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Daily and seasonal variation in water relations of macchia shrubs and trees in France (Montpellier) and Turkey (Antalya)

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Abstract

Based upon two different research studies in the mediterranean regions of France and Turkey, drought resistance strategies were investigated in a broad group of species. The diurnal and seasonal patterns of the water relations of different lifeforms from the thermo-mediterranean to submediterranean lifezones were compared. Three sites near Montpellier, in Southern France, and five sites near Antalya, Turkey were used for this comparison. Xylem pressure potential and relative stomatal aperture were the key water relations parameters collected in France while these parameters as well as osmotic potential and leaf conductance were studied in Turkey.

From the 26 different study species investigated in France, 7 distinct types of stomatal control were observed, with the deciduous lifeforms showing the least control, the sclerophyllous and coniferous evergreens the greatest control and the malacophyllous shrublets intermediate levels of control. Predawn water potential values provided a means of classifying species according to their temporal and spatial utilization of site water reserves. The comparison of turgor potentials (difference between water and osmotic potentials) gave an insight into leaf adaptations to site moisture. Species with high predawn water potentials generally maintain positive turgor even at midday during the summer, whereas species with low predawn values were frequently at zero turgor even at predawn. *Phlomis grandiflora* was the most extreme species with mid-summer predawns and midday water potentials of −6 MPa and osmotic potentials never more negative than −2.4 MPa.

Introduction

The paper presented here is the result of two studies; the first by the senior author at three research sites near Montpellier (France) and the second by both authors at five sites near Antalya (Turkey). The overall goal of both projects was to document the water relations of different lifeforms using comparative day courses within a seasonal context. The lifeforms considered included deciduous submediterranean trees and shrubs, mesophyllous and sclerophyllous evergreens, and malacophyllous (drought deciduous)

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shrubs (Table 1). Thus the research design, originally utilized by Braun-Blanquet and Walter (1931), focussed on the comparative water relations of these various lifeforms. Specifically, the daily courses of xylem pressure potential (pressure chamber) and relative stomatal aperture (stomatal infiltration method) were generated on a wide variety of species over a range of seasonal phenological and drought conditions. In addition to these data, information on leaf conductance and osmotic potential were collected in Turkey. These data enabled us to compare the water relations of a large number of species at one site, between sites and finally over a distance of some 2300 km.

Methods and materials

Research sites

France: The Montpellier area known as the Bas-Languedoc is part of the Mediterranean basin west of the Rhone estuary. The gentle rolling hills of the lowlands increase in elevation both towards the Cevennes in the north and the Jurassic plateaus (ca. 800–1000 m) to the northwest. The final ascent both to the plateaus and the crest of the Cevennes is very dramatic; this is also documented by the change in precipitation from 770 mm in the vicinity of Montpellier to 2175 mm on Mt. Aigoual (1567 m), the highest peak of the Cevennes and by the change in vegetation from true mediterranean sclerophyllous shrub and forest through sub-mediterranean summer green oak forests to mountain beech forests.

The summer drought rarely exceeds two months in the Montpellier area and thus this lowland climate is termed subhumid. In addition, mean summer temperatures do not often exceed 30° and then for only very short periods. Based upon climate, the Antalya region of Turkey is quite different from Montpellier because the drought period lasts 4 to 5 months longer and midday temperatures in the summer are frequently 10 °C warmer.

Turkey: The Antalya region of Turkey encompasses an area of some 1150 km^2 which lies between 29° 30′ and 31° 30′ east longitude and 36° 10′ and 37° 40′ north latitude. This region was selected because (1) it represents the classical macchia type of the eastern mediterranean and (2) there are both National Parks and Forest Service lands and these lands can be used for study. The climate of the area is typically mediterranean and is characterized by warm, dry summers and cool, wet winters. The Mediterranean Sea to the south, the Bey Mountain Range to the west and the Toros Mountain Range to the north and east exert a moderating influence on the climate. Rainfall ranges from a low of 475 mm per year in Korkuteli to a high of 1351 mm at Akseki (NE of Manavgat at 1150 m). Precipitation is generally high near the coast (from 906 mm at Kas to 1571 mm at Kemer), increases with elevation and then decreases dramatically in the lee of the coast mountains. August is the warmest month with maximum temperatures averaging between 31.8 and 33.6 °C along the coast and decreasing with elevation. January mean temperatures range from 6.3 to 9.7 °C along the coast to as low as −1.7 °C at Elmali in the interior. The topography of the area is steep, rugged and spectacular. The highest peak in the Bey Mountain Range is 3086 m, which is only 37 km from the coast. The geology of the area is characterized by limestone and dolomitic formations resulting in an highly weathered and dissected character. In many areas a karst topography exists. Generally, the soils of the region are red and red brown mediterranean wood soils derived from limestone and dolomitic parent material.

Study sites

France: Three study sites were chosen ranging from 90 m to nearly 700 m above mean sea level. Each site provided a range of different species, for which the daily course of water relations of 10 to 11 individuals was measured. Measurements were taken several times during May, July–August and September–October; three periods that defined the three major stages of the growing season.

Table 1. List of lifeforms, associated species and number of sites on which these species were studied at each site (France and Turkey).

Lifeform	Species	Code	Montpellier, France			Antalya, Turkey				
			1	2	3	1	2	3	4	5
Evergreen, sclerophyll	*Arbutus andrachne*	Aran					x	x	x	
	Arbutus unedo			x						
	Buxus sempervirens		x		x					
	Ceratonia siliqua	Cesi				x	x			
	Laurus nobilis	Lano								x
	Olea europaea	Oleu				x	x	x	x	x
	Phillyrea angustifolia			x						
	Phillyrea latifolia	Phla		x		x	x	x	x	x
	Phillyrea media	Phme		x						
	Pistacia lentiscus			x						
	Quercus calliprinos	Quca				x	x	x	x	x
	Quercus coccifera		x							
	Quercus ilex		x	x						
	Rhamnus alaternus			x						
Evergreen, conifer	*Juniperus communis*				x					
	Juniperus oxycedrus	Juox	x				x	x		x
	Juniperus phoenicea		x				x			
Evergreen malacophyll	*Citus albidus*		x							
	Lavandula angustifolia				x					
	Lavandula latifolia		x							
	Phlomis grandiflora	Phgr						x		x
	Rosmarinus officinalis		x							
	Salvia ssp.									x
Wintergreen	*Quercus infectoria*	Quin						x		x
Summergreen	*Acer campestre*			x						
	Acer monspessulanum		x		x					
	Amelanchier ovalis		x							
	Cornus mas		x							
	Corylus avellana				x					
	Crataegus monogyna	Crmo			x				x	x
	Ostrya carpinifolia	Osca								x
	Pistacia terebinthus	Pite		x		x	x			
	Prunus mahaleb			x	x					
	Pyrus amygdaliformis	Pyam		x				x	x	
Quercus aegilops	*Quae*							x		
	Quercus pubescens				x					
	Sorbus aria				x					
	Styrax officinalis	Stof				x				x
	Ulmus minor				x					

France: 1 Guzargues (90 m)
2 Aumelas (220 m)
3 La Vacquerie (70 m)

Turkey: 1 Kas Beach (12 m)
2 Beskonak (320 m)
3 Lower Termessus (400 m)
4 Kas Gravel (500 m)
5 Upper Termessus (840 m)

Turkey: Five study sites were selected which ranged from 12 m to nearly 840 m above mean sea level. These sites provided a range of elevations, species, and site evaporative demand. Each site was visited at least once in the spring (April–May 1979), summer (July–August 1979) and fall (October–November 1978) for day course and pressure-volume curve sampling.

Study species

The species studied at each location are listed in Table 1. On each study site, representative individuals of the study species with a healthy, relatively full crown were chosen.

Methods

Common elements of the research program for both study areas consisted of (1) characterizing the water relations of a large number of species representing different lifeforms, (2) the use of the daily pattern for this characterization and (3) the development of daily patterns during three parts of the growing season. These parts were: (1) mid-spring to examine the interaction between leaf development, high soil moisture and moderate evaporative demand on the water relations of the study species, (2) mid-summer to document the effect of low soil moisture and high evaporative demand, and (3) mid-fall to examine the recovery as a result of fall rains.

France: For each study day, as many as 11 different species (Table 1) were sampled from before sunrise to after sunset. Paired readings of xylem pressure potential and relative stomatal aperture were taken every two hours on each species.

Turkey: For each study day, five to seven study species were selected and were sampled hourly from before sunrise until after sunset. Each hour, beginning with species 1 and continuing through species 5 to 7, five to eight leaves (or two twigs and three to five leaves) were removed from each study species. Leaf or twig xylem pressure potential readings were made on two of the leaves (or on twigs for *Juniperus oxycedrus*, *J. phoenicea*, *Phillyrea latifolia* and *Quercus coccifera*), stomatal infiltration pressure was determined on one to four leaves and leaf conductance was measured on one or two of the sampled leaves. An effort was made to sample (or to pair samples) from a small region of the crown that was exposed to the sun, see Figure 1 and discussion below. Only two shrubs were sampled at once and foliage was stored in the shade and in plastic bags with moist paper towels (leaf or twig xylem pressure potential and stomatal infiltration) or without moisture paper towels (leaf conductance) between readings. It took between 25 and 40 min to sample all species.

The procedures in France and Turkey which were the same are as follows. Stomatal infiltration pressure was measured using a modified in-

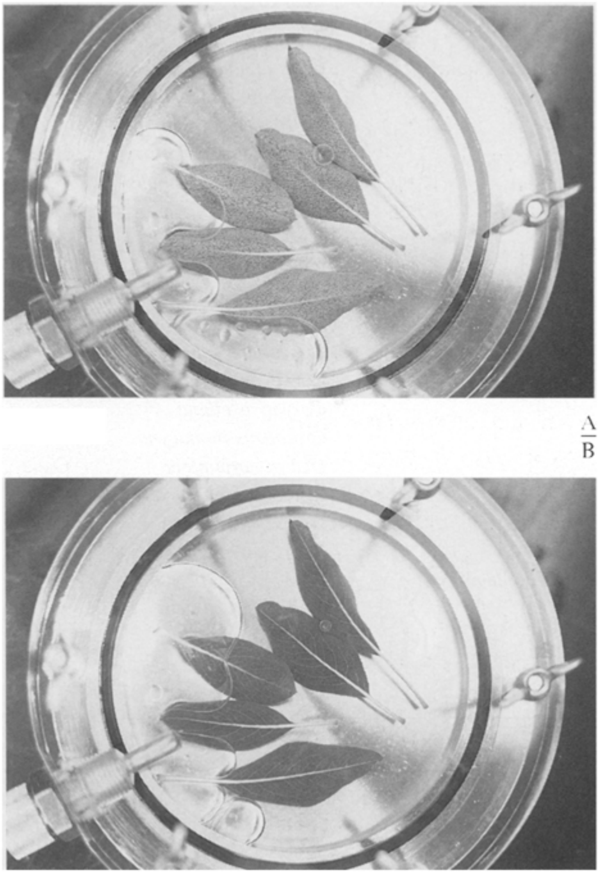


Fig. 1. Infiltration chamber with *Pyrus amygdaliformis* leaves at (A) beginning of infiltration and (B) at 90% infiltration.

filtration chamber suitable for leaves up to 10 cm in diameter (Duhme 1974; cf. Froeschel 1951; Fry & Walker 1967). The pressure at which infiltration first occurred (Fig. 1A) and the pressure at which 90% (Fig. 1B) of the stomata were infiltrated were recorded. If 90% of the stomata were not infiltrated at an applied pressure of 0.8 MPa, the percentage of stomata infiltrated was recorded. In an earlier paper (Hinckley *et al.* 1980), the relationship between stomatal infiltration pressure and leaf conductance was described (e.g., Figs. 7, 8 and 9 on pages 138 and 139). The infiltration device has the advantage of being robust, not dependent upon an external supply of electricity and indicative of the nature of within as well as between leaf variation in stomatal aperture and, therefore, leaf conductance. Leaf conductance (Turkey only) was estimated using a ventilated porometer described by Körner and Cernusca (1976). Leaf water potential (Ψ_t) was measured with a pressure chamber using the procedure given by Ritchie and Hinckley (1975). In order to develop a sampling procedure for leaf water potential, pressure chamber readings were recorded as often as once every 2 min on two differently exposed *Quercus ilex* shrubs (Fig. 2). These two *Quercus ilex* shrubs were used to provide three sets of leaves with very different exposures: (1) full sun, (2) partial sun and (3) complete shade. Within thirty minutes following sunset, leaf water potential values were identical for all leaves on the two shrubs.

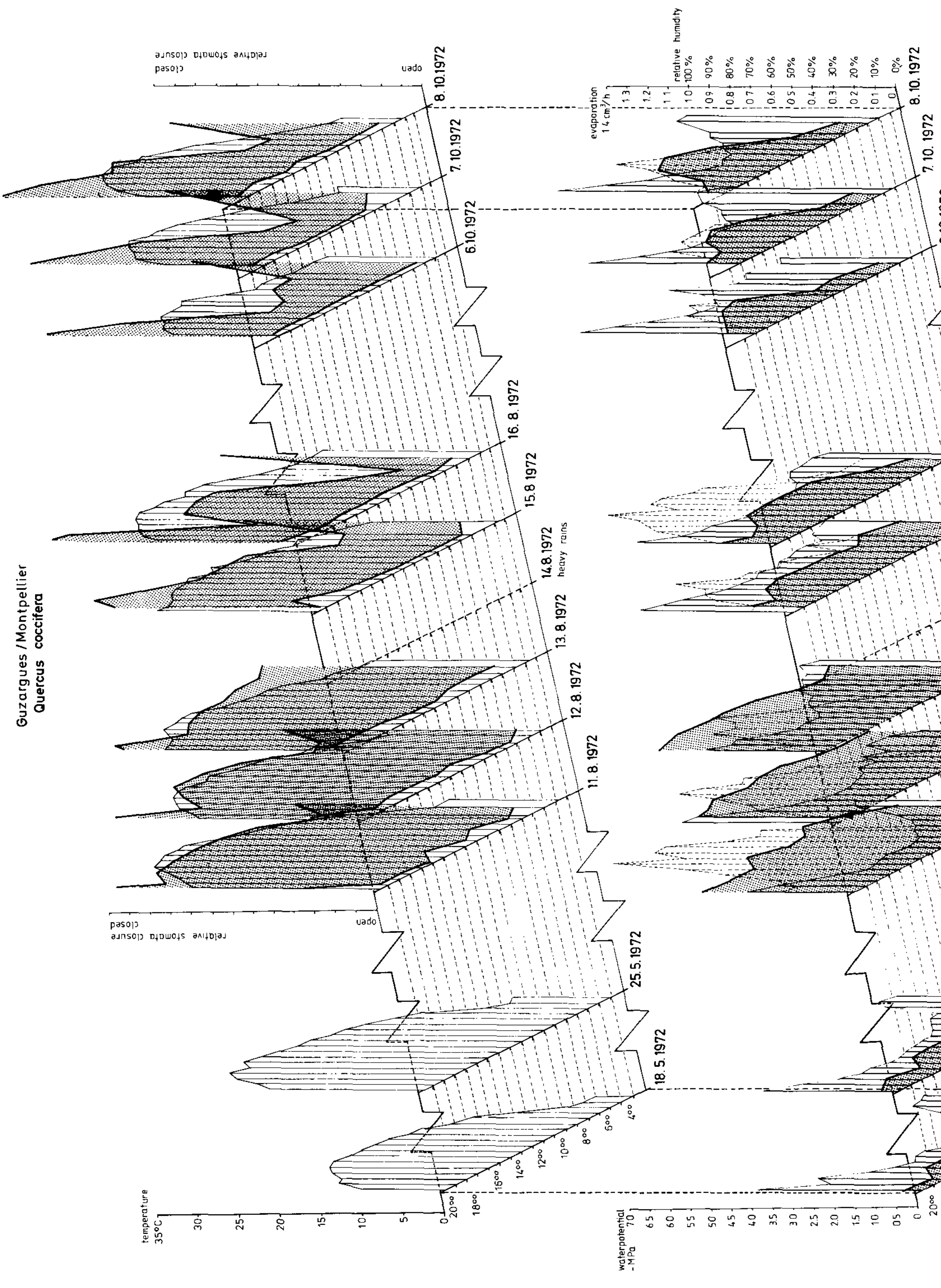
From this finding we drew three conclusions. First, with good water availability, the activity of the leaves is directly correlated with the radiation gain and thus more negative leaf water potentials indicate higher flow resistances in the conductive system. Second, it is important to match the light environment of the foliage sample with the light environment of the shrub. Third, sampling once every two hours provides an accurate measure of the daily pattern on relatively clear days.

Prior to, and immediately following, each hourly set of readings, relative humidity and air temperature, photosynthetic photon flux density and potential evaporation were measured with an Assman psychrometer, a Licor 185S quantum sensor and a Piche evaporimeter, respectively. These environmental measurements were taken at 2 m where all the equipment was on a portable wooden tower. Two towers were placed on each site, one in a very open position and the other in a more sheltered position.

In order to determine osmotic potential using the pressure-volume curve technique (based on the results obtained in Turkey), a leafy branch from each species was collected, stored in a plastic sack and brought as rapidly as possible to the laboratory. The branch was recut under water, covered with plastic and left overnight to resaturate. The following day, a fully resaturated leaf (or a twig for *Juniperus oxycedrus*, *J. phoenicea*, *Phillyrea latifolia* and *Quercus coccifera*) was removed from the branch and weighed, Ψ_t was determined and the leaf was reweighed. Then repeated fresh weights before and after each pressure chamber reading of Ψ_t were made on the leaf using procedures described in detail by Hinckley *et al.* (1980, 1983). For each species, a minimum of three leaves (twigs) within a given age class of foliage were sampled. During the spring and occasionally in summer, evergreen shrubs contained both young and old foliage. Both age classes were sampled.

Results

Figure 3 shows the diurnal as well as the seasonal progression of stomatal infiltration pressure and leaf water potential for *Quercus coccifera* and the environmental variables, air temperature, relative humidity and evaporation. In May, both predawn and midday leaf water potential were relatively high (greater than −0.5 and −1.5 MPa, respectively). However in early August both had decreased appreciably (approximately −4.5 MPa). Following heavy rains on August 14, predawn and midday water potential recovered. Before the mid-August rain, stomatal infiltration pressure indicated that stomata were completely closed. Following the rain, stomata opened slightly, particularly during the morning. Leaf water potential in October was somewhat similar to that observed


Guzargues / Montpellier
Quercus coccifera
temperature
35°C
30
25
20
15
10
5
0
relative stomata closure
closed
open
waterpotential
- MPa
7.0
6.5
6.0
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0
evaporation
1.4 cm³/h
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
relative humidity
100 %
90 %
80 %
70 %
60 %
50 %
40 %
30 %
20 %
10 %
0%
20⁰⁰
18⁰⁰
16⁰⁰
14⁰⁰
12⁰⁰
10⁰⁰
8⁰⁰
6⁰⁰
4⁰⁰
18.5.1972
25.5.1972
11.8.1972
12.8.1972
13.8.1972
14.8.1972
heavy rains
15.8.1972
16.8.1972
6.10.1972
7.10.1972
8.10.1972

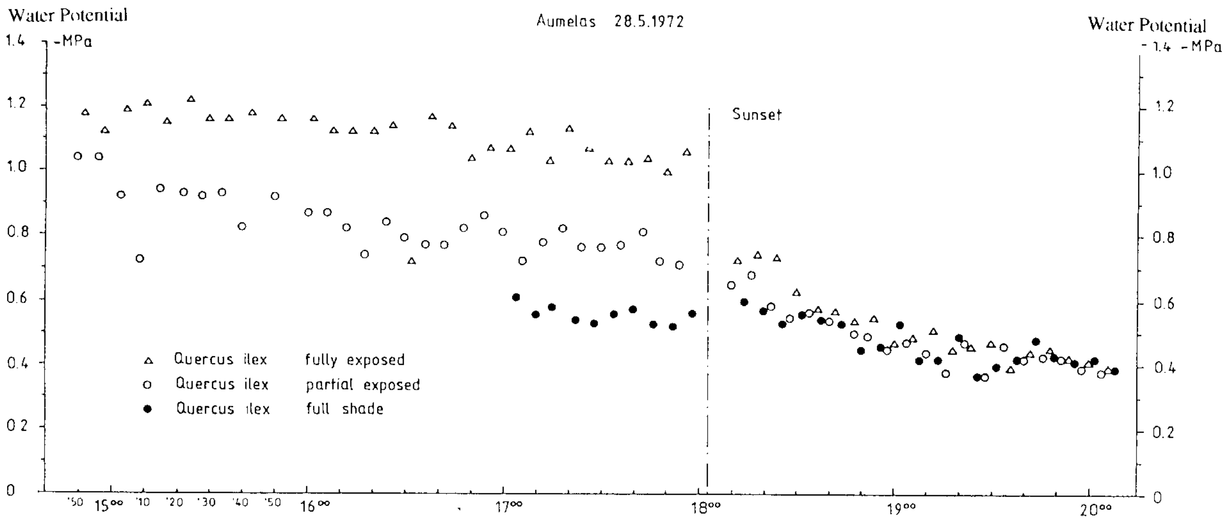


Fig. 3. Daily and seasonal development of stomata control (upper section) and leaf water potential.

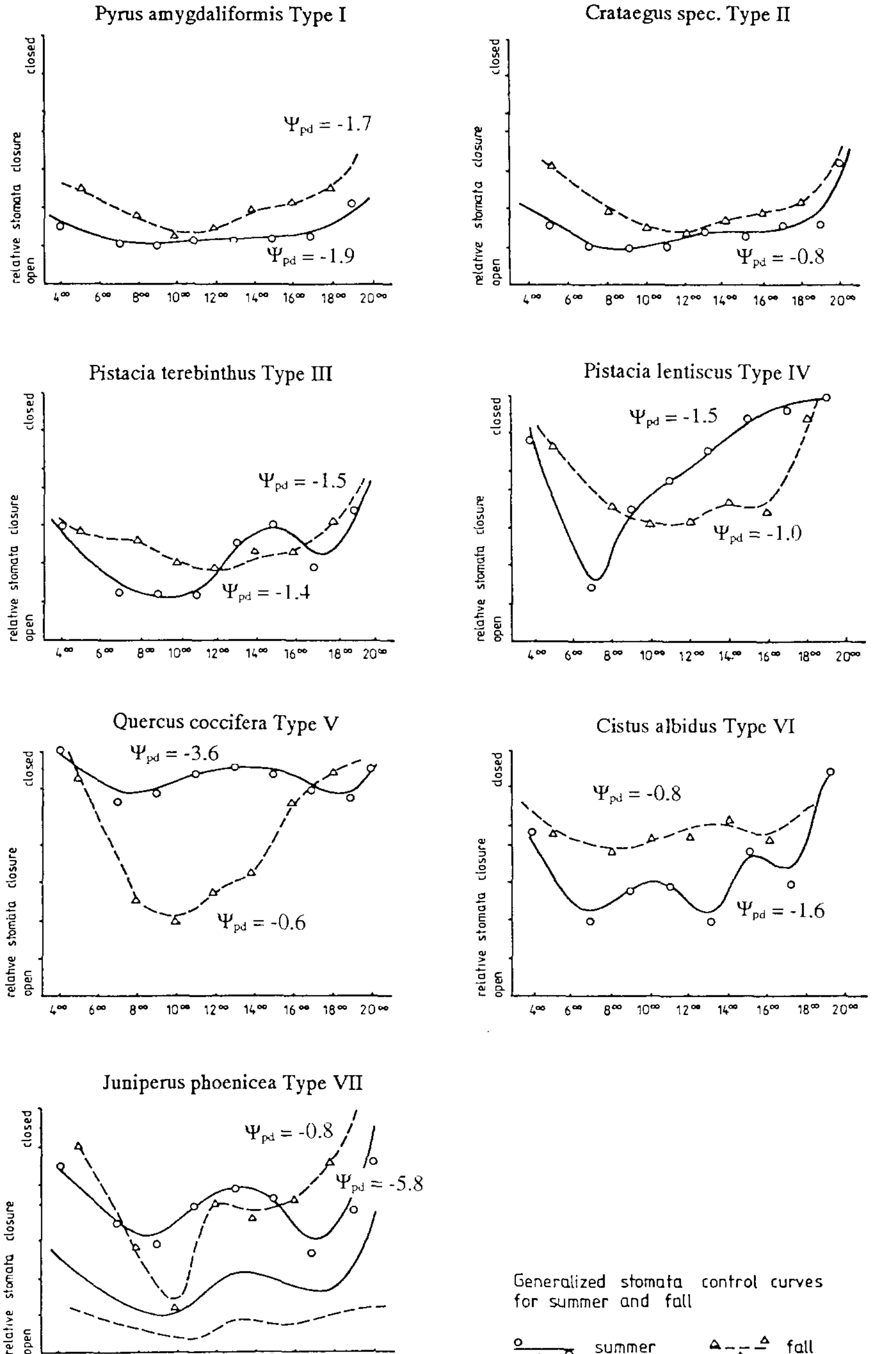
in spring; however, midday values were more negative. Stomata were more open in the fall.

Seven different summer – fall patterns of stomatal behavior were identified for the 26 different study species from France and are summarized in Figure 4. By using *Quercus coccifera* (Type V Pattern of stomatal control) as an example, a transition from Figure 3 and 4 may be developed. Only slight early morning and late afternoon opening was observed in *Quercus coccifera* during the summer (before the August 14 heavy rain). Stomata were open to a greater extent and for a longer period of time during the fall in *Quercus coccifera*. In contrast to the Type V pattern, the Type I pattern, as illustrated by *Pyrus amygdaliformis*, indicated no stomatal closure during the summer and only slight, perhaps in association with leaf senescence, in the fall. Changes from the Type I to II and eventally to V were as a result on increasing stomatal closure, particularly in the afternoon. A shift from the Type I to the Type V pattern, is accompanied by an increase in stomatal control hence the ability to control appears to be associated with leaf persistence, with the least control occurring in the deciduous (Types I to III) and the most control in the evergreen species. This relationship is very pronounced with control Types I through V and even

Table 2. Stomatal control types, associated lifeforms and species which illustrate them (see Figure 4 for illustrations of each type).

Type	Lifeform	Species (France)	Species (Turkey)
I	Summergreen, nonmediterranean	*Pyrus amygdaliformis*	*Pyrus amygdaliformis*
II	Summergreen, submediterranean	*Crataegus monogyna*	*Crataegus monogyna*
III	Summergreen, mediterranean	*Pistacia terebinthus*	*Pistacia terebinthus*
IV	Evergreen laurel type	*Pistacia lentiscus*	*Laurus nobilis*
V	Evergreen sclerophyll	*Quercus coccifera*	*Quercus calliprinos*
VI	Malacophyllic – drought deciduous	*Cistus albidus*	*Phlomis grandiflora*
VII	Evergreen conifer	*Juniperus oxycedrus* *Juniperus plhoenicaea*	*Juniperus oxycedrus* *Juniperus phonicaea*

Fig. 2. Dependance of insertion points of reference leaves in relation to direct radiation on *Quercus ilex* bushes.



Pyrus amygdaliformis Type I

Crataegus spec. Type II

Pistacia terebinthus Type III

Pistacia lentiscus Type IV

Quercus coccifera Type V

Cistus albidus Type VI

Juniperus phoenicea Type VII

Fig. 4. Generalized stomata control types for 26 different woody species from the Montpellier study site.

with type VII where the specific xylem and needle structure of the coniferous *Juniper* group may influence the response observed (Table 2). The Type VI pattern, illustrated by *Cistus albidus*, is not entirely clear – a moderate level of stomatal control may occur in this group. These drought

Table 3. Predawn water potentials (MPa) by site of the various study species.

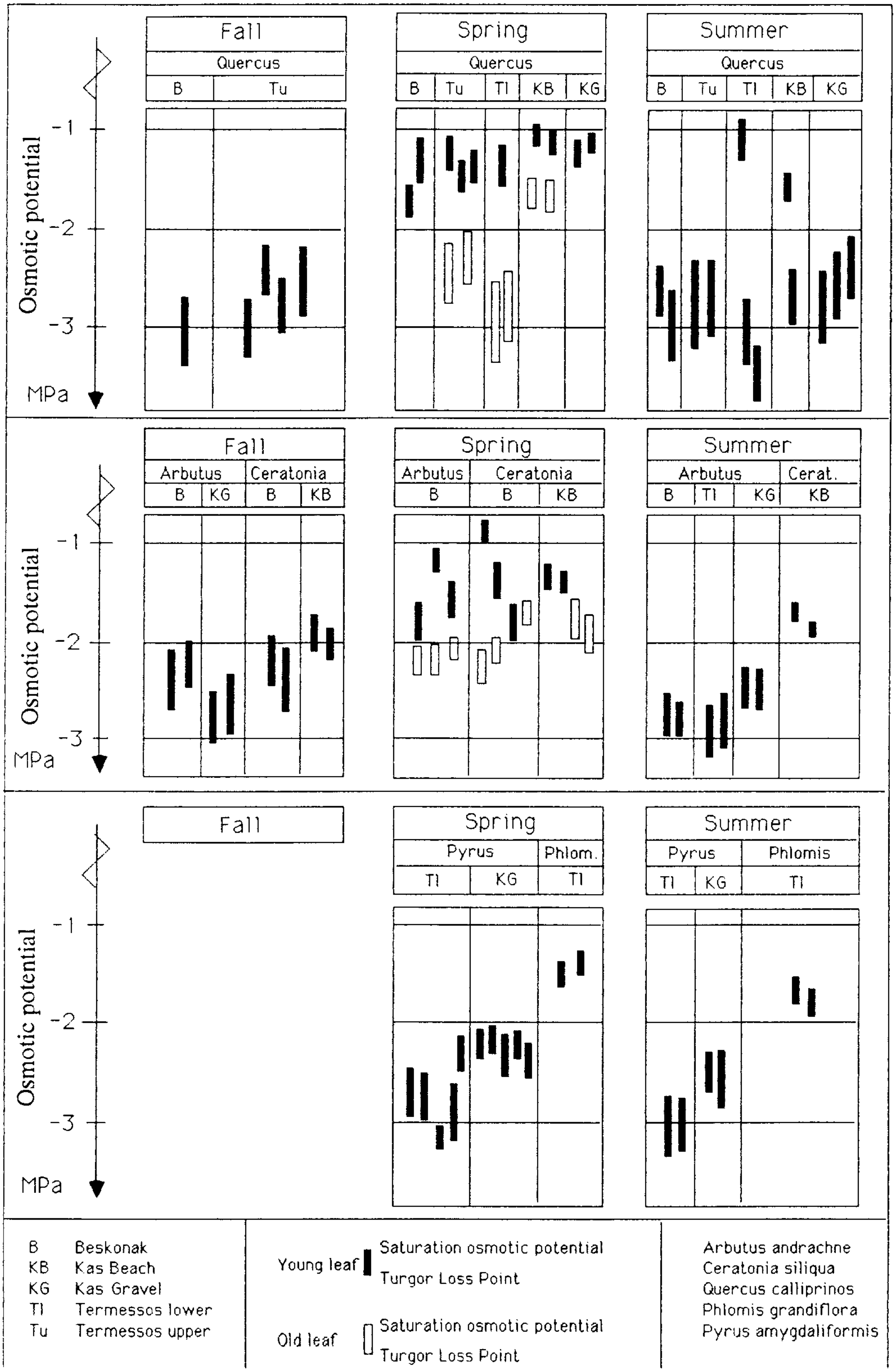
Species	Code	Montpellier, France			Antalya, Turkey				
		1	2	3	1	2	3	4	5
Arbutus andrachne	Aran					-0.70	-4.04	-0.86	
Arbutus unedo			-2.10						
Buxus sempervirens		-1.55		-1.70					
Ceratonia siliqua	Cesi				-0.83	-0.77			
Laurus nobilis	Lano								-1.72
Olea europaea	Oleu				-2.92	-2.39	-3.28		-2.24
Phillyrea angustifolia			-1.18						
Phillyrea latifolia	Phla		-1.72		-3.48	-2.56	-5.07	-2.76	-1.47
Phillyrea media	Phme		-3.27						-2.41
Pistacia lentiscus			-1.55						
Quercus calliprinos	Quca				-0.91	-0.84	-1.07	-0.95	-1.01
Quercus coccifera		-3.68							
Quercus ilex		-1.15	-1.82						
Rhamnus alaternus			-1.42						
Juniperus communis				-0.85					
Juniperus oxycedrus	Juox	-3.05				-1.32			-2.27
Juniperus phoenicea	Juph	-6.06				-1.36			
Cistus albidus			-2.05						
Lavandula angustifolia				-0.80					
Lavandula latifolia		-2.27							
Phlomis grandiflora	Phgr						-5.63		-2.83
Rosmarinus officinalis		-3.75							
Quercus infectoria	Quin						-1.39		-0.82
Acer campestre			-1.58						
Acer monspessulanum		-1.66		-0.80					
Amelanchier ovalis		-3.32		-0.75					
Cornus mas		-3.35							
Corylus avellana				-0.52					
Crataegus monogyna	Crmo			-1.55				-2.89	-1.87
Ostyra carpinifolia	Osca								-1.30
Pistacia terebinthus	Pite		-1.80		-1.85				
Prunus mahaleb			-1.02	-0.97					
Pyrus amygdaliformis	Pyam		-1.97				-1.44	-0.81	
Quercus aegilops	Quae							-0.68	
Quercus pubescens				-0.52					
Sorbus aria				-1.00					
Styrax officinalis	Stof				-2.08				-1.67
Ulmus minor				-1.10					

France: 1 Guzargues (90m)
2 Aumelas (220 m)
3 La Vacquerie (700 m)

Turkey: 1 Kas Beach (12 m)
2 Keskonak (320 m)
3 Lower Termessus (40 m)
4 Kas Gravel (500 m)
5 Upper Termessus (840 m)

tolerant deciduous shrubs obviously do not follow the aforementioned control patterns.

Another useful way of comparing these species is to examine the minimum predawn water potentials and their association with species and microsite preference (Table 3). The most negative


Fall
Quercus
B
Tu
Spring
Quercus
B
Tu
Tl
KB
KG
Summer
Quercus
B
Tu
Tl
KB
KG
Osmotic potential
-1
-2
-3
MPa
Fall
Arbutus
Ceratonia
B
KG
B
KB
Spring
Arbutus
Ceratonia
B
B
KB
Summer
Arbutus
Cerat.
B
Tl
KG
KB
Osmotic potential
-1
-2
-3
MPa
Fall
Spring
Pyrus
Phlom.
Tl
KG
Tl
Summer
Pyrus
Phlomis
Tl
KG
Tl
Osmotic potential
-1
-2
-3
MPa
B Beskonak
KB Kas Beach
KG Kas Gravel
Tl Termessos lower
Tu Termessos upper
Young leaf
Saturation osmotic potential
Turgor Loss Point
Old leaf
Saturation osmotic potential
Turgor Loss Point
Arbutus andrachne
Ceratonia siliqua
Quercus calliprinos
Phlomis grandiflora
Pyrus amygdaliformis

predawn Ψ_t value from Turkey during the summer was observed in *Phlomis grandiflora* (−5.63 MPa) located at Lower Termessus while the highest predawn Ψ_t was observed in *Quercus aegilops* (−0.68 MPa) from Kas Gravel. When all species from Turkey and for the summer measurement period were averaged for a site, the following ranking from most negative to least negative predawn Ψ_t was found: Lower Termessus (−3.13 MPa, $n = 7$) < Kas Beach (−2.01, $n = 6$) $\# \leq$ Upper Termessus (−1.78, $n = 11$) < Kas Gravel (−1.49, $n = 6$) $\# \leq$ Bekonak (−1.42, $n = 7$). These site differences were due both to inherent differences in the sites as well as to the species chosen on each site. However, when species that occurred on all sites were compared (*Phillyrea latifolia* and *Quercus calliprinos*), the site ranking did change slightly: Lower Termessus (−3.07 MPa) < Kas Beach (−2.20) < Kas Gravel (−1.86) < Upper Termessus (−1.71 = Beskonak (−1.70).

Arbutus andrachne and *Ceratonia siliqua* generally occur on more mesic sites than does *Quercus calliprinos*. Their pattern of osmotic potential is similar to that of the evergreen oak but differences between older and newly expanding foliage in the spring is somewhat less pronounced. In addition, the *Cerationia siliqua* from Kas Beach was growing next to a dry stream bed and, as a consequence, has far less negative osmotic potential values in the summer than either *Arbutus andrachne* or *Quercus calliprinos*.

In the lower part of Figure 5, one can compare the osmotic potentials of *Pyrus amygdaliformis* and *Phlomis grandiflora*. *Phlomis grandiflora* is morphologically quite similar to the *Cistus albidus* studied in France and, therefore, belongs to the malacophyllic shrublets of the mediterranean basin. The rapid development of the leaves of *Pyrus amygdaliformis* resulted in relatively negative osmotic potential values in late April and early May. This difference in the rate of leaf maturation becomes apparent when one compares emerging leaves of the evergreen shrubs (e.g., *Quercus calliprinos*) with those of this deciduous shrub. In the summer, osmotic potential values are only slightly more negative in *Pyrus*. For neither the broad, long leaves observed on *Phlomis grandiflora* in the spring, nor the much smaller leaves found in the summer, were osmotic potentials more negative than −2.0 MPa observed.

Figure 6 illustrates species differences in predawn and midday water potential and in the osmotic potential at the turgor loss point in mature tissue sampled during the spring (top) and summer (bottom). The data presented for the summer begins from the left with the most negative predawn water potential and proceeds to the right with increasing predawn water potential (from *Phlomis grandiflora* at −4.2 MPa to *Quercus aegilops* at −0.68 MPa). In general, more negative midday water potentials were associated with more negative predawn water potentials; however, the relationship was not a strong one ($r = 0.62$). Within this arrangement of increasing predawn water potentials from left to right, the osmotic potential at turgor loss did not show any consistent relationship with either predawn ($r = 0.03$) or midday water potential ($r = 0.09$). A general tendency is apparent in species on the left hand side of Figure 6 with osmotic potentials at turgor loss that are less negative than the midday or even the predawn water potentials while those on the right hand side have osmotic potentials at turgor loss always more negative or equivalent to the midday water potentials.

From Figure 6 one may also conclude that *Phlomis grandiflora* is probably the least adapted species to drought. It had the most negative predawn and midday water potentials and the least negative osmotic potential at turgor loss. For example at Lower Termessus, values of −5.63, −6.06 and −1.93 MPa for predawn, midday and turgor loss point were noted during the summer, respectively. Two of the evergreen species, *Phillyrea media* and *Olea europaea*, had pre-

Fig. 5. Comparative summary of variance and seasonal development of saturation osmotic potential and turgor loss point of *Arbutus andrachne*, *Ceratonia siliqua*, *Quercus calliprinos*, *Phlomis grandiflora*, and *Pyrus amygdaliformis* at various sites.

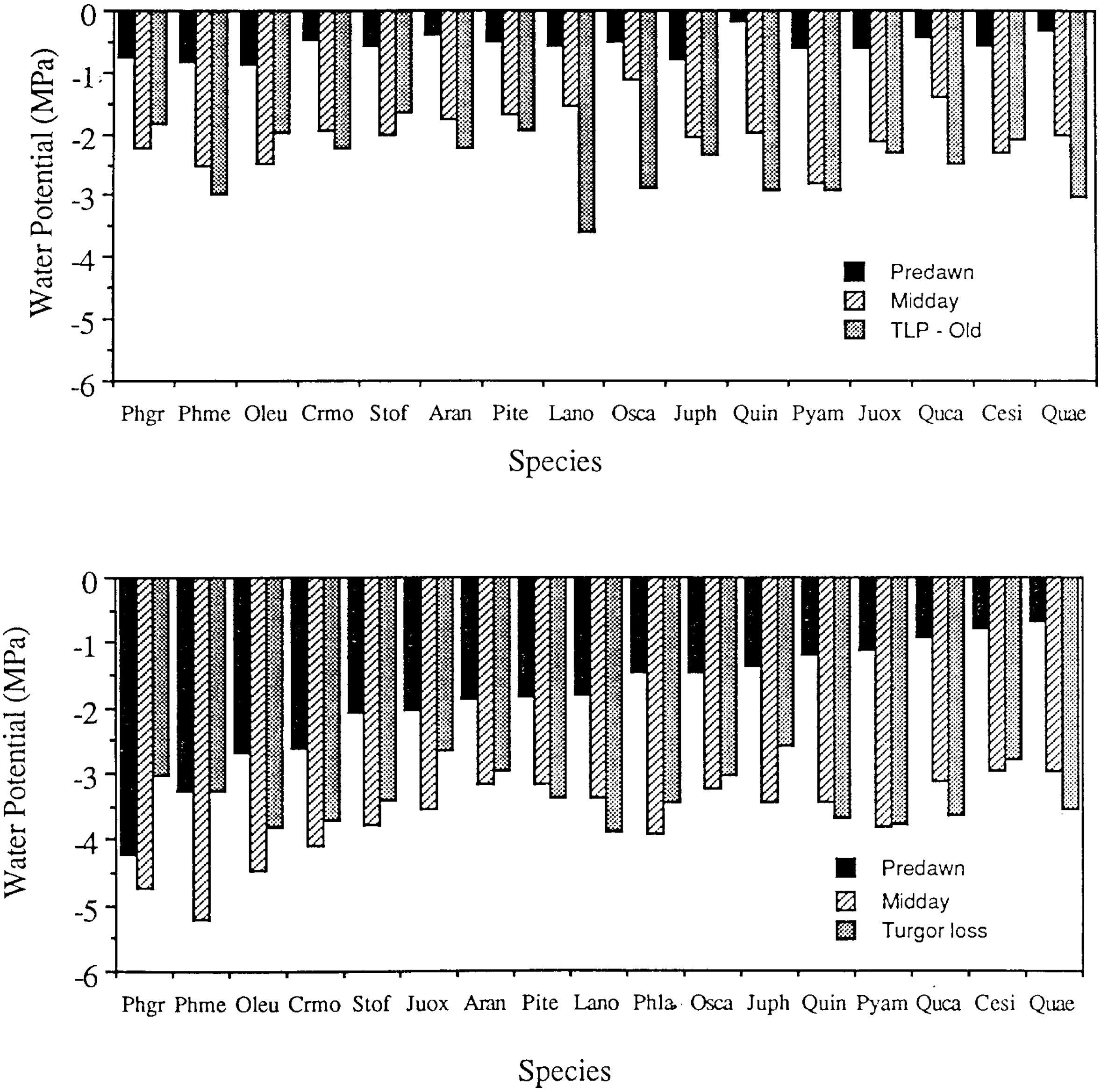


Fig. 6. Summary of species differences in predawn and midday water potential and in water potential at the turgor loss point in spring (top) and summer (bottom).

dawn and midday water potential values that approached those of *Phlomis grandiflora* (predawn values were −5.07 and −3.28, respectively, while midday values were −5.85 and −5.28, respectively). For these two evergreen species, the osmotic potential at the turgor loss point was −3.26 and −3.98, respectively.

In contrast to *Phlomis grandiflora*, *Pyrus amygdaliformis*, a deciduous tree, had corresponding values of predawn and midday water potential and osmotic potential at the turgor loss point (−1.44, −3.69, and −3.77 respectively) that suggested greater drought adaptation. In *Pyrus amygdaliformis*, the rapid decrease in osmotic potential with leaf maturation (see Figure 6, spring) compensated for the daily minima in water potentials. In addition, relatively high predawn water potential values (only three species had higher average predawn water potentials) indicated an ability to extract considerable water from the soil for night-time recovery. *Phlomis grandiflora* failed to cope with both daily atmospheric evaporative demand and seasonal decreases in soil moisture. Because of its relatively high osmotic potentials, it was wilting during the summer measurement period.

Discussion

At the research sites in France, *Quercus ilex* bushes were examined under different habitat conditions; at Aumelas, one specimen grew in the richer colluvium of a valley bottom which was formerly used for agriculture, while the other was located at mid-slope not far away from the Pistacias and the Pyrus. In both situations, *Quercus ilex* performance reflected a stomata control type IV pattern which is characterized by high water potentials and a very pronounced stomata reaction behaviour during the day course. At Guzargues, scattered specimens of *Quercus ilex* were intermixed with the more dominant *Q. coccifera* which occurred in a very stunted form reaching only up to 1.5 m. Under these probably identical site conditions *Q. coccifera* behaved very much like *Juniperus phoenicea* (control type VI) which tolerates much higher water stress. Based upon the response of co-occurring species at each site, we can conclude that *Q. ilex* is the most effective species in respect of drought avoidance.

Although *Quercus calliprinos* in Turkey is defined taxonomically as belonging to *Quercus coccifera* (Hedge & Yaltirik 1982, p. 681), all our ecophysiological findings suggest a much stronger link with *Q. ilex*. Obviously, further taxonomic research is warranted.

For the results from Turkey, some additional discussion is needed for *Phlomis grandiflora* and *Pyrus amygdaliformis*. From an ecological context, the contradictory drought strategies of *Phlomis grandiflora* and *Pyrus amygdaliformis* are much easier to understand than from the water relations data alone. *Phlomis grandiflora*, similar to other shrubby species such as *Salvia* and *Cistus*, is only abundant in non-competitive, early successional stages (e.g., immediately after fire) or under extreme conditions of overgrazing as it is relative unpalatable in comparison to the other macchia trees and shrubs. Thus the survival of these malacophytic shrubs is only partially dependent on drought resistance qualities; they are shortlived with a pronounced reproductive capacity and, at the population level, they are not forced to persist as living plants. They may perpetuate themselves in a seed stage and thus escape drought. In addition, they do appear to be able to tolerate very low water potentials.

Pyrus amygdaliformis possesses considerable drought resistance properties, in particular it shows a rapid maturation of its foliage and thus low osmotic potentials and has an extensive rooting system. However, even a highly adapted deciduous hardwood will never play more than a marginal role within any Mediterranean biome because of the superior competitive ability of the evergreen sclerophyll lifeform. In the long run, deciduous hardwoods are shaded out by the evergreens. In colder regions, the evergreen form will be excluded because of its relatively low frost resistance (Larcher 1963). From plant geography, it is well documented that in winter cold, summer dry areas, deciduous hardwoods such as *Pyrus amygdaliformis* (and a large number of other members of the Rose family such as *Crataegus*, *Prunus*, etc.) form a dominant part of the community (cf. Ayasligil 1987).

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