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Growth and early survival seedling of zeen oak under shade and moderate drought: comparative study of two provenances

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Abstract – The effects of drought and light on survival and growth traits was assessed in seedlings of zeen oak (*Quercus canariensis* Willd.) originating from Spain and Tunisia. Plants from both 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. Survival rate varied from 82.8 to 92.1%, with no significant differences between groups of treatments. Seedling diameter was similar in both provenances, while seedling height was significantly higher in the Spanish provenance. None of the provenances seemed to be more tolerant to water stress, while the Tunisian provenance showed a greater ability to acclimate to deep shade. However, when both factors (light and water) acted in concert the Tunisian provenance showed a greater ability to cope with low water availability under moderate shade, whilst the Spanish provenance showed a greater ability to cope with low water availability under deep shade.

Keywords: *Quercus canariensis*, provenance, light, water stress

1. Introduction

Zeen oak (*Quercus canariensis* Willd.) is a one of the most valuable species in the Mediterranean region due to its high ecological and social value. It is a shade-tolerant species (Perez-Ramos et al. 2010) that grows usually at moderate altitudes (700–1100 m) (Schoenenberger and Salsac 1970), under 1000 to 1150 mm of precipitation and on deep soils (Quero et al. 2008).

Like most Mediterranean species, zeen oak experiences an important drought during the summer season. The effects of drought are highly variable and depend on length of stress imposition, stage of plant development, and plant response to stress through a complex net of physiological and morphological changes (Pimentel 2004). At the tree level, a water deficit can affect above- and below-ground growth, leading to reductions in diameter, height (Zine El Abidine 2003) and root development (Ksontini 1996). On the other hand water stress reduces the ability of trees to withstand other environmental stresses and affects the photoassimilates partitioning (Zine El Abidine 2003). At the forest population level, water stress increases mortality and can result in the replacement of the existing species by more resistant ones (Teskey and Hinckley 1986; Aussenac 1993; Aussenac 2000).

A lack of light results in a reduction of stem diameter (Pierson et al. 1990), and in an increase of the shoot elongation (Daas-Ghrib 2009). Under low light, first-year oak seedlings are more likely to produce one growth unit (Phares 1971; Crow 1988), 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 (Hodges and Gardiner 1993). A common response to shade reported in many studies is also a reduced allocation to roots (Zollinger and Kells 1991; Thompson et al. 1992; Messier 1992). On the other hand light intensity affects photosynthesis, which in turn is related to the accumulation of organic matter and biomass.

The interaction of light and water stresses may be a compromise between contradictory patterns on seedlings' morphological response (Mechergui and Pardos 2016). According to the *trade-off hypothesis* mentioned by Holmgren (2000) and Sack and Grubb (2002), drought has a stronger impact on individuals grown in deep shade than on those grown under high irradiances. A contrary hypothesis (the *facilitation hypothesis*) predicts that drought has a weaker impact on plants in shade, because of lower air temperatures and vapour pressure deficits in shaded microsites (Holmgren 2000; Johnson et al. 1997). Studies which have been carried out on growth response of oak seedlings to either water stress or shading were often limited to height, diameter and biomass measurements (Rao and Singh 1986; Messina and

Duncan 1993; Wang and Bauerle 2006; Březina and Dobrovolný 2011). However, like other oak species (Champagnat et al. 1986; Harmer 1990), zeen oak has a typically rhythmic pattern of height growth (Mechergui et al. 2012). 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 objective of this study was to compare the effects of water stress and/or shading on early survival seedling and growth of containerized zeen oak seedlings, originating from Spain and Tunisia, testing the two hypotheses (trade-off, facilitation).

2. Materials and methods

2.1. Plant material and experimental design

The study was carried out in a greenhouse at INIA (Madrid—Spain, (40º27'20''N, 3º44'58''W, 595 m a.s.l.)), during the period December 2009 to December 2010. Two provenances of zeen oak, sampled from Tunisia and Spain, were grown in 3-L pots (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 moss peat and fine sand (3:1, v:v). Pots were kept well-watered three days per week (15 min) inside a greenhouse from December 2009 until mid-March 2010.
On 15 March 2010, seedlings from each provenance were randomly assigned to two light treatments. Sixteen plants were placed into each of two metal frames covered with layers of neutral shade white cloth (Polysack Plastic Industries Ltd., Israel) to produce the two light environments. The percentage of photosynthetic photon flux density (PFD) inside and outside (greenhouse) metal frames was 5% (90 $\mu mol \cdot m^{-2} \cdot s^{-1}$) and 15% (250 $\mu mol \cdot m^{-2} \cdot s^{-1}$) of full-light, respectively. They correspond to deep and moderate shades (Puértolas et al. 2008), respectively. Light level inside the greenhouse and metal frames was calculated as a percentage of light outside the greenhouse.
Within each light treatment, seedlings were randomly divided into two watering treatments, W+ (well-watered treatment) and W- (water stressed treatment). The W+ treatment was watered to field capacity, while W- treatment was watered at 60% of field capacity. The volume of water supplied in the W- treatment, for each irrigation, was a function of the volume of water lost under the low photosynthetic photon flux density (PFD), which had the minimum water losses. By this means, a slow rate of imposition of the water stress conditions was assured. The experiment included in total 32 seedlings for each provenance, allocated between four treatment combinations (15% of full-light and W+, 15% of full-light and W-, 5% of full-light and W+, 5% of full-light and W-).

2.2. Assessments

At the end of the experiment (December 2010), height and basal diameter of all plants were recorded, for each provenance, along with mortality. All plants were then harvested, and cut at the root-collar and separated into shoots and roots to determine above and below-ground biomass, respectively. The weight of the above- and below-ground biomass was obtained after drying at 60°C for one week. Additional parameters deduced from the above were: height-to-diameter (H/D) ratio, root-to-shoot ratio (calculated by dividing below-ground biomass by above-ground biomass) and total plant biomass (which corresponds to the sum between the above- and above-ground biomass).
Zeen oak's growth is a rhythmical growth resulting in an alternation of rest and elongation phases during which a portion of stem or growth unit (GU) is established (Mechergui et al. 2012). Two variables were thus measured at the main stem, at the end of the growing season, are the number and length of the GU.

2.3. Data analysis

A three-way ANOVA (provenance, light, water) was conducted for quantitative variables (seedling height, basal diameter, height-to-diameter ratio, below- and above-ground biomass, root-to-shoot ratio, total biomass, GU length) and comparisons between treatment means were made using Tukey test. 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 Chi^2 test with the PROC FREQ procedure. Differences, between means or proportions, were considered significant at $P \leq 0.05$. All data analyses were carried out with SAS 9.2 software (SAS Institute Inc., Cary, NC).

3. Results and Discussion

3.1. Survival

Survival at the end of the growing season varied between 82.8 per cent and 92.1 per cent. There were no significant differences between treatments (Table 1).

Table 1. Analysis for survival rate. P_{-Chi}^2 = value of chi-square (Chi^2) test. Factors are provenance, light, water, and their interaction.

Factors	P_{-Chi}^2
Light	0.5930
Water	0.1088
Provenance	0.2850
Light × Water	0.6975
Provenance × light	0.8447
Provenance × water	0.8339
Light × water (for the Spanish provenance)	0.5711
Light × water (for the Tunisian provenance)	1.0000

3.2. Height growth, basal diameter and height-to-diameter (H/D) ratio

Significant factors for height growth were provenance and light intensity, while no significant effect was found for diameter growth (Table 2). Seedling height in the Spanish provenance was 2-fold the height in the Tunisian provenance (Fig. 1A). Independently of their provenance, seedlings were 28% taller under 5% of light than under 15% of full-light (Fig. 1B).

The height-to-diameter ratio was significantly different between provenances (Table 2) with greater value for the Spanish than for the Tunisian provenance (Fig. 1C), as well as between light intensities (Table 2) with greater value under 5% than under 15% of light (Fig. 1D).

Table 2. Analysis of variance for height, diameter and height-to-diameter ratio (H/D). Factors are provenance, light, water, and their interaction.

Factors	Height (Pr > F)	Diameter (Pr > F)	H/D ratio (Pr > F)
Light	0.0008*	0.6266	<0.0001*
Water	0.6972	0.0960	0.3458
Provenance	<0.0001*	0.4224	<0.0001*
Light × Water	0.5990	0.4439	0.7901
Provenance × light	0.3547	0.0547	0.8257
Provenance × water	0.0946	0.0512	0.3778
Provenance × light × water	0.5281	0.0756	0.5108

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

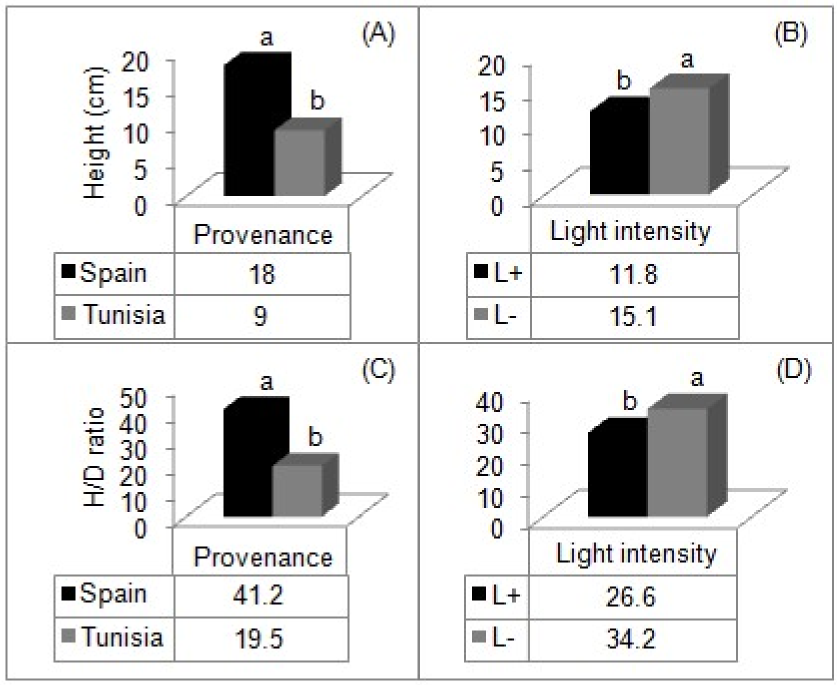

Figure 1. Height and height-to-diameter ratio (H/D ratio) according to provenance (A, C) and light intensity (B, D) (L+, (15% of full-light); L-, (5% of full-light)). Means marked with different letters are significantly different at p ≤ 0.05 level.

3.3. Number and length of growth unit (GU)

The decomposition of the main stem in GU showed that both provenances established 1 to 2 GU during the growing season. The number of established GU was not dependent neither on light intensity (P = 0.5668) nor on water regime (P = 0.3465), while a significant difference (P < 0.0001) between the provenances was found. The Tunisian provenance had more tendency to produce only one GU (75.4%), while the Spanish provenance usually produced two GU (85.7%).

With regard to GU length, significant factors for the first GU were provenance and light intensity, while significant factors for the second GU were provenance and light intensity in addition to the significant light × water regime interaction (Table 3). Both GU were longer for the Spanish than for the Tunisian provenance (Fig. 2A, Fig. 3A) and both GU were longer under 5% than under high 15% of full-light (Fig. 2B, Fig. 3B). However, as revealed by the light × water regime interaction, the effect of water regime on the second GU was dependent on light environment. Thus, under 5% of full-light GU length was significantly greater in well-watered than in water-stressed seedlings, while under 15% of full-light the difference was not significant (Fig. 3C).

Table 3. 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.

Factors	GU1	GU2
Light	0.0048*	0.0434*
Water	0.4973	0.9530
Provenance	0.0009*	0.0024*
Light × water	0.3444	0.0065*
Provenance × light	0.5950	0.0514
Provenance × water	0.3672	0.6722
Provenance × light × water	0.9321	0.4320

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

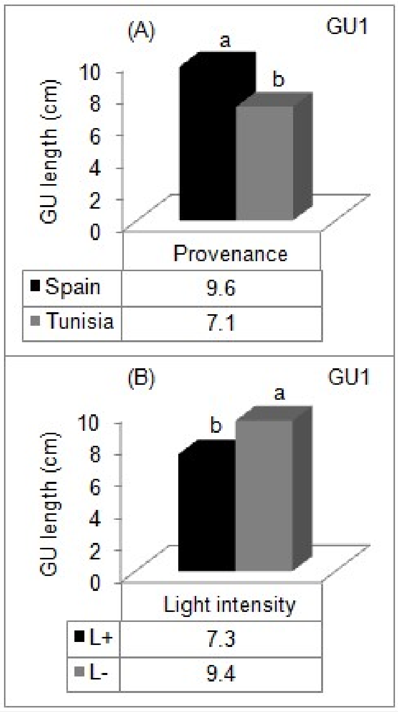

Figure 2. Growth unit (GU) length of the first (GU1) **GU** according to provenance (A) and light intensity (B) (L+, (15% of full-light); L-, (5% of full-light)). Means marked with different letters are significantly different at $p \leq 0.05$ level.

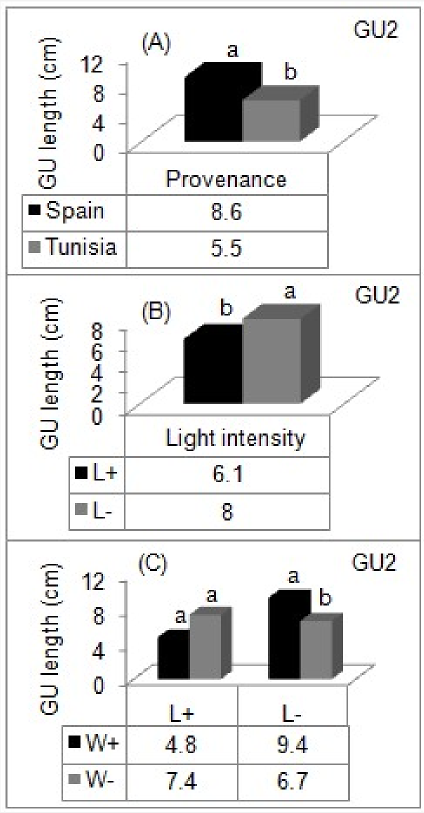

Figure 3. Growth unit (GU) length of the second (GU2) GU according to provenance (A), light intensity (B) (L+, (15% of full-light); L-, (5% of full-light)) and light intensity and water regime (W+, well-watered seedlings; W–, moderate water-stressed seedlings) (C). Means marked with different letters are significantly different. Letters show in (C) significant differences within each light treatment at $p \leq 0.05$ level.

3.4. Biomass growth and root-to-shoot ratio

None of the studied factors had a significant effect on above-ground biomass (Table 4). By contrast, the below-ground biomass was significantly different between light intensities, with lower value under 5% than under 15% (9.8 ± 0.70 g *vs*. 7.7 ± 0.74 g (± SE)), as well as between water regimes with higher values under no limiting water conditions than under water stress (10.5 ± 0.74 g *vs*. 7.0 ± 0.70 g). Other significant factors included the two-way provenance × light intensity interaction and the three-way provenance × light intensity × water regime interaction indicating, respectively, that the effect of light intensity and the two-way light intensity × water regime interaction varied between both provenances. Thus, for the Spanish provenance the below-ground biomass was significantly higher under 15% than under 5% of full-light, while for the Tunisian provenance the difference was not significant (Fig. 4 A). On the other hand, while the Spanish provenance showed a significantly higher value of the underground biomass in well-watered than in water-stressed seedlings under 15% of full-light and similar values under 5% of full-light, the Tunisian provenance showed a significantly higher value in well-watered than in water-stressed seedlings under 5% of full-light and similar values under 15% of full-light (Fig. 4B, C).

Table 4. Analysis of variance for below- (BGB) and above-ground (AGB) biomass, total biomass (TB) and root-to-shoot ratio (RSR). Factors are provenance, light, water, and their interaction.

Factors	BGB	AGB	TB	RSR
Light	0.0395*	0.5888	0.0889	<0.0001*
Water	0.0010*	0.1712	0.0022*	0.0705
Provenance	0.2675	0.7196	0.3102	0.0013*
light × Water	0.5995	0.9051	0.6370	0.3742
Provenance × light	0.0153*	0.1177	0.0136*	0.0990
Provenance × water	0.3501	0.2340	0.3198	0.3306
Provenance × light × water	0.0028*	0.1375	0.0037*	0.1251

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

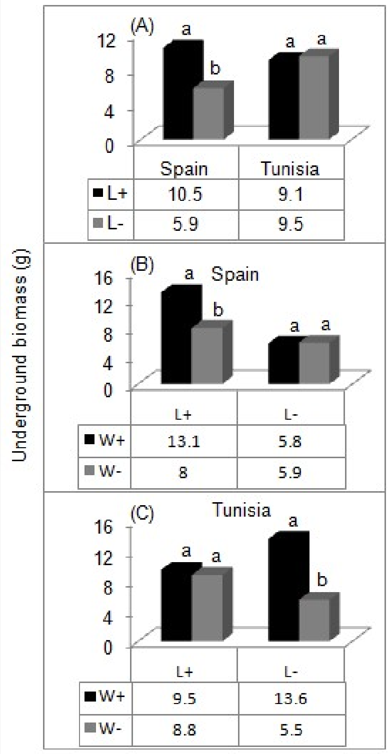

Figure 4. Underground biomass according to provenance (A) and light intensity (L+, (15% of full-light); L-, (5% of full-light)) and water regime (W+, well-watered seedlings; W–, moderate water-stressed seedlings) (B, C). Means marked with different letters are significantly different. Letters show in (A) significant differences within each provenance and in (B, C) significant differences within each light treatment at p ≤ 0.05 level.

Significant factors for the total biomass were water regime, the two-way provenance × light intensity interaction and the three-way provenance × light intensity × water regime interaction (Table 4).
The effect of water regime resulted in a significantly higher total biomass in well-watered than in water-stressed seedlings (Fig. 5A), while the effect of the two-way provenance × light intensity interaction resulted in significantly higher total biomass under 5% than under 15% of full-light for the Spanish provenance, and in similar values for the Tunisian provenance (Fig. 5B). The three-way provenance × light intensity × water regime interaction resulted in a significantly difference in total biomass only under 15% of full-light for the Spanish provenance and under 5% of full-light for the Tunisian provenance, with significantly higher value in well-watered than in water-stressed seedlings (Fig. 5C, D).
The root-to-shoot ratio was significantly different between provenances (Table 4), with a greater value for the Tunisian (8 ± 0.31) than for the Spanish (6.4 ± 0.34) provenance, and between light intensities (Table 4) with lower value under 5% of full-light (5.8 ± 0.34) than under 15% of full-light (8.4 ± 0.32).

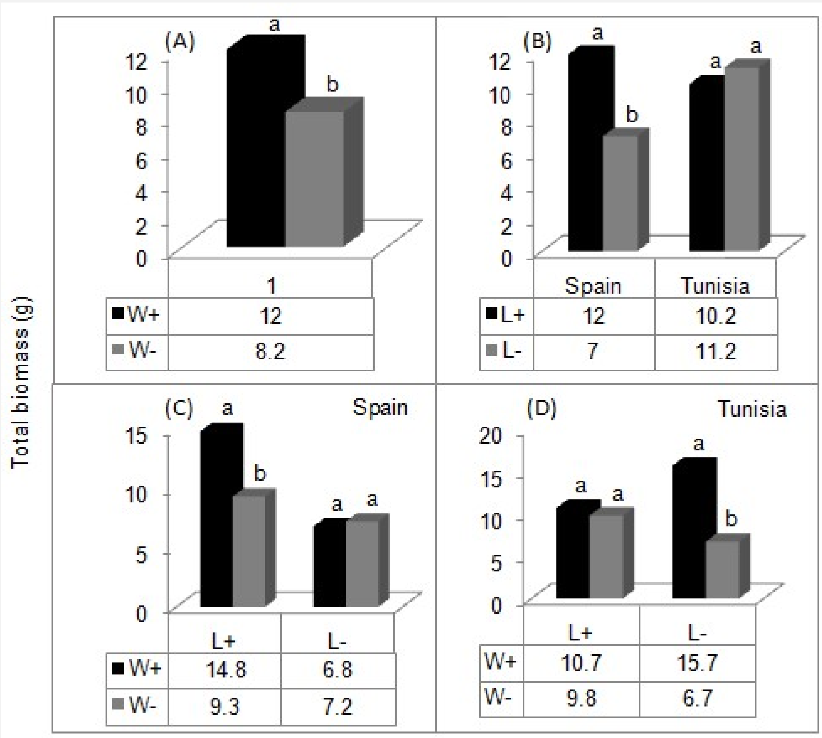

Figure 5. Total biomass according to water regime (W+, well-watered seedlings; W–, moderate water-stressed seedlings) (A), provenance (B), and light intensity (L+, high light intensity (15% of full-light); L-, low light intensity (5% of full-light)) and water regime (C, D). Means marked with different letters are significantly different. Letters show in (B) significant differences within each provenance and in (C, D) differences within each light treatment at p ≤ 0.05 level.

Our results show that survival rate was independent of studied factors, provenance, light and water regime, and hence seedling mortality may be attributed to other factors rather than these factors.
A greater degree of shading stimulates the seedlings to grow more in height to reach available light (Jacobs and Steinbeck 2001). This was the reason for having significantly greater height growth under deep shade (5% of full-light) than under moderate shade (15% of full-light). Increased height-to-diameter ratio under deep shade comparatively to moderate shade reveals an unbalanced growth between height and basal diameter (Mechergui 2016). However, this unbalanced growth was a function of height growth as there was no reduction in diameter growth. The difference in this ratio between provenances, with greater value for the Spanish provenance, is a result of a difference in height growth which was also greater for the Spanish provenance (diameter growth was not different between provenances).
The decomposition of the main stem in GU showed that seedlings grown under deep shade expressed a significantly greater GU length for both GU, while the difference concerning the number of established GU was not significant, compared to seedlings grown under moderate shade. Accordingly, the greater

height growth attributed to seedlings grown under deep shade is only the result of the increase in GU length. The comparison between provenances showed that the Spanish provenance had longer GU and tended to establish more GU. Hence, seedling height was significantly greater for the Spanish than for the Tunisian provenance as a result of an increase in both the number and the length of the produced GU on the main stem. It is important to remember that for the second GU water stress reduced length of this GU under deep shade, but not under moderate shade where the difference between water regimes was not significant. This indicates that deep shade altered seedlings' ability to acclimate to water stress. This finding is in accordance with the *trade-off hypothesis* (Holmgren 2000; Sack and Grubb 2002; Smith and Huston 1989) that drought should have stronger impact in deep shade because of reduced root investment.

While they showed a greater height growth, seedlings grown under deep shade did not show a difference in their above-ground biomass compared to those grown under moderate shade. This indicates that this increase in height was not due to an increase in dry matter production, but rather of reallocation of growth in favor of shoot elongation. Root biomass of trees has been found to be adversely affected by water regime (Fabião et al. 1995) and light (Dias-Filho 1995). This may be confirmed in our work, which shows that root biomass decreased under both water stress and low light availability (deep shade). 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 photosynthates in favour of the aerial part of plants causing a reduction in the root-to-shoot ratio (Burger et al. 1997). In this study, the reduction in root biomass under low light availability is due to the unbalance in the distribution of photosynthates between the aerial and below-ground parts of plant, as revealed by the reduction in root-to-shoot ratio. However, the reduction in root biomass under water stress is not due to an unbalance in the distribution of photosynthates between the aerial and below-ground parts of plant, as the root-to-shoot ratio was not affected, but rather to reduced overall photosynthates pool as revealed by the reduction in total biomass. Reduced below-ground and total biomasses under low light conditions only for the Spanish provenance (see fig. 4A and fig. 5B) suggests that the Tunisian provenance is more adapted to shade conditions. When light and water acted in coordinate way, two different situations according to the seedlings' provenance were highlighted: for the Spanish provenance water stress reduced both below-ground and total biomasses under moderate shade (15%) but had no effect on both biomasses under deep shade (5%), thus providing support for the *facilitation hypothesis* that drought has a weaker impact under shade than under high light intensity because of improved microclimatic conditions. For the Tunisian provenance water stress had no significant effect on neither below-ground nor total biomasses under moderate shade, but reduced both biomasses under deep shade which is in line with the *trade-off hypothesis*. This trade-off implies that plants adapted to shade would be worse adapted to drought than other seedlings growing under high light levels (Puértolas et al. 2008). This may confirm our suggestion, as previously mentioned, that the Tunisian provenance is more adapted to shade conditions than the Spanish provenance. This variability appeared to be geographically structured and would be mainly genetically controlled, as zeen oak provenances were cultivated under the same environmental conditions.

4. Conclusion

Our results show that water stress significantly affected 2 of the 10 of studied traits. By contrast, light affected 5 of the 10 traits studied which indicates that it acted as a predominant factor. None of the provenances seemed to be more tolerant to water stress, while the Tunisian provenance showed a greater ability to acclimate to low light availability. However, when both factors (water and light) acted together the Spanish provenance showed a greater acclimation to water stress under deep shade, while the Tunisian provenance showed a greater acclimation to water stress under moderate shade. This suggests as both factors may act in concert in Mediterranean conditions, as our results show, that the Spanish provenance may constitute a better material for afforestation under deep shade, whereas the Tunisian provenance may constitute a better material for afforestation under moderate shade.

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