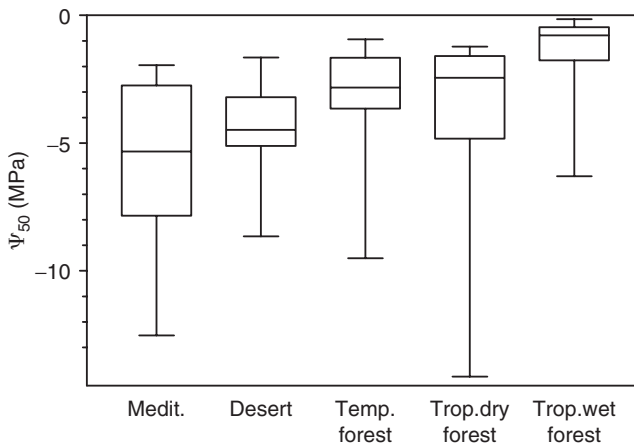


FIGURE 9.5 Box and whisker plots for the distribution of vulnerability to water stress-induced cavitation (as determined by plant water potential at which 50% cavitation occurred, Ψ_{50}) for 167 woody species grouped into five vegetation types (after Maherali et al. 2004). The number of species for the vegetation types are 16, 20, 71, 19, and 41 for Mediterranean, desert, temperate forest, tropical dry forest, and tropical rain forest, respectively. The corresponding medians are -5.3 , -4.5 , -2.8 , -2.4 , and -0.8 MPa.

CARBON ASSIMILATION: LEAF PHOTOSYNTHETIC PERFORMANCES

ASSIMILATION IN RELATION TO ENVIRONMENTAL CONDITIONS

Net CO₂ Assimilation in Optimal Conditions

The photosynthetic performance of Mediterranean species does not differ particularly from that of species from other biomes (Rambal 2001). For example, in the genus *Quercus*, Damesin et al. (1998a) analyzing the literature found that the Mediterranean species do not differ in their maximum assimilation—mean value of $16.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ calculated over five species—from non-Mediterranean species—mean value of $17.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ calculated over five species. Numerous studies have been conducted concerning species of the Californian chaparral and the Chilean matorral (Oechel et al. 1981) on the South African fynbos (Mooney et al. 1983, Van der Heyden and Lewis 1989) and on the shrublands and woodlands around the Mediterranean Sea (Tenhunen et al. 1987, Damesin et al. 1998a). Differences have been demonstrated between growth forms (Oechel et al. 1981) or guilds, and between restioid–ericoid and proteoid species (Van der Heyden and Lewis 1989). A robust relationship between nitrogen content of the leaves and their photosynthetic capacities has often been found in natural vegetation for a wide variety of plants (Wright et al. 2005). This correlation appears to be a consequence of the limitations on photosynthetic capacity imposed by the levels of the enzyme RuBP carboxylase and of the pigment–protein complexes. Mediterranean species do not deviate from this rule (Field 1991).

This relationship holds for species with low nitrogen content as observed with 36 evergreen sclerophyllous species growing at two sites in the coastal and mountain fynbos of South Africa. Herppich et al. (2002) averaged mass-based leaf nitrogen content of 0.52 ± 0.13 , 0.76 ± 0.18 , 0.55 ± 0.10 , 1.00 ± 0.29 for proteoid, ericoid, restioid, and other sclerophylls in their coastal location and 0.74 ± 0.13 , 1.29 ± 0.24 , 0.60 , 1.08 ± 0.31 for the same groups in their mountain location. They found a unique linear relationship between maximal light-saturated photosynthesis and nitrogen content for all the species except the coastal proteoid. Coastal proteoid too displayed a linear relationship with a steeper slope, that is, more photosynthesis with the same amount of nitrogen. Evergreen species might allocate less N to photosynthetic functions or they might allocate the same amount of N to photosynthetic functions but allocate that N inefficiently (Warren and Adams 2004).

Response to Water Constraint and Photoprotection

Mediterranean climate leaves have to cope with excess intercepted solar radiation when carbon assimilation is limited either by stomatal closure or a decrease of photosynthetic capacity due to water stress and high temperatures (summer) or low temperatures (winter). Indeed, absorption of light energy may be in excess of that required for carbon fixation and may result in damage to the photosystem. Different physiological regulatory mechanisms have been shown to occur during diurnal cycles to dissipate the excess of absorbed energy without any damage for cells: a downregulation of photosynthesis via a decrease of the photochemical efficiency of PSII (F_v/F_m) (Demmig-Adams et al. 1989, Damesin and Rambal 1995, Faria et al. 1996, Méthy et al. 1996) or via a decrease of chlorophyll content (Kyparissis et al. 1995), a change in the components of the xanthophyll cycle, a high antioxidative potential (Faria et al. 1996). It is difficult to assess if Mediterranean species have a more efficient photoprotection mechanism than temperate or tropical species. In particular, it would be interesting to examine if the Mediterranean species responses to high irradiance are acclimation or adaptation. On that account, a great proportion of the plant species growing in MTE produce and accumulate volatile organic compound (VOC) which may also serve as an excess energy dissipation system during a period of restricted growth

(Kesselmeier and Staudt 1999) although several studies pointed out that there is not necessarily a specific role for every VOC emitted (see Peñuelas and Llusia 2004 for a comprehensive account on this subject).

Modeling

Functioning at the biochemical level of the photosynthetic system, described by Farquhar and von Caemmerer (1982), can be summarized by both maximum carboxylation V_{cmax} and electron transport rates J_{max} . Mediterranean species fit in with the general scheme in terms of this functioning, if reference is made to the few Mediterranean species included in Wullschleger's (1993) review, although this author did not propose a separate grouping for these species. They do not deviate significantly from the empirical linear relation between V_{cmax} and J_{max} that he observed. Other data support this trend for Mediterranean oaks and *Arbutus unedo* (Hollinger 1992, Damesin et al. 1998a). This leaf photosynthesis model can be next integrated in a canopy level carbon balance model (Hollinger 1992, Sala and Tenhunen 1996). Relations between stomatal conductance (g_s) and assimilation (A) could be simulated following the empirical model proposed by Ball et al. (1987). That is the so-called coupled photosynthesis Ball–Berry stomatal model

$$g_s = g_0 + g_{\text{fac}} \frac{AR_h}{C_a},$$

in which A is net assimilation rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$), g_0 is a value representing the stomatal conductance when $A=0$ at the light compensation point (generally set to about $10 \text{ mmol m}^{-2} \text{s}^{-1}$), g_{fac} is a dimensionless empirical factor expressing the relation of g_s to A , to relative humidity at the leaf surface R_h (decimal fraction), and to CO_2 concentration at the leaf surface C_a ($\mu\text{mol mol}^{-1}$).

The functional dependency of g_{fac} on predawn leaf water potential (Ψ_{pd}) was measured in the field for *Q. ilex* (Sala and Tenhunen 1996) and *Q. pubescens* (Damesin and Rambal 1995). Both studies showed linear relationships for Ψ_{pd} equal or lower than -1 MPa , that is, during periods of reduced water availability (Figure 9.6). Xu and Baldocchi (2003) observed a strong correlation between g_s and AR_h/C_a during the growing season in *Quercus douglasii*. They suggested that leaf age and severe water stress did not alter g_{fac} ; a constant g_{fac} of 8–10 seems typical for oaks (Goulden 1996, Xu and Baldocchi 2003). However, the effect of decreasing

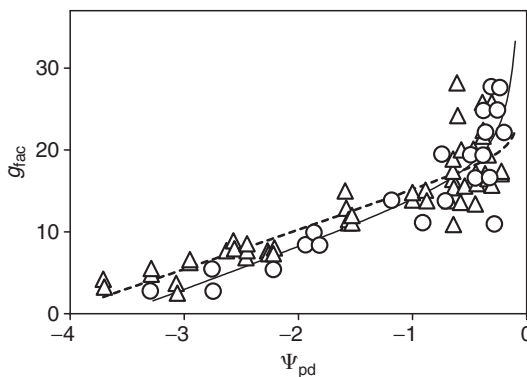


FIGURE 9.6 Relationships between g_{fac} and predawn water potential Ψ_{pd} for *Quercus ilex* and *Quercus pubescens*. The data for the former oak species have been obtained by Sala and Tenhunen (1996) (empty circle), and those for *Q. pubescens* by Damesin and Rambal (1995) (empty triangle up). For both data sets, we fitted the equation $g_{\text{fac}} = (a/\Psi_{\text{pd}}) + (b\Psi_{\text{pd}} + c)$. For *Q. ilex* (dotted), we obtained, $a = -0.31$, $b = 4.76$, $c = 19.6$, and $r^2 = 0.76$; for *Quercus pubescens* (solid line), $a = -1.64$, $b = 4.97$, $c = 17.35$, and $r^2 = 0.78$.

soil water content and consequently predawn leaf water potential Ψ_{pd} on g_{fac} is still in dispute. Some works assert that g_{fac} decreases as the soil dries. On the other hand, some others observed that g_{fac} remains constant and V_{cmax} decreases as the soil dries. A number of important gaps in our knowledge about photosynthetic downregulation and inhibition under water stress have been listed by Flexas et al. (2004).

ASSIMILATION IN RELATION TO WATER LOSS

One way to estimate water-use efficiency (ratio of photosynthesis and transpiration) in C_3 plants is to use leaf carbon isotope composition. Its measurement, easier than that of gaseous exchanges, allows the study of intraspecific and interspecific variability in field conditions (Damesin et al. 1998b).

Interspecific Variability

The creation of a superclass for Mediterranean species could be made on the basis of the discrimination (Δ) against $^{13}CO_2$ during the photosynthesis. For the xerophytic woods and scrubs superclass (which includes *Heteromeles arbutifolia*, *Nerium oleander*, and *Eucalyptus socialis*), Lloyd and Farquhar (1994) gave a surprising low Δ value of 12.9%. By comparison, this discrimination reaches 18.3% for the superclass cool or cold mixed forest they proposed and averaged 17.8% for all the C_3 plants. This distinction in term of Δ values implies a segregation of the long-term estimates of the ratio c_i/c_a between the intercellular CO_2 concentration within leaves and the atmospheric CO_2 concentration and therefore of leaf performance and water use efficiency. This approach has been extended by Beerling and Quick (1995) who used it both for superclasses and at the scale of the individual plant.

They estimated V_{cmax} and J_{max} both from Δ and from maximum assimilation. What values of Δ should be adopted for Mediterranean species? From a study conducted at 25 stations in southern France (Damesin et al. unpublished results) with four species of co-occurring trees or shrubs the following values were obtained: 18.20 ± 0.65 for *Pinus halepensis*, 18.86 ± 1.53 for *Quercus pubescens*, 19.50 ± 0.52 for *Q. coccifera*, and 19.88 ± 0.68 for *Q. ilex*. Only *P. halepensis* deviated significantly from the other three species. A similar distinction was recorded by Williams and Ehleringer (1996) between *Q. gambelii* and *P. edulis*. Values obtained on Californian oaks (Goulden 1996) and on *Q. ilex* at other sites (Fleck et al. 1996) confirm these orders of magnitude. However, all these values are subject to averaging procedures to overcome the great individual variation in Δ (Damesin et al. 1997).

Intraspecific Variability

Differential responses of species to local variations of resources could be analyzed through isotopic measurements. For example, Williams and Ehleringer (1996) explained the between-site variability in Δ along a summer monsoon gradient in southwestern USA using a parameter that integrated both the water balance and the climatic demand throughout the growing season. Similarly, Damesin et al. (1998b) took into account both within- and between-site variability among two deciduous and evergreen Mediterranean oaks using the minimum seasonal leaf predawn potential. This type of response, which tends to optimize water resource utilization, can be extended to entire plant communities growing along a water availability gradient (Stewart et al. 1995).

ASSIMILATION IN RELATION TO LEAF LIFE SPAN

In Mediterranean communities, evergreen species are more abundant than deciduous ones (Mooney and Dunn 1970, Cody and Mooney 1978, di Castri 1981). As a consequence,

ecological studies have largely focused on evergreen and sclerophyllous-leaved species and less attention was devoted to deciduous species. Nevertheless, Mooney and Dunn (1970) presented a conceptual model comparing the functioning of evergreen chaparral shrubs versus drought-deciduous species of the coastal sage community. The basic assumptions of this model were that the leaves of evergreen sclerophyllous have a relatively low photosynthetic capacity, compared with the malacophyllous, drought-deciduous leaves, but can amortize their cost of production over a longer period of time. Although the woody shrub growth-form is an important vegetation element in the MTE, the situation of co-occurrence of winter-deciduous and evergreen trees is not infrequent at least in California and Mediterranean Basin where many species of co-occurring *Quercus* exhibit the two habits (Hollinger 1992, Damesin et al. 1996, 1998a,b). How do these winter-deciduous species compete with their evergreen neighbors? Researches have been mainly oriented toward the mechanisms of seedling installation. However, trees generally have a long life span, and adult survival can thus also determine the abundance of a species in a given region. If the survival of a perennial species depends on its ability to maintain a positive carbon balance over the year (Givnish 1988), the winter deciduous habit could a priori present two disadvantages as compared with the evergreen one: (1) it implies a shorter photosynthetically active period and (2) the active period coincides with the most important constraint imposed by the Mediterranean climate, that is, the summer drought.

This distinction is in agreement with a validation of a cost-benefit model at the leaf level (Mooney and Dunn 1970). In this model, deciduous species compensate their lower leaf life span by a higher carbon assimilation by unit of time and a lower leaf production cost. This model was successfully tested for two coexisting Californian oaks (Hollinger 1992), but does not hold for two other oaks co-occurring in the North of the Mediterranean Basin where *Q. pubescens* has a lower area-based construction cost than *Q. ilex*, but does not have a higher photosynthetic capacity (Damesin et al. 1998a). Despite differences in biochemical composition, size, and mass per unit area, the leaves of the two species respond similarly to water-limited conditions and have similar intrinsic water use efficiencies (Damesin et al. 1997, 1998b). These results indicate that key factors distinguishing the functioning of the deciduous species from evergreen ones are more important at the higher level of organization (individual and ecosystem) than at the leaf level.

High level of secondary metabolites, essential oils, and resins, with their associated volatiles, characterize plants of semiarid regions (Kesselmeier and Staudt 1999). These secondary metabolites and VOCs represent an important part of the costs of construction of the leaves. Production of VOC has shown a great intraspecific variability (Staudt et al. 2001, 2004) and its regulation by environmental conditions have to be specified (Loreto et al. 1996, Lerda et al. 1997). There has been rapid progress in understanding how the emission of volatiles is regulated, mostly focusing on enzymatic activity (Fischbach et al. 2002) and on biochemical control (Niinemets et al. 2004). The effect of stomatal conductance and drought still remains in debate (Staudt et al. 2002).

POTENTIAL MULTIEFFECT OF AN INCREASE OF CO₂

Anticipating the responses of vegetation to increasing CO₂ concentration is critical attempting to predict the effect of global change on primary production, on vegetation spatial distribution, and on potential sinks for carbon, which may be provided by terrestrial ecosystems. Results obtained on greenhouse experiments shown that net CO₂ assimilation of *Q. suber* seedlings, in conditions of moderate drought, was at least twice as great in elevated atmospheric CO₂ conditions, but stomatal conductance was unchanged (Damesin et al. 1996). In addition, shoot and root biomass, stem height, and total leaf area were increased by elevated CO₂ as well as root and stem ramifications. Comparing tree ring chronologies of *Q. ilex* growing in natural CO₂ springs in Italy with those growing in ambient CO₂ control

sites, Hättenschwiler et al. (1997) showed that trees grown under high CO₂ for 30 years showed a 12% greater final radial stem width. This stimulation was largely due to responses when trees were young in accordance with the previously cited study. Increasing CO₂ concentration could affect different leaf functional characteristics. The leaves of *Q. pubescens* grown under elevated CO₂ do not show changes in the number or size of stomata but on the size of the guard cells (Miglietta et al. 1995). In contrast, *Q. ilex* leaves (Paoletti and Gellini 1993) and *Pistacia lentiscus* (Peñuelas and Matamala 1990) collected in herbaria showed a reduction of stomatal density with increasing atmospheric CO₂ as shown for temperate species (Woodward 1987).

NUTRIENT REGULATION: INDIVIDUAL AND ECOSYSTEM LEVELS

NUTRIENT UPTAKE AND TROPHIC TYPES

The five regions supporting MTEs differ largely concerning their nutrient level (see Section “Substrate”). As a consequence, belowground structures do not show convergence, although majority of plants form vesicular–arbuscular (VA) mycorrhizae in all regions (Allen et al. 1995). In Mediterranean Basin forests, ectomycorrhizal (ECM) fungi are known to play a fundamental role in enhancing the acquisition of resources by the host plant. de Roman and de Miguel (2005) and Richard et al. (2005) found a striking diversity of ECM fungi in *Q. ilex* forests. Nevertheless, exhaustive inventory of the diversity is a real challenge due to the large number of rare types.

The benefits that ECM fungi confer on their host plants can lead to improved growth and greater drought tolerance. Nevertheless, very few field experiments have addressed how changes in climate, such as increased drought, might quantitatively or qualitatively influence these ECM communities. ECM fungal community composition also may shift in response to drought and soil warming (Rygiewicz et al. 2000, Shi et al. 2002, Swaty et al. 2004).

High proportion of the Proteaceae in South Africa are nonmycotrophic species and there appear to be no ECM plants. In Australia, nonmycorrhizal species are confined among woody species to root hemiparasites or species bearing proteoid cluster roots (Lamont 1984). The N₂-fixing plants carry strong root specialization of presumed significance in absorption of phosphorous (Pate 1994). The Australian species of Epacridaceae form very peculiar ericoid-type mycorrhizae in extremely nutrient-deficient soils (Read 1992). High incidence of ECM trees as well as VA mycorrhizal grasses and shrubs characterize the other MT regions. This pattern is probably related to contrast between the very old and phosphorous-deficient South African and Australian soils and the relatively high phosphorous Mediterranean, Chilean, and Californian soils (Allen et al. 1995). In Australian nutrient-impooverished heathlands, Pate (1994) emphasized that the mycorrhizal association is just one of many nutrient-acquiring specializations in natural ecosystems, including various forms of parasitism, epiparasitism, and autotrophy with and without mycorrhizal associations.

NUTRIENT USE EFFICIENCY, SCLEROPHYLLY, AND EVERGREENNESS

The dominance of sclerophyllous—leathery, rigid, and heavily cutinized leaves—evergreen plants in the five MTEs of the world has been interpreted since a long time as a convergent adaptation in responses to the unique environmental conditions associated with Mediterranean climate. Seddon (1974) presents a historical discussion of concepts of sclerophylly and xeromorphy. The possible functional role of sclerophylly has been interpreted in diverse directions: (1) adaptation to drought, thick cell walls can better resist negative turgor pressure under water stress (Lo Gullo and Salleo 1988, Salleo et al. 1997), (2) leaf hardness is a epiphenomenon of phosphorous deficiency in soils (Loveless 1961, Monk 1966, Rundel

1988), and (3) sclerophylly is an adaptation to herbivory. In fact, similarities of sclerophylly in MTE is presently interpreted as linked to the long-term persistence of tertiary lineages that evolved under a subtropical climate and is not interpreted as an adaptation to Mediterranean climate (Herrera 1992, Joffre and Rambal 2002, Verdú et al. 2003, Thompson 2005).

Rundel (1988) supported interpretations that leaf nutrition may be a critical factor in the evolution of leaf characteristics as evergreenness or leaf life span. Since the study of Monk (1966) postulating that the habit of evergreens an adaptation to low nutrient availability, several researches have emphasized that evergreens, due to their long leaf life-spans have a higher nutrient use efficiency (productivity per unit nutrient uptake) than deciduous species. Several researches (Pugnaire and Chapin 1993, Aerts 1995, 1996, Killingbeck 1996) show that nutrient resorption of nitrogen was significantly lower for evergreens than that for deciduous. In southern France, the proportion of nitrogen in fallen leaves was 78% of that in mature leaves in *Q. ilex* and 44% in *Q. pubescens* (Damesin et al. 1998a). This comparison suggests that the deciduous *Q. pubescens* have a more efficient mechanism for removing nitrogen from senescing leaves. This result is in agreement with that obtained by Del Arco et al. (1991) on five oak species. They found a positive relation between the percentage of nitrogen translocated and the nitrogen concentration of the mature leaves, which was itself negatively related to the life span of the leaves.

Leaf longevity appears more important than resorption efficiency as a nutrient conservation mechanism. Resorption efficiency has to be considered as one of the internal mechanisms of nutrient regulation involving the relative pool sizes of mobile and insoluble nutrients as well as the capacity to store and mobilize energy as carbohydrates and lipids (Escudero et al. 1992). Cherbuy et al. (2001) showed that remobilization of carbohydrates, lipids, nitrogen, and phosphorous from 1 year leaves of mature *Q. ilex* participates in supplying carbon and nutrients for the new growth in spring. Although substantial differences in seedling storage ability between seeder and resprouter species have been shown in five prevalent MTEs of southwestern Australia (Pate et al. 1990), there is actually no strong corpus of evidence showing clear differentiation between storage patterns of mature deciduous and evergreen plants in MTEs.

NUTRIENT RELEASE AND DECOMPOSITION

Nitrogen and phosphorous release patterns during leaf litter decomposition varied considerably between species. We illustrate the importance of growth form in the nutrient cycling at ecosystem level comparing the decomposition patterns of the deciduous and evergreen oaks (*Q. pubescens* and *Q. ilex*) in southern France. Gillon et al. (1994) showed that nitrogen was released quickly by *Q. ilex*. In this species, the first stage, in which there was a strong decrease in nitrogen amount, corresponded to the release of soluble nitrogen (Ibrahima et al. 1995). In contrast, nitrogen was strongly immobilized by *Q. pubescens* litter. Increases in the nitrogen amount immobilized in the litter during decomposition may be partly explained by microbial and fungal incorporation of nitrogen from soil organic matter. This net accumulation of nitrogen in litter during the early stages of decomposition would alter the rates and patterns of nitrogen uptake by trees and may limit tree production. The difference in litter composition is also associated with a difference in the timing of leaf fall. In *Q. ilex* canopies, there are typically two peaks, one in spring and the other in autumn, or sometimes a single peak in spring. In *Q. pubescens* canopies, leaf fall starts in autumn, but since the species is marcescent, there is also some leaf fall in winter. The difference in mineral input to the soil between both species is accentuated by a difference in the intensity of leaching by precipitation. These differences certainly imply difference in the regulation of nitrogen turnover in the forest floor. These results are in agreement with the hypothesis that functional differences between evergreen and deciduous species depend on the management of nutrients and particularly nitrogen (Monk 1966, Moore 1980, Aerts 1995).

SUMMARY

Five regions throughout the world, that is, the Mediterranean Basin itself, California, central Chile, the Cape region of south Africa, and parts of southwestern and southern Australia, are characterized by the same climatic regime marked by a strong seasonality in temperature and precipitation that leads to a hot drought period in summer and a cool wet period in winter. Their vegetation type presents numerous structural and functional affinities that has led to define MTEs. The aim of this chapter is to discuss some aspects of the functioning of the woody Mediterranean species.

The main climatic factor controlling the functioning of these ecosystems is water availability, which varies greatly in time and space, imposing strong constraints over the plant. Moreover, a general consensus of global circulation models indicates an increase of summer drought and of extreme events occurrences during the twenty-first century. Different mechanisms acting at several scales and levels illustrate how individuals and ecosystems cope with and control water uptake, water loss, and water transfer through the soil–plant–atmosphere continuum.

Carbon assimilation characteristics are presented in relation to environmental conditions. In optimal conditions, the photosynthetic performance of Mediterranean species does not differ particularly from that of species from other biomes. Nevertheless, their leaves have to tolerate high irradiance and they have to cope with excess intercepted solar radiation when carbon assimilation is limited either by stomatal closure or a decrease of photosynthetic capacity due to water stress and high temperatures (summer) or low temperatures (winter). A great proportion of the plant species growing in MTE produce and accumulate aromatic volatile oils that may also serve as an excess energy dissipation system during a period of restricted growth. The functioning of evergreen and deciduous species is presented and some assumptions based on a cost-benefit model explaining their coexistence are discussed.

The five regions supporting MTEs show very distinct nutrient level. As a consequence, some differences occur concerning the belowground structures and the role of mycorrhizae. In Australian and south African nutrient impoverished heathlands, some specific root adaptations are presented. The possible functional role of sclerophylly as a nutrient conservation mechanism is discussed. Relations between leaf life span, resorption efficiency, and nutrient-use efficiency differ between evergreen and deciduous species. Decomposition and release of mineral forms have contrasted patterns between these two groups of species. These differences certainly imply difference in the regulation of nitrogen turnover in the forest floor and seem to be in agreement with the hypothesis that functional differences between evergreen and deciduous species depend on the management of nutrients. In conclusion, the remarkable combination of gradient of natural resources and obviously different anthropic management in the five Mediterranean regions of the world leading to a great diversity of adaptive strategies and functional attributes in the MTEs is highlighted.

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