

Article

Light Transmissivity of Tree Shelters Interacts with Site Environment and Species Ecophysiology to Determine Outplanting Performance in Mediterranean Climates

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Abstract: Plastic tree shelters are commonly used in plantations under Mediterranean climates to protect against herbivory and enhance outplanting performance. However, effects on outplanting performance cannot be generalized due to the complexity of plant responses to microenvironmental conditions within the tube wall. The interactions between the light transmissivity of the tubes and species-specific responses to light and site environment on two-year outplanting performance were studied in two species with contrasting shade tolerance planted inside tree shelters with four different light transmissivities and a non-tree shelter control at two Mediterranean sites with contrasting rainfall and temperature. In general, increasing light transmissivity enhanced biomass accumulation, suggesting that the use of clear tubes might be advisable. However, the shade-tolerant *Q. ilex* did not benefit from the greater light transmissivity in the most arid site, indicating that the positive effect of clear tubes depends on water stress experienced by seedlings, which ultimately is determined by drought resistance strategies and site conditions. The growth of both species and survival of *P. halepensis* were higher within clear tubes in the continental site than in unsheltered plants, which suggests that factors other than light, such as warmer daytime temperatures or the prevention of dust deposition, can explain this beneficial site-dependent effect of tree shelters. In conclusion, our results confirm the hypothesis that the effect of tree shelter and its light transmission on outplanting performance is site and species-specific, but further research is needed to identify the effect of other effects not related to light transmission.

Keywords: forest restoration; forestation; Mediterranean climate; tree shelters; transplanting performance; *Pinus halepensis*; *Quercus ilex*; water potential; root growth



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1. Introduction

Tree planting is recognized as an effective way to conduct forest landscape restoration in all biomes [1,2]. However, restoration initiatives are often at risk due to low survival rates of transplants. Both abiotic and biotic constraints compromise the performance of planted seedlings. In particular, planting in dry areas such as Mediterranean forests is particularly challenging. Shallow and unfertile soils are frequent in these biomes [3]; biotic stress such as predation by small mammals, birds or ungulates is a common disturbance in these landscapes that hampers survival and growth [4,5]. Along with these factors, intense summer drought occurring in Mediterranean areas simultaneously with high radiation levels is the main source of abiotic stress, causing significant failures and subsequent economic loss [6,7]. The current scenario of climate change, with higher probabilities of extreme, harsh summers [8], suggests that the success of restoration programs in dry

Mediterranean environments will require improvements in planting techniques aimed at ameliorating the degree of stress affecting the seedlings [9,10].

Many of the ecotechnological tools commonly used in dry and arid environments have focused on deterring seedling predation or improving microsite conditions and resource availability [1,11]. One of the most widespread cultural practices in restoration programs in the Mediterranean over the past few years is the use of tree shelters. Along with protecting seedlings from animal predation, an overall positive effect of shelters on survival has been observed in planting experiments with predation exclusion, as shown by a meta-analysis about ecotechnologies for dryland restoration [11]. However, single studies show that the effects of tree shelters are species and site-specific [12]. Planting experiments in the Mediterranean suggest that tree shelters improve the survival of many shade-tolerant Mediterranean species [10,13,14], particularly in harsh areas [15,16]. However, the mechanisms explaining this response are far from being clarified. Tree shelters are complex systems in which light interacts with other environmental variables, such as temperature and soil water availability, with feedback effects on plant physiology [17–19]. Some experiments suggest a positive effect of tree shelters on the abiotic stress incidence of shade semi-tolerant species [20,21], but other studies show that light reduction within the tree shelter limits the survival of shade-intolerant species [13,15,22].

Low light levels inside tree shelters elicit well-known physiological and morphological responses [23], such as an increase in leaf specific area, stomatal density and biomass allocation to shoots, and a reduction in root growth [23]. These responses have been reported to decrease plants' overall resistance to drought stress [24]. However, this trade-off in resistance is not universal and can depend on species shade and drought tolerance and environmental conditions [25]. Limited root development during the growing (wet) period is a major factor precluding the summer survival of planted trees in Mediterranean areas. A deep root system allows plants to escape the desiccation of top soil layers that occurs during the dry season [26], especially in zones with harsh summers. This could explain the lower survival rates of pines and other shade-intolerant species in planting experiments with tree shelters [13], especially within dark tubes with low light transmissivity [15]. Due to light reduction in shelters, these species would not take advantage of the elevated temperatures inside the tree shelters in winter and spring that could potentially enhance photosynthesis rates and, consequently, root growth. In contrast, even though shade semi-tolerant species such as the Mediterranean *Quercus* species also experience that reduction in root growth [17], the lower plasticity of the root growth of these species in response to light levels compared to shade-intolerant ones [21] would explain their better performance in tree shelters.

In contrast, alleviation of the harmful combination of high radiation and water stress during the Mediterranean dry summer has been demonstrated to be an important factor explaining the effect of tree shelters on the seedling survival of shade semi-tolerant species [21]. Under drought stress, stomatal closure impedes CO₂ entering the leaf. The excess of energy that cannot be used for carbon fixation provokes the degradation of the photosynthetic machinery and oxidative damage, which can lead to seedling death [27]. Therefore, under drought conditions, reducing light intensity attenuates that excess of energy and, therefore, oxidative damage. However, this potential alleviation also depends on the species characteristics and environmental conditions. Thus, shade-intolerant species that possess enhanced mechanisms to cope with radiation excess would not benefit from light sheltering as much as shade-tolerant species [25].

Another important feature of tree shelters to understand their physiological effects is the inextricable relation between their transmissivity and air temperature [28]. The heating effect of tree shelters during daylight hours in summer is well known. This effect becomes more intense in shelters with high transmissivities. Differences as high as 6 °C in mean temperatures in summer between clear tubes and open air have been detected [20,29]. These elevated temperatures inside tree shelters can become stressful under the hot Mediterranean summer conditions, which can counterbalance the alleviating effect of shading, in particular

for transplants of semi-tolerant species [14,21,28]. However, this stressing effect of more transparent tubes was not detected under controlled experiments with no limiting water conditions [17,29].

For a given light transmissivity of the tree shelter wall, the interaction of the physiological (root growth, photosynthetic performance) and microclimatic factors inside the tube (temperature and light) described above results in complex responses that depend on species' physiological characteristic features (light radiation tolerance/plasticity and drought resistance) and site conditions (temperature, radiation and soil moisture). Therefore, we hypothesize that the light transmissivity of tree shelters can be tailored to specific conditions of the planting area, in particular to the combination of site environmental conditions (temperature and average water availability) and species. To our knowledge, there are no previous experiments specifically aimed at testing this combination of factors.

In this experiment, we analyze the effects of the light transmissivity of tree shelters on the post-transplant morphology and physiology of two Mediterranean forest species with contrasted ecology (*Quercus ilex* L. subsp. *ballota* (Desf.) Samp. and *Pinus halepensis* Mill.) during establishment at two dry Mediterranean zones: an inland (continental) dry area and a coastal semiarid warm site. Both sites share a common dry hot summer, but drought intensity, temperatures and rainfall during the wet season can broadly vary. The studied species are commonly used in restoration programs in Spain [30] and exhibit strong ecological differences according to their successional stage and phylogeny: the pioneer, shade-intolerant, isohydric *P. halepensis* and the late successional, anisohydric intermediate shade-tolerant *Q. ilex* [31,32], with shade tolerance indexes of 1.35 and 3.02, respectively [33]. Two hypotheses were tested: (1) the light transmission of tree shelters differently affects the response of both species, with *Q. ilex* having better planting performance under intermediate or low light transmissivities of tubes, and *P. halepensis* showing an opposite response; and (2) this effect depends on the environmental conditions of the planting area, with higher affinity for lower transmissivities of *Q. ilex* under harsher (warm and semiarid) conditions of the coastal site. The objective of this study is to find a more specific adjustment of the light transmission of tree shelters to functional traits of species and site conditions for Mediterranean areas.

2. Materials and Methods

2.1. Study Sites, Plant Material and Experimental Layout

The experimental study was replicated in two recently abandoned flat cropland sites with contrasted climatic conditions of Mediterranean Spain. Alcázar de San Juan (39°20' N, 3°14' W, 640 m a.s.l., Appendix A Figure A1) is an inland location of central Spain that, according to Köppen's classification, has a continental semi-arid Mediterranean climate with warm summers and cold winters (Bsk type [34]); the annual precipitation is 365 mm, with mean temperature of 14.8 °C and 69 mm of precipitation during summer months (June to September [35]). The other site is located on the south-east coast of the Iberian Peninsula (38°23' N, 0°26' W, 80 m a.s.l., Alicante, Figure A1), which according to Köppen's classification has an arid Mediterranean sub-desertic climate with warm summers and winters (Bsh type [34]); the annual precipitation is 279 mm, with mean temperature of 18.2 °C and 85 mm of precipitation during summer months (June to September [35]). Rainfall during studied period was 659 and 470 mm in Alcázar, and 325 and 284 mm in Alicante (years 2010 and 2011, respectively). Mean temperature was 15.2 and 16.1 °C in Alcázar and 18.0 and 18.9 °C (years 2010 and 2011, respectively) in Alicante. Summer temperature in both sites was similar, but winters of Alicante were much warmer (Figure 1). Rainfall was higher than average in both sites and years. During planting year (2010), summer months (from June to September) were wetter than average, with rainfall higher in Alcázar (145.8 mm) than in Alicante (87.6 mm, Figure 1). Aridity period (the number of months with higher mean temperature than two times rainfall) during planting year (2010) was much longer in Alicante (5 months) than in Alcázar (2 months). During 2011,

summer rainfall was lower than average, but also higher in Alcázar (36.6 mm) than Alicante (15.9 mm), and aridity period was 5 months in both sites (Figure 1).

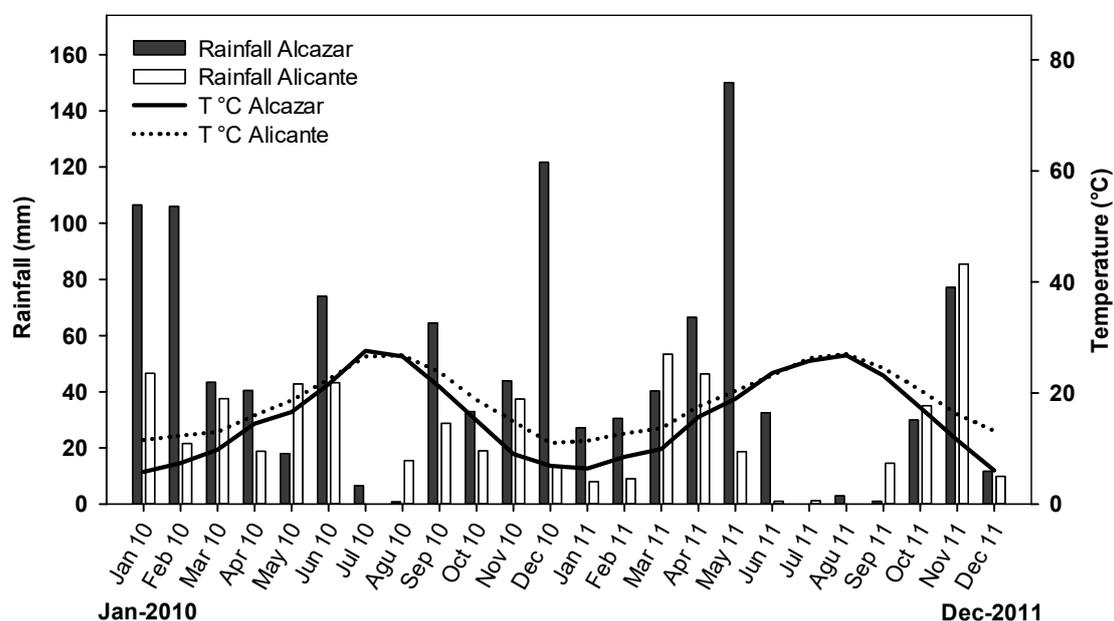


Figure 1. Climatic conditions in the two sites during study period. Rainfall (mm) and mean monthly temperatures (°C). Data from National Agency of Meteorology, Agriculture and Environment Department, Spanish Government.

In both sites, natural soils belong to FAO unit Calcisol, which suggests abundance of calcic carbonate in depth [36]. Three composite soil samples per site were collected at 0–40 cm depth. According to soil analysis from these samples, soil texture in Alcázar de San Juan is essentially silt and silt–loam, with 34.5 ± 2.4 of sand percentage. For Alicante, the results showed clay and clay–silt soils reaching 26.2 ± 1.0 of sand percentage. Both soils have high pH, although electric conductivity of Alcázar was five times higher than in Alicante. Active limestone and carbonate contents are high in both sites, although values for Alicante were superior (Appendix A Table A1).

Both sites were cross subsoiled prior to planting at a 60 cm depth with two rippers 0.5 m apart to reduce soil compaction. After soil preparation, they were planted in February 2010 with one-year-old seedlings of *Pinus halepensis* and *Quercus ilex* from the same stock-lot. Seedlings of *P. halepensis* were raised from seeds of La Mancha provenance [37] and cultivated in 200 cm³ cells. Seedlings of *Q. ilex* were raised from seeds of Extremadurensis provenance [37] and cultivated in 300 cm³ cells. Prior to planting, seedling height, root collar diameter, and shoot and root biomass were 18.4 ± 3.66 cm, 3.67 ± 0.38 mm, 3.85 ± 0.05 g, and 1.88 ± 0.04 g, respectively, for *P. halepensis*, and 18.1 ± 5.91 cm, 3.47 ± 0.60 mm, 3.50 ± 0.16 g, and 4.79 ± 0.15 g, respectively, for *Q. ilex* ($n = 10$). Experimental zone was split in two parts, each one containing one species. In Alcázar de San Juan, seedlings were manually planted 3 × 3 m apart, while in Alicante plants were placed 2 × 1 m apart. Weed control was conducted manually and by herbicide application (Alicante) around each seedling, and by mechanical harrowing in Alcázar de San Juan. Once planted, shelter treatments were randomly assigned to each seedling. The experimental design was a 2 × 5 factorial design, with the following factors and levels: (1) sites (Alcázar de San Juan vs. Alicante), and (2) light transmissivity of the plastic wall of the tube (values around 20, 40, 60 or 80%, and a control not protected by a tree shelter but with a mesh, Figure A2). The wall of the tree shelters was made from plastic material supplied by Repsol Química (Spain). Additives were added to the copolymer base to reach the light transmissivities tested in this experiment, maintaining the red/far red ratio around 1 (neutral shade) [29]. Hand-made tubes using the plastic sheets were circular, single-walled tubes, 50 cm tall ×

10 cm wide, with four ventilation holes facing each other of 2.5 cm width and situated at 18 and 36 cm in height. Tubes were stabilized by fixing a plastic stake with clamps and burying the shelter in the soil. Herbivory protection for control seedlings was achieved by using a mesh tree shelter that consisted of a 60 cm tall \times 15 cm wide cylindrical blue polyethylene net with mesh holes 0.8 \times 0.8 cm (Redplanton, Projar SA, Valencia, Spain) and a light transmission coefficient of 83% [29], similar to the highest transmission tree shelter. Mesh size is big enough to allow normal air circulation, so no differences exist in air temperature and relative humidity between the inside and outside of the mesh shelter [29]. Two hundred fifty seedlings of *P. halepensis* and *Q. ilex* were planted at each site with 50 seedlings per shelter treatments per site.

2.2. Outplanting Performance and Physiological Measurements

Seedling survival, height and root collar diameter were measured in all seedlings two times (November 2010 and November 2011). Stem volume was calculated from height and root collar diameter by applying the formula of a cone. Seedling biomass and root development were evaluated from five randomly chosen seedlings per treatment species and sites (100 plants in total) that were destructively harvested on February 2011. Using small hand tools, root systems were carefully excavated from soil up to a depth of 70 cm and taking care to retain roots $>$ 1 mm diameter. This depth is beyond subsoiling limits, where most new root tissues of planted seedlings presumably thrive [26]. Shoots were separated from the roots at the root collar and all parts were frozen until processing. Roots protruding out of the plug were excised and washed free from soil with tap water, and dry mass of each component (leaves, stem, within plug roots and protruding roots) was determined by oven drying them at 65 °C for 48 h and weighing. Physiological measurements took place at the end of the first summer, in August 2010, in six to ten seedlings per shelter type, species and site. Shoot xylem water potential was measured at predawn (Ψ_{pd}) and at noon (Ψ_{md} 11.00–13.00 solar time). A 3–7 cm healthy twig of the upper third of the plant was excised, wrapped in aluminum foil, kept in sealed polyethylene bags, and refrigerated in an ice box. Water potential was measured within 3 h using a pressure chamber (Model 1000[®], PMS Instruments Company, Albany, OR, USA).

2.3. Statistical Analyses

For survival analyses, Wald chi-squared tests were carried out to determine the significance of the explanatory variables (site and shelter treatments). A Tukey post hoc pairwise comparison was used to compare among the different shelter treatments within a site and species.

Normality and homoscedasticity were tested for morphology, water potential, and dry mass after planting. The 2010 diameter and 2011 height growth from *P. halepensis* and 2010 and 2011 height growth from *Q. ilex* were log-transformed. Additionally, the predawn water potential values from *P. halepensis* and dry mass from *Q. ilex* were log-transformed to meet the assumptions for the analysis. A two-way ANOVA analysis (main factors were species and shelter type) was conducted for each site in all variables except water potential. For water potential, due to much higher variability in the Alicante site, one-way ANOVA, with shelter type as factor, was carried out for each species \times site combination. For all variables, post hoc Tukey tests (α -value = 0.05) were used to assess differences between shelter types within each site and species. The R software version 4.0.2 was used (R Core Team 2020 Vienna, Austria), and the Sigma Plot (2012, Inc., San Jose, CA, USA) was used for the figures.

3. Results

Survival measured at the end of both growing seasons (November 2010 and 2011) was high (above 80% for all shelter \times species \times site combinations at the end of the second season, Table 1). Nevertheless, *Q. ilex* survival was significantly lower at the coastal sub-desertic site (Alicante), while for *P. halepensis* it was generally lower at the continental

semi-arid site (Alcázar) (Tables 1 and 2). In general, mortality rates in those sites and species with the lowest survival at the end of the studied period occurred in the second season, except for control *Q. ilex* in Alicante, which already had a relatively low survival rate (compared to the rest of treatments) after the first season (85.7%). For *P. halepensis*, a significant site \times shelter interaction was observed during the second year of planting (Table 2), as the control plants had significantly lower survival than the tree shelters only in Alcázar, with very high survival in Alicante in all treatments for this species. In contrast, *Q. ilex* survival was very high in Alcázar and lower in Alicante, but with no differences between treatments within each site. In summary, tree shelters improved survival rates compared to control plants, but for each species this effect was dependent on site conditions and the season after planting.

Table 1. Survival rates (% , $n = 50$) in both planting sites at the end of the first (November 2010) and second (November 2011) years after planting for the different shelter types (control mesh plus a gradient of wall light transmissivity ranging from 20 to 80% of incident radiation). Different letters following survival values denote distinct groups in percentage values within the same year and species across the two different sites (binomial model Tukey post hoc analysis, $\alpha = 0.05$).

Treatment	<i>Pinus halepensis</i>		<i>Quercus ilex</i>	
	Alcázar	Alicante	Alcázar	Alicante
First Year				
Control	96.0 ^a	100 ^a	100 ^a	85.7 ^a
LT80%	98.0 ^a	92.0 ^a	100 ^a	94.1 ^b
LT60%	94.0 ^a	100 ^a	100 ^a	94.0 ^b
LT40%	94.0 ^a	100 ^a	100 ^a	96.0 ^b
LT20%	94.0 ^a	98.0 ^a	100 ^a	96.0 ^b
Second Year				
Control	81.8 ^a	100 ^a	100 ^a	81.8 ^a
LT80%	95.5 ^b	91.1 ^a	100 ^a	82.6 ^a
LT60%	85.0 ^b	100 ^a	100 ^a	91.1 ^a
LT40%	92.9 ^b	100 ^a	98.0 ^a	86.7 ^a
LT20%	92.5 ^b	97.7 ^a	98.0 ^a	93.3 ^a

Table 2. Wald test analysis of factor significance of the logistic model of survival evaluated at the end of the first (November 2010) and second (November 2011) years after planting. Significant effects are highlighted in bold.

	d.f	<i>P. halepensis</i>		<i>Q. ilex</i>	
		Chi ² Test	<i>p</i>	Chi ² Test	<i>p</i>
First Year					
Site	1	3.7	0.05	18.5	<0.001
Shelter	4	0.8	0.93	3.7	0.5
Site \times Shelter	4	6.3	0.16	3.7	0.5
Second Year					
Site	1	12.0	0.001	26.6	<0.001
Shelter	4	2.8	0.60	3.3	0.5
Site \times Shelter	4	9.2	0.04	5.2	0.3

In general, seedlings grew more in root collar diameter (RCD) and height in Alcázar during the first year, while the opposite trend was observed in the second year (except for height growth in *Q. ilex*, where no differences between sites were observed, Tables 3 and 4). Growth was generally higher during the second season, except for *Q. ilex* in Alcázar and control *P. halepensis* plants in Alcázar. For both species, control (meshed) seedlings grew less in RCD and height in Alcázar, with differences between control and tree shelter seedlings particularly large for *P. halepensis* in the second growing season. These growth patterns

resulted in smaller control seedlings compared with those growing in tree shelters in Alcázar for both species at the end of the second growing season, whereas in Alicante control seedlings were not different in RCD and stem volume from those in the clearer tubes and were even generally bigger than in the darker tubes (Figure 2). Within tree shelters (i.e., excluding control treatment), the effect of light transmissivity followed a similar trend in both sites and species, with RCD and stem volume lower in the darkest tube (LT20%, Figure 2C–F). However, the RCD and stem volume of *P. halepensis* increased linearly with transmissivity in Alcázar but saturated at LT40% in Alicante. For *Q. ilex*, this saturation was observed at LT40% in both sites. Height and RCD also varied slightly differently depending on the species and site, with the H/RCD relationship decreasing linearly with light transmissivity in Alcázar for *Q. ilex* and in Alicante for *P. halepensis*, but not that clearly in the other two site × species combinations (Figure 2G,H). There was a different H/RCD pattern across species and sites: while this trait was higher in Alcázar than in Alicante for *Q. ilex*, the opposite was true for *P. halepensis*. In conclusion, light transmissivity tended to increase post-planting growth in both species and sites, but in the continental site (Alcázar) light tree shelters (high transmissivity values) improved it greatly compared to control plants.

Table 3. Height and root collar diameter absolute growth (mean ± standard error; $n = 50$ for the first growing season and 35–45 for the second) for both species at the two sites during the first (November 2010) and second (November 2011) years after planting for the different shelter types (control mesh plus a gradient of wall light transmissivity ranging from 20 to 80% of incident radiation). Different letters following height or diameter denote distinct groups for each species, year, and site (Tukey, $\alpha = 0.05$).

Site	<i>Pinus halepensis</i>				<i>Quercus ilex</i>			
	Height (cm)		Root Collar Diameter (mm)		Height (cm)		Root Collar Diameter (mm)	
	Alcázar	Alicante	Alcázar	Alicante	Alcázar	Alicante	Alcázar	Alicante
First Year								
Control	14.3 ± 0.9 ^a	9.5 ± 0.6 ^a	3.0 ± 0.1 ^a	3.1 ± 0.2 ^c	7.7 ± 0.6 ^a	4.0 ± 0.6 ^a	1.1 ± 0.0 ^a	0.8 ± 0.1 ^b
LT80%	25.2 ± 1.4 ^b	15.5 ± 1.2 ^b	4.2 ± 0.2 ^b	2.8 ± 0.2 ^{bc}	14.9 ± 1.0 ^b	5.9 ± 0.8 ^{ab}	1.9 ± 0.1 ^b	1.0 ± 0.1 ^c
LT60%	25.1 ± 1.3 ^b	17.0 ± 1.0 ^{bc}	4.2 ± 0.2 ^b	2.7 ± 0.1 ^{bc}	13.5 ± 0.9 ^b	7.0 ± 1.0 ^b	1.7 ± 0.1 ^b	1.0 ± 0.1 ^c
LT40%	24.9 ± 1.3 ^b	20.7 ± 1.2 ^c	3.3 ± 0.2 ^a	2.6 ± 0.1 ^b	13.7 ± 0.9 ^b	8.0 ± 1.2 ^b	1.4 ± 0.1 ^{ab}	0.9 ± 0.1 ^c
LT20%	22.8 ± 1.3 ^b	19.8 ± 1.1 ^c	2.4 ± 0.1 ^a	1.8 ± 0.1 ^a	13.3 ± 0.9 ^b	8.7 ± 1.0 ^b	1.0 ± 0.0 ^a	0.5 ± 0.0 ^a
Second Year								
Control	4.0 ± 1.0 ^a	37.9 ± 3.0 ^{ab}	1.8 ± 0.2 ^a	7.7 ± 0.4 ^c	2.8 ± 0.6 ^a	8.9 ± 1.5 ^a	0.6 ± 0.1 ^a	2.4 ± 0.4 ^b
LT80%	37.8 ± 2.3 ^c	41.0 ± 2.5 ^{ab}	6.9 ± 0.3 ^d	5.5 ± 0.4 ^b	10.9 ± 0.9 ^b	11.4 ± 1.7 ^a	1.9 ± 0.1 ^b	2.1 ± 0.3 ^b
LT60%	30.7 ± 1.4 ^{bc}	43.4 ± 2.5 ^b	5.0 ± 0.5 ^{cd}	5.0 ± 0.3 ^b	11.3 ± 1.0 ^b	11.5 ± 1.6 ^a	1.5 ± 0.1 ^b	2.4 ± 0.3 ^b
LT40%	28.7 ± 2.9 ^{bc}	39.5 ± 2.2 ^{ab}	5.2 ± 0.4 ^c	5.4 ± 0.3 ^b	12.8 ± 1.2 ^b	9.8 ± 1.4 ^a	1.4 ± 0.1 ^b	2.0 ± 0.3 ^b
LT20%	19.2 ± 2.3 ^b	33.7 ± 1.8 ^a	3.9 ± 0.3 ^b	4.1 ± 0.3 ^a	9.5 ± 0.7 ^b	8.9 ± 1.6 ^a	0.7 ± 0.1 ^a	1.1 ± 0.2 ^a

Table 4. Analysis of variance of root collar diameter (RCDG) and height (HG) absolute growth for each of the two studied species at the end of the first (November 2010) and second (November 2011) years after planting. Degrees of freedom (d.f.), F-statistic (F) and p -values (p) are shown for each of the two factors and their interaction. Significant effects are highlighted in bold.

	d.f.	<i>Pinus halepensis</i>				<i>Quercus ilex</i>			
		HG		RCDG		HG		RCDG	
		F	p	F	p	F	p	F	p
First Year									
Site	1	72.9	<0.001	59.2	<0.001	92.2	<0.001	72.8	<0.001
Shelter	4	28.8	<0.001	18.8	<0.001	10.3	<0.001	13.9	<0.001
Site × Shelter	4	2.0	0.09	6.6	<0.001	2.3	0.05	1.4	0.2
Second Year									
Site	1	73.5	<0.001	12.8	<0.001	0.02	0.88	22.9	<0.001
Shelter	4	14.7	<0.001	10.8	<0.001	22.7	<0.001	11.9	<0.001
Site × Shelter	4	9.4	<0.001	27.9	<0.001	11.0	<0.001	4.5	<0.001

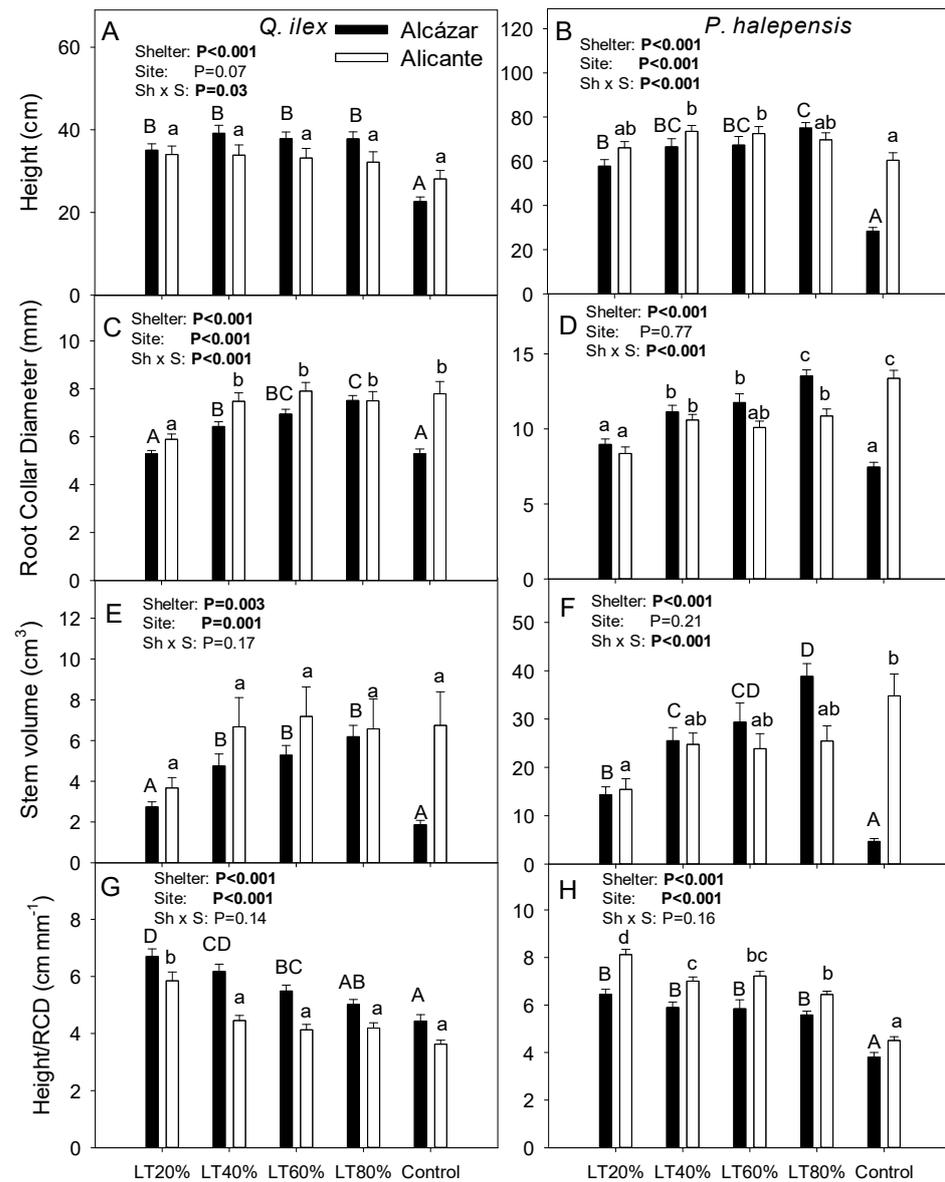


Figure 2. Mean values ($n = 35\text{--}45$) of morphological traits at the end of the second season year (November 2011) of *Q. ilex* and *P. halepensis* seedlings growing under the five different shelter treatments (control mesh plus a gradient of wall light transmissivity ranging from 20 to 80% of incident radiation) in the two sites (Alcázar and Alicante). (A,B) Height; (C,D) Root collar diameter; (E,F) Sem volume; (G,H) Sturdiness quotient. Error bars represent standard error. Different capital letters denote homogenous groups of shelter treatments within Alcázar, while small letters apply to Alicante (Tukey, $\alpha = 0.05$). For each variable and species, the results of the two-way ANOVA (Shelter, Site) are depicted in the corresponding panel.

In general, *Q. ilex* had lower plasticity in biomass accumulation than *P. halepensis* in response to shelter treatments (Figure 3). In the former species, only the biomass of the newly emerged roots from the plug was higher (double) in the clearest tube (LT80%) compared to the rest of the shelter treatments in the continental semi-arid site (Alcázar, Figure 3C). In contrast, differences in height and RCD growth during the first year were reflected in biomass accumulation in *P. halepensis*. Shoot and root biomass increased with shelter transmissivity and was maximum at LT80%, while control plants had significantly less biomass than this shelter type and were not significantly different from those with lower transmissivity (LT60% and below, Figure 3B,D,F). Shoot-to-root ratio was similar across shelter types and sites for both species (Figure 3G,H). Thus, even though *Q. ilex*

biomass responses to light transmission tubes were less plastic than in *P. halepensis*, the clearest tube (LT80%) enhanced the growth of roots outside the plug compared to the rest of the treatments, especially in *Q. ilex* in Alcázar (but not in Alicante for this species).

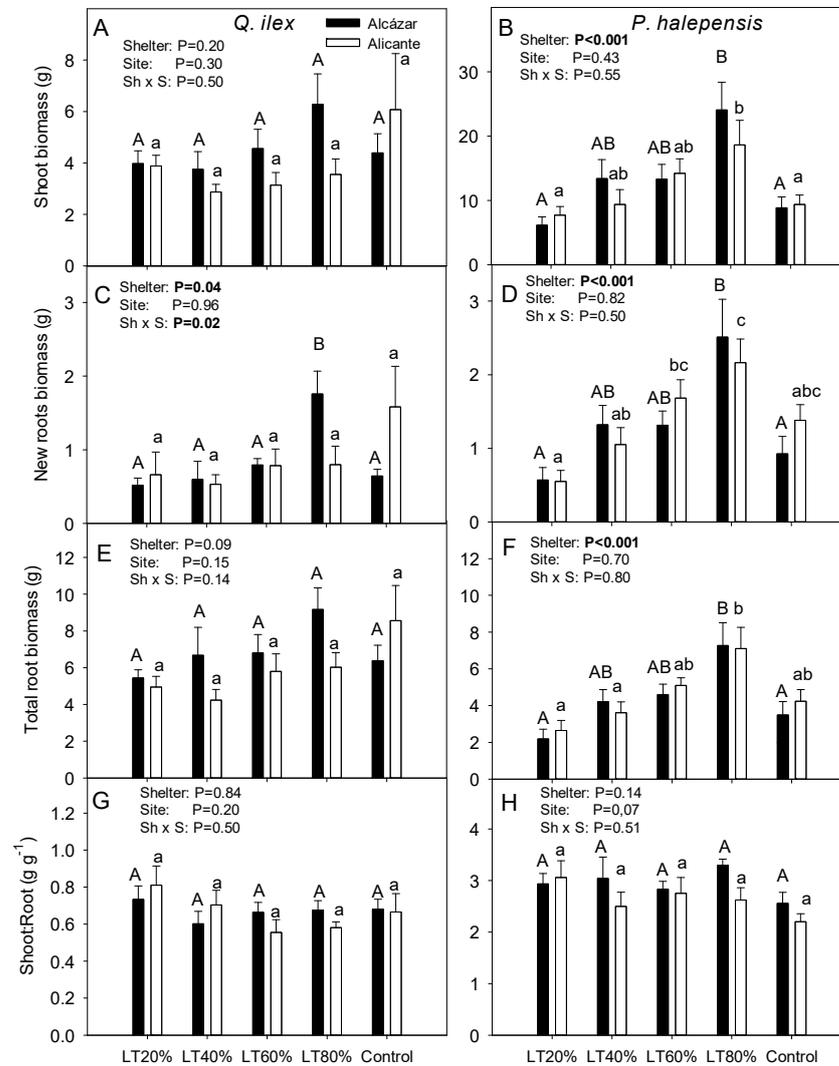


Figure 3. Mean values ($n = 6-10$) of shoot (A,B), newly emerged root (C,D) and total root (emerged + plug, E,F) biomass and shoot-to-root biomass ratio (G,H) of *Q. ilex* (A,C,E,G) and *P. halepensis* (B,D,F,H) seedlings harvested between first and second growing season (February 2011) for the different shelter treatments (control mesh plus a gradient of wall light transmissivity ranging from 20 to 80% of incident radiation) in each site (Alcázar and Alicante). Error bars represent standard error. Different capital letters denote homogenous groups of shelter treatments within Alcázar, while small letters apply to Alicante (Tukey, $\alpha = 0.05$). For each variable and species, the results of the two-way ANOVA (Shelter, Site) are depicted in the corresponding panel.

Predawn (Ψ_{pd}) and midday (Ψ_{md}) water potential at the end of August of the first planting year was lower in the coastal sub-desertic site (Alicante) for both species (Figure 4). For *Q. ilex*, Ψ_{pd} was 1 MPa higher (less negative) in LT80% than the darkest tubes (LT20% and LT40%) and the control seedlings (Figure 4A), but only in Alcázar. In contrast, in Alicante, differences were marginally significant, and Ψ_{pd} decreased with light transmissivity and was lowest (more negative) in control plants. Thus, decreasing light transmissivity attenuated differences in Ψ_{pd} between sites, from 2 MPa in unshaded seedlings (control) to 0.5 MPa in the darkest tubes (LT40% and LT20%, Figure 4A). The midday water potential of *Q. ilex* followed a similar trend as for Ψ_{pd} , but differences were only marginally

significant for Alicante (Figure 4C). For *P. halepensis*, there were no significant differences for any of the two variables in both sites, although Ψ_{md} tended to be more negative with tube transmissivity but higher (less negative) in control plants (Figure 4D). In summary, seedling water status was only clearly ameliorated by LT80% tubes in *Q. ilex* growing in the continental site (Alcázar).

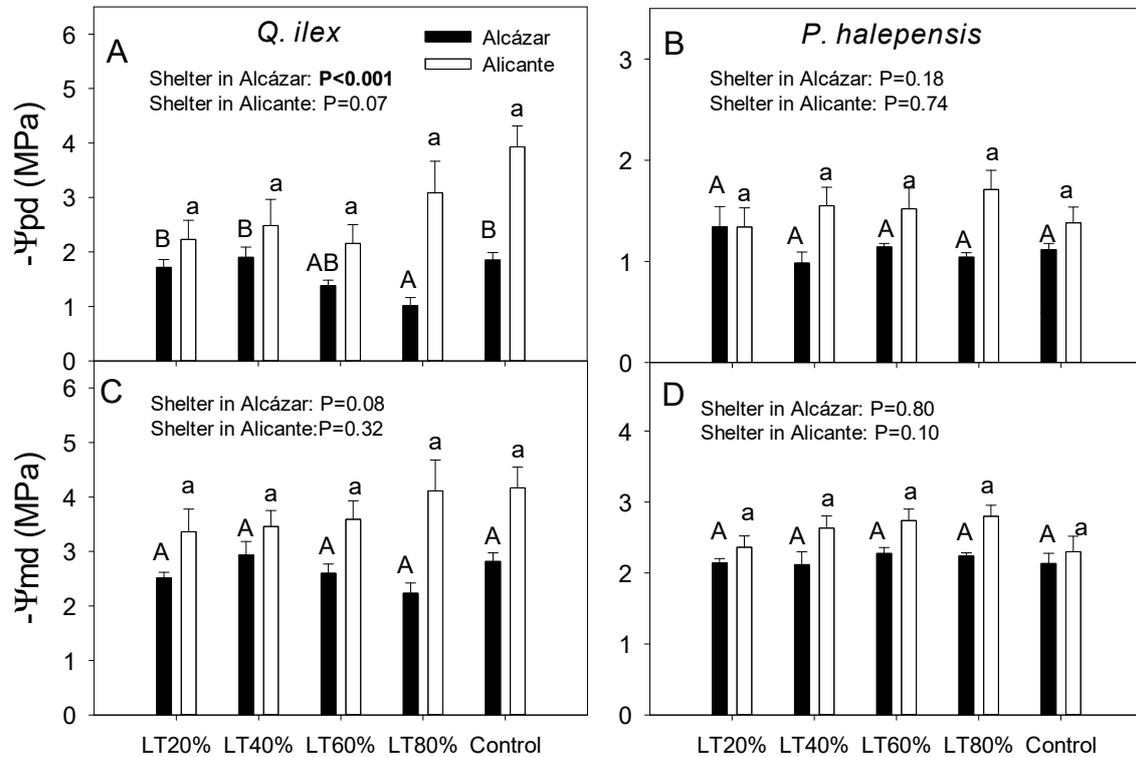


Figure 4. Mean values ($n = 6-10$) of predawn (Ψ_{pd} , A,B) and midday Ψ_{md} , C,D) water potential of *Q. ilex* (A,C) and *P. halepensis* (B,D) seedlings at the end of the first dry season (end of August 2010) for the different shelter treatments (control mesh plus a gradient of wall light transmissivity ranging from 20 to 80% of incident radiation) in each site (Alcázar and Alicante). Error bars represent standard error. Different capital letters denote homogenous groups of shelter treatments within Alcázar, while small letters apply to Alicante (Tukey, $\alpha = 0.05$). For each variable, species, and site, the results of the one-way ANOVA (Shelter) are depicted in each panel.

4. Discussion

The results confirmed our hypothesis that plant responses to tree shelters and their light transmissivity are species and site-specific, which supports the idea that all these factors (presence/absence of tubes, transmissivity, species ecophysiology, site environment) need to be considered carefully when designing post-planting care treatments. However, some of the observations made here highlight the complexity of tree shelter effects in Mediterranean climates and suggest interactive effects on plant physiology of the site environment with other shelter factors beyond light transmissivity.

4.1. Effects of Light Transmissivity of Tree Shelters on Post-Planting Performance

The general effects of light transmissivity on plant morphology and physiology within tree shelters and the differences between species are in agreement with previous studies reporting an increase in biomass accumulation in clearer tubes but more pronounced effects on the shade-intolerant *Pinus halepensis* compared to *Quercus ilex* [21,29]. However, the comparison across sites with contrasting soil water availability (as planned and confirmed by the differences in predawn water potential between the drier sub-desertic Alicante site and continental semi-arid Alcázar) shows the stability of responses across sites of the

shade-intolerant species but a more differentiated response of the shade-tolerant *Q. ilex*. This was particularly evident when assessing the growth of new roots emerging from the plug during the first season after planting (Figure 3C, D), which increased with light transmissivity in all species and site combinations, except for *Q. ilex* in Alicante. This interactive effect of light environment and soil moisture availability has been previously observed on *Quercus suber* gas exchange [38]: under low soil water content (such as in the Alicante site), water stress provokes stomatal closure preventing CO₂ uptake, so increases in light radiation (higher light transmissivity) cannot be translated into increases in carbon gain. Moreover, decreased turgor impedes cell elongation and therefore growth even before any limitation to photosynthesis occurs [39]. Therefore, the lack of responses to light availability in *Q. ilex* in the sub-desertic site might be explained by the lower average water potential experienced in that plot compared to the other site × species combination (below −2.0 and −3.0 MPa for all treatments at predawn and midday, respectively, Figure 4A). Additionally, the higher summer temperature measured within light tubes (LT80% [14]) in seedlings of this species planted in sub-desertic Alicante increased the evaporative demand and thus water stress of seedlings [17], as supported by a marginally lower predawn water potential in LT80% (Figure 4A), which reinforces the feedback process that leads to stomatal closure and contributes to explain the lack of growth response to increasing light in this species × site combination.

This lack of growth response of *Q. ilex* to light transmissivity in the most arid site explained by high water stress contrasts with the strong positive effect of clear tubes (LT80%) on root proliferation in the continental site (Figure 3C). In this site (Alcázar), midday water potential was far above the turgor loss point for this species across treatments (−3.4 MPa [40], Figure 4C). Even though this climatic species is not considered to be plastic in response to light [41], a previous experiment with tree shelters with the same range of transmissivity showed a good response under optimal soil moisture conditions, not very different from *P. halepensis* [29].

The better water status of *Q. ilex* seedlings in clear tubes (Figure 4A) compared to the rest of the treatments could be likely explained by enhanced new root growth (Figure 3C). This suggests that the use of clearer tubes than those typically found in the market, which are similar or even below 20% of transmissivity [13,41], can further enhance post-planting performance in Mediterranean *Quercus* species when planted at continental semi-arid sites. In the same vein, the better water status of *P. halepensis* compared to *Q. ilex* at both sites can also be explained by the greater proliferation of roots after planting, in particular in plants growing in clear tubes (Figure 3C,D). However, the positive response of new root growth to light transmissivity did not translate into a better water status, which was homogenous across treatments (Figure 4B,D). While the lack of differences in Ψ_{md} can be explained by the isohydric water use strategy of this species [32], the lack of differences in Ψ_{pd} across the light transmissivity gradient might indicate higher water consumption in clearer tubes (with high vapor pressure deficit), counterbalancing the greater water acquisition by roots. Thus, species differences in the interactive response of light and soil availability seem to be eventually explained by the pioneer behavior of *P. halepensis* in comparison with the slower growing climatic *Q. ilex*.

4.2. Effect of Tree Shelters versus Non-Shelter Control

We hypothesized that light transmissivity would govern shelter type × site × species interactions [21,42]. However, the poor growth of control seedlings in Alcázar, in contrast with Alicante, in which stem volume growth increased with light environment regardless of tube presence or absence (Figure 2E,F), indicates that these interactions are affected by other microclimatic features occurring inside tree shelters [18].

Different possibilities could explain the greater growth in tubes of both species planted in Alcázar compared to control (mesh) seedlings. First, diurnal warmer temperatures inside tree shelters, in particular in the clearer ones (see previous section of the Discussion), can be beneficial during winter and early spring months, as they activate growth earlier and

keep the growing rate high while the soil is still moist. In coastal Alicante, by contrast, warmer winter and spring temperatures (Figure 1) attenuate the heating effect of solid wall shelters, mostly in *Q. ilex*. The slower shoot growth during the first season in control *P. halepensis* seedlings that was also observed in Alicante (Figure 3B) might indicate that this impact can also be important in warmer sites for pioneer species such as *P. halepensis*. This species is highly plastic in response to air temperature and soil moisture and can resume growth as soon as conditions are favorable [43].

Besides, slightly but significantly lower survival rates of *P. halepensis* in control seedlings at the continental site would also support the hypothesis of temperature-related effects of tubes explaining site \times shelter interactions. This species is relatively cold sensitive [44,45] and, even though they can thrive in inland locations, the optimal conditions are coastal Mediterranean areas with mild winters [46]. In the continental conditions of Alcázar, sub-zero temperatures can occur during sunny days for several days, which can be challenging for this species during early establishment. Even though tree shelters slightly decrease nighttime temperatures [17,18], higher temperature inside tubes during daytime could contribute to avoiding winter damage in continental sites. However, this hypothesis would be disproved by early studies reporting decreasing frost hardiness inside tree shelters for deciduous temperate species, which was more evident in clear tubes [47]. Whether the frost resistance of evergreen Mediterranean species is lost inside clear tree shelters merits further attention.

Once a higher impact of winds in the continental site is discarded [48], as the inland Spanish plateau where the continental site is located is not windier than the coastal location [35], another possible explanation for the lower growth in control plants only observed in Alcázar might be dust deposition. In Alcázar, a sheep herd used to graze in nearby lands, raising a great amount of dust in their movements, which resulted in shoots of control seedlings being covered in dust, while tubes sheltered seedlings from dust covering (personal observation). Dust deposition has been shown to decrease the photosynthesis and growth of several forest species, and this effect is species-specific [49].

5. Conclusions

In general, our results support the use of tree shelters with higher light transmission than those usually commercialized regardless of species and site environment, as they maximize early post-planting growth. However, afforestation managers need to be cautious with species with slow root growth planted in water-limited environments, as higher light availability does not translate into enhanced growth when plants experience water stress.

As observed previously, shelters generally enhanced outplanting performance under Mediterranean conditions, but species \times site interactions suggest that the positive effect cannot be solely attributed to light transmissivity but other microclimatic features that deserve further research to optimize the design of tree shelters.

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Appendix A



Figure A1. Location of experimental plantations in Spain: inland Alcázar de San Juan site (semi-arid Mediterranean with cold winters (Bsk)) and coastal Alicante site (arid Mediterranean sub-desertic with warm summers and winters (Bsh)).

Table A1. Mean \pm standard deviation of soil index from Alcázar and Alicante sites. Three composite soil samples were collected from establishment sites.

	Alcázar	Alicante
pH	8.6 \pm 0.1	8.5 \pm 0.2
Conductivity (mS/cm)	2.5 \pm 0.2	0.5 \pm 0.1
Sand (g/100 g)	34.5 \pm 2.4	26.2 \pm 1.0
Silt (g/100 g)	48.1 \pm 1.9	36.3 \pm 5.7
Clay (q/100 g)	17.5 \pm 1.2	37.5 \pm 6.4
Oxidable organic matter (g/100 g)	1.2 \pm 0.1	1.7 \pm 0.6
Carbonates (CaCO ₃ /100 g)	26.6 \pm 1.1	55.4 \pm 5.7
Active limestone (g/100 g)	9.8 \pm 0.2	13.9 \pm 0.3
Soluble phosphorus (mg/kg)	9.83 \pm 0.8	8.5 \pm 2.7
Soluble potassium (mg/kg)	628.3 \pm 54.9	396.3 \pm 136.4
Soluble calcium (meq/100 g)	72.1 \pm 20	42.7 \pm 1.3
Soluble magnesium (meq/100 g)	2.8 \pm 0.2	4.4 \pm 0.4
Soluble sodium (meq/100 g)	0.06 \pm 0.0	0.6 \pm 0.0

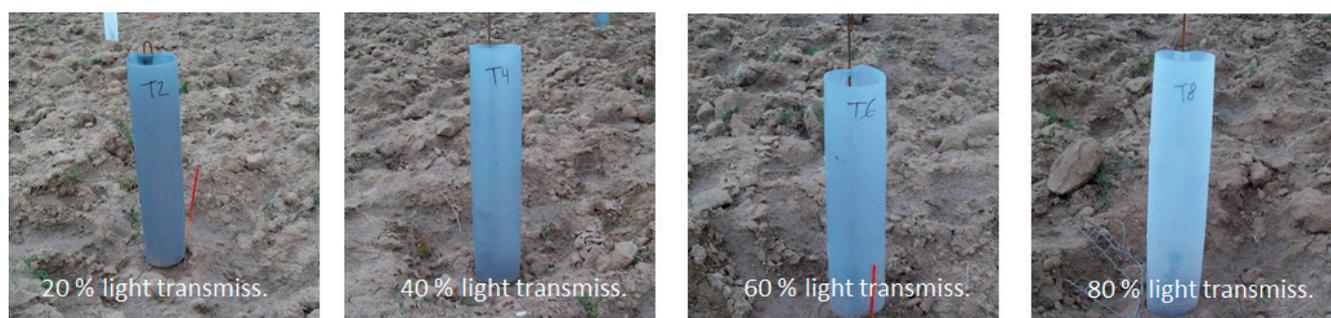


Figure A2. Tree shelters of four light transmissivities (from 20 to 80%) tested in the experiment.

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