

## Ecophysiological responses of some maquis (*Ceratonia siliqua* L., *Olea oleaster* Hoffm. & Link, *Pistacia lentiscus* and *Quercus coccifera* L.) plant species to drought in the east Mediterranean ecosystem

Munir Ozturk<sup>\*1</sup>, Yunus Dogan<sup>2</sup>, M. Serdal Sakcali<sup>3</sup>, Andreas Doulis<sup>4</sup> and Fadi Karam<sup>5</sup>

<sup>1</sup>Department of Botany, Ege University - 35100, Bornova-Izmir, Turkey

<sup>2</sup>Department of Biology, Faculty of Education, Dokuz Eylul University - 35160, Buca-Izmir, Turkey

<sup>3</sup>Department of Biology, Fatih University - 34500, B. Cekmece, Hadimkoy, Istanbul, Turkey

<sup>4</sup>Biotechnology Unit, Nagref - 73100, Heraklion, GR-71110, Greece

<sup>5</sup>Department of Irrigation and Agrometeorology, P.O. 287, Lebanese ARI, Tal Amara, Zahle, Lebanon

(Received: January 20, 2009; Revised received: May 15, 2009; Accepted: September 18, 2009)

**Abstract:** The objective was to examine the adaptation strategies of four maquis species to drought prone environments; typical of the east Mediterranean area in degraded and healthy sites in Turkey. A comparison made between sites for *Pistacia lentiscus* and *Quercus coccifera* shows higher net daily photosynthesis in the degraded site, when compared with the healthy site; but *Ceratonia siliqua* and *Olea oleaster* exhibited no difference in their photosynthetic activity in environmentally contrasting conditions. The pattern of daily transpiration shows higher values in the degraded site in the case of *P. lentiscus* and *Q. coccifera*, while no site effect was observed for *C. siliqua* and *O. oleaster*. In the case of *Q. coccifera*, a behavior similar to *C. siliqua* was observed. A comparison made between *C. siliqua* and *O. oleaster* to observe seasonal differences in daily patterns of net photosynthesis and transpiration reveals that *Q. coccifera* had the highest water use efficiency (slope= 2.88;  $r^2= 0.61$ ), followed by *C. siliqua* (slope= 2.74;  $r^2= 0.7$ ), *P. lentiscus* (slope= 2.56;  $r^2= 0.52$ ) and *O. oleaster* (slope= 2.40;  $r^2= 0.78$ ). *Olea oleaster* and *P. lentiscus* performed as a drought tolerant species, being more resistant to aridity and thus indicative of the degradation state of the site. *Ceratonia siliqua* and *Q. coccifera* were found avoiding drought by adopting first a water-spending strategy, and then a water-saving strategy.

**Key words:** Drought, Maquis plants, Photosynthesis, Transpiration, Water use efficiency

PDF of full length paper is available online

\* Corresponding author: [munirozturk@gmail.com](mailto:munirozturk@gmail.com)

### Introduction

Almost all countries around the Mediterranean basin are facing a mass habitat destruction due to several anthropogenic activities like fires, over grazing, wood cutting and uncontrolled urbanization (Ozturk *et al.*, 2008). The basin is characterized by mild and short rainy winters but long and dry summers and poor soils. All these influence the water availability of plants (Vertovec *et al.*, 2001; Loreto and Centritto, 2004; Centritto and Loreto, 2005). In addition to abiotic destructions the anthropogenic stresses duplicate the influence of water scarcity in the area and of course in plant behavior (Sakcali and Ozturk, 2004; Sakcali *et al.*, 2008). Low water availability is considered as one of the main environmental factors limiting photosynthesis and, consequently, plant growth and yield worldwide. It can induce morphological and ecophysiological changes in plants affecting their growth, survival, distribution and abundance (Flexas *et al.*, 2006). Most Mediterranean sclerophyllous plants develop numerous morphological and physiological adaptations like small, thick and microphyllous leaves, dense pubescence, deep water extraction system, high water use

efficiencies in frequent drought stress during the long and dry summer period. Strong diversity in physiological adaptations to the intense insolation and high temperature environments, likely to be of adaptive value, such as the specificity factor of Rubisco; the response of relative growth rate and its components to water stress; or leaf water relations and stomatal control (Faria *et al.*, 1999; Galmes *et al.*, 2005).

Lately, attempts have been made to generalize the responses of photosynthesis to water stress in higher plants (Lawlor and Cornic, 2002; Chaves *et al.*, 2002). There has been a long-standing controversy as to whether drought mainly limits photosynthesis through diffusive resistances or by metabolic impairment. Measurements based on the photosynthetic response to chloroplast CO<sub>2</sub> often confirm that the photosynthetic capacity is preserved, but photosynthesis is limited by diffusive resistances under drought conditions. These evaluations reveal that diffusion limitations on photosynthesis predominate under most water-stress situations which not only involve closure of stomata, but also

decreased mesophyll conductance to CO<sub>2</sub> ( $g_s$ ) (Ennahli and Earl, 2005; Pons et al., 2009).

A general failure of metabolism is reported to occur when daily maximum stomatal conductance ( $g_s$ ) drops below 0.1 mm<sup>2</sup>s<sup>-1</sup> H<sub>2</sub>O (Flexas et al., 2004; Garatani, 1997), but very little information is available in this connection on natural vegetation of different origins. Indeed, many studies have described reductions in photochemical efficiency and low photosynthetic rates during summer drought (Damesin and Rambal, 1995; Tazoe et al., 2009). In addition, temperature during Mediterranean summer may reach potentially damaging thresholds for physiological processes (Epron, 1993), especially when drought-induced stomatal closure limits the ability of plants to avoid heat stress by transpirational cooling (Ladjal et al., 2007).

The natural vegetation of the Mediterranean basin is the proper area to understand the photosynthesis response of plants to drought due to land degradation continuing from centuries. The objectives of this study were 1) to examine as to whether future warming and extended drought events could have a different effect on the physiological performance and water use of some Mediterranean sclerophyllous species, 2) how changes occur in the photosynthetic response of selected plant species to water stress in degraded and healthy areas, 3) to find the most suitable species for reclamation of degraded areas of the Mediterranean basin and 4) to evaluate the suitable parameter for indication of the level of degradation in this area.

### Materials and Methods

Two different areas were selected as study sites situated on the Aegean coast of Eastern Mediterranean basin. First site was chosen in National Park, in the northern side of Dilek Peninsula (37°41' 46" N latitude, 29°09' 44" E longitude) classified as healthy site (H). It lies very near to the coast at an altitude of 10 m, with a total rainfall of 600-700 mm yr<sup>-1</sup>. The dominant plant cover is represented by *Ceratonia siliqua*, *Pistacia lentiscus*, *Olea oleaster*, *Quercus coccifera*, *Phillyrea latifolia*, *Pinus brutia*, *Arbutus andrachne* and *Laurus nobilis*. The second site is Karina, at the south of Dilek Peninsula (37°37' 53" N latitude, 27°07' 11" E longitude) classified as degraded site (D), with poor vegetation cover since it was burnt. This site too lies at an altitude of 10 m facing the coast, with an annual precipitation of 600-700 mm. The dominant species are *P. brutia*, *Q. coccifera*, *Q. ilex*, *C. siliqua*, *O. oleaster*, *L. nobilis*, *P. lentiscus*, *P. terebinthus*, *P. latifolia*, *Styrax officinalis*, *Calicotome villosa* and *Arbutus* species.

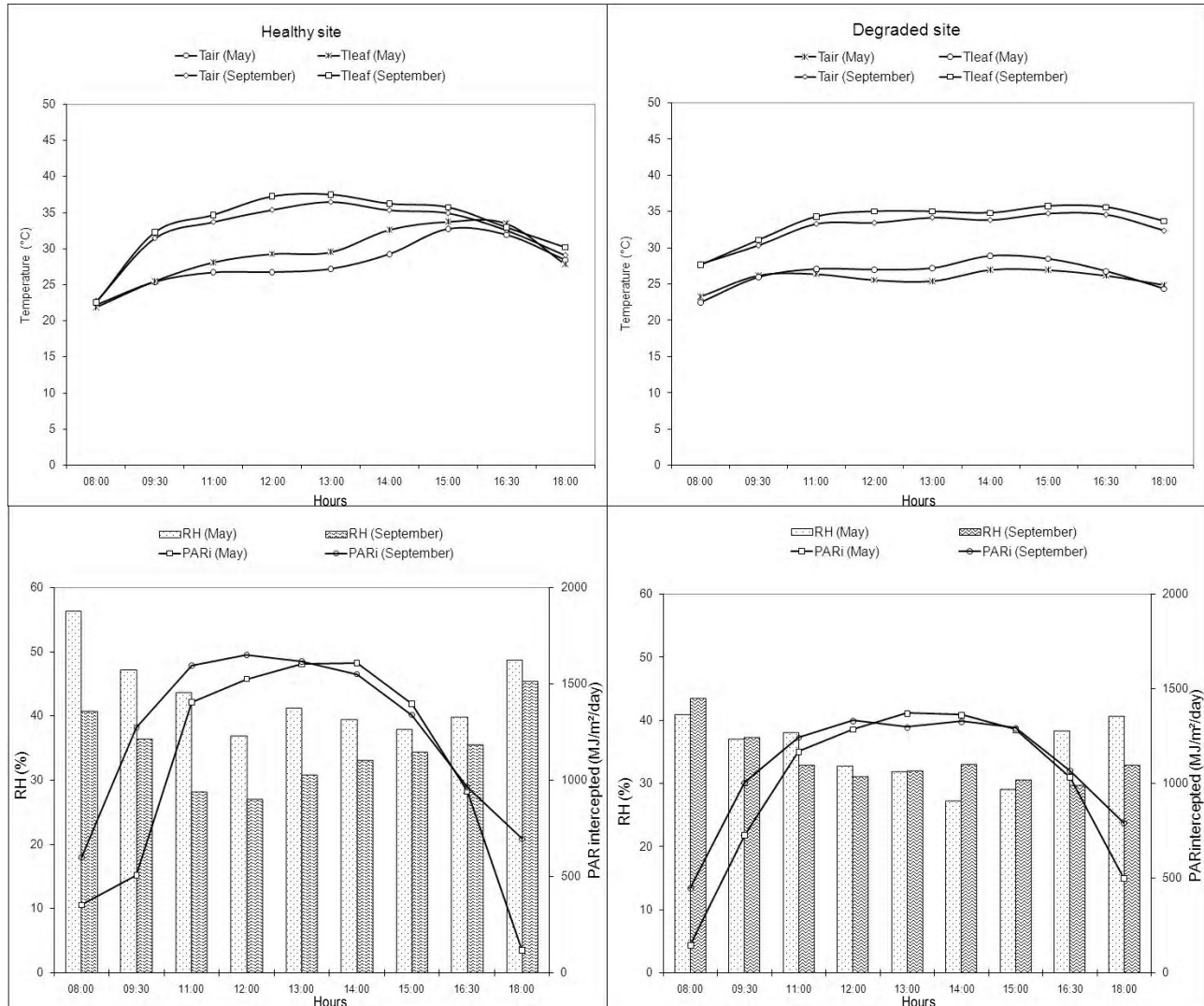
The selection of the species and the experimental sites was done upon considerations of diffusion and relevance on the whole environment. Measurements of CO<sub>2</sub> exchange, air temperature, PAR (photosynthetic active radiation) and transpiration were made in the field on sunny leaves of single trees of *Ceratonia siliqua* L., *Olea oleaster* Hoffm. and Link, *Pistacia lentiscus* L. and *Quercus coccifera* L. LI-COR (Lincoln, NE) LI-6000 Portable Photosynthesis

System (Li-Cor, 1991) was used for photosynthetic measurements. Diurnal time course of measurements were started before sunrise and completed after sunset.

Sampled leaves were chosen in full sunlight. The attached leaves remained in their natural orientation for approximately 45-60s inside the cuvette. One single leaf per tree was selected for measurements and two replicates of diurnal patterns of the ecophysiological parameters were made on hourly basis from sunrise to sunset so as to examine the response of the species under question to different levels of daily stress, and to characterize hourly variability of environmental conditions. The same individual trees of all species were measured in May and September. Data was collected and treated using the C6000 software program available from LI-COR (Leuning and Sands, 1989).

### Results and Discussion

Diurnal variations of air and leaf temperatures, relative humidity and PAR intercepted were measured in both healthy and degraded sites in May and September (Fig. 1). The daily pattern of net photosynthesis with emphasis to site varied among species (Fig. 2). A comparison made between sites for *P. lentiscus* and *Q. coccifera* shows higher net daily photosynthesis in the degraded site, when compared to the healthy site. A similar behavior was observed by Fleck et al. (1998) in *Q. ilex*. Such behavior can result from the reduced plant competition in degraded sites, which increases the availability of water and other nutrients (Vertovec et al., 2001). An increase in the net assimilation rate per unit of leaf area also occurs due to reduced leaf area index as observed in fire-exposed plants. Flexasa et al. (2001) examined the variations in net photosynthesis, stomatal conductance, and several other parameters in *P. lentiscus*. The net photosynthesis peaked in spring and autumn, when water was abundant and temperature was moderately high. It was reduced in winter paralleling reduced carboxylation efficiency. Photosynthesis was at the annual minimum in summer due to drought-induced stomata closure. This data coincides with our observations. *Q. coccifera* experiences lower transpiration rates and higher net photosynthetic rates and water use efficiency than *P. latifolia*. Under severe summer drought conditions none of the two species was able to reach a positive carbon gain. *P. latifolia* was able to increase WUE by reducing transpiration losses during midday. According to Galmes et al. (2007a) there is a general pattern of photosynthetic response to water stress when stomatal conductance is used as a reference parameter and as the values decrease the total photosynthetic limitation rises. The studies on the leaf gas exchange and fluorescence of *P. latifolia*, *P. lentiscus* and *Q. ilex* saplings under severe drought and high temperature conditions revealed that the watered plants of *Q. ilex* had lower photosynthetic activity and stomatal conductance than *P. latifolia* and *P. lentiscus* (Filella et al., 1998), which indicates a different relationship between photosynthetic activity and electron transport rate in *Q. ilex* compared to the other two species which are better adapted to severe drought, but to compare different adaptative strategies it is better to conduct long term experiments (Tretiach, 1993; Galle et al., 2009).



**Fig. 1:** Seasonal variation of weather parameters during the measurement days. Degraded site (D) Karina, Healthy site (H): National park, PARI: Photosynthetically active radiation intercepted ( $\text{MJ m}^{-2} \text{day}^{-1}$ ), RH: Relative humidity

The thermophilic species *C. siliqua* and *O. oleaster* show no significant difference in the photosynthesis between healthy and degraded sites (Fig. 2). This may be primarily due to their mesomorphic leaves, which appear to be unable to prevent wilting under daily water stress if conditions of high evaporation demand prevail, resulting thus in a reduction of the photosynthesis as postulated by Lo Gullo *et al.* (1986). The pattern of daily transpiration shows higher values in the degraded site in the case of *P. lentiscus* and *Q. coccifera*, while no site effect is observed for *C. siliqua* and *O. oleaster* (Fig. 3). A comparison was made between *C. siliqua* and *O. oleaster* to show the seasonal differences in daily patterns of net photosynthesis and transpiration. Fig. 4 shows the average across healthy and degraded sites in photosynthesis rates. This figure shows that *O. oleaster* has high rates of daily photosynthesis in May. The highest values were reached in the morning followed by an immediate depression at midday that continues in the afternoon to less consistent values. In September, the hourly values were

significantly lower than those obtained in May. In contrast, data on *C. siliqua* indicates higher values in September, stressing thereby the fact that the strategy adopted by these species to withstand water stress was completely different from *O. oleaster*. In the case of *Q. coccifera*, a behavior similar to *C. siliqua* was observed, where the lowest values were obtained in May and the highest in September.

The low net  $\text{CO}_2$  assimilation rate observed at the beginning of the growing season may be attributed to the fact that *Q. coccifera* is classified as a drought resistant species and thus it may require conditions of water stress before the stomata start to act effectively (Rambal, 1984). In *P. lentiscus*, no clear difference was observed, which leads to assume the insensitivity of this species to water stress, with regard to seasonal variation. Similar findings are reported by Ogaya and Penuelas (2003) in their studies on the photosynthetic response to experimental drought conditions in *Q. ilex* and *P. latifolia*.

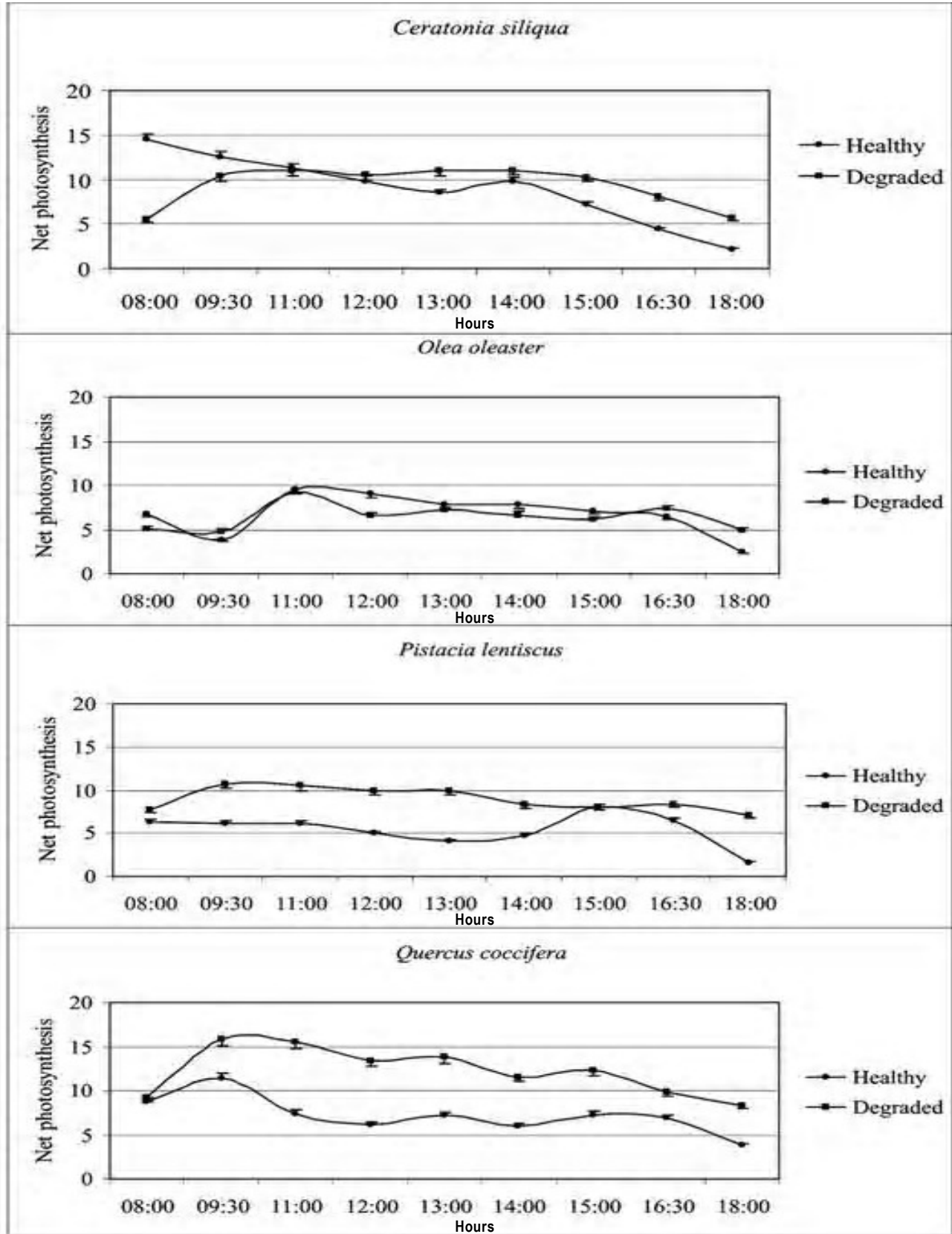


Fig. 2: Daily pattern of net photosynthesis: comparison among species with emphasis to site (unit of measurement: mmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>)

The effects of drought on three Mediterranean cedar species by Ladjal *et al.* (2007) point out that moderate drought provokes a decrease in osmotic potential at full leaf turgor and a long-lasting osmotic adjustment, net photosynthesis ( $A$ ) and stomatal conductance ( $g_s$ ) are lower under dry conditions as compared to the wet.

Plants following water spending strategy for water stress avoidance are incapable of reducing significantly their water loss, and as a consequence are characterized by maintaining high levels of hydration when exposed to external water stress. This means that water can be extracted from soil rapidly enough to compensate for water loss by transpiration, which in turn leads to a sharp decrease in plant water potential in response to water loss. Some Mediterranean plants such as *P. lentiscus* and *C. siliqua* and *O. oleaster* (Lo Gullo *et al.*, 1986; Angelopoulos *et al.*, 1996) appear to adopt this strategy to withstand water stress. These three species are characterized by mesomorphic leaves that show wide variation in daily water potential, which might be achieved by rapid changes in turgor pressure (Ozturk *et al.*, 1983), in response to a change in the air temperature and relative humidity, as well as in soil water availability. However, a night recovery of the plant water status is made possible in response to a decrease in the vapor pressure deficit of the air and an increase in the soil water potential. *C. siliqua* and *O. europaea* are accepted as a paradigm for drought tolerance in the Mediterranean. Fig. 5 shows that the average values between healthy and degraded sites of transpiration rates. Figure reveals that the transpiration rates of *C. siliqua* and *Q. coccifera* were much higher in September than in May. In contrast, as the season progressed, and consequently water stress episode became more severe, *O. oleaster* plants appeared to be unable to prevent dehydration in spite of consistent decrease of transpiration when exposed to prolonged water stress. Stomatal closure in fact, was not sufficient to prevent water loss in September where water stress is at its maximum. As a result, *O. oleaster* behaved in such a way as to maintain its frequency constant even in degraded site, although at the cost of strongly reducing plant size. The investigations undertaken on olive show that this species possesses a series of physiological mechanisms to tolerate drought stress and grows under adverse climatic conditions like carob. The olive plants can lower the water content and water potentials of their tissues, establishing a particularly high potential gradient between leaves and roots, and stop canopy growth but not photosynthetic activity and transpiration (Sofa *et al.*, 2007). At severe drought-stress levels some antioxidant enzymes involved in the scavenging of activated oxygen species increase during a period of drought. Fig. 6 gives the slope of the correlation curve between net photosynthesis and transpiration, or water use efficiency. It can be noticed that *Q. coccifera* has the highest water use efficiency (slope = 2.88;  $r^2 = 0.61$ ), followed by *C. siliqua* (slope = 2.74;  $r^2 = 0.7$ ), *P. lentiscus* (slope = 2.56;  $r^2 = 0.52$ ) and *O. oleaster* (slope = 2.40;  $r^2 = 0.78$ ). Fig. 7 shows the values of average seasonal net photosynthesis and transpiration. *C. siliqua* has the highest rate of net photosynthesis early in the season when water stress episodes are not as much as

to affect seriously plant behavior. Late in the season, low values of net photosynthesis and transpiration were obtained, indicating thus the susceptibility of this species to severe water shortage periods. In terms of water loss, *C. siliqua* behaves as an efficient water spender, but late in the season, this species is no longer capable of compensating for water loss during severe summer water stress, than it does in early season when water stress intensity is mild. In conclusion, this species switched to a water saving strategy.

Early in the season, photosynthesis and transpiration rates are relatively low except for *O. oleaster* where the range of variation of these two parameters is higher than the other species. In that period of the year, the lowest values of photosynthesis and transpiration were observed in *Q. coccifera*, resulting thus in higher water use efficiency in comparison with other species under study. Late in the season, photosynthesis and transpiration decrease drastically in *O. oleaster*, while they increase significantly in *C. siliqua*. For *Q. coccifera*, the increase was slight in the healthy site in comparison with the degraded site. In both sites, a contrasted behavior can be identified between *O. oleaster* and *Q. coccifera*. Meanwhile the first species seems to have higher photosynthesis and transpiration late in the season; these two parameters are very low in the case of *Q. coccifera*. In September, when water stress reaches its maximum, *Q. coccifera* shows higher photosynthesis and transpiration than *O. oleaster* and this difference was mostly evident in degraded site as compared to the healthy one. Our results are in agreement with other reports showing different behavior of photosynthetic activity and water use efficiency on daily and seasonal basis (Tenhunen *et al.*, 1985; Penuelas *et al.*, 2000) as well as the findings of Tretiach (1993), Penuelas *et al.* (2001), Asensio *et al.* (2007) on the response of gas exchanges to the drought in the Mediterranean on seasonal basis. All species develop different physiological responses to the drought.

In the marked seasonality of Mediterranean climate conditions, drought has strongly influenced evolution and plant life (Pereira and Chaves, 1995). Predicted water stress in the Mediterranean Basin (Houghton *et al.*, 2001) may be associated with physiological and phenological responses in plant species (Penuelas and Filella, 2001), but different species can develop different responses to these climatic changes. It is likely that more drought- and heat-resistant species such as *P. latifolia* will tolerate the increase of temperature and dry conditions better than more mesic ones. These physiological responses could be followed by changes in carbon acquisition of Mediterranean forests, and in a long term, by changes in species distribution conferred by the different capacity of different species to survive under the new climatic constraints. The ecophysiological characteristics described in this study are in agreement with the different distribution of these species. They are in agreement with predictions of a possible change in dominance of species with similar adaptations to drought in a warmer drier climate such as the one predicted in the Mediterranean region by global change circulation models (Houghton *et al.*, 2001).

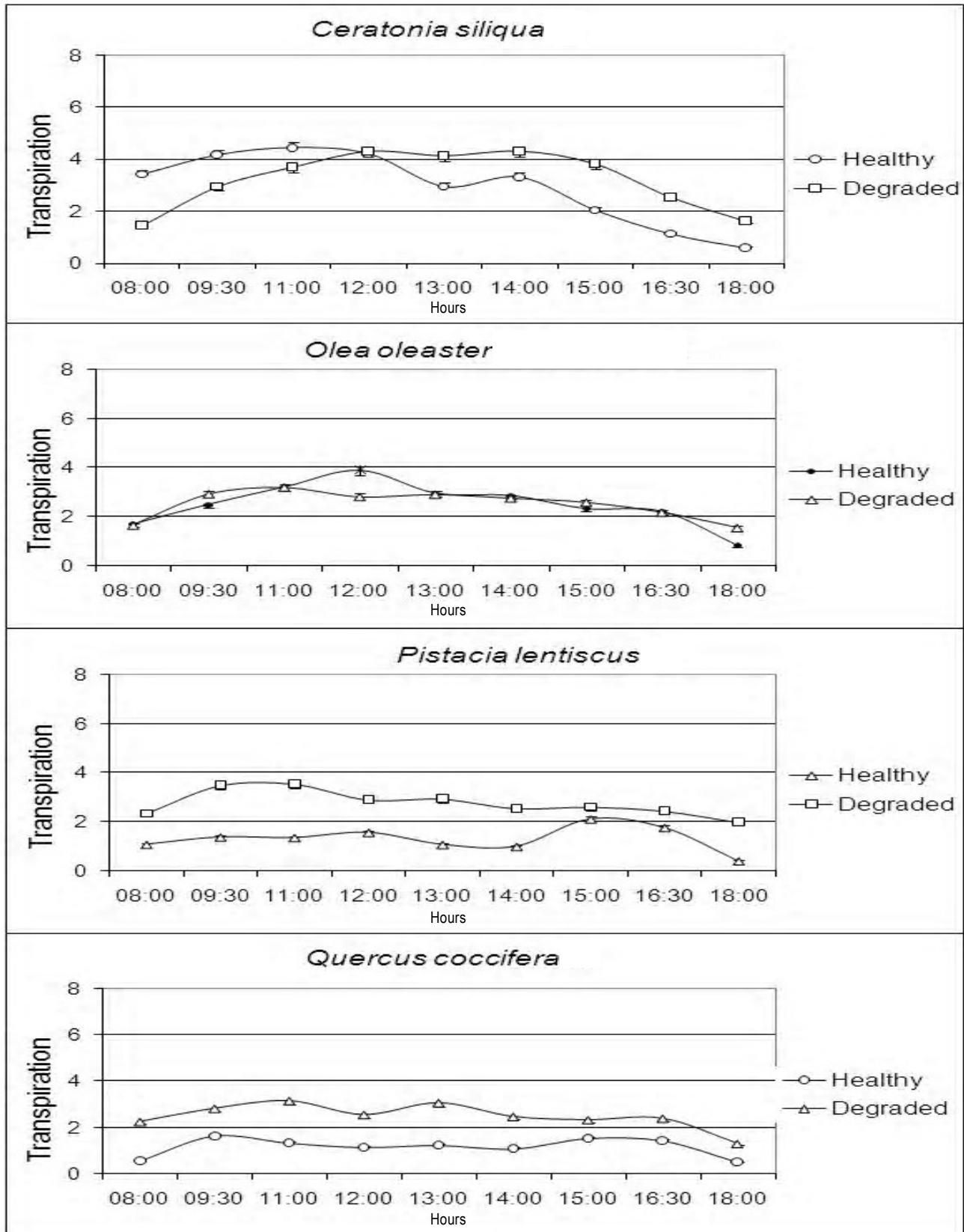


Fig. 3: Daily pattern of transpiration: comparison among species with emphasis to site (unit of measurement: mmol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>)

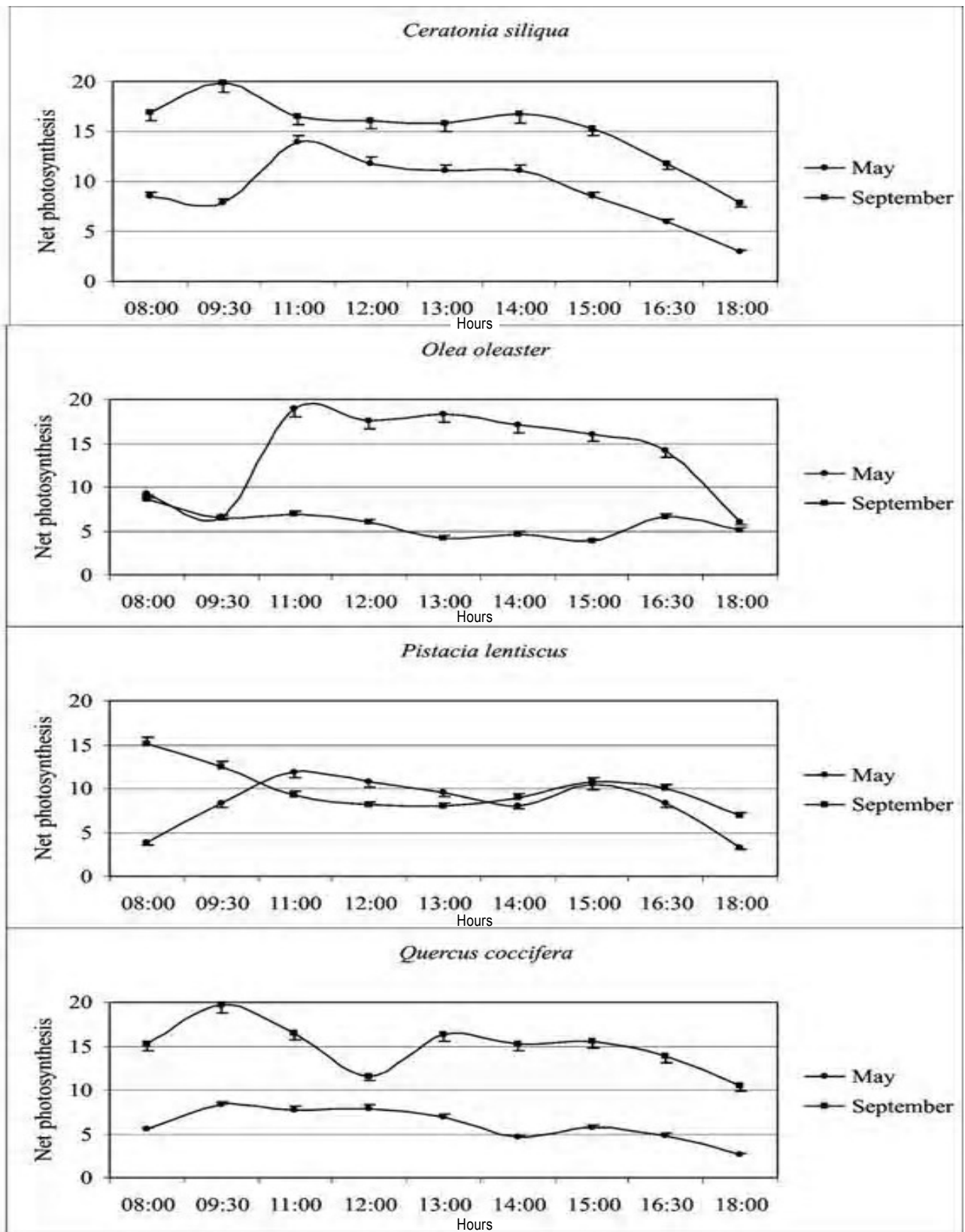


Fig. 4: Daily pattern of net photosynthesis: comparison among species with emphasis to season (unit of measurement: mmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>)



The consistent global climate change will definitely introduce changes in the plant growth therefore data is needed for the most important tree crops to make long term prediction in this connection. Although stress is laid on the CO<sub>2</sub> increase, the extent to which annual temperature and rainfall patterns will be altered is very important in determining if local species will be benefited by the increased photosynthesis and water use efficiency. Most probably a combination of higher temperature, reduced availability of water and increased use of saline irrigation waters will enhance several stressing factors that will be very difficult to overcome. Local variability in the climate can cause dramatic differences in photosynthesis among populations within short distances. These differences are likely to be translated into large differences in the annual carbon balance between local populations of the same species. It is therefore very important that conservation and sustainable use of water resources should be planned now particularly in the Mediterranean basin. The shrub species show lower shoot water potentials, transpiration rates and stomatal conductance under drought and there is a significant reduction in the overall leaf net photosynthetic rates depending on the species. The drier and warmer conditions may change the competitive relationship among species of Mediterranean scrublands. The future drier conditions may decrease the annual productivity of Mediterranean shrubs, although the magnitude of such decreases will be species-specific, and warmer conditions could alleviate the low temperature constraints on the photosynthetic performance during the colder seasons, possibly increasing the length of the growth period. The evergreen oaks have the capability of exploring larger soil volumes thus surviving the drought and assimilating some carbon using the water stored in the soil free from the competition of other plants. The closed canopy plantation seems to be less sensitive to moderate droughts, but more vulnerable to severe droughts than the systems dominated by herbaceous plants. *Q. coccifera* is found to be a drought resistant species. This has been observed on the basis of seasonal average net photosynthesis and transpiration that showed a strategy of water loss avoidance. *P. lentiscus* and *O. oleaster* are found to be water spender species since they suffer from water stress problems much earlier than do *C. siliqua* and *Q. coccifera*. *O. oleaster* is shown to be unable to prevent the negative effects of prolonged water stress. Seasonal values of water use efficiency of the species under study are presented in Table 1. According to this table, *P. lentiscus* and *Q. coccifera* exhibit similar seasonal values of water use efficiency and the highest values were observed in September, i.e. at the end of the drought period. In contrast, in the case of *C. siliqua* and *O. oleaster* the highest values were obtained in early spring. The results of the of photosynthesis and transpiration measurements demonstrated that *C. siliqua* and *Q. coccifera* are species that can be considered as suitable candidates for natural reforestation of degraded areas of the east Mediterranean Basin. Although *P. lentiscus* and *O. oleaster* proved to be sensitive to aridity, wild olive species proved to be a suitable indicator of the degree of degradation of the different areas under study. *Q. coccifera* and *C. siliqua* proved to be drought resistant species, while *O. oleaster* suffered water stress, largely. *Q. coccifera* should be

planted first, because it is drought resistant and, in fact, is affected by environmental aridity.

The diurnal and seasonal trends of the measured parameters, with regard to site and seasonal variation depict that differences between species are evident and explain different responses to the environmental pressure, based on proper physiological demand. In particular, differences help to discriminate between drought avoiding or resistant species (*Q. coccifera* and *C. siliqua*) and drought tolerant or vulnerable to aridity (*O. oleaster*). This means that different species can be differently used with regard to desertification monitoring attitude. *O. oleaster* behaves as water-spender, while *Q. coccifera* behaves as a water-saver. On the basis of our data and in accordance with previous reports (Lo Gullo and Salleo, 1988; Giorio et al., 1999) *O. oleaster* can be regarded as a desiccation tolerant (drought avoider) species in accordance with the definition of Levitt (1980). *C. siliqua* shows low photosynthesis and transpiration at the beginning of the growing season and these two parameters tend to increase remarkably in September with the acceleration of the water stress period. As far as for *P. lentiscus*, the situation was less clear as compared to the other species. However, results showed that this species had relatively low photosynthesis and transpiration rate in comparison with other species, which however did not differ significantly between sites. Our results agree with well-known patterns of annual variation of gas exchange in Mediterranean evergreen shrubs. Initially, stomatal control is the major cause of photosynthetic depression during summer. The main control of photosynthesis is through stomatal limitation, triggered by variation in water availability. The stomatal control requires both hydraulic and chemical signaling to be effective. The stomatal conductance represents an optimal solution of a hierarchically structured system.

Low photosynthetic rates have been reported during winter. Some investigators suggest that winter cold stress plays a relevant role in the development and distribution of Mediterranean evergreen species (Tretiach, 1993; Karavatas and Manetas, 1999). Low photosynthetic rate in dry summer period is almost due to the stomatal control in evergreen species of Mediterranean basin as reported by several investigators (Tenhunen et al., 1990; Filella et al., 1998; Penuelas et al., 1998; Galmes et al., 2007b). A marked decline in maximal rate of photosynthesis at saturating irradiance and high

**Table - 1:** Seasonal water use efficiency for the species under study (mmol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>)

	<i>C. siliqua</i>	<i>O. oleaster</i>	<i>P. lentiscus</i>	<i>Q. coccifera</i>
<b>Healthy site</b>				
May	2.61	2.44	3.65	3.71
September	3.26	3.63	4.80	4.15
Average	2.93	3.03	4.22	3.93
<b>Degraded site</b>				
May	2.80	2.66	3.72	3.35
September	2.94	2.39	3.97	3.93
Average	2.87	2.52	3.84	3.64



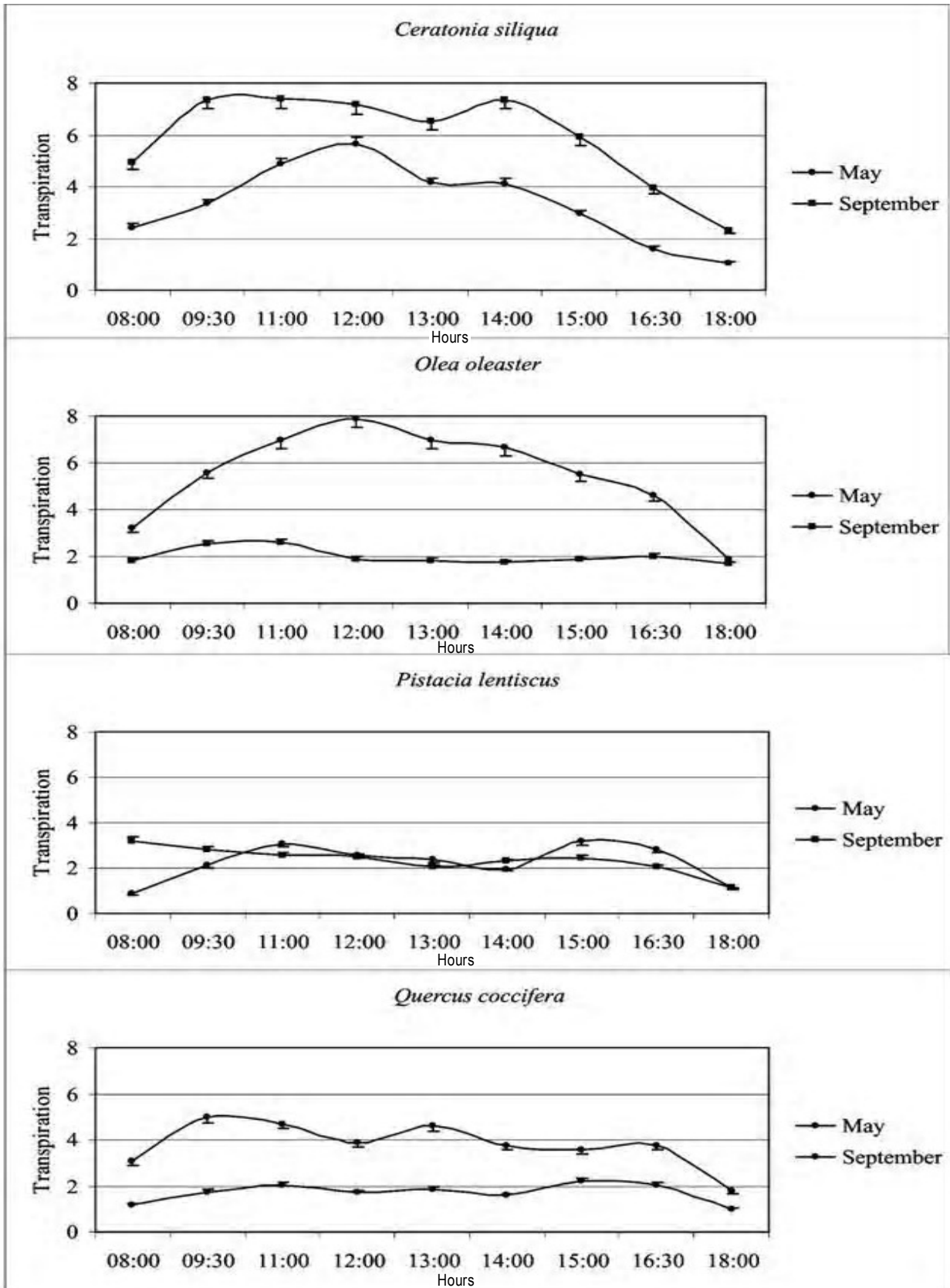


Fig. 5: Daily pattern of transpiration: comparison among species with emphasis to season (unit of measurement:  $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$ )

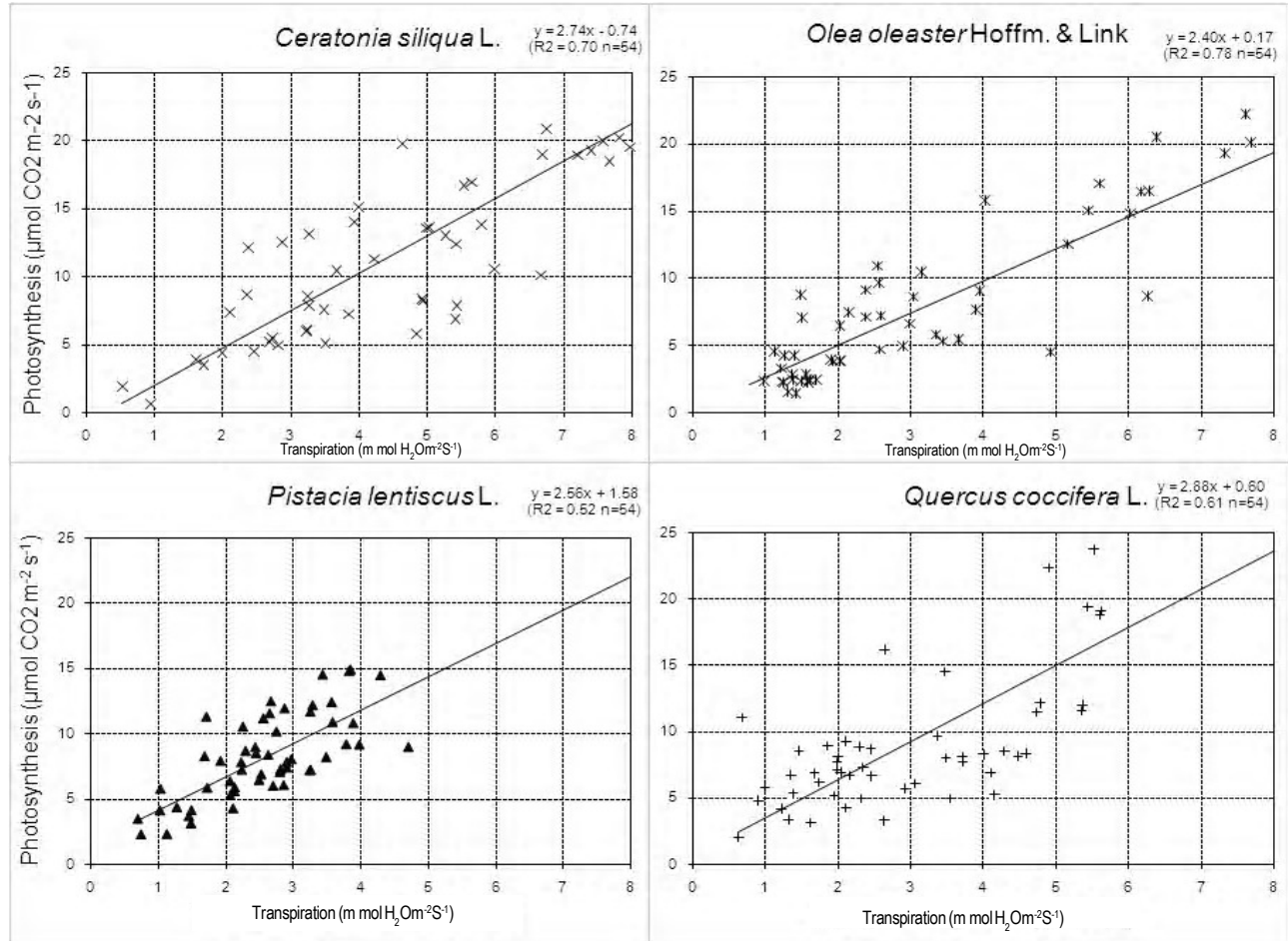


Fig. 6: Photosynthesis versus transpiration comparison between species

internal CO<sub>2</sub> concentration has been observed at temperatures ranging from 35 to 40°C (Tenhunen *et al.*, 1985; 1990; Niinemets *et al.*, 2005). Therefore, an increase in the duration and severity of summer drought as well as indirect effects of future warming, can significantly increase leaf heat stress, limiting growth and survival of plants due to severe restrictions on photosynthesis, and may affect the physiological activity of the Mediterranean plants. Osmond *et al.* (1980) demonstrated that the greatest effect of water stress on plants is observed in coincidence of peak irradiance, either on daily or seasonal bases. The midday stomatal closure observed in many Mediterranean species has been reported by Vardar and Ozturk (1972), Sheikh (1976) and Tenhunen *et al.* (1985) as a feature of these species, which allows them to limit water loss when the atmospheric demand is at its maximum during the course of the day. The relation between photosynthesis and transpiration requires a certain degree of stomatal aperture, but not necessarily maximum aperture, which is important for the success of plants in habitats, which are partially or entirely dry. The balance between carbohydrates and nitrogen may have a triggering role in plant response under elevated CO<sub>2</sub>. Carbon export rates by the

leaves seem to be independent of total carbon assimilation, suggesting a sink limiting effect on growth and photosynthesis under elevated CO<sub>2</sub> (Chaves *et al.*, 2002).

The global change is expected to produce an effect on the photosynthesis and productivity of plants, but it will vary with the regions depending on the pre-existing climatic conditions and the adaptation potential of the species (Niinemets *et al.* 2009). The carbon balance of a plant enduring a water-stress depends on the rate and degree of photosynthetic recovery as well as its decline during water depletion (Centritto *et al.* 2009; Flexas *et al.* 2009). There is a strong relationship between stomatal conductance and environmental factors under Mediterranean climatic conditions therefore high temperature and low rainfall will lead to high evapotranspiration losses, increasing the water stress problems, thus crops in the Mediterranean will have to grow under more hot and dry environment (Chartzoulakis & Psarras, 2005; Vitale *et al.* 2007; Galle *et al.* 2009). Seasonal gradients are important to characterize the intensity of water stress duration of different species. In particular, in view of the recently highlighted importance

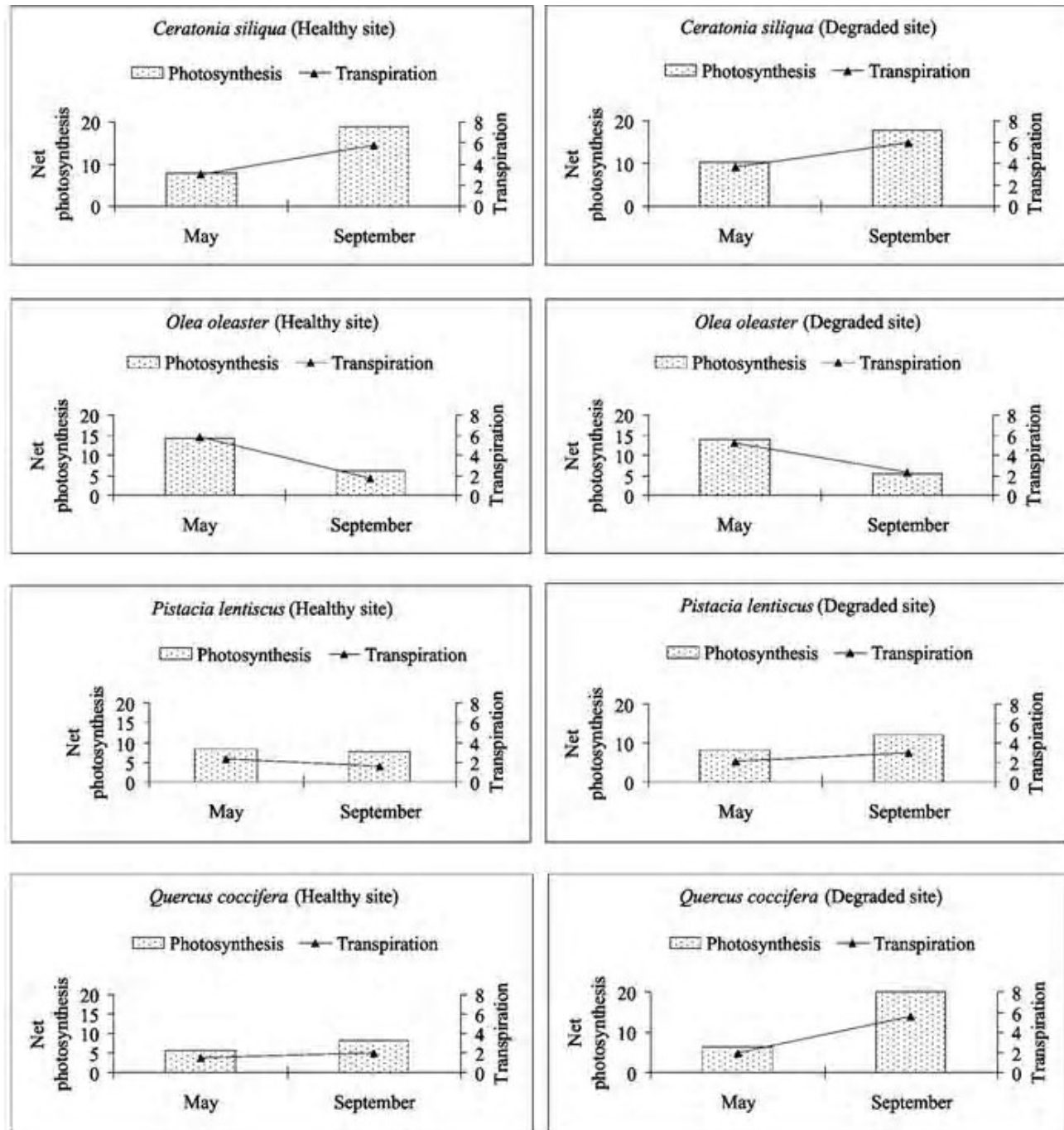


Fig. 7: Average seasonal net photosynthesis (mmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>) and transpiration (mmol H<sub>2</sub>O m<sup>-2</sup> s<sup>-1</sup>): comparison among species with emphasis to site and season

of decreased  $g_i$  in the regulation of photosynthesis during water stress, this parameter will attract more attention under natural conditions. The results presented here underline the response in terms of photosynthesis and transpiration variation on both daily and seasonal bases. The correlation between these two parameters, called also water use efficiency, WUE, gives an indication of the degree of adaptation of each species to the environmental condition.

**Acknowledgments**

This work was done with the support from the European Community Project INCO-DC ERBIC18CT970153 Desertification in the Mediterranean Drylands: development of a monitoring system based on plant ecophysiology (DEMOS).

We greatly acknowledge the help rendered to us in the field by Mediterranean Agronomic Institute, Chania-73100 Crete, Greece



through Mr. P. Akl and Mrs. T. Shahsuvaroglu. Our thanks go to Prof. S. Salleo and Prof. E. Feoli, (Department of Biology, Univ. of Trieste, Italy) for their helpful discussions during the course of this investigation. Our special thanks go to the Forest Directorate Kusadasi National Park for permitting us to work in the area.

### References

- Angelopoulos, K., B. Dichio and C. Xiloyannis: Inhibition of photosynthesis in olive trees (*Olea europaea* L.) during water stress and rewatering. *J. Exp. Bot.*, **47**, 1093-1100 (1996).
- Asensio, D., J. Penuelas, R. Ogaya and J. Llusia: Seasonal soil and leaf CO<sub>2</sub> exchange rates in a Mediterranean holm oak forest and their responses to drought conditions. *Atmos. Environ.*, **41**, 2447-2455 (2007).
- Centritto M., M. Lauteri, M. C. Monteverdi and R. Serraj: Leaf gas exchange, carbon isotope discrimination and grain yield in contrasting rice genotypes subjected to water deficits during the reproductive stage. *J. Exp. Bot.*, **60**, 2325-2339 (2009).
- Centritto, M. and F. Loreto: Photosynthesis in a changing world: Photosynthesis and abiotic stresses. *Agric. Ecosys. Environ.*, **106**, 115-117 (2005).
- Chartzoulakis, K. and G. Psarras: Global change effects on crop photosynthesis and production in Mediterranean: The case of Crete, Greece. *Agric. Ecosys. Environ.*, **106**, 147-157 (2005).
- Chaves, M.M., J.S. Pereira, J. Maroco, M.L. Rodrigues, C.P.P. Ricardo, M.L. Osorio, I. Carvalho, T. Faria and C. Pinheiro: How plants cope with water stress in the field. Photosynthesis and growth. *Ann. Bot. London*, **89**, 907-916 (2002).
- Damesin C. and S. Rambal: Field study of leaf photosynthetic performance by a Mediterranean deciduous oak tree (*Quercus pubescens*) during a severe summer drought. *New Phytol.*, **131**, 159-167 (1995).
- Ennahli, S. and H.J. Earl: Physiological limitations to photosynthetic carbon assimilation in cotton under water stress. *Crop Sci.*, **45**, 2374-2382 (2005).
- Epron, D. and E. Dreyer: Long-term effects of drought on photosynthesis of adult oak trees *Quercus petraea* (Matt.) Liebl. and *Quercus robur* L. in a natural stand. *New Phytol.*, **125**, 381-389 (1993).
- Faria, T., M. Vaz, P. Schwanz, A. Polle, J.S. Pereira and M.M. Chaves: Responses of photosynthetic and defence systems to high temperature stress in *Quercus suber* L. seedlings grown under elevated CO<sub>2</sub>. *Plant Biol.*, **1**, 365-371(1999).
- Filella, I., J. Llusia, J. Pinol and J. Penuelas: Leaf gas exchange and fluorescence of *Phillyrea latifolia*, *Pistacia lentiscus* and *Quercus ilex* saplings in severe drought and high temperature conditions. *Environ. Exp. Bot.*, **39**, 213-220 (1998).
- Fleck, I., K.P. Hogan, L. Lorens, A. Abadaia and X. Aranda: Photosynthesis and photoprotection in *Quercus ilex* resprouts after fire. *Tree Physiol.*, **18**, 607-614 (1998).
- Flexas J., J.J. Bota Galmes, H. Medrano and M. Ribas-Carbo: Keeping a positive carbon balance under adverse conditions: Responses of photosynthesis and respiration to water stress. *Physiol. Plantarum*, **127**, 343-352 (2006).
- Flexas, J., J. Guliasa, S. Jonassonb, H. Medranoa and M. Musa: Seasonal patterns and control of gas exchange in local populations of the Mediterranean evergreen shrub *Pistacia lentiscus* L. *Acta Oecol.*, **22**, 33-43 (2001).
- Flexas, J., M. Baron, J. Bota, J. Ducruet, A. Galle, J. Galmes, M. Jimenez, A. Pou, M. Ribas-Carbo, C. Sajnani, M. Tomas and H. Medrano: Photosynthesis limitations during water stress acclimation and recovery in the drought-adapted vitis hybrid richter-110 (*V. berlandierix*, *V. rupestris*). *J. Exp. Bot.*, **60**, 2361-2377 (2009).
- Flexasa, J., J. Guliasa, S. Jonassonb, H. Medranoa and M. Musa: Seasonal patterns and control of gas exchange in local populations of the Mediterranean evergreen shrub *Pistacia lentiscus* L. *Acta Oecol.*, **22**, 33-43 (2001).
- Galle, A., I. Florez-Sarasa, M. Tomas, A. Pou, H. Medrano, M. Ribas-Carbo and J. Flexas. The role of mesophyll conductance during water stress and recovery in tobacco (*Nicotiana sylvestris*): Acclimation or limitation?. *J. Exp. Bot.*, **60**, 2379-2390 (2009).
- Galmés J., J. Cifre, H. Medrano and J. Flexas: Modulation of relative growth rate, its components by water stress in Mediterranean species with different growth forms. *Oecologia*, **145**, 21-31 (2005).
- Galmés J., J. Flexas, R. Savé and H. Medrano: Water relations and stomatal characteristics of Mediterranean plants with different growth forms and leaf habits: Responses to water stress and recovery. *Plant Soil*, **290**, 139-155 (2007b).
- Galmés, J., H. Medrano and J. Flexas: Photosynthetic limitations in response to water stress and recovery in Mediterranean plants with different growth forms. *New Phytol.*, **175**, 81-93 (2007a)
- Garatani, L.: Structural and ecophysiological plasticity of some evergreen species of the Mediterranean maquis in response to climate. *Photosynthetica*, **31**, 335-343 (1997).
- Giorio, P., G. Sorrentino and R. d'Andria: Stomatal behaviour, leaf water status and photosynthetic response in field-grown olive trees under water deficit. *Environ. Exp. Bot.*, **42**, 95-104 (1999).
- Houghton, J.T., Y. Ding, D.J. Griggs, M. Noguer, P.J. Van der Linden, X. Dai, K. Maskell and C.A. Johnson: The scientific basis, contribution of working group I. In: IPCC, Climate change. Third Assessment Report of Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge (2001).
- Karavatas, S. and Y. Manetas: Seasonal patterns of photosystem 2 photochemical efficiency in evergreen sclerophylls and drought semi-deciduous shrubs under Mediterranean field conditions. *Photosynthetica*, **36**, 41-49 (1999).
- Ladjal, M., N. Deloche, R. Huc and M. Ducrey: Effects of soil and air drought on growth, plant water status and leaf gas exchange in three Mediterranean cedar species: *Cedrus atlantica*, *C. brevifolia* and *C. libani*. *Trees*, **21**, 201-213 (2007).
- Lawlor, D.W. and G. Cornic: Photosynthetic carbon assimilation and associated metabolism in relation to water deficits in higher plants. *Plant Cell Environ.*, **25**, 275-294 (2002).
- Leuning, R. and P. Sands: Theory and practice of a portable photosynthesis instrument. *Plant Cell Environ.*, **12**, 669-678 (1989).
- Levitt, J.: Responses of Plants to Environmental Stresses. New York: Academic Press (1980).
- Li-Cor: Plant Canopy Analyser Instruction Manual. Li-Cor, Lincoln, NE, USA (1991).
- Lo Gullo, M.A. and S. Salleo: Different strategies of drought resistance in three Mediterranean sclerophyllous trees growing in the same environmental conditions. *New Phytol.*, **108**, 267-276 (1988).
- Lo Gullo, M.A., S. Salleo and R. Rosso: Drought avoidance strategy in *Ceratonia siliqua* L., a mesomorphic-leaved tree in the xeric Mediterranean area. *Ann. Bot.*, **58**, 745-756 (1986).
- Loreto, F. and M. Centritto: Photosynthesis in a changing world. *Plant Biol.*, **6**, 239-241 (2004).
- Niinemets, U., A. Cescatti, M. Rodeghiero and T. Tosens: Leaf internal diffusion conductance limits photosynthesis more strongly in older leaves of Mediterranean evergreen broad-leaved species. *Plant Cell Environ.*, **28**, 1552-1566 (2005).
- Niinemets, U., A. Diaz-Espejo, J. Flexas, J. Galmes and C.R. Warren: Role of mesophyll diffusion conductance in constraining potential photosynthetic productivity in the field. *J. Exp. Bot.*, **60**, 2249-2270 (2009).
- Ogaya, R. and J. Penuelas: Comparative field study of *Quercus ilex* and *Phillyrea latifolia*: Photosynthetic response to experimental drought conditions. *Environ. Exp. Bot.*, **50**, 137-148 (2003).
- Osmond, C.B., K. Winter and S.B. Powles: Adaptive significance of carbon dioxide cycling during photosynthesis in water-stressed plants. In: Adaptation of plants to water and high temperature stress (Eds.: N.C. Turner and P.J. Kramer). New York: John Wiley and Sons, Inc. pp. 139-154 (1980).

- Ozturk, M., E. Yucel, S. Gucl, S. Sakcali and A. Aksoy: Plants as Biomonitor of Trace Elements Pollution in Soil. *In: Trace Elements as Contaminants and Nutrients: Consequences in Ecosystems and Human Health* (Ed.: M.N.V. Prasad MNV). John Wiley and Sons, Inc., Hoboken, N.J.. pp. 721-742 (2008).
- Ozturk, M., O. Seçmen and K. Kondo: Transpirational studies in some macchia elements. *Memoirs Faculty of Integrated Arts and Science Hiroshima University*, **8**, 60-76 (1983).
- Penuelas, J., F. Lloret and R. Montoya: Severe drought effects on Mediterranean woody flora in Spain. *For. Sci.*, **47**, 214-218 (2001).
- Penuelas, J., I. Filella, F. Lloret, J. Pinol and D. Siscart: Effects of a severe drought on water and nitrogen use by *Quercus ilex* and *Phillyrea latifolia*. *Biol. Plantarum*, **43**, 47-53 (2000).
- Penuelas, J., I. Filella, J. Llusia, D. Siscart and J. Pinol: Comparative field study of spring and summer leaf gas exchange and photobiology of the Mediterranean trees *Quercus ilex* and *Phillyrea latifolia*. *J. Exp. Bot.*, **49**, 229-238 (1998).
- Pereira, J.S. and M.M. Chaves: Plant responses to drought under climate change in Mediterranean-type ecosystems. *In: Global change and Mediterranean-type ecosystems* (Eds.: J.M. Moreno and W.C. Oechel). Ecological Study, Springer, New York, **117**, 140-160 (1995).
- Pons, T.L., J. Flexas, S. Caemmerer, J.R. Evans, B. Genty, M. Ribas-Carbo and E. Bruognoli: Estimating mesophyll conductance to CO<sub>2</sub>: Methodology, potential errors and recommendations. *J. Exp. Bot.*, **60**, 2217-2234 (2009).
- Rambal, S.: Water-balance and pattern of root water-uptake by a *Quercus coccifera* evergreen shrub. *Oecologia*, **62**, 18-25 (1984).
- Sakcali, M.S. and M. Ozturk: Eco-physiological behaviour of some mediterranean plants as suitable candidates for reclamation of degraded areas. *J. Arid Environ.*, **57**, 141-153 (2004).
- Sakcali, M.S., H. Bahadir and M. Ozturk: Eco-physiology of *Capparis spinosa* L.: A plant suitable for combating desertification. *Pak. J. Bot.*, **40**, 1481-1486 (2008).
- Sheikh, K.H.: Variations in leaf hydration and stomatal openings of some maquis in response to changes in some environmental factors. *In: Proceedings of the third mediterranean plant physiology meeting* (Eds.: Y. Vardar, K.H. Sheikh and M. Ozturk). Izmir, Ege University Press. pp. 24-36 (1976).
- Sofa, A., S. Manfreda, B. Dichio, M. Fiorentino and C. Xiloyannis: The olive tree: A paradigm for drought tolerance in Mediterranean climates. *Hydrological Earth Systematic Sciences*, **4**, 2811-2835 (2007).
- Tazoe, Y., S. von Caemmerer, M.R. Badger and J.R. Evans: Light and CO<sub>2</sub> do not affect the mesophyll conductance to CO<sub>2</sub> diffusion in wheat leaves. *J. Exp. Bot.*, **60**, 2291-2301 (2009).
- Tenhunen, J.D., A. Sala, P.C. Harley, R.L. Dougherty and J.F. Reynolds: Factors influencing carbon fixation and water use by Mediterranean sclerophyll shrubs during summer drought. *Oecologia*, **82**, 381-393 (1990).
- Tenhunen, J.D., O.L. Lange, P.C. Harley, W. Beyschlag and A. Meyer: Limitations due to water stress on leaf net photosynthesis of *Quercus coccifera* in the Portuguese evergreen Scrub. *Oecologia*, **67**, 23-30 (1985).
- Tretiach, M.: Photosynthesis and transpiration of evergreen Mediterranean and deciduous trees in an ecotone during a growing season. *Acta Oecologia*, **14**, 341-360 (1993).
- Vardar, Y. and A.M. Ozturk: Relative transpiration of the old and young leaves of some macchia elements. *Phyton*, **14**, 251-262 (1972).
- Vertovec, M., S. Sakcali, M. Ozturk, S. Salleo, P. Giacomich, E. Feoli and A. Nardini: Diagnosing plant water status as a tool for quantifying water stress on a regional basis in Mediterranean drylands. *Ann. For. Sci.*, **58**, 113-125 (2001).
- Vitale, M., S. Anselmi, E. Salvatori and F. Manes: New approaches to study the relationship between stomatal conductance and environmental factors under Mediterranean climatic conditions. *Atmos. Environ.*, **41**, 5385-5397 (2007).