EFFECTS OF MODERATE WATER STRESS AND SHADING ON SURVIVAL, GROWTH AND RESOURCE ALLOCATION OF TWO CORK OAK (QUERCUS SUBER L.) PROVENANCES

Taher MECHEGUI1 & Marta PARDO2

1Faculté des Sciences de Bizerte (FSB), Jarzouna – 7021. Tunisie. E-mail: mecherguit@yahoo.fr (corresponding author)
2Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (INIA). Centro de Investigacion Forestal.
Ctra. de La Coruña, Km. 7.5. 28040 Madrid. Spain. E-mail: pardos@inia.es

SUMMARY.— Sixty-four plants of Cork oak (Quercus suber L.) originating from Spain and Tunisia provenances were grown under a combination of two light levels (15 % (moderate shade) versus 5 % (deep shade) of full-light) and two water regimes (well-watered versus moderate water stress) in a nursery in Spain. Ten response variables including seedling survival, height, diameter, height-to-diameter ratio, above- and below-ground biomass, total biomass, root-to-shoot ratio, number and length of growth unit were measured for each provenance. In average, seedling survival was 89 % and was independent of the studied factors (provenance, light, water regime). Seedling height was similar in both provenances, while diameter was significantly larger in the Spanish provenance. Water stress adversely affected the balance between height and diameter for the Spanish provenance, but not for the Tunisian provenance, while light, and independently of seedlings’ provenance, affected 80 % (8/10) of traits studied. Thus, the Tunisian provenance seemed to be more tolerant to water stress while none of both provenances seemed to be more tolerant to shade. However, when considering both factors the Spanish provenance showed a better seedlings’ acclimation to water stress under deep shade and may constitute accordingly a better material for afforestation as in Mediterranean conditions, as our results show, light and water stress may act in a coordinate manner. This variability would be mainly genetically controlled, as both provenances were cultivated under the same environmental conditions. Our results may be helpful in regeneration, cultivation and afforestation of cork oak.

Light (Castell et al., 1994; Tognetti et al., 1994; Valladares & Pearcy, 1997) and soil water moisture (Méthy et al., 1996; Nardini et al., 1999) may be considered among the most important environmental factors constraining primary productivity of Mediterranean species and, thus, that may contribute significantly to the future stand composition. Like most Mediterranean species, cork oak, light-demanding species (Hasnaoui, 1992), that grows at altitudes less than 700 m
(Schoenenberger & Salsac, 1970), under 650 to 980 mm of precipitation and on shallow soils (Perez-Ramos et al., 2010), experiences an important drought during the summer season. Furthermore, it is known that light and drought stress can co-occur in Mediterranean conditions; therefore, their interaction must be considered (Valladares & Pearcy, 1997). Evaluating cork oak seedlings’ responses under the combination of light and water availability is of major interest for designing the optimal regeneration strategies in different sites. The combination of these two factors may help to explain species niche differentiation (Walters & Reich, 1997; Kollmann & Grubb, 1999; Sack & Grubb, 2002), predict seedling performance at given microsites (Holmgren et al., 1997; Sack & Grubb, 2002) and define patterns of recruitment (Callaway, 1992; Valladares et al., 2002). The interaction between light and water stress may be a compromise between contradictory patterns of morphological and physiological response of seedlings (Kubiske et al., 1996; Pardos et al., 2005). Thus, it can be hypothesized that the combined effects of irradiance and water is characterized by a trade-off between drought tolerance and shade tolerance (the trade-off hypothesis) (Niinemets et al., 2004; Smith & Huston, 1989; Vance & Zaerr, 1991). According to the trade-off hypothesis, drought should have a stronger impact in shade than in high light, because shaded plants invest relatively less in roots, and therefore less access to soil water. However, there is strong evidence that under shade conditions drought has a weaker impact on plants because of improved microclimatic conditions, i.e. the facilitation hypothesis (Holmgren et al., 1997, 2000). All plants require light, water and nutrients for their survival, growth and reproduction. Accordingly, reduced availability in any one of these resources may lead to reduced survival and growth (resource limitation hypothesis, Quero et al., 2008).

Past studies investigating the growth response of oak seedlings to either water stress or shading were often limited to height, diameter and biomass measurements (Rao & Singh, 1986; Messina & Duncan, 1993; Wang & Bauerle, 2006; Březina & Dobrovolný, 2011). However, like other oak species (Champagnat et al., 1986; Harmer, 1990), cork oak has a typically rhythmic pattern of height growth (Mechergui et al., 2013; Mechergui & Pardos, 2017). The study of the periodic height growth pattern of oak species allows the main stem to be divided on other morphological entities called the growth unit (GU) and gives useful information on this growth response characterization. In addition, studies involving the effects of water stress and/or shading were limited to cork oak seedlings of a local provenance. The objective of this work was to examine the effects of water stress and/or shading on early seedling performance of two provenances of containerized cork oak seedlings, originating from Spain and Tunisia. The specific objectives were: 1) to assess survival and seedling growth under individual and combined effects of water stress and shading, and 2) to compare the degree of tolerance of both provenances to water and light stresses (water deficit & low light availability). Three hypotheses were tested: 1) drought and shade would reduce seedling growth and survival as a result of a lower resource availability (the resource limitation hypothesis), 2) drought survival may be higher under shade than in high light (the facilitation hypothesis) and 3) drought may have a stronger impact in shade than in high light (the trade-off hypothesis).

MATERIALS AND METHODS

PLANT MATERIAL AND TREATMENTS

A factorial experiment with three factors (provenance, light and water) of two levels each (2 provenances (Spanish & Tunisian), 2 light intensities (S & 15 % of full-light), and 2 watering regimes (well-watered & moderate water stress)) was designed to test for main effects and interactions on the different studied traits.

Ripe acorns were collected from Cork oak (Quercus suber L.) trees at Oued Elballout (36°44'57.53"N, 8°54'33.57"E, altitude 200 m a.s.l.) for the Tunisian provenance, and from trees at Sierra del Aljibe (36°20'59"N, 5°35'50"W, altitude 769 m a.s.l.) for the Spanish provenance. The main ecological attributes for each of the two provenances are shown in table 1.
The experiment was conducted in a greenhouse at INIA experimental centre (Madrid, Spain: 40°27′20″N, 3°44′58″W, 595 m a.s.l.). Acorns were kept in moist plastic bags at 4°C until germination in December 2009. One germinated acorn was planted in each 3-L pot (truncated square pyramid containers, 25 cm height, 169 cm² and 64 cm³, upper and lower cross-sectional areas, respectively), filled with a mixture of moss peat and fine sand (3:1, v:v). Thirty-two acorns by provenance were sown. Pots were kept well watered three days per week (15 min) inside a greenhouse until mid-March 2010. On 15 March 2010, seedlings from each provenance were randomly divided in two groups according to the two light environments, one of which was grown under metal frames (50 × 80 × 150 cm) covered with layers of neutral shade white cloth (Polysack Plastic Industries Ltd., Israel) to produce the two light environments. The design of the frame was optimized to avoid any effect on the temperature of the air in contact with the plants. The average photosynthetic photon flux density (PFD) inside and outside (greenhouse) of the metal frames was 5 (90 µmol·m⁻²·s⁻¹) and 15 % (250 µmol·m⁻²·s⁻¹) of full sunlight, respectively. They correspond to deep and moderate shades (Puértolas et al., 2008), respectively, which allows to study well the behaviour of the species under low irradiances (because the studied species is a light-demanding species).

Seedlings growing under each light treatment were randomly divided in two groups, for the water treatment assignments, one group was watered to field capacity (W+), while the other group was watered at 60 % of field capacity (W−). The choice of the application of a moderate water stress is justified by the fact that under this water stress this type of Quercus is working, which is not the case for instance under a severe water stress where this plant is not working at all (Jiménez, personal communication). The exact amount of water supplied in the W− treatment was a function of the volume of water lost under the low photosynthetic photon flux density (PFD), which had the minimum evaporative demands. By this means, a slow rate of imposition of the water stress conditions was assured. Eight plants from each provenance were grown under each combination of water × light treatment, which makes a total of 64 plants (8 plants × 2 provenances × 2 light levels × 2 water regimes). The experiment was conducted inside a greenhouse to avoid the entry of rain.

MEASUREMENTS AND ANALYSES

Ten response variables were studied, for each provenance, on each surviving seedling at the end of the experiment (December 2010). Studied parameters at the whole-plant were basal diameter, height growth, height-to-diameter ratio, above- and below-ground biomass, total biomass, shoot-to-root ratio and survival. The weight of the above- and below-ground biomass was measured after drying at 60 °C for one week.

Cork oak is a species that shows a rhythmic growth. Each year, growth occurs in one or more bouts of elongation during which growth units (GU) are formed (see Mechergui et al., 2013). Thus, the measured parameters at the stem level, at the end of the growing season, were the number and length of the GU established by the main stem.

An analysis of variance (ANOVA), using the PROC GLM procedure, was conducted to compare height and diameter growths, height-to-diameter ratio, GU length, biomass, and shoot-to-root ratio (quantitative variables) among treatments. When the ANOVA analysis found significant differences between treatments, Tukey’s test was conducted to detect differences between individual treatment level means. The remainder of variables, survival and number of GU established on the main stem (qualitative variables), were expressed in percentage (%). A comparison of mean percentages was then performed using a Chi² test with the PROC FREQ procedure. All statistical analyses were performed, at a 95 % confidence level, using the SAS software package (SAS Institute Inc., Cary, NC).

RESULTS

SURVIVAL

Survival at the end of the growing season was 90.6 % in the Spanish provenance and 87.5 % in the Tunisian provenance. There were no significant differences between treatments (Tab. II).
TABLE II
Analysis for survival rate
Factors are provenance, light, water, and their interaction. $P_{\chi^2}$ = value of chi-square ($\chi^2$) test

<table>
<thead>
<tr>
<th>Factors</th>
<th>$P_{\chi^2}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Light</td>
<td>0.2435</td>
</tr>
<tr>
<td>Water</td>
<td>0.6975</td>
</tr>
<tr>
<td>Provenance</td>
<td>0.6975</td>
</tr>
<tr>
<td>Light $\times$ water</td>
<td>0.9257</td>
</tr>
<tr>
<td>Provenance $\times$ light</td>
<td>0.9257</td>
</tr>
<tr>
<td>Provenance $\times$ water</td>
<td>0.9282</td>
</tr>
<tr>
<td>Light $\times$ water (for the Spanish provenance)</td>
<td>0.8998</td>
</tr>
<tr>
<td>Light $\times$ water (for the Tunisian provenance)</td>
<td>0.7961</td>
</tr>
</tbody>
</table>

GROWTH

Height growth and basal diameter

Height growth was significantly influenced by the light intensity (Tab. III), with an average height greater under L- (5 % of full-light) than under L+ (15 % of full-light) by 6.2 cm (17 ± 0.80 cm vs. 23.2 ± 0.82 cm (± SE)). A significant three-way provenance $\times$ light intensity $\times$ water regime interaction, which reveals that the effect of light intensity $\times$ water regime interaction varied between both provenances, was also found.

TABLE III
Analysis of variance for height, diameter and height-to-diameter ratio ($H/D$ ratio)
Factors are provenance, light, water, and their interaction

<table>
<thead>
<tr>
<th>Factors</th>
<th>Height ($Pr &gt; F$)</th>
<th>Diameter ($Pr &gt; F$)</th>
<th>$H/D$ ratio ($Pr &gt; F$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Light</td>
<td>&lt;0.0001*</td>
<td>&lt;0.0001*</td>
<td>&lt;0.0001*</td>
</tr>
<tr>
<td>Water</td>
<td>0.8123</td>
<td>0.1878</td>
<td>0.2566</td>
</tr>
<tr>
<td>Provenance</td>
<td>0.0519</td>
<td>0.0003*</td>
<td>0.9184</td>
</tr>
<tr>
<td>Light $\times$ water</td>
<td>0.6722</td>
<td>0.2615</td>
<td>0.4417</td>
</tr>
<tr>
<td>Provenance $\times$ light</td>
<td>0.4881</td>
<td>0.8050</td>
<td>0.9174</td>
</tr>
<tr>
<td>Provenance $\times$ water</td>
<td>0.1034</td>
<td>0.5232</td>
<td>0.0003*</td>
</tr>
<tr>
<td>Provenance $\times$ light $\times$ water</td>
<td>0.0054*</td>
<td>0.2419</td>
<td>&lt;0.0001*</td>
</tr>
</tbody>
</table>

Asterisk (*) shows significant differences between treatments at $P \leq 0.05$

![Figure 1](image)

Figure 1.— Height growth according to light intensity (L+, moderate shade (15 % of full-light); L-, deep shade (5 % of full-light)) and water regime (W+, well-watered seedlings; W-, moderate water-stressed seedlings) in the Spanish (A) and Tunisian (B) provenance. Means ± standard error (SE). Means marked with different letters within each light treatment are significantly different at $P \leq 0.05$ level.
For the Spanish provenance, average height growth was similar for both water regimes under both light intensities (Fig. 1). By contrast, two cases were highlighted for the Tunisian provenance: (1) under L+, average height growth was similar for both well-watered and water-stressed seedlings, while (2) under L-, this height was significantly greater for well-watered seedlings.

Significant effects on basal diameter were found for the provenance and light intensity (Tab. III). Average basal diameter was greater for the Spanish than for the Tunisian provenance by about 14% (4.1 ± 0.091 mm vs. 3.6 ± 0.092 mm). Contrary to height growth, average basal diameter was greater under L+ (4.1 ± 0.090 mm) than under L- (3.5 ± 0.092 mm).

**Height-to-diameter (H/D) ratio**

The H/D ratio was significantly different between both light intensities (Tab. III), with a higher value, on average, under L- than under L+ (41.4 ± 1.6 vs. 64.2 ± 1.7). Other significant factors included the two-way provenance × water regime interaction, and the three-way light intensity × water regime × provenance interaction (Tab. III) indicating, respectively, that both effects of water regime and light intensity × water regime interaction on H/D were dependent on provenance.

For the Tunisian provenance H/D ratio was similar under both water regimes, while for the Spanish provenance this ratio was significantly higher under water stress than under no limiting water conditions (Fig. 2). On the other hand, none of both provenances showed a significant difference in H/D ratio between both water regimes, when grown under L+, while each of both provenances showed a significant difference in H/D ratio between both water regimes when grown under L- (Fig. 2). However, while the Spanish provenance showed a significantly higher H/D under water stress, the Tunisian provenance showed a significantly higher H/D under no limiting water conditions.

![Figure 2](image_url)

Figure 2.— Height-to-diameter ratio (H/D ratio) according to water regime (W+, well-watered seedlings; W–, moderate water-stressed seedlings) (A, B), and water regime and light intensity (L+, moderate shade (15 % of full-light); L–, deep shade (5 % of full-light)) (C, D) in the Spanish (left) and Tunisian (right) provenance. Means ± SE. Means marked with different letters are significantly different at *P* ≤ 0.05 level. Letters show in (C, D) significant differences within each light treatment.
**Number and length of growth unit (GU)**

The decomposition of the main stem in GU showed that both provenances established during all the growing season 1 to 2 GU. The number of established GU was not dependent neither on the seedlings’ provenance ($P = 0.7015$) nor on water regime ($P = 0.6711$), while a significant effect of light intensity was found ($P = 0.0005$). There was no significant difference in the percentage of plants having established 1 and 2 GU under L+ (Fig. 3).

Figure 3.— Frequency (%) of seedlings having established 1 (1 GU) and 2 (2 GU) growth unit (GU) (A) and GU length of the first (GU1) and second (GU2) GU (B, C), according to light intensity (L+, moderate shade (15 % of full-light); L-, deep shade (5 % of full-light)). Means ± SE, and seedlings percentage ± likelihood confidence limits. Means marked with different letters are significantly different at $P \leq 0.05$ level. Letters show in (A) significant differences within each light treatment.

**TABLE IV**

*Analysis of variance for length of growth unit (GU). GU1 and GU2: first and second GU, respectively. Factors are light, water, provenance and their interaction.*

<table>
<thead>
<tr>
<th>Factors</th>
<th>GU1</th>
<th>GU2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Light</td>
<td>&lt;0.0001*</td>
<td>0.0258</td>
</tr>
<tr>
<td>Water</td>
<td>0.9429</td>
<td>0.4188</td>
</tr>
<tr>
<td>Provenance</td>
<td>0.0751</td>
<td>0.1140</td>
</tr>
<tr>
<td>Light $\times$ water</td>
<td>0.8100</td>
<td>0.4674</td>
</tr>
<tr>
<td>Provenance $\times$ light</td>
<td>0.6702</td>
<td>0.5945</td>
</tr>
<tr>
<td>Provenance $\times$ water</td>
<td>0.0472</td>
<td>0.5308</td>
</tr>
<tr>
<td>Provenance $\times$ light $\times$ water</td>
<td>0.1346</td>
<td>0.5988</td>
</tr>
</tbody>
</table>

Asterisk (*) shows significant differences between treatments at $P \leq 0.05$

By contrast, there was a significant difference under L-, where the percentage of plants having established 1 GU was significantly higher than that of plants having established 2 GU.

As shown in table IV, only the effect of light intensity was significant for length of the first (GU1) and the second (GU2) GU. Both GU were, on average, longer under L- than under L+ (Fig. 3).
Biomass growth and shoot-to-root ratio

Both underground biomass and total biomass were significantly affected by light intensity and water regime, while no significant effect was found for the above-ground biomass (Tab. V). The shoot-to-root ratio was significantly affected only by light intensity (Tab. V).

### TABLE V

Analysis of variance for below-ground (BGB) and above-ground (AGB) biomass, total biomass (TB) and shoot-to-root ratio (SRR). Factors are provenance, light, water, and their interaction

<table>
<thead>
<tr>
<th>Factors</th>
<th>BGB</th>
<th>AGB</th>
<th>TB</th>
<th>SRR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Light</td>
<td>&lt;0.0001*</td>
<td>0.7576</td>
<td>&lt;0.0001*</td>
<td>&lt;0.0001*</td>
</tr>
<tr>
<td>Water</td>
<td>0.0105*</td>
<td>0.1298</td>
<td>0.0094*</td>
<td>0.6186</td>
</tr>
<tr>
<td>Provenance</td>
<td>0.1938</td>
<td>0.1967</td>
<td>0.2796</td>
<td>0.1685</td>
</tr>
<tr>
<td>Light × water</td>
<td>0.7805</td>
<td>0.4380</td>
<td>0.7229</td>
<td>0.7486</td>
</tr>
<tr>
<td>Provenance × light</td>
<td>0.8782</td>
<td>0.9164</td>
<td>0.8921</td>
<td>0.7160</td>
</tr>
<tr>
<td>Provenance × water</td>
<td>0.8504</td>
<td>0.4652</td>
<td>0.9265</td>
<td>0.9038</td>
</tr>
<tr>
<td>Provenance × light × water</td>
<td>0.4121</td>
<td>0.6857</td>
<td>0.4099</td>
<td>0.4668</td>
</tr>
</tbody>
</table>

Asterisk (*) shows significant differences between treatments at $P \leq 0.05$

Figure 4.— Underground biomass (A, B) and total biomass (C, D) according to water regime (W+, well-watered seedlings; W–, moderate water-stressed seedlings) (left) and light intensity (L+, moderate shade (15 % of full-light); L–, deep shade (5 % of full-light)) (right). Means ± SE. Means marked with different letters are significantly different at $P \leq 0.05$ level.

Both underground biomass and total biomass were, on average, greater for well-watered than for water-stressed seedlings (Fig. 4). On the other hand, they were greater under L+ than under L– (Fig.4). For the shoot-to-root ratio, this ratio was, on average, higher under L- than under L+ (0.085 ± 0.0121 vs. 0.159 ± 0.0123).

**DISCUSSION**

**SURVIVAL**

Our results did not show differences in survival rate neither between light nor water treatments, which contrasts with our hypotheses that drought and shade would reduce seedling survival because of a lower resource availability (the resource limitation hypothesis) and that drought survival may be higher under shade (L-) than under high light (L+) because of improved microclimatic conditions (the facilitation hypothesis), and with results of Amissah et al. (2015) where both hypotheses were proved for other forest species. This suggests that water stress and shade applied in this study were not at levels that could trigger differences in seedling survival.
between treatments. This trend is true for both provenances, as they did not show significant differences in survival rate neither for light levels and water regimes nor for their interaction.

**GROWTH**

**Height growth and basal diameter**

The greatest height which occurred under L- (deep shade), reflects investment in the production of photosynthetic structures to overcome light limitation (Ortega *et al.*, 2006), especially since cork oak is a light-demanding species (see introduction). In the Tunisian provenance water stressed seedlings showed a reduction in height growth under L-, comparatively to well-watered seedlings, which was not the case under L+ (moderate shade) where seedlings were indifferent to water stress (Fig. 1B). These results are seemingly in line with the *trade-off hypothesis*, which states that drought has a stronger impact in deep shade than in high irradiances (Smith & Huston, 1989; Holmgren, 2000; Sack & Grubb, 2002) because of reduced root investment, thus making shaded plants more sensitive to drought (Smith & Huston, 1989). They clearly indicate, on the other hand, that deep shade decreased seedlings’ acclimation to water stress. However, like most Mediterranean species cork oak experiences an important drought during the summer season (Jiménez *et al.*, 2009), which may prevent the species (which is already characterized by a slow height growth) to achieve maximum growth when grown in shaded habitats. Contrary to the Tunisian provenance, the Spanish provenance did not lose seedlings’ acclimation to water stress under L- (see fig. 1A). This suggests that water stress was more important than the cost imposed by dearth of light, but also that the Spanish provenance acclimates better to water stress under shade conditions compared to the Tunisian provenance. In a general way, these differences in response to growth would be mainly genetically controlled, as cork oak provenances were cultivated under the same environmental conditions. Gandour *et al.* (2007) reported from a study of twenty-six provenances of cork oak originating from Portugal, Spain, Italy, Morocco, Algeria, and Tunisia, that the Spanish provenance had a thick diameter. In our growth conditions, we noticed also that diameter growth was greater in the Spanish than in the Tunisian provenance. Apart from the provenance effect, seedlings exhibited larger diameter under L+ than under L- which is in accordance with the results of Daas-Ghrib (2009) who observed under different light regimes that seedlings diameter increased with increasing light intensity.

**Height-to-diameter ratio**

Increased height-to-diameter ratio under L- clearly indicates that seedlings invested more in height growth than in stem diameter (Mechergui & Pardos, 2017), which can be explained as a strategy for maximizing light interception. Indeed, it was observed under various light intensities that this ratio decreased with increasing light intensity (Daas-Ghrib, 2009). There is no available information in the literature about the effect of water stress on height-to-diameter ratio, and consequently on the balance between height and diameter growth, in broad-leaved species including cork oak species. However, in a study conducted by Espinoza *et al.* (2013) on a coniferous species (*Pinus radiata* D. Don) these authors observed that water stress significantly increased height-to-diameter ratio comparatively to well-watered treatment. The same response was observed in our study where water stress effect, highlighted for the Spanish, resulted also in a significant increase in a height-to-diameter ratio compared to well-watered seedlings. When both factors operate simultaneously, water stress in combination with exposure to low light availability (L-) affected balance between height and diameter in both provenances. However, while the Spanish provenance showed an increase in height-to-diameter ratio suggesting that seedlings put more resources towards height than towards diameter growth, the Tunisian provenance showed, in contrast, a decrease in this ratio suggesting that seedlings put more resources towards diameter.
than towards height growth. The reason for that is not quite clear, but may reflect a strong plasticity of the species.

**Number and length of GU**

At the end of the growing season, seedlings had one to two GU. They did not show, however, a clear trend to establish one or two GU, when grown under L+ (the difference was not significant). By contrast, they showed a higher trend to produce one GU than two GU when grown under L- (see fig. 3A). It has also been reported since long that under low light conditions oak seedlings generally produce only one GU in the course of the first year (Phares, 1971; Crow, 1988). On the other hand, although they exhibited a clear trend to produce one rather than two GU, L- seedlings were significantly higher than L+ seedlings. Accordingly, the greater height growth attributed to L- seedlings comes only from the increase of the length of the produced GU on the main stem.

**Growth biomass**

Although they had a greater height growth, L- seedlings did not show a difference in their above-ground biomass compared to L+ seedlings suggesting that this increase in height was not a result of an increase in dry matter production, but of reallocation of growth in favour of shoot elongation (Mechergui & Pardos, 2017; Famiani *et al.*, 2007). Root biomass of trees has been shown to be adversely affected by water regime (Fabião *et al.*, 1995) and light (Dias-Filho, 1995). This is in agreement with the results of our work, which show that root biomass decreased under both water stress and low light availability. Burger *et al.* (1997) reported that the reduction in root biomass could be the result of a reduced overall photosynthate pool (reflected by the reduction in total biomass production) and/or a repartition in photosynthate in favor of the aerial part of plant causing a reduction in the root-to-shoot ratio. In this study, the reduction in root biomass under low light availability is due to reduced overall photosynthate pool, as revealed by the reduction in total biomass, as well as to the unbalance in the distribution of photosynthate between the aerial and underground parts of plant, as revealed by the increase in shoot-to-root ratio. However, the reduction in root biomass under water stress is not due to an unbalance in the distribution of photosynthate between the aerial and underground parts of plant, since the shoot-to-root ratio was not affected, but rather to reduced overall photosynthate pool as revealed by the reduction in total biomass.

**CONCLUSION**

Our results suggest that both provenances may survive well under a water stress at a level such as applied in this study. The water stress (60 %) applied here (in this study) may be considerate as moderate. Hence, mortality of cork oak seedlings in the Mediterranean region which can reach up to 90 %, in open areas, due to summer drought (Hasnaoui, 1992) seems to be occurring under a water stress much more intense than that applied in this study. None of both provenances seemed to be more tolerant to shade, while the Tunisian provenance seemed to be more tolerant to water stress. However, when considering both factors water stress in combination with exposure to low light availability was found to affect 20 % of traits studied for the Tunisian provenance. By contrast only 10 % of traits studied were found to be affected for the Spanish provenance which seems to be, thus, more drought-tolerant under low light conditions and may constitute accordingly a better material for afforestation, since in Mediterranean conditions, as our results show, light and water stress may act in concert. Yet, both provenances showed a decrease in seedlings’ acclimation to water stress only when grown under low light availability. To avoid this scenario, especially since the Mediterranean region is characterized by reduced soil moisture
availability, cork oak plantations should be established under not very close overstory, in order to optimize light-water resource. At the level of aged populations, increased light availability, in order to favour natural regeneration of young plants, may be ensured through silvicultural treatments (i.e., thinning, canopy opening (canopy gaps), reduction of the undergrowth density). According to our study, moderate shade level (15 % of full sunlight) appears to be enough to favour cork oak regeneration in nursery culture, even under drought, but may be also in natural stands or in plantation since it minimizes water needs without impairing seedlings development (under this light intensity water stress had no effect on seedling growth).

ACKNOWLEDGEMENTS

This research received financial support from the Superior Education Ministry and Scientific Research from Tunisia. The authors would like to thank the Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (Madrid, Spain) for the assistance on this research. Special thanks are given to Enrique Garriga for helping in the setup of the experiment and to two anonymous referees for their useful comments.

REFERENCES


