Environmental control of CO$_2$ assimilation rates and stomatal conductance in five oak species growing under field conditions in Greece

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Summary — The present study compared CO$_2$ assimilation rate and stomatal conductance of five oak species from the beginning of May through November 1993 under similar natural conditions. Gas exchange, leaf characteristics and water status were measured on 30-year-old Quercus ilex, Q macrolepis, Q pedunculiflora, Q pubescens and Q trojana growing in experimental plots in northern Greece. The seasonal pattern of assimilation rates was similar for all study species but differences occurred between the species. After initial leaf expansion, all species rapidly developed high photosynthetic rates. In addition, assimilation rates were high in all species in May and November after rain events. No significant differences in stomatal conductance were observed among species during the growing season. The relationships between assimilation rate and stomatal conductance displayed variation in the slopes among species and months.

Quercus sp / assimilation rate / stomatal conductance / seasonality / drought

Résumé — Effets de l'environnement sur l'assimilation nette de CO$_2$ et la conductance stomatique de cinq espèces de chênes en plantation en Grèce. Cette étude a permis la comparaison des niveaux d'assimilation nette de CO$_2$ et de conductance stomatique de cinq espèces de chênes en plantation comparative dans le nord de la Grèce, au cours d'une saison de végétation (mai–novembre 1993). Les échanges gazeux, les caractéristiques foliaires et l'état hydrique ont été déterminés sur des arbres de 30 ans de Quercus ilex, Q macrolepis, Q pedunculiflora, Q pubescens et Q trojana. La dynamique saisonnière d'assimilation nette était très semblable entre espèces. Des différences significatives sont apparues à certains moments. Après la phase d'expansion initiale des feuilles, toutes les espèces présentaient de fortes valeurs d'assimilation, de même que pendant les périodes pluvieuses en mai et en novembre. Peu de différences interspécifiques de conductance stomatiques ont été détectées au cours de la saison. Cependant, les relations entre conductance stomatique et assimilation nette ont fortement différé suivant les espèces et les périodes de mesure.

Quercus / assimilation nette de CO$_2$ / conductance stomatique / variations saisonnières / sécheresse
INTRODUCTION

Oak forests in Greek cover about 23% of the total forest area. Oak species occurring in Greece are generally considered to be drought resistant and suitable for forest regeneration in the Mediterranean zone characterized by frequent summer droughts. Drought adaptation has been shown to govern species distribution (Bahari et al, 1985; Dafis, 1986). Drought is the result of a combination of environmental factors including low precipitation, irregular rainfall distribution, low air humidity and high air temperature. Limited soil moisture, high evaporation demand and high temperature can have negative effects on gas exchange. The knowledge of how environmental conditions influence gas exchange may improve the understanding of oak species habitat within the Mediterranean forest complex. There is a lack of knowledge about the physiological features of drought adaptation in Greek oak species.

Eleven oak species occur in Greece. They grow in habitats widely differing in extent of drought. The following rating of drought tolerance based on species distribution has been suggested (Athanasiadis, 1986; Dafis, 1986): Quercus pedunculiflora (least tolerant) < Q ilex < Q trojana < Q macrolepis < Q pubescens (most tolerant). However, these apparent differences in drought tolerance have not yet been confirmed by comparative studies on trees growing in natural conditions.

The present study was undertaken to identify differences in drought adaptation between these species. Stomatal conductance and CO₂ assimilation behavior were compared.

MATERIALS AND METHODS

Study area

The experimental area is located near the Forest Research Institute of Thessaloniki (latitude 40°35’N, longitude 22°58’E, altitude 10 m). The area consists of experimental plots of the following species: Quercus ilex L., Q macrolepis, Kotschy, Q pedunculiflora Koch, Q pubescens Willd. and Q trojana Webb. Each plot occupies an area of 1 550 m² (45 x 30 m), the planting space was 3 x 3 m and had been planted 30 years before the study (table I). In each plot, nine dominant trees were selected for further measurements.

The area displays an Emberger coefficient of 50.8 and the climate is characterized as a semi-arid Mediterranean bioclimate with dry and hot summers and cold winters (Mauromatis, 1980). The area belongs to the Ostryo-carpinion vegetation zone (Dafis, 1973). The study was conducted at a site where Q pubescens would occur naturally.

The mean annual precipitation is 409 mm (range 211–704 mm) for the 30 year period. The summer dry period begins in June and lasts until October. The driest months are August and September with a mean monthly precipitation of 22 and 21 mm, respectively. A weather station, located at the study site, was used to record hourly the average of the following parameters:

Table I. Main characteristics of the study stands.

<table>
<thead>
<tr>
<th></th>
<th>Q ilex</th>
<th>Q macrolepis</th>
<th>Q pendunculiflora</th>
<th>Q pubescens</th>
<th>Q trojana</th>
</tr>
</thead>
<tbody>
<tr>
<td>Years</td>
<td>30</td>
<td>30</td>
<td>30</td>
<td>30</td>
<td>30</td>
</tr>
<tr>
<td>Mean height (m)</td>
<td>4.32 (0.50)</td>
<td>8.2 (0.72)</td>
<td>9.34 (0.80)</td>
<td>8.4 (0.60)</td>
<td>7.96 (0.55)</td>
</tr>
<tr>
<td>Stand density</td>
<td>70%</td>
<td>72%</td>
<td>75%</td>
<td>71%</td>
<td>73%</td>
</tr>
</tbody>
</table>
total incoming radiation, air temperature, relative humidity, precipitation, barometric pressure, wind speed and wind direction.

The soil belongs to soil brun Mediterranean type and consists of sand and clay with pH(H2O) 7.7 in the surface layer and 8.0 in deeper layers. The texture varies between clay and loam.

**Leaf water status**

Leaf (xylem) water potential (Ψ) was measured with a pressure chamber on two or three leaves per sampled tree, harvested between 1130 and 1400 hours. The sample leaves were enclosed in plastic sheaths immediately before cutting (Turner, 1981).

**Gas exchange**

Gas exchange measurements were made using a portable closed-loop photosynthesis system (Li 6200, Li-Cor, Inc, Lincoln, NE, USA) with a 1/4 L leaf cuvette (Li-6200-13). The leaf was enclosed in the cuvette for 12–45 s with each measurement of gas exchange. Photosynthetically active radiation (PAR), air and leaf temperature, and relative air humidity were also recorded. Net CO₂ assimilation rates and stomatal conductance (gₛ) were estimated on a project area basis. Gas exchange measurements were made on two mid-canopy, south-facing branches on each of the nine selected trees per examined plot. The same branches were used throughout the growing season. Measurements were taken in three different positions on each selected branch on one or two fully expanded leaves from the upper canopy. Days with no clouds occurred; consequently, there were no values of PAR below 700 μmol m⁻² s⁻¹. Measurements were made at seven different times during the growing period, which started in May and ended in November 1993.

**Data analysis**

Analysis of variance and the Duncan test were used. Average standard error was calculated from the residual mean square from the analysis of variance. The relationship between the assimilation rate (A) and stomatal conductance (gₛ) was also subjected to regression analysis. Mean values per selected tree were used. Differences between slopes of regression lines were tested according to Yates (1982).

**RESULTS AND DISCUSSION**

**Weather conditions during the measured period**

Seasonal changes in daily air temperature (mean, minimum and maximum) are shown in figure 1a. Consistently high temperatures were recorded in July and August. Similar to temperature, relative humidity fluctuated during the experimental period; however, the highest values were noted in April and November (fig 1b). Rainfall occurred until mid-June, after which there was almost no rain until the end of October; during this period, soil moisture declined.

The weather conditions during the study period differed from the long-term average

<table>
<thead>
<tr>
<th></th>
<th>May</th>
<th>June</th>
<th>July</th>
<th>Aug</th>
<th>Sept</th>
<th>Oct</th>
<th>Nov</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>for last 30 years</td>
<td>40</td>
<td>37</td>
<td>30</td>
<td>22</td>
<td>21</td>
<td>38</td>
<td>64</td>
<td>252</td>
</tr>
<tr>
<td>for 1993</td>
<td>84</td>
<td>28</td>
<td>4</td>
<td>5</td>
<td>4</td>
<td>7</td>
<td>31</td>
<td>163</td>
</tr>
</tbody>
</table>
Except in May when rainfall was high, the other months were much drier than the average. The total rainfall between 1 July and 26 October 1993 was 13 mm while the normal rainfall for this period is 111 mm.

**Plant water status**

Figure 2a shows the seasonal progression of midday water potential (Ψ) of the five study species. There were no significant differences in Ψ between the species during...
the measured period. Lowest values of Ψ were consistently recorded in Q pedunculiflora. Values of Ψ at the beginning and end of the study period were high (between -0.5 and -1.0 MPa) and these high values coincided with relatively high soil moisture. Values of Ψ declined rapidly from early June and reached values less than -4 MPa in mid-September. The minimum values of Ψ that appear in the five study species seem to be comparable to those of other Quercus sp growing under water stress. Values of -3.5, -2.8 and -3.4 MPa, respectively, were recorded for Q suber, Q coccifera and Q petraea (Hinckley et al, 1983; Tenhunen et al, 1984; Rhizopoulou and Mitrakos, 1990; Cochard et al, 1992). The Ψ values such as those reported here are easily found also in the literature for other trees of the Mediterranean ecosystem (Nunes et al, 1992). The capacity of many species to develop very low leaf water potential is well recognized (Sobrado, 1986) and all the studied oaks belong to these species.

**Phenological data**

According to table III, new leaves appeared approximately on 11 April. The leaves com-

**Table III.** Leaf area/leaf (cm²).

<table>
<thead>
<tr>
<th></th>
<th>11 Apr</th>
<th>27 Apr</th>
<th>6 May</th>
<th>27 May</th>
<th>16 June</th>
<th>22 June</th>
<th>15 July</th>
</tr>
</thead>
<tbody>
<tr>
<td>Q ilex</td>
<td>4.34</td>
<td>4.55</td>
<td>4.57</td>
<td>4.85</td>
<td>4.8</td>
<td>4.87</td>
<td>4.9</td>
</tr>
<tr>
<td>Q macrolepis</td>
<td>4.57</td>
<td>14.27</td>
<td>15.24</td>
<td>17.77</td>
<td>17.83</td>
<td>17.91</td>
<td>17.95</td>
</tr>
<tr>
<td>Q pendunculiflora</td>
<td>8.3</td>
<td>22.74</td>
<td>29.09</td>
<td>33.89</td>
<td>35.56</td>
<td>37.14</td>
<td>35.34</td>
</tr>
<tr>
<td>Q pubescens</td>
<td>1.09</td>
<td>15.93</td>
<td>11.54</td>
<td>18.82</td>
<td>19.38</td>
<td>21.33</td>
<td>22.05</td>
</tr>
<tr>
<td>Q trojana</td>
<td>1.74</td>
<td>8.78</td>
<td>10.1</td>
<td>10.73</td>
<td>11.84</td>
<td>11.84</td>
<td>11.95</td>
</tr>
<tr>
<td>SEM</td>
<td>0.41</td>
<td>0.91</td>
<td>0.73</td>
<td>0.75</td>
<td>0.8</td>
<td>0.79</td>
<td>0.76</td>
</tr>
</tbody>
</table>
pleted development around 22 June. On 7 May, the leaves were 88, 79, 51 and 88% of the full expanded size for *Q. macrolepis*, *Q. pedunculiflora*, *Q. pubescens* and *Q. trojana*, respectively. All species develop early and quickly the final leaf area.

**Seasonal trends in assimilation rate**

The seasonal pattern of net assimilation (*A*) was similar in all study species (fig 3a). During May under high soil moisture conditions, the assimilation rates at midday were high-

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**Fig 3.** Seasonal variation in assimilation rate (*A*) (a) and in stomatal conductance (*gₛ*) (b) of five oak species. Vertical bars indicate ± SEM. Photosynthetic active radiation ranged between 700 and 1 400 μmol m⁻² s⁻¹, leaf temperature 26 to 43 a and relative humidity 30 to 60%.
est in all species and particularly for *Q. macrolepis*. As the soil dried, the assimilation rate decreased in all species. *Q. macrolepis* had the highest assimilation rate and *Q. trojana* the lowest. By 9 August, the lowest A values were either reached or approached. This was a month before the lowest Ψ values were observed. On 9 August, *Q. ilex* had the highest A values and *Q. trojana* the lowest.

Photosynthetic rates recovered in all species by early November after the drought had ended. *Q. ilex*, *Q. pedunculiflora* and *Q. pubescens* had the highest values and *Q. trojana* the lowest. In general, the highest values of A were observed during early November. Leaves were fully mature and the microclimate within the cuvette was less stressful in November versus early June (data not shown). As noted by Dougherty and Hinckley (1981), the maintenance of the high photosynthetic potential for most of an oak leaf's life is important. Consequently, the ability of oak species to keep a high photosynthetic rate in November is advantageous for tree growth.

All study species developed rapid high photosynthetic rates. On 7 May, the leaves were not fully enlarged, the assimilation rates of which were high. Others have noted that A in deciduous leaves approaches maximum values before leaves are fully expanded (Dougherty et al., 1979). The early development of photosynthetic capacity is especially advantageous for tree growth in a Mediterranean climate where the drought starts early. It was reported for *Robinia pseudocacia* that the maximum photosynthetic rate was achieved 20–39 days after leaf emergence (Medrahtu and Hanover, 1991). Early development of high photosynthetic rate was reported for conifers such as *Pinus taeda* (Radoglou and Teskey, 1993). This behavior also characterizes fast growing species and species growing in warm climates.

The recorded values were found to be in the range reported for oak species (Tenhunen et al., 1987a; Ceulemans and Saugier, 1991). The potential rates of net CO₂ assimilation of oak leaves were probably much higher than those reported here. Such values may not be reached under all conditions. High photosynthetic rates for deciduous and evergreen sclerophyllous oak species were also reported (Dreyer et al., 1992; Epron and Dreyer, 1993). It is well known that drought does not only decrease A and gs but also changes the diurnal pattern of gas exchange (Tenhunen et al., 1987b). Higher rates of assimilation than those reported here may therefore be reached, particularly in the morning.

**Seasonal trends in stomatal conductance**

The seasonal variation of stomatal conductance was similar for all study species (fig 3b). There were no significant differences in gs during the growing season between study species, except in November when *Q. trojana* had high values. Maximum leaf conductance was reached in May and November under high air humidity and soil moisture conditions. Throughout the season, low values of gs appeared. Values of recorded gs were similar to those reported for leaves from other Quercus species (Ni and Pallardy, 1991) and for *Ceratonia siliqua* in the Mediterranean area (Nunes et al., 1992). This has been observed for five different oak species of the robur section (*Q. robur*, *Q. petraea*, *Q. pubescens*, *Q. pyrenaica* and *Q. canariensis*), which submitted to drought in parallel; the decline in gs was almost the same magnitude and precocity (Dreyer et al., 1993).

**Assimilation in relation to stomatal conductance**

The ratio of CO₂ assimilation rate to stomatal conductance (A/gs) is a major determi-
nant of instantaneous water use efficiency of plants. The $A/g_s$ ratio has been shown to be under close physiological regulation and found to differ considerably among forest tree genotypes (Farquhar et al., 1989; Guehl et al., 1991). These differences may be associated with differential drought adaptation and consequently may have great ecological significance (Schulze, 1986).

Linear regressions applied to all the values reported, means for each selected tree for all study species and measured days. The relationship between $A$ rates and $g_s$ from June to November for $Q$ macrolepis

![Graph](image_url)

**Fig 4.** Relationship between stomatal conductance ($g_s$) and net photosynthesis ($A$) of $Q$ macrolepis (a) and $Q$ pedunculiflora (b) throughout the growing season between 1000 and 1300 hours under steady-state condition, with irradiance higher than 700 $\mu$mol m$^{-2}$ s$^{-1}$. Data points represent different trees.
and *Q pedunculiflora* appears in figure 4a, b. Table IV shows the slopes of linear regressions of the relationship between $A$ and $g_s$. The initial slope was different between species and during the growing season. Water use efficiency (WUE) increased as water stress was induced in the trees. *Q macrolepis* experienced the least amount of changes of the slope. Trees of *Q macrolepis* kept their stomata significantly open even at low soil water availability, low air humidity and low WUE. In other cases, the slope of *Q pedunculiflora* and *Q ilex* greatly increased and presented higher WUE. In all study species, the water use efficiency was not maintained constant during the growing period and the $g_s$ was more affected by environmental changes than $A$.

The rating according to the maximum value of the slope was *Q pedunculiflora* < *Q ilex* < *Q trojana* < *Q pubescens* < *Q macrolepis*. The results were consistent with those reported for other *Quercus* species (Delucia and Heckathorn, 1989; Ni and Pallardy, 1991); for *Artemisia tridentata*, a desert shrub; and for *Pinus ponderosa*, a more mesic species. High WUE and an inconstant state were also observed in xeric plants in other studies (Levitt, 1980; Schulze and Hall 1982; Field et al, 1983).

**Table IV. Sensitivity of $A$ to $g_s$ (µmol m$^{-2}$ s$^{-1}$)/(mmol m$^{-2}$ s$^{-1}$).**

<table>
<thead>
<tr>
<th></th>
<th>14 June</th>
<th>15 July</th>
<th>6 Aug</th>
<th>1 Sept</th>
<th>16 Sept</th>
<th>14 Oct</th>
<th>9 Nov</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Q ilex</em></td>
<td>68.653</td>
<td>37.065</td>
<td>31.772</td>
<td>30.652</td>
<td>106.93</td>
<td>35.69</td>
<td>21.426</td>
</tr>
<tr>
<td></td>
<td>(0.97)</td>
<td>(0.93)</td>
<td>(0.94)</td>
<td>(0.93)</td>
<td>(0.87)</td>
<td>(0.92)</td>
<td>(0.89)</td>
</tr>
<tr>
<td><em>Q macrolepis</em></td>
<td>69.663</td>
<td>39.433</td>
<td>27.787</td>
<td>31.149</td>
<td>75.952</td>
<td>49.576</td>
<td>34.783</td>
</tr>
<tr>
<td></td>
<td>(0.98)</td>
<td>(0.97)</td>
<td>(0.79)</td>
<td>(0.97)</td>
<td>(0.97)</td>
<td>(0.94)</td>
<td>(0.91)</td>
</tr>
<tr>
<td><em>Q pendunculiflora</em></td>
<td>118.648</td>
<td>52.096</td>
<td>56.937</td>
<td>74.978</td>
<td>70.568</td>
<td>34.699</td>
<td>21.741</td>
</tr>
<tr>
<td></td>
<td>(0.92)</td>
<td>(0.84)</td>
<td>(0.91)</td>
<td>(0.85)</td>
<td>(0.88)</td>
<td>(0.80)</td>
<td>(0.73)</td>
</tr>
<tr>
<td><em>Q pubescens</em></td>
<td>100.53</td>
<td>64.817</td>
<td>81.55</td>
<td>31.673</td>
<td>92.306</td>
<td>52.545</td>
<td>30.86</td>
</tr>
<tr>
<td></td>
<td>(0.98)</td>
<td>(0.91)</td>
<td>(0.84)</td>
<td>(0.83)</td>
<td>(0.87)</td>
<td>(0.95)</td>
<td>(0.91)</td>
</tr>
<tr>
<td><em>Q trojana</em></td>
<td>65.872</td>
<td>32.808</td>
<td>60.14</td>
<td>34.049</td>
<td>99.89</td>
<td>30.173</td>
<td>15.974</td>
</tr>
<tr>
<td></td>
<td>(0.92)</td>
<td>(0.84)</td>
<td>(0.91)</td>
<td>(0.85)</td>
<td>(0.88)</td>
<td>(0.80)</td>
<td>(0.73)</td>
</tr>
<tr>
<td>SEM</td>
<td>5.9</td>
<td>5.1</td>
<td>4.3</td>
<td>4.1</td>
<td>7.3</td>
<td>5.2</td>
<td>3.6</td>
</tr>
</tbody>
</table>

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