Impact of moderate drought and shading on morphological traits of *Quercus suber* L. and *Quercus canariensis* Willd seedlings

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Abstract: *The main objective of this study was to investigate the effect of shading and water availability on tree seedling growth of cork oak (Quercus suber L.) and zeen oak (Quercus canariensis Willd). To reach this objective, two light intensities (moderate (L+) versus low (L-) intensity) and two water regimes (well-watered (W+) versus moderate drought (W-)) were applied. Cork oak seedlings growing under well-watered conditions were able to increase their height in response to low light intensity, while those growing under water deficit were not. By contrast, zeen oak's response to light was independent of water regime with greater height under L- than under L+. Diameter growth was lower under L- than under L+ for cork oak, and similar under both light intensities for zeen oak. Balance between height and diameter was adversely affected under L- for both oaks, while that between shoot and root biomass was adversely affected only for cork oak, compared to L+. The effect of water stress resulted in a reduction in diameter growth, root biomass, and total biomass and an increase in shoot-to-root ratio for zeen oak. Our results suggest that low water availability may be the bottleneck for recruitment of cork oak seedlings in shaded habitats.*
Keywords: *cork oak, drought, light, regeneration bottleneck, zeen oak*

I. Introduction

Light and water are the main factors that determine plants' growth and distribution [1]. Both factors may act in a non-coordinate manner rendering a segregation in species regeneration niches [2, 3]. Light is an energy source for plants. It acts at least on three processes: the photosynthesis of the assimilates by the leaves, the elongation of the stem (photomorphogenesis) [4] and the development of the root system which will be affected in the first place by a decrease on photosynthesis [5]. Certain plants are more or less demanding in light. The difference in light consumption between light-demanding species and shade-tolerant species is between 50 to 100 times [6]. A lack of light involves a reduction of stem diameter [7] and an increase in the shoot elongation [8], chlorophyll content [9], leaf area [8, 10, 11], surface mass [8], length of the petioles [10, 11] and internodes [10, 11]. Under low light, first-year oak seedlings usually produce only one growth unit [12, 13], which is determined by stored reserves in the acorns. Once the reserves are depleted, survival and growth of oak seedlings are dependent on photosynthates produced by new leaves [14]. Acclimation to different light environments occurs on the whole-plant scale as well as on the leaf scale [15]; leaf acclimation could be morphological, anatomical or physiological [16].

Water is everywhere the paramount factor (85 to 90%) of the total fresh weight of the plants. It conditions the forest production both for its qualitative (spatial distribution of the species) and quantitative effect on the growth [6]. The effects of water stress are numerous and vary according to the genotype, the developmental stage of the plant and the severity and the duration of the stress [17]. The water stress appears in two forms, the lack of water and its excess. In this study we were interested only in the lack of water. At the level of the tree, a water deficit can affect the components of its two parts, aerial and underground. Thus, water stress reduces the diameter and height growth, weakens the capacity of trees to withstand the other stresses of the environment, affects the allocation of the assimilates and influences other development processes, namely flowering, fructification and reproduction [17]. At the forest population level, water stress increases mortality and can result in the replacement of the existing species by more resistant ones. It also reduces the leaf area [17] which leads to a reduction of foliar transpiration, by increasing the resistance of stomata, but also to a reduction of the available assimilates [18] by reducing the photosynthetic activity. Zahner [19] reported also a high sensitivity of the shoot growth to a water restriction. In addition, the annual increment can be reduced if one of the growth units underwent a water deficit during its development [20]. A water restriction can be also responsible for the premature senescence of leaves and sometimes their fall [20]. Nevertheless, under difficult conditions, characterized mainly by a water deficit, this premature fall of leaves can constitute a strategy of resistance of plants to water stress enabling them to reduce the losses of water and to prolong their lifetime [21]. With regard to the underground part, a high degree of sensitivity was proven for oaks under a water restriction

[22, 23]. In an experiment with three oak species (*Quercus suber*, *Q. canariensis* and *Q. coccifera*), Ksontini [24] observed that water stress resulted in a reduction in root development.

For the experiment, we used saplings of two Mediterranean oak species, the semi-deciduous zeen oak (*Quercus canariensis* Willd.) and the evergreen sclerophyllous cork oak (*Quercus suber* L.). Zeen oak is a shade-tolerant species [25] that grows usually at moderate altitudes (700–1100 m) [26], under 1000 to 1150 mm of precipitation and on deep soils [27]. Cork oak grows at lower altitudes (< 700 m) [26], under 650 to 980 mm of precipitation and on shallow soils [25]. It is usually exposed to more severe drought during the summer [27], being a typical sclerophyllous species, with lower tolerance than zeen oak to shade [25]. In Tunisia, both cork oak and zeen oak are mainly located in the northwest region, the most humid area of the country, occupying an area of 70113 and 8332 ha, respectively [28]. Both species have a high ecological, social and economic value. However, nowadays, the Tunisian cork oak and zeen oak forests suffer from very low regeneration success [8] because of the high seed predation, the inability of young plants to successfully compete for light and soil resources [4], and the high early seedling mortality rate usually due to water stress. In this study we focused light and water stress factors. Both factors may be considered as the main climatic limiting factors that control regeneration success of forest tree species in the Mediterranean forests [29]. Experiments examining the effect of water stress and shade are often carried out separately. In addition, studies investigating the growth response of oak seedlings to either water stress or shade were often limited to height, diameter and biomass measurements [30, 31, 32, 33]. However, like other oak species [34, 35], zeen oak [36] and cork oak [37] have a typically rhythmic pattern of height growth. 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. The experiment was set up to ascertain 1) the effect of water stress and/or light intensity on the morphological traits of containerised cork oak and zeen oak seedlings and 2) to determine if water stress decreases seedlings' acclimation to shade. We tested the following hypotheses: (1) shade and water stress will affect seedling growth in a different way depending on the trait considered, and (2) water stress may overrule the morphological acclimation to shade.

II.   Materials and methods

2.1. Plant material and experimental design

The experiment was arranged as a factorial design with two watering regimes (well-watered versus moderate stress) and two light levels (moderate versus low light intensity). Two oak species, cork oak (*Quercus suber* L.) and zeen oak (*Quercus canariensis*) were used for this experiment. Acorns were harvested from trees at Oued elballoutin in Northwestern Tunisia (36°44'57.53''N, 8°54'33.57''E, elevation 200 m a.s.l.). The study was carried out in a greenhouse at INIA (Madrid—Spain, (40º 27' 20'' N, 3º 44' 58'' W, 595 m a.s.l.)).

Collected 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 cm^2 and 64 cm^2, upper and lower cross-sectional area, respectively), filled with a mixture of peat moss (KEKKILA 50/50) and vermiculite (1:3, v/v). Sixty four acorns by species 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 were randomly divided in two groups according to the water regime, one group was watered to field capacity three days (15–20 min) per week (W+), while the other group (W–) was watered one day per week (15–20 min). Volumetric soil water content in the well-watered seedlings (W+) was maintained at field capacity, while seedlings subjected to moderate stress (W–) were allowed to dry to a water content at 60% of field capacity. 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.

Seedlings under each water regime were randomly divided in two groups according to the two light environments, one of which was grown under metal frames (50 × 80 ×150 cm) with different 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 PFD inside and outside metal frames was 200 µmol·m^{-2}·s^{-1} and 90 µmol·m^{-2}·s^{-1}, respectively. They correspond to moderate (L+) and low (L-) light intensities, respectively. Sixteen plants from each species were grown under each combination, which makes a total of 64 plants by species.

2.2. Growth measurements

Measurements were made on all seedlings of each species at the end of the experiment (December 2010). Measured parameters for each species at the whole-plant were basal diameter, height growth, height-to-diameter ratio and biomass of the different fractions. The weight of the above- and below-ground biomass was measured after drying at 60°C for one week. Total biomass was obtained by making the sum between the above- and below-ground biomass.

Oak height growth occurs in a rhythmic pattern with periods of uninterrupted terminal bud growth (flushes) alternating with periods of bud development and apparent rest [35]. During each growth flush, a distinct portion of the stem called the GU is established. Thus, the measured parameters at the stem level, at the end of the growing season, were the number of flushes established by the main stem and length of the GU for each flush.

2.3. Statistical analysis

Quantitative variables such as height growth, basal diameter, height-to-diameter ratio, GU length, biomass, and shoot-to-root ratio were subjected to a two-way ANOVA (water regime and light intensity), using the PROC GLM procedure. For each analysis, when the ANOVA was significant, statistically significant differences between means were identified using Tukey test.

Qualitative variable (number of GU established on the main stem) was expressed in percentage (%). A comparison of mean percentages was then performed using a χ^2-test with the PROC FREQ procedure. Differences, between means or proportions, were considered significant at $P \leq 0.05$.

All statistical analyses were performed using SAS program, version 9.2.

III. Results

3.1. Height

Height growth was significantly impacted by water regime, light intensity, and their interaction in cork oak, but by light intensity in zeen oak (Table I). Zeen oak's height growth was, on average, greater under low than under moderate light intensity (Fig. 1A). This trend was also observed in well-watered cork oak seedlings (Fig. 1B), while height growth in water stressed cork oak seedlings was similar under both light intensities.

Table I. Analysis of variance for height growth in cork oak and zeen oak seedlings. Factors are light, water, and their interaction.

Variable	Factors	Cork oak	Zeen oak
Height	Water	0.0327*	0.2052
	Light	0.0021*	< 0.0001*
	Water × light	0.0311*	0.2564

Asterisk (*) shows significant differences between treatments at $P \leq 0.05$ (ANOVA, Tukey test).
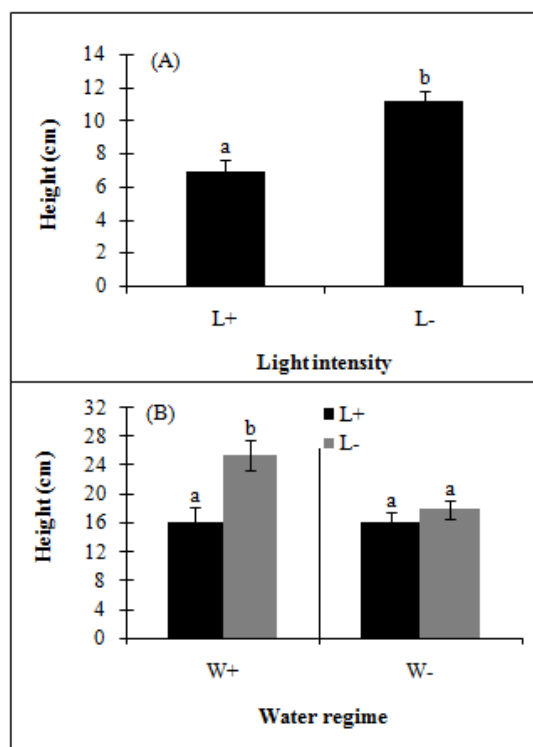
figure 1. Height growth according to light intensity (moderate (L+) versus low (L-) light intensity) for zeen oak (A), and water regime (well-watered (W+) versus moderate stress (W-)) and light intensity (moderate (L+) versus low (L-) light intensity) for cork oak (B). Means ± standard error (SE). Letters show in (A) significant differences between light levels, and in (B) light levels within each water treatment.

3.2. Basal diameter and height-to-diameter (H/D) ratio

Basal diameter growth was significantly influenced by light intensity for cork oak, and by water regime for zeen oak; the interaction between water regime and light was not significant in either species (Table II). Average basal diameter was greater for well-watered than for water stressed seedlings (4.8 ± 0.1 vs. 4.1 ± 0.1 mm). Contrary to height growth, average basal diameter was greater under moderate than under low light intensity (3.9 ± 0.09 vs. 3.3 ± 0.1 mm). Height-to-diameter ratio was significantly different between light intensities for both cork oak and zeen oak (Table II). It was, on average, higher under low than under moderate light intensity for both oaks (Fig. 2).

Table II. Analysis of variance for basal diameter and height-to-diameter ratio in cork oak and zeen oak seedlings. Factors are light, water, and their interaction.

Variable	Factors	Cork oak	Zeen oak
Diameter	Water	0.0775	0.0075*
	Light	0.0001*	0.0699
	Water × Light	0.9651	0.0564
Height-to-diameter ratio	Water	0.1265	0.9485
	Light	<0.0001*	<0.0001*
	Water × Light	0.1384	0.6793

Asterisk (*) shows significant differences between treatments at $P \leq 0.05$ (ANOVA, Tukey test).
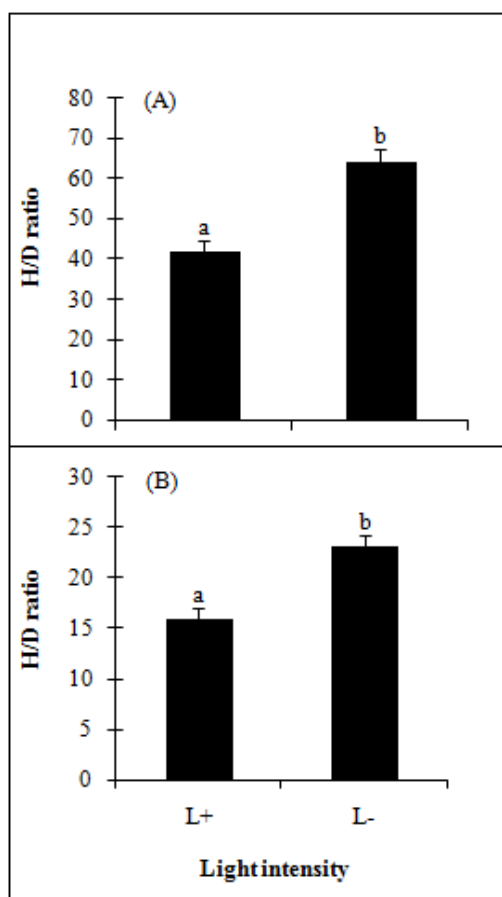
figure 2. Height-to-diameter ratio on cork oak (A) and zeen oak (B) seedlings according to light intensity (moderate (L+) versus low (L-) light intensity). Means ± SE. Letters show significant differences between light levels.
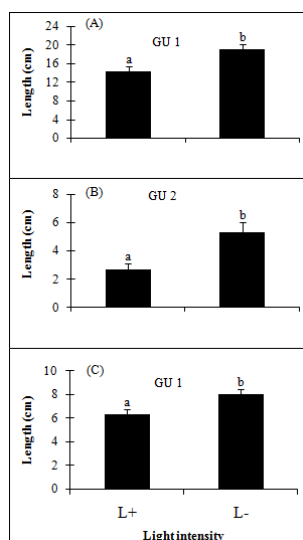
3.2. GU Length

The decomposition of the main stem in GU showed that seedlings established during all the growing season 1 to 2 GU. This trend was observed for both species. Both the first and the second GU were significantly affected by light intensity in cork oak (Table III). However, only the first GU was significantly affected by light intensity in zeen oak. Water regime and its interaction with light intensity had no significant effect neither for the first GU nor for the second GU, for both oaks. For both species, GU was, on average, longer under low than moderate light intensity (Fig. 3).

Table III. Analysis of variance for growth unit (GU) in cork oak and zeen oak seedlings. Factors are light, water, and their interaction.

| Variable	Factors	Cork oak	Zeen oak
First GU	Water	0.2070	0.7875
	Light	0.0083*	0.0064*
	Water × Light	0.4034	0.3015
Second GU	Water	0.7492	0.8065
	Light	0.0057*	0.0594
	Water × Light	0.1409	0.0875

Asterisk (*) shows significant differences between treatments at $P \leq 0.05$ (ANOVA, Tukey test).

figure 3. Growth unit (GU) length of the first (GU1) and the second (GU2) GU on cork oak seedlings (A, B), and of the first GU on zeen oak seedlings (C) according to light intensity (moderate (L+) versus low (L-) light intensity). Means ± SE. Letters show significant differences between light levels.

3.3. Number of GU

The number of GU was not dependent neither on water regime (P = 0.1049) nor on light intensity (P = 0.1913) for zeen oak. For cork oak, this number was significantly dependent on light intensity (P = 0.0178), but independent of water regime (P = 0.7639). There was no significant difference in the percentage of plants having established 1 GU under both light intensities (Fig. 4). By contrast, there was a significant difference in the percentage of plants having established 2 GU, with a lower value under low than under moderate light intensity.
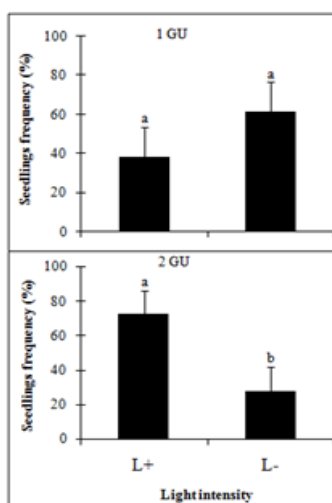
figure 4. Frequency of cork oak seedlings (%) with one (1 GU) and two (2 GU) growth unit (GU) according to light intensity (moderate (L+) versus low (L-) light intensity). Seedling percentage ± likelihood confidence limits, at 5% threshold. Letters show significant differences between light levels.

3.5. Biomass growth and shoot-to-root ratio

Neither water availability nor light had a significant effect on above-ground biomass for both oak species (Table IV). However, both underground biomass and total biomass were significantly affected by light intensity for cork oak, and by water regime for zeen oak.
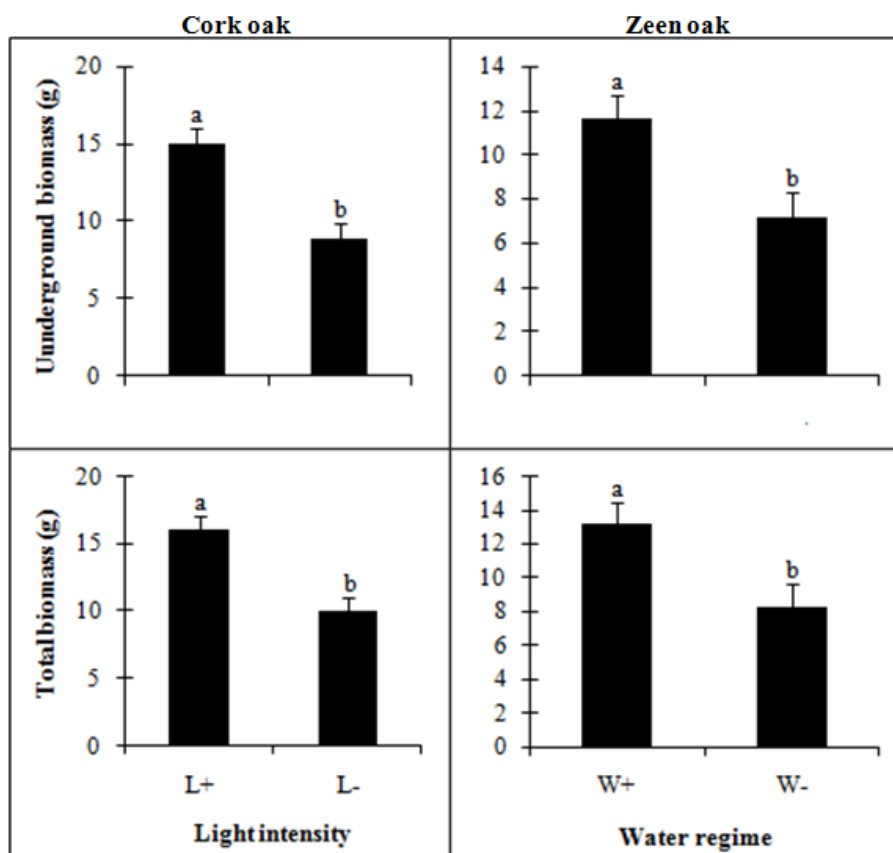
For water regime, both underground biomass and total biomass were, on average, greater for well-watered than water stressed seedlings (Fig. 5). For light intensity, average underground biomass and total biomass was lower under low than under moderate light intensity (Fig. 5).

The shoot-to-root ratio was significantly affected by light intensity in cork oak, and by water regime and light intensity in zeen oak (Table IV). For water regime, the shoot-to-root ratio was, on average, lower for well-watered than for water stressed seedlings (0.132 ± 0.008 vs. 0.159 ± 0.009). For light intensity, this ratio was, on average, higher under low than under moderate light intensity for both species (Fig. 6).

Table IV. Analysis of variance for above-ground biomass, underground biomass, total biomass and shoot-to-root ratio in cork oak and zeen oak seedlings. Factors are light, water, and their interaction.

Variable	Factors	Cork oak	Zeen oak
Above-ground biomass	Water	0.1189	0.1076
	Light	0.7724	0.0662
	Water × Light	0.4100	0.1629
Underground biomass	Water	0.1426	0.0068*
	Light	<0.0001*	0.8055
	Water × Light	0.4999	0.1236
Total biomass	Water	0.1180	0.0103*
	Light	<0.0001*	0.6127
	Water × Light	0.4649	0.1314
Shoot-to-root ratio	Water	0.6997	0.0414*
	Light	0.0177*	<0.0001*
	Water × Light	0.5139	0.1191

Asterisk (*) shows significant differences between treatments at $P \leq 0.05$ (ANOVA, Tukey test).

figure 5. Underground biomass and total biomass according to light intensity (moderate (L+) versus low (L-) light intensity) for cork oak (left) and water regime (well-watered (W+) versus moderate stress (W-)) for zeen oak (right). Means ± SE. Letters show significant differences between light levels (left) and between water regimes (right).
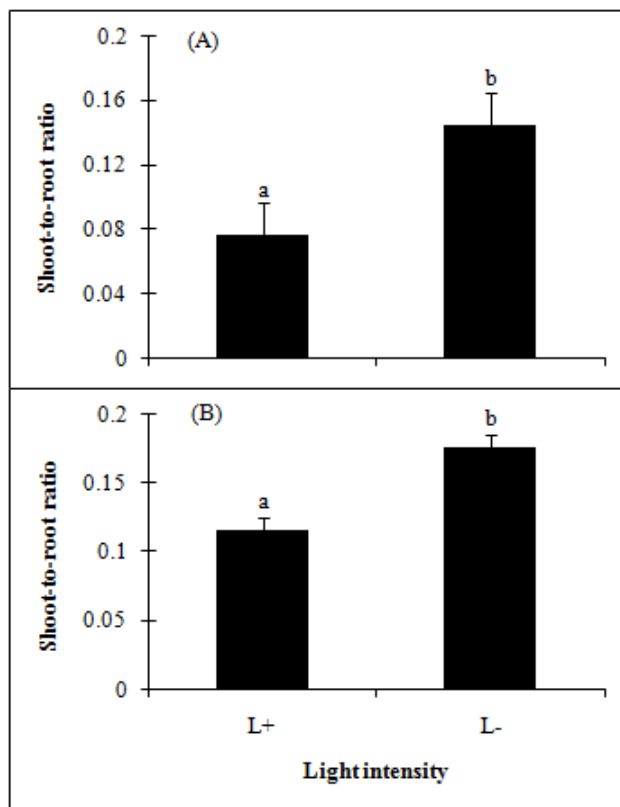
figure 6. Shoot-to-root ratio on cork oak (A) and zeen oak (B) seedlings according to light intensity (moderate (L+) versus low (L-) light intensity). Means ± SE. Letters show significant differences between light levels.

IV. Discussion

It has been reported since long that the first response to shade conditions is shoot elongation [38]. This was the reason for having, for both species, greater height growth under low than under moderate light intensity. Under shade conditions, seedlings are forced to grow towards light, to ensure their needs in this resource, and consequently to grow more in height [39]. It is important to note, however, that for cork oak increased height growth under low light intensity took place for well-watered seedlings, but nor for water stressed seedlings indicating that low water availability limited the seedlings' ability to cope with shading. This is because the water availability is the dominant stress factor. On the other hand, this means that water stress may aggravate growth of seedlings which are exposed to shading.

The increased height-to-diameter ratio observed for both oak species under low light level was also reported by Daas-Ghrib [8]. It attests for an unbalanced growth between height and basal diameter [40]. For cork oak, unbalanced growth is due to an increase in height and a decrease in diameter growth. For zeen oak, unbalanced growth was a function of height growth as there was no reduction in diameter growth, which reveals a progressive re-establishment of the plant growth balance.

Thanks to the primary growth decomposition, in GU, different growth characteristics can be underlined between seedlings grown under moderate and low light intensities. Seedlings grown under low light intensity expressed a significantly greater GU length for both established GU in cork oak, and for the first GU in zeen oak. Therefore, the greater height growth attributed to seedlings grown under low light level comes from the increase in GU length of the first GU for zeen oak, but also of the second GU for cork oak. Increased height growth in zeen oak only by increasing the first GU might indicate that after the establishment of this GU, seedlings ensured their needs in light. As previously reported, the stimulation of height growth under shade conditions stops when the plant reaches the demanded level of light [8]. As mentioned before, cork oak is described as less shade tolerant than zeen oak. For that reason perhaps there was a growth stimulation of both established GU for cork oak, which allows plant to profit the possible maximum from the available light, but only of the first GU for zeen oak. The increase in GU length accompanied by a decrease in the polycyclism rate observed in this study for cork oak confirms the results of Chaar et al [41] and Mechergui et al [37], who reported for the same species that GU length tends to be shorter as the polycyclism rate increases.

Although they had a greater height, seedlings grown under low light intensity did not express, in both oaks, an increase in their above-ground biomass compared to those grown under moderate light intensity. This indicates that this increase in height was not a result of an increase in dry matter production, but of a different

allocation of assimilates which favored height growth and development of shoots in the distal part of the trees [40, 42]. Root biomass of trees has been shown to be adversely affected by water regime [43] and light [44]. In our study, root biomass growth was dependent on water regime for zeen oak, and on light level for cork oak. This is because deciduous species (i.e., zeen oak) are more shade-tolerant and water-demanding than evergreen species (i.e., cork oak) [45], which could explain also why diameter growth was independent of light intensity, and significantly reduced under water stress only for zeen oak. Burger et al. [46] 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 favour the aerial part of plant causing a reduction in the root-to-shoot ratio. In this study, the reduction in root biomass of cork oak and zeen oak seedlings under low light intensity and water stress, respectively, is due to reduced overall photosynthate pool as well as to the unbalance in the distribution of photosynthate between the aerial and underground parts of plant, as both biomass production (total biomass) and shoot-to-root ratio were affected. Decreased allocation to roots in response to shade has been demonstrated in many studies [47, 48, 49, 50]. However, increased investment in above-ground plant part under water stress, as suggested by the increased in the shoot-to-root ratio, is contradictory with what was established for along that under water deficit plant invests in root development [51, 52, 53, 54]. In a general way, this morphological plasticity enables a plant to change its growth pattern when it encounters different stresses [55] and to enhance, consequently, its ability to face these stresses.

V.   Conclusion

The study of cork oak and zeen oak seedlings' responses under changing light and water availability is of major interest, because the impact of the interaction between light and water availability can greatly help to understand regeneration success and niche differentiation in Mediterranean ecosystems. In this study, there was interaction between light and water availability for cork oak; thus, seedlings growing under no limiting water conditions were able to increase their height in response to low light intensity, while those growing under water stress were not. This suggests that cork oak can acclimate perfectly to shade conditions, when water conditions are not limiting. However, like most Mediterranean species, cork oak experiences an important drought during the summer season [56]; water stress may be, therefore, the bottleneck for recruitment of cork oak seedlings in shaded habitats. To avoid this situation, silvicultural treatments in cork oak stand under shaded conditions (i.e., forest gap, the reduction of undergrowth density or of tree density) in order to increase light penetration inside the population, and to favor consequently the regeneration of young plants, appear therefore necessary. Contrary to cork oak, shoot elongation in zeen oak was not significantly affected by an interaction between water and light, but by light alone. This demonstrates that water availability did not interfere with the response to light and that light affected the shoot elongation whatever the water regime applied. Contrary to cork oak, zeen oak did not lose its ability to acclimate to shade under water stress. It seems, thus, that zeen oak acclimated to shade conditions better than cork oak under water stress. Hence, the regeneration of zeen oak under shade and water stress would be more favored than that of cork oak. This implies that the ability of regenerated seedlings to respond to shade conditions under drought might influence patterns of forest distribution. The water stress applied in this study is a mild stress. Therefore, a higher intensity of water stress may increase the differences found in the range of applied water regimes. In addition, the responses reported at present may be linked to a threshold irradiance; hence, it is interesting to evaluate the combined application of light and water stress in a wider range of irradiance and water availability.

Acknowledgements

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