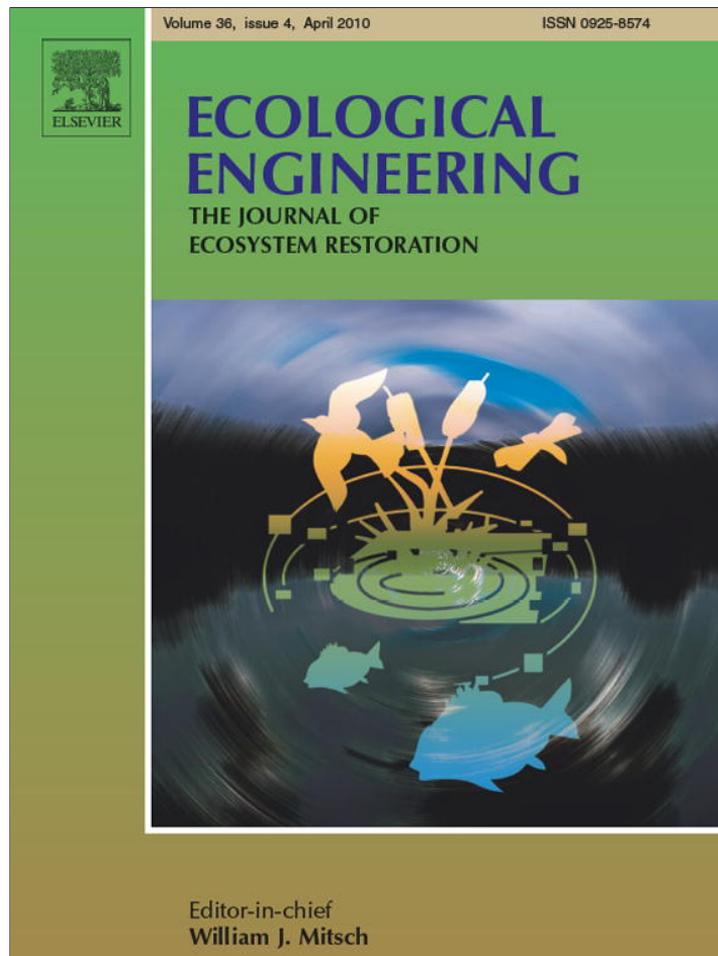


Provided for non-commercial research and education use.  
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Contents lists available at ScienceDirect

Ecological Engineering

journal homepage: [www.elsevier.com/locate/ecoleng](http://www.elsevier.com/locate/ecoleng)

## Evaluation of unventilated treeshelters in the context of Mediterranean climate: Insights from a study on *Quercus faginea* seedlings assessed with a 3D architectural plant model

J. Pemán<sup>a</sup>, J.J. Peguero-Pina<sup>b</sup>, F. Valladares<sup>c</sup>, E. Gil-Pelegrín<sup>b,\*</sup>

<sup>a</sup> Department of Crop and Forest Sciences, University of Lleida, Alcalde Rovira Roure 191, E-25198 Lleida, Spain

<sup>b</sup> Unit of Forests Resources, CITA de Aragón, Apdo. 727, E-50080 Zaragoza, Spain

<sup>c</sup> Centro de Ciencias Medioambientales, CSIC, Serrano 115, E-28006 Madrid, Spain

### ARTICLE INFO

#### Article history:

Received 10 July 2009

Received in revised form 26 October 2009

Accepted 23 November 2009

#### Keywords:

Afforestation  
Treeshelter  
*Quercus faginea*  
Photoinhibition  
Photosynthesis  
Shade  
Y-Plant

### ABSTRACT

Unventilated treeshelters have been widely used to protect seedlings against animal browsing and prevent seed predation by rodents, when the method used is seeding instead of planting. This last method has been a common practice in reforestation with oak species in Spain, because it prevents acorn predation. Although unventilated treeshelters have been widely used in this country, the performance of such devices under Mediterranean climatic conditions is a matter that deserves further investigations. To find out if treeshelters also provide protection against abiotic stress and improve the potential carbon gain in sheltered seedlings, we carried out a light and thermal characterization of the atmosphere inside the treeshelter. Moreover, we assessed the impact of treeshelters on light capture parameters, transpiration and photosynthesis using a Y-Plant model with *Quercus faginea* seedlings. Simulations with Y-Plant have shown that the growth in sheltered seedlings was mainly in spring and was limited by the low light levels. On other hand, in summer, the low values of potential carbon gain and water use efficiency in the sheltered seedlings could limit the seedling establishment. The main limiting factor during this season was the high temperatures. Therefore, the choice of the suitable treeshelter in this region must be carefully evaluated. The treeshelter must warranty high light levels and an optimal air renovation. Photoinhibition risks in leaves of sheltered and control seedlings have not been previously shown.

© 2009 Elsevier B.V. All rights reserved.

### 1. Introduction

Seedling establishment has been considered to be influenced by seedling quality, time of planting and site environmental conditions (Burdett, 1990). However, the relative contribution of any of these factors may change when a particular reforestation program is undertaken. Thus, Palacios et al. (2009) showed that the role of the previous site preparation may be more critical than seedling quality, when reforestation with holm oak under Mediterranean conditions is considered. The response of the seedling to the environmental conditions and its ability to develop roots determines whether a seedling will survive the planting process (Grossnickle, 2005; Pemán et al., 2006). Sites to be restored can show extreme environmental conditions, which alter heat exchange processes and soil water relations in the plant, specially under subtropical

(Wang et al., 2007) or Mediterranean climatic conditions (Tormo et al., 2006; Matesanz and Valladares, 2007).

Soil and atmospheric water deficits are the main limiting factors for photosynthesis and growth, although high irradiance and temperature also contribute to the reduction in leaf CO<sub>2</sub> assimilation; which may ultimately affect seedling establishment (Faria et al., 1998). Thus, shade can be beneficial in hot arid environments by reducing leaf temperatures, transpiration and photoinhibition (Valladares and Pearcy, 1997; Gómez-Aparicio et al., 2004; Estes et al., 2006). The reduction of incident solar radiation in seedlings has been one of the main objectives in afforestation programs in the Mediterranean region. The traditional forest restoration models in Spain suggested the use of pine species in order to facilitate the further establishment of late successional species (Ortigosa et al., 1990), being the shading one of the most important benefits provided by these plantations. Nowadays, the use of treeshelters in afforestation could be a feasible alternative for the introduction of late successional species.

Treeshelters, which are widely used in Spanish afforestation programs, have been revealed as a valuable method for the

\* Corresponding author. Tel.: +34 976 716394; fax: +34 976 716335.  
E-mail address: [egilp@aragon.es](mailto:egilp@aragon.es) (E. Gil-Pelegrín).

improvement of some late successional tree species under limiting ecological conditions, which are common in the reforestation of Mediterranean areas (Navarro Cerrillo et al., 2005). Several different models have been used in these programs, with differential effects on sheltered seedlings (Bellot et al., 2002; Oliet et al., 2003). Previous studies registered the microclimatic conditions inside the treeshelter in Mediterranean regions, which were characterized by a reduction of radiation and wind, increase of temperature and marked daily changes in air humidity and CO<sub>2</sub> concentration (Bellot et al., 2002; Oliet et al., 2003; Navarro Cerrillo et al., 2005). Although the use of ventilated treeshelters reduces the negative influence of air confinement, unventilated treeshelters has been widely used for the reforestation with oak species, due to the extra protection against rodents predation when seeding instead of planting is the method used (Pemán and Gil-Peigrín, 2008).

Several studies show that the use of treeshelters have a clear positive influence on plant survival, shoot height, internode length, leaf area and length, and number of leaves (Fabiao and Silva, 1996; Leroy and Caraglio, 2003) and some other effects on stem diameter and total biomass (Burger et al., 1996; Bellot et al., 2002; Quilhó et al., 2003; Navarro Cerrillo et al., 2005). However, few studies have dealt with the photosynthetic performance of sheltered seedlings, because it is very difficult to measure directly inside the treeshelters (Kjelgren et al., 1997; Bergez and Dupraz, 1997; Dupraz and Bergez, 1999; Oliet and Jacobs, 2007). Although CO<sub>2</sub> concentration inside the treeshelters is considered a major limiting factor for CO<sub>2</sub> assimilation in sheltered seedlings under well-watered conditions (Dupraz and Bergez, 1999; Bergez and Dupraz, 2000), its influence remains unclear when Mediterranean conditions (high temperature and soil water deficit) are considered. In addition, to the extend of our knowledge, there are not published results about the relationship between shoot architecture in sheltered seedlings and (i) the efficiency of light capture and (ii) the increase in susceptibility to photoinhibition under Mediterranean climate conditions. Thus, the study of the effect of the treeshelter on microclimatic conditions affecting plant growth will allow the design of a treeshelter with an improved performance under Mediterranean climate conditions. In this way, the study of the structural and physiological changes, mainly related to the photosynthetic activity, of sheltered plants will also improve the design of the treeshelter.

Several computer models have been developed to simulate the shoot architecture, and accordingly estimate light interception, transpiration and carbon gain by the whole plant (Percy and Yang, 1996). By measurements of shoot geometry, physiological and morphological leaf parameters and environmental conditions, these models can reconstruct a three-dimensional image of the shoot and can estimate the gas exchange parameters and the efficiency in the use of light and water. So, these models could be a useful tool to characterize the sheltered seedlings.

*Quercus faginea* is a Mediterranean oak species that have been widely used with treeshelters in Spanish afforestation programs. Nowadays, more than 2000 ha have been reforested with this species. In this sense, the questions that we raised were: (1) Do summer microclimatic conditions inside treeshelters affect photosynthesis in these plants and, therefore, do they limit their possibilities of establishment in the field? (2) Do treeshelters provide protection against photoinhibition and, therefore, do they improve growth on *Q. faginea* seedlings? (3) How can we modify the microclimatic conditions around the seedlings to improve the growth during the spring without the risk of harmful temperature levels in summer?

## 2. Materials and methods

### 2.1. Plant material

Acorns of *Q. faginea* from “Alcarria y Serranía de Cuenca” (Spain) provenance region (altitude: 800–1200 m, annual precipitation: 460–993 mm) were sown in 500 cm<sup>3</sup> pots in March 2002. A mixture of peat and silt (3:1, v/v) substrate was employed. A slow-release fertiliser (OSMOCOTE® Mini 18 + 6 + 11, 5–6 months of longevity at 21 °C) was incorporated into the bulk substrate in a dose of 3.5 g l<sup>-1</sup>. Seedlings were kept well-watered during the growing period. Twenty-five seedlings were grown outside treeshelters (control) and twenty-five seedlings were grown inside treeshelters (Tubex®, 60 cm tall, 8 cm diameter, unventilated, double-wall, green colour). The study was carried out during the first growth period of the plants in the experimental installations of CITA (Zaragoza, Spain, 41°47'N, 0°50'W), under the meteorological conditions existing in this site. The plants were lifted in October 2002.

### 2.2. Microclimatic conditions of light and temperature inside treeshelters

The microclimatic conditions inside the treeshelters were monitored by measuring air temperature and light transmission, which were then compared with measurements made on control treatment (outside). The measurement period was in spring and summer of 2002. To estimate air temperature we used six double-wired Pt100 temperature probes, with an accuracy of 0.5 °C. We recorded temperatures every 5 min from March to October in three replicates for treatment. The probes were placed 20 cm above the ground, both inside and outside the treeshelters. The probes located outside were installed inside a solar shield. To estimate light transmission inside the shelters we used a UniSpec Spectral Analysis System (PP Systems, Herts, UK) at wavelengths from 306 to 1138 nm, coupled with a cosine receptor in order to collect the total amount of incident radiation from all angles. Light transmission was calculated as the ratio of the incident radiation inside treeshelter to the incident radiation outside. Data were recorded on the spring equinox and summer solstice at noon when light levels were expected to be high and stable, or on the next clear day when these selected days were overcast. To differentiate between the radiation that crosses the wall of the treeshelter and the radiation that penetrates through the top opening of the treeshelter, we measured with and without the wall of the treeshelter covered by a piece of black felt. The measurement taken without the black felt estimated the total radiation. The radiation measured inside treeshelters covered by the black felt represents the zenithal component, which is principally direct solar radiation. The lateral component was estimated by the difference between total radiation and zenithal component. The lateral component is diffuse solar radiation. These measurements were made, without seedlings inside treeshelters, at 0, 20 and 40 cm above the ground, in order to make a better characterization of the light ambient inside treeshelter during the growing period. Three replicates were made in all light measurements.

### 2.3. Modelling of canopy architecture and whole crown gas exchange

The three-dimensional computer model Y-Plant (Percy and Yang, 1996) was used to simulate the shoot architecture, and hence, the light interception, carbon gain and transpiration for whole shoot. The crown architectural information required by Y-Plant was obtained from measurements on four plants randomly selected per treatment (treeshelter and control). Considering the

plant as a series of articulated nodes (intersection point on the shoot of a stem, branch or leaf), the shoot architecture was defined by parameters of shoot (diameter, length, elevation angle and azimuth), branch and petiole (diameter, length, elevation angle and azimuth), and leaf (length, azimuth, elevation angle and orientation). These parameters were measured following the methodology described by Percy and Yang (1996). Carbon gain was calculated by Y-Plant using the values of light interception by the three-dimensional plant crown together with mean values of maximum light-saturated assimilation rate, dark respiration rate, photosynthetic quantum yield and curvature factor of the light response curve and light absorbance measured in single leaves. The assimilation rate of each leaf type was modelled using the rectangular hyperbolic response to photosynthetic photon flux density (*PPFD*) (Thornley, 1976). These parameters were estimated in one fully expanded current-year leaf of 5 unsheltered seedlings with a portable gas exchange system (ADC-LCA4, Analytical Development Co., Hoddesdon, UK). The physiological leaf parameters were only estimated in unsheltered seedlings because inside the treeshelter it became logistically impossible to make gas exchange measurements without altering too much the plant; besides, other studies have not revealed significant changes in photosynthetic capacity under the different environmental conditions imposed by the tube; although the performance is different, the potential performance (i.e. the maximum rates and the shape of the light curve) remains constant (Valladares and Percy, 1998). The version used in this work is an update of the original model (Valladares et al., 2005). The modifications include (i) a leaf energy balance model for computation of leaf temperature and transpiration rates, (ii) the Ball–Woodrow–Berry model (BWB model; Ball et al., 1986) model of stomatal conductance, (iii) the Farquhar–von Caemmerer–Berry model (FvCB model; Farquhar et al., 1980) for CO<sub>2</sub> assimilation, and (iv) the Ögren and Sjöström (1990) model for photoinhibition as implemented by Werner et al. (2001). Values of the maximum carboxylation capacity ( $V_{cmax}$ ) and electron transport capacity ( $V_{jmax}$ ) required for the FvCB model of leaf assimilation were also estimated. Values of  $V_{cmax}$  and  $V_{jmax}$  were derived from assimilation versus CO<sub>2</sub> dependence ( $A/C_i$ ) curves. The FvCB model was used primarily to calculate  $A_{max}$  at light saturation and the current intercellular CO<sub>2</sub> pressure and leaf temperature, and then it was applied to the rectangular light response model. The advantage of this approach is that it gives much better fits in the transition from light limitation to saturation than the FvCB model alone, which often has an unrealistically sharp transition. Simulations with Y-Plant gave the diffuse and direct light interception, assimilation rate and transpiration rate for each leaf in the crown, and subsequently by integration, the corresponding whole crown values. Simulations were carried out at 30 min intervals between sunrise and sunset for spring equinox and summer solstice at 42°N latitude.

Y-Plant estimates the efficiency of light capture as the ratio of the mean *PPFD* absorbed by the crown to the *PPFD* incident on a horizontal surface. This efficiency includes both the effects of the leaf angle and leaf overlap (self-shading) on light interception. Two additional parameters of light capture, projection and display efficiency, provide a quantitative indication of the roles of leaf orientation and shelf shading on light interception. The projection efficiency ( $E_p$ ) is the ratio between the potential projected leaf area and the actual leaf area. The projected leaf area, normal to a direction of incident *PPFD*, is the actual leaf area reduced by the cosine of incidence. This efficiency expresses the angular effects on light interception in the absence of leaf overlap in this direction. The display efficiency ( $E_d$ ) is the ratio of the displayed area to the actual leaf area. The displayed area is the projected area as reduced by leaf overlap. Plant light use efficiency (*LUE*) was calculated as daily carbon gain divided by *PPFD* absorbed, and plant water use

efficiency (*WUE*) was calculated as daily carbon gain divided by transpiration. Both values were estimated for seedlings ( $n=4$ ) in both treatments for the whole crown with Y-Plant.

In order to estimate the effect of a reduction on radiation received by the seedling, without any other modification of the other environmental variables, temperature and air humidity, we simulated with Y-Plant the effect of shading in plants grown inside treeshelters (i.e. leaving air conditions equal to those outside the treeshelter). The lack of a commercial shade mesh with stability in the field prevented its use in this study.

Leaf area was measured using a leaf area meter (Area Measurement System, Delta-T Devices, UK).

#### 2.4. Chlorophyll fluorescence

To characterize the photoinhibition process in sheltered seedlings we used chlorophyll fluorescence techniques. Modulated chlorophyll (Chl) fluorescence was measured on attached leaves of 5 plants per treatment in September 2002 with a PAM 2000 portable fluorometer (Heinz Walz, Effeltrich, Germany). We measured the leaves located at the upper third, medium third and lower third of the plants grown inside the treeshelter. In order to check for possible effects of self-shading, we distinguished between sun and shade leaves in the medium third of the plants. In the upper and lower third, we considered a uniform light environment and therefore we did not distinguish between sun and shade leaves. In plants grown outside the treeshelter, we made a distinction between sun (without self-shading) and shade leaves (with self-shading), but we assumed the influence of the position of the leaf on the shoot to be negligible for the control plants. We measured at 9, 12 and 15 h (solar time), following the methodology described by Morales et al. (2000). Leaves were covered with a black bag and kept in darkness for 30 min to estimate the minimum ( $F_0$ ) and maximum ( $F_M$ ) Chl fluorescence in dark-adapted leaves. The same leaves were used for all subsequent Chl fluorescence measurements. The steady-state value of fluorescence ( $F_S$ ) was measured after the leaves were uncovered and a second pulse of high-intensity white light was used to determine maximum fluorescence in the light-adapted state ( $F_M'$ ). The leaves were covered again and the basic fluorescence after induction was determined ( $F_0'$ ). We also estimated  $F_0$  and  $F_M$  under dark conditions at predawn. The variable fluorescence in the dark ( $F_V$ ) is defined as  $F_M - F_0$ , whereas the variable fluorescence in light-adapted state ( $F_V'$ ) is  $F_M' - F_0'$ . The ratio  $F_V/F_M$  estimates the maximum potential photosystem II (PSII) efficiency in the dark (Abadía et al., 1996). Actual ( $\Phi_{PSII}$ ) and intrinsic ( $\Phi_{exc}$ ) PSII efficiencies were estimated as  $(F_M' - F_S)/F_M'$  and  $(F_V'/F_M')$  respectively. Photochemical quenching ( $qP$ ), which indicates the fraction of light energy that is used for photosynthesis processes, was calculated as  $(F_M' - F_S)/F_V'$  according to Van Kooten and Snel (1990). Non-photochemical quenching ( $NPQ$ ), which indicates the thermal dissipation of the excess of light energy, was calculated as  $(F_M/F_M') - 1$ . To determine the influence of *PPFD* in  $\Phi_{PSII}$  in plants grown both inside and outside treeshelters, we measured  $\Phi_{PSII}$  for several values of *PPFD*: 25, 50, 100, 200, 400, 600, 1000, 2000 and 2500  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  in 5 plants per treatment.

#### 2.5. Statistical analysis

In order to evaluate differences in the morphology of light capture between treatments, morphological data were subjected to analysis of variance (ANOVA) for a completely randomised design. Repeated measures ANOVA was conducted on all chlorophyll fluorescence variables. The effect of the position of the leaves was analyzed independently of the rest of the main factors, treatment and type of leaves. The models used were the following: (i) To

evaluate position effect (upper vs lower):  $Y = \mu + \tau$  (position) +  $\omega$  (time) +  $\tau\omega + \varepsilon$ . (ii) To evaluate treatment (shelter vs control) and type of leaf (sun vs shade):  $Y = \mu + \varphi$  (treatment) +  $\pi$  (type of leaf) +  $\omega$  (time) +  $\varphi\omega + \pi\omega + \varepsilon$ . For the models presented above:  $\mu$ : overall mean,  $\tau$ : fixed effect of position,  $\omega$ : fixed effect of time,  $\tau\omega$ : position by time interaction effect,  $\varphi$ : fixed effect of the treeshelter,  $\pi$ : fixed effect of type of leaf,  $\varphi\omega$ : treeshelter by time interaction effect,  $\pi\omega$ : position by time interaction effect, and  $\varepsilon$ : experimental error. These different analyses are justified by the design conducted and the impossibility to cross all the factors. To evaluate position effects we used the variables that correspond to the lower and upper position of sheltered plants and to evaluate the effect of the treatment and type of leaf we used the variables that correspond with control plant and medium part of sheltered plant. All analyses were performed using standard SAS/STAT procedures (SAS, 2001).

### 3. Results

#### 3.1. Microclimatic conditions

Total light transmission inside treeshelters at the spring equinox ranged from 8% to 24% for photosynthetic active radiation (PAR) (Fig. 1a). At the summer solstice, the solar angle increase reduced the total light transmission inside treeshelters. The principal component was the lateral radiation (Fig. 1b) that showed a similar pattern than the total radiation. The zenithal component was similar in both seasons with a slightly increase in summer (Fig. 1c).

The daily air temperature curves inside the treeshelter (Fig. 2) showed a heating period ( $t_{inside} > t_{outside}$ ) between 9 and 15 h (solar time) at the spring equinox. Immediately afterward the temperature decreased until it matched the ambient temperature during the night. However, at the summer solstice, the air temperature inside the treeshelter increased between 9 and 11 h and was constant between 11 and 18 h. Subsequently, the air temperature decreased quickly and was lower than the ambient temperature over night. The duration of the heating period of the air inside treeshelter was 24 and 11 h at the spring equinox and summer solstice respectively. The maximum temperature registered inside the treeshelter was 52.2 °C in summer (2 August), with values above 50 °C for 145 min. The mean heating of the air inside treeshelter was 16 °C in the spring and 13 °C in the summer. On the other hand, the mean temperature decrease of the air inside in relation to the air outside the treeshelter ( $t_{inside} < t_{outside}$ ) was 0.2 °C in the spring and 4.2 °C in the summer.

#### 3.2. Shoot architecture

Light environment inside the treeshelter modified several structural parameters of the seedlings (Table 1). Sheltered seedlings were three times taller than control seedlings. Furthermore, the number of leaves and the leaf area were respectively 2 and 2.5 times higher in seedlings grown inside the treeshelters. Leaf length and internode length were higher in sheltered seedlings. Root collar diameter and foliar angle, by contrast, were approximately 1.5 times higher in control seedlings. During the experiment we did not observe that the leaves of the sheltered seedlings were in contact with the walls of the treeshelter, and so, we considered that the foliar angle was not influenced by the proximity of the wall.

#### 3.3. Crown light capture and gas exchange

The parameters used in Y-Plant simulations (Tables 2 and 3) were those estimated by the physiological measurements made in leaves of control seedlings and those obtained by microclimatic characterization. Although the values of light transmission were

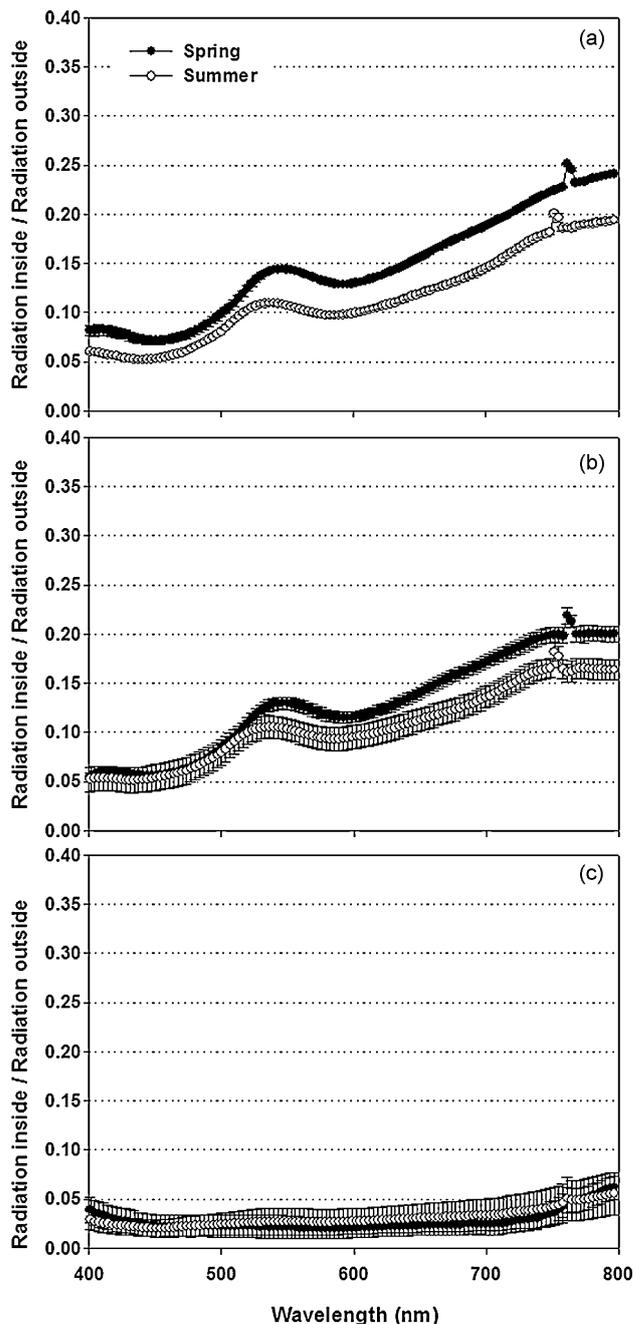


Fig. 1. Total (a), lateral (b) and zenithal (c) composition of light transmitted inside treeshelter in spring equinox (closed symbol) and summer solstice (open symbol). Measurements inside treeshelter were made without seedlings (mean  $\pm$  SE,  $n = 3$ ).

different in spring and summer, we considered the same in order to analyze the influence of the rest of the parameters in the model. The value of light transmission considered is considerably low and the slightly differences registered in both seasons would not be relevant in the model.

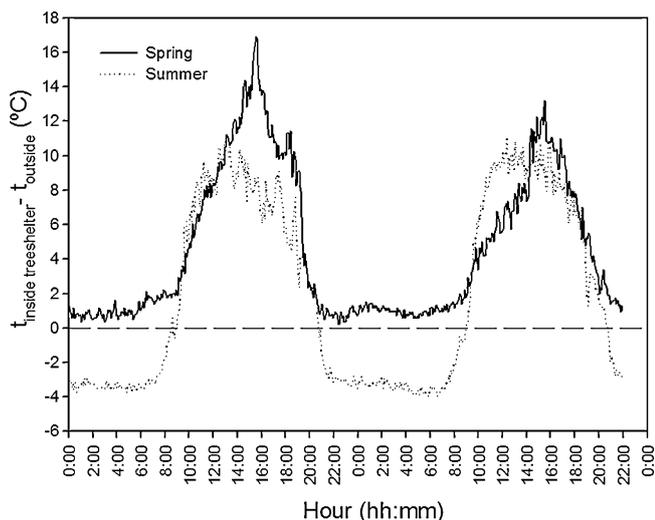
Projected and illuminated leaf area ( $E_p$  and  $E_d$ ) and self-shading area did not show significant differences between the two treatments, for the range of values of solar angle considered for the latitude of the distribution area of *Q. faginea* (Fig. 3).

Simulations with Y-Plant yielded absorbed PPFD values of  $9.4 \pm 0.7$  and  $25.8 \pm 0.7$  mol photons  $m^{-2} d^{-1}$  in treeshelter and control respectively. In spring this value was  $16.3 \pm 0.7$ , whereas in summer it was  $18.9 \pm 0.7$ . The gas exchange variables showed

**Table 1**  
Morphological variables of *Quercus faginea* seedlings after one growing period (mean ± SE, n = 4).

	Sheltered seedlings	Control seedlings	p
Height (cm)	31.36 ± 2.23a	9.91 ± 1.41b	<0.001
Root collar diameter (mm)	2.8 ± 0.2b	4.0 ± 0.4a	<0.05
Number of leaves	34.0 ± 2.1a	17.0 ± 1.2b	<0.001
Internode length (mm)	9.3 ± 0.2a	5.7 ± 0.6b	<0.05
Leaf area (cm <sup>2</sup> )	120.7 ± 12.8a	46.2 ± 20.8b	<0.001
Leaf angle (°)	19.0 ± 0.9b	26.9 ± 1.4a	<0.001
Leaf length (mm)	32.1 ± 0.9a	26.2 ± 1.9b	<0.05

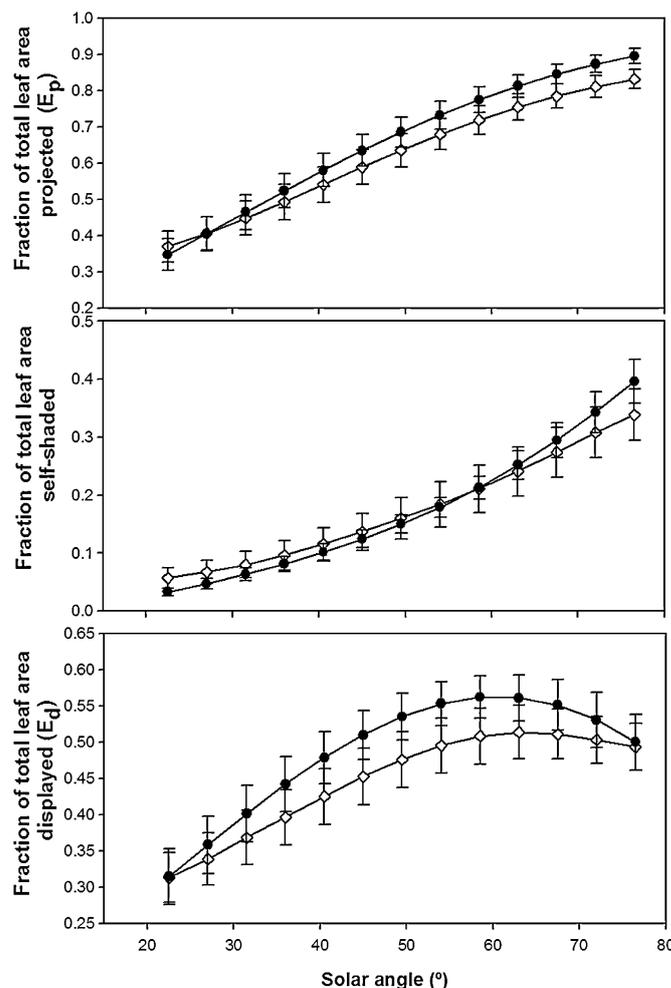
Different letters denote significant differences (Tukey Test, n = 4).



**Fig. 2.** Heating variation of the air inside treeshelters in spring equinox (continuous line) and summer solstice (dotted line) for a period of 48 h.

**Table 2**  
Physiological leaf parameters estimated in control *Quercus faginea* seedlings (mean ± SE; n = 5).

Parameters	Value
Maximum light-saturated assimilation rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	11.5 ± 0.8
Dark respiration ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	-1 ± 0.07
Photosynthetic quantum yield	0.06 ± 0.004
Curvature factor	0.81 ± 0.006
Leaf absorptance	0.86 ± 0.06
Leaf reflectance	0.08 ± 0.006
Maximum carboxylation capacity ( $V_{cmax}$ )	95 ± 6.7
Electron transport capacity ( $V_{jmax}$ )	130 ± 9.1
Photon yield electron transport	0.15 ± 0.011



**Fig. 3.** Projection efficiency ( $E_p$ ) (a), self-shading (b) and display efficiency ( $E_d$ ) (c) as a function of solar angle for *Quercus faginea* seedlings estimated with Y-Plant (mean ± SE, n = 4).

**Table 3**  
Environment parameters used in Y-Plant simulations.

	Spring		Summer	
	Outside	Inside treeshelter	Outside	Inside treeshelter
Temperature (°C) (daily range)	10–23	10–35	20–38	20–45
Relative humidity (%) (daily range) <sup>a</sup>	38–80	48–90	25–45	12–45
Hour minimum temperature	6:30 AM	6:30 AM	5:30 AM	5:30 AM
Hour maximum temperature	13:00 PM	13:00 PM	14:00 PM	14:00 PM
CO <sub>2</sub> concentration (ppm) (daily mean) <sup>a</sup>	360	370	360	370
Wind speed (m s <sup>-1</sup> )	1	1	1	1
Photon flux density (mol m <sup>-2</sup> d <sup>-1</sup> )	2450	735	2450	735
Diffuse coefficient	0.1	1	0.1	1

<sup>a</sup> Data did not estimate. Values were obtained from other studies (Oliet and Jacobs, 2007).

**Table 4**  
Environment parameters used in Y-Plant shading simulation.

	Spring	Summer
Temperature (°C) (daily range)	10–23	20–38
Relative humidity (%) (daily range) <sup>a</sup>	38–80	25–45
Hour minimum temperature	6:30 AM	5:30 AM
Hour maximum temperature	13:00 PM	14:00 PM
CO <sub>2</sub> concentration (ppm) (daily mean) <sup>a</sup>	360	360
Wind speed (m s <sup>-1</sup> )	1	1
Photon flux density (mol m <sup>-2</sup> d <sup>-1</sup> )	735	735
Diffuse coefficient	1	1

<sup>a</sup> Data did not estimate. Values were obtained from other studies (Oliet and Jacobs, 2007).

significant differences ( $p < 0.001$ ) for the interaction between treatment and season (Fig. 4). Transpiration and potential net assimilation did not register differences in spring, but in summer the values were about 42% and 56% lower in sheltered seedlings than in control seedlings, respectively (Fig. 4a and b). The sheltered seedlings were more efficient in *LUE* and *WUE* than control seedlings in spring (Fig. 4c and d). In summer *LUE* was similar in control and sheltered seedlings, while *WUE* in control seedlings were about 62% higher than in sheltered seedlings.

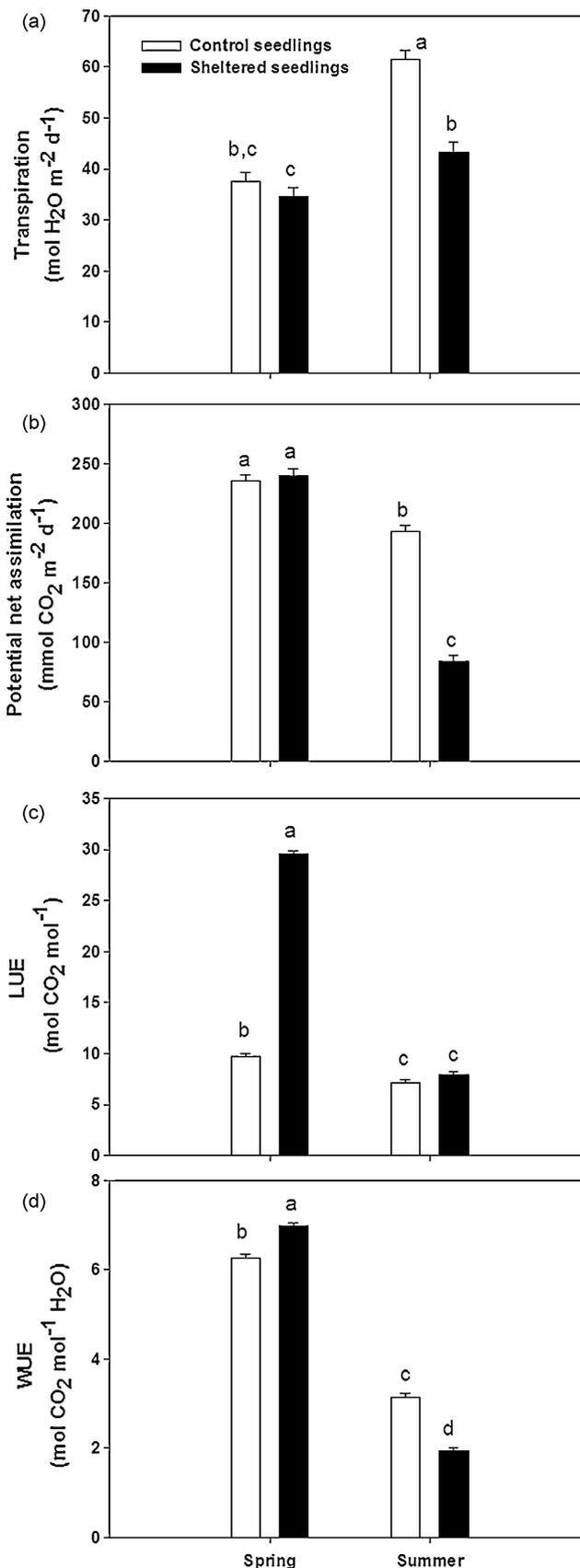
In the study of a daily cycle, during spring, the sheltered seedlings showed similar values of potential carbon gain and transpiration than control seedlings (Fig. 5). Only at the beginning of the morning the potential carbon gain was higher in the sheltered seedlings. On the other hand, in summer, the transpiration and potential carbon gain in control seedlings were higher than sheltered ones. While the transpiration rate of the control seedlings reached  $3 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$  at midday, the transpiration rate of the sheltered seedlings remained fairly constant around  $1 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ . The potential carbon gain of the control seedlings reached  $9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  at the end of the morning falling progressively thereafter. In sheltered seedlings the potential carbon gain reached  $7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  at eight o'clock (solar time) and then registered negative values during the afternoon.

The simulation of single effect of shading (Table 4) showed significant differences ( $p < 0.001$ ) for the interaction between treatment and season (Fig. 6). During summer, the shaded seedlings registered the highest values for the potential net assimilation, *LUE* and *WUE* (around twofold higher than sheltered seedlings for all the variables and 1.4 and 2.2 higher than control seedlings for *LUE* and *WUE* respectively). During the spring, the potential net assimilation was 25% and 27% lower in shaded seedlings than control and sheltered seedlings respectively; and *WUE* was about 16% and 29% higher in shaded seedlings than in sheltered and control seedlings, respectively.

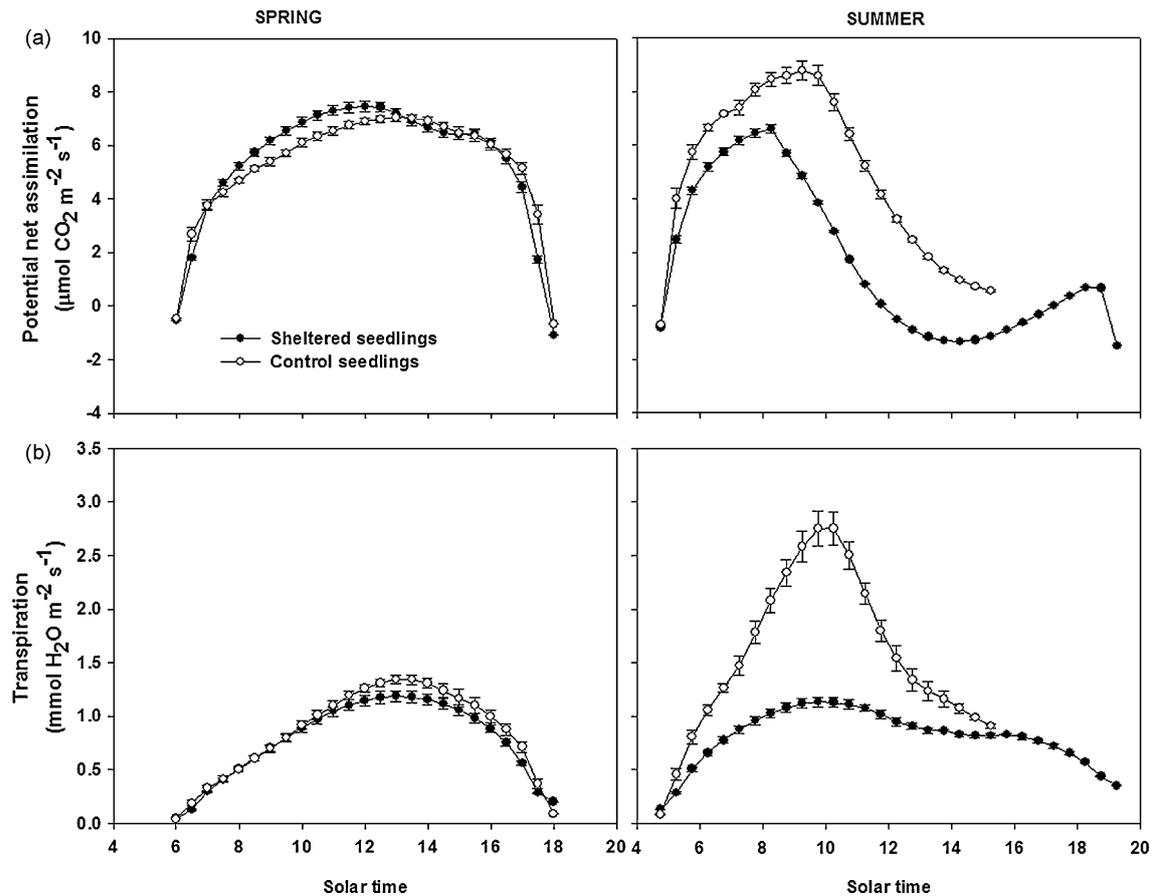
During summer, the potential net assimilation was similar in control and shaded seedlings and around twofold higher than sheltered seedlings. In this season, the shaded seedlings registered values of *LUE* and *WUE*, 1.4 and 2.2, are higher than control seedlings respectively. During the spring, the shaded seedlings registered lower values in potential net assimilation and *LUE* than sheltered seedlings, 27% in both variables, but, as in summer, showed the highest values of *WUE*.

### 3.4. Chlorophyll fluorescence

There were no significant differences in fluorescence parameters between leaf types (sun and shade) and between leaf positions along the shoot (upper third leaves and lower third leaves).  $F_V/F_M$  at predawn was around  $0.80 \pm 0.02$  for control seedlings and around  $0.82 \pm 0.01$  for sheltered seedlings. There were no significant differ-



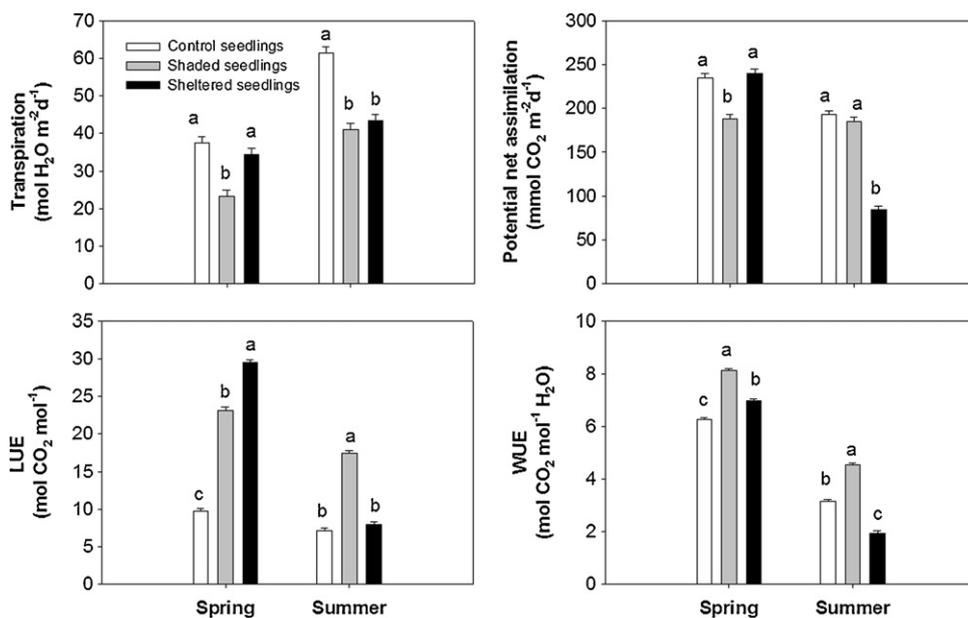
**Fig. 4.** Transpiration, potential net assimilation, light use efficiency (*LUE*) and water use efficiency (*WUE*) in control and sheltered *Quercus faginea* seedlings for different seasons simulated with Y-Plant (mean  $\pm$  SE,  $n = 4$ ). Different letters denote significant differences ( $p < 0.001$ ).



**Fig. 5.** Daily potential net assimilation and transpiration in control and sheltered *Quercus faginea* seedlings for spring equinox and summer solstice estimated with Y-Plant (mean  $\pm$  SE,  $n=4$ ).

ences in the diurnal time course of  $F_V/F_M$ . The diurnal time course of  $\Phi_{PSII}$  and  $\Phi_{exc}$  for sheltered and control seedlings exhibited a midday reduction in both parameters, although later, it reached its maximum value at 15 h (Fig. 7). This reduction was higher in the

control seedlings. As expected,  $NPQ$  exhibited the reverse pattern, with the highest values at midday, 1.91, and the minimum at 15 h, 1.12. The  $NPQ$  was 1.77 for sheltered seedlings, whereas it was 1.22 for control seedlings.



**Fig. 6.** Transpiration, potential net assimilation, light use efficiency ( $LUE$ ) and water use efficiency ( $WUE$ ) in control, shaded and sheltered *Quercus faginea* seedlings for different seasons simulated with Y-Plant (mean  $\pm$  SE,  $n=4$ ). Different letters denote significant differences ( $p < 0.001$ ).

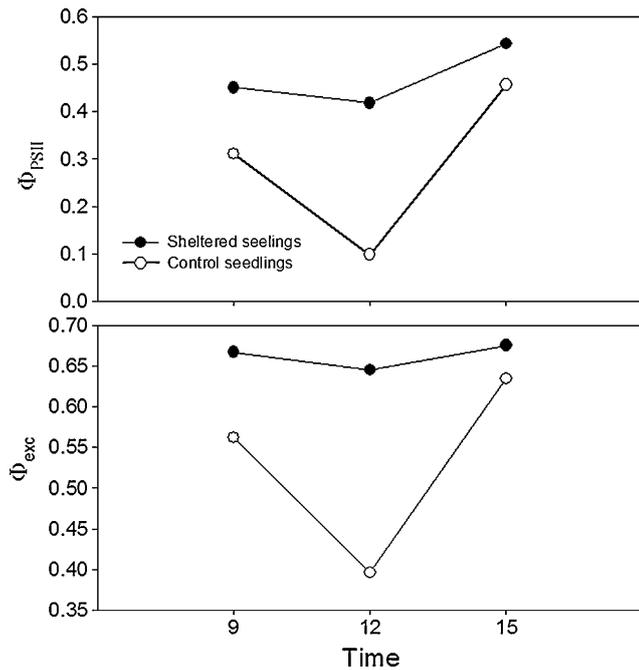


Fig. 7. Diurnal time course of quantum yield of PSII ( $\Phi_{PSII}$ ) and intrinsic efficiency of PSII ( $\Phi_{exc}$ ) in *Quercus faginea* seedlings grown inside treeshelters and outside (control) (mean  $\pm$  SE,  $n = 5$ ).

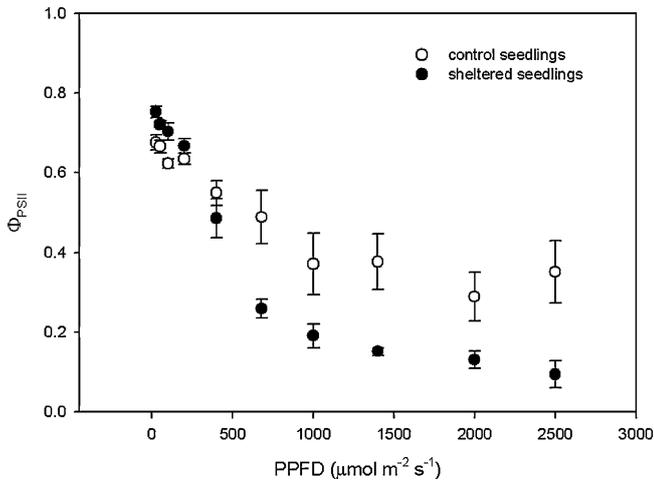


Fig. 8. Relationship between photosynthetic photon flux density (PPFD) and quantum yield of PSII ( $\Phi_{PSII}$ ) in *Quercus faginea* seedlings (mean  $\pm$  SE,  $n = 5$ ).

$\Phi_{PSII}$  decreased with increasing PPFD in both shoot architectures;  $\Phi_{PSII}$  was significantly higher in control than in sheltered seedlings for the different photosynthetic photon flux densities (Fig. 8). The decrease in  $\Phi_{PSII}$  with PPFD was more accentuated in sheltered than in control seedlings:  $\Phi_{PSII}$  decreased by 81% from 400 to 2500  $\mu\text{mol photons m}^{-2} \text{s}^{-1}$  in the former, while it decreased only by 36% in the latter.

#### 4. Discussion

This study has confirmed the previous findings with regard to the low level of solar radiation inside treeshelters (Potter, 1991; Bergez, 1993; Kjelgren and Rupp, 1997; Bellot et al., 2002; Sharew and Hairston-Strang, 2005;) and the inverse relationship between solar angle and radiation inside the treeshelter (Bergez, 1993; Bergez and Dupraz, 2009). Therefore, when the solar angle is low,

the radiation is perpendicular to the treeshelter and the transmissivity of the wall is high, causing the difference registered in radiation inside treeshelter between seasons. In addition, the low PPFD values measured inside the treeshelter reduces the  $\text{CO}_2$  assimilation and could increase the susceptibility to biotic factors (Kozłowski et al., 1991). The diffuse radiation is the principal component inside the treeshelter, whereas the direct radiation was only significant at very high solar angles. The advantages of the diffuse radiation inside the treeshelter include higher LUE and protection against photoinhibition processes.

Furthermore, the inverse relationship between solar angle and radiation inside the treeshelter explained the higher rates of air heating inside treeshelter during the spring, and the quick increase of temperature at the beginning of the morning (Bergez, 1993; Bergez and Dupraz, 2009). Temperature increment suggests that treeshelters could enhance growth in sheltered seedlings during the spring, while in summer the high temperatures registered within treeshelter could limit the photosynthetic activity (Seeley and Kammereck, 1977) and induce damage due to heat stress.

The morphological variables of the shoot in sheltered seedlings suggest that plants grown inside a treeshelter could develop a shade acclimation modulated by the intensity and duration of shading. This idea is supported by the increase of height, internode length, number of leaves, leaf area and length, and the reduction in root collar diameter and leaf angle. These results agree with previous studies that have reported that sheltered seedlings were 1.3–3.2 times taller than control plants (Ponder, 1991; Burger et al., 1992; Kittredge et al., 1992), had a root collar diameter 1.4–1.6 times smaller than control plants (Burger et al., 1992; Kjelgren et al., 1997) and had more leaves or longer internodes than control plants (Kittredge et al., 1992; Bellot et al., 2002; Leroy and Caraglio, 2003). Moreover, Valladares et al. (2000) found that *Quercus ilex* and *Quercus coccifera* shaded plants had longer internodes and larger total leaf area but had lower leaf angle than their sun counterparts in both oak species. Leaf angle decreased in sheltered seedlings, but it was higher than the values reported for *Heteromeles arbutifolia* by Valladares and Percy (1999). Leaf angle is a structural parameter with great plasticity that is used to maximize carbon gain and minimize the time that leaf surfaces are exposed to saturating light (Valladares and Percy, 1999; Falster and Westoby, 2003). High leaf angles reduce light capture when solar angle increases, showing its minimum values at midday and in summer in relation to daily and seasonal variation respectively. The benefits of high leaf angles reported by different studies include an increase in midday WUE, a decrease in overheating risk and a decrease in the susceptibility of photoinhibition processes (Cowan, 1982; King, 1997).

Although no significant differences were found for displayed, projected and self-shading leaf areas between treatments, seedlings grown inside treeshelters showed a tendency to increase the self-shaded leaf area for maximum solar angles, due to their high leaf number and low leaf angle. Leaf area values subjected to solar radiation of about 0.4 corresponded with avoiding strategies of evergreen shrubs that tend to sacrifice high radiation rates in order to maintain a high productive capacity. The reduction in daily PPFD absorbed in sheltered seedlings was due to a reduction in PPFD inside the treeshelter.

Seasonal course of transpiration rates showed the influence of temperature in this parameter, as a consequence of changes in respiration rate. The daily course of the transpiration in summer is similar to the pattern registered by Bergez and Dupraz (1997) in *Prunus avium*. These authors found a constant transpiration rate around a 1  $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$  in the sheltered seedlings. The low values of transpiration rates of the sheltered seedlings could be explained to restricted air movement in the shelters that severely reduced boundary layer conductance (Kjelgren et al., 1997). These

low transpiration rates may help conserve water reserves of the soil, and delay the occurrence of a water deficit for the seedling during the dry season (Bergez and Dupraz, 1997).

The environmental conditions inside the treeshelter did not improve assimilation rates, as compared to the outside environment in spring, due to a temperature increase. The low values of light transmission considered in the model (30%) could be the principal limitation; therefore, treeshelters with high light transmittance could increase the potential carbon gain in this season where the temperatures registered do not reach supraoptimal levels. In this sense, simulations with Y-Plant with values of light transmission about 50% (data not shown) registered values of potential net assimilation about 28% higher than values of light transmission about 30%. On the other hand, in summer, potential carbon gain was significantly lower in sheltered than in control seedlings. These results agree with those found for *Fraxinus pennsylvanica* by Kjelgren et al. (1997), with a reduction between 50% and 70% in net photosynthesis in relation to the outside environment. These low values could be explained by the daily course of potential carbon gain, which showed positive values at early morning hours when the optimal temperature for assimilation process is registered (Oliet and Jacobs, 2007) and negative values at midday. Therefore the potential carbon gain in this season could be due to the photosynthetic activity at the beginning of the morning, when the temperature is similar to the optimal for assimilation process but the light level is low, yet. The negative values registered in summer by the daily course of potential carbon gain at midday could explain the CO<sub>2</sub> concentration increase inside the treeshelter observed by other authors (Frearson and Weiss, 1987; Mayhead and Jones, 1991).

The reduction in the risk of heat stress and the CO<sub>2</sub> concentration increase in summer suggest the relevance of an optimal air renovation inside treeshelter (Bergez, 1993; Dupraz and Bergez, 1999; Bergez and Dupraz, 2000). Light reduction, without further effects on the microclimate inside the treeshelter, could be a good option in warm climates. In this sense, shading simulations with Y-Plant have demonstrated that the only effect of shading improves the potential net assimilation and *LUE* and *WUE* in summer of the seedlings, which in xeric environments may improve seedling establishment (Retana et al., 1999; Cardillo and Bernal, 2005). New commercial products such as light shading mesh-tube could be a feasible alternative, because it only changes incident solar radiation without changes in temperature.

In conclusion, the treeshelters modify significantly the shoot architecture of the sheltered seedlings. The Y-Plant simulations do not show an increase in potential carbon gain during the spring in sheltered seedlings, due to shade and air temperature increase. However, in summer, the high temperature inside treeshelters induces a decrease in net photosynthesis and *WUE*. It should be noted that water stress could make these decreases more intense (Peguero-Pina et al., 2009). Because of the experimental complexity, the effect of a progressive drought on seedling physiology has not been incorporated in this study. However, this fact deserves further investigation in order to reach more realistic conclusions. The severity of heat stress will determine the effects on seedling performance. Shade without modification of other microclimatic parameters could be a good choice in warm environments. Photoinhibition risks in sheltered or control seedling leaves have not been observed after their first growing period.

## References

- Abadía, A., Gil, E., Morales, F., Montañes, L., Montserrat, G., Abadía, J., 1996. Marcescence and senescence in a submediterranean oak (*Quercus subpyrenaica* E.H. del Villar): photosynthetic characteristics and nutrient composition. *Plant Cell Environ.* 19, 685–694.
- Ball, J.T., Woodrow, I.E., Berry, J.A., 1986. A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In: Biggins, J. (Ed.), *Progress in Photosynthesis Research*. Martinus Nijhoff, Dordrecht, pp. 221–224.
- Bellot, J., Ortiz de Urbina, J.M., Bonet, A., Sánchez, J.R., 2002. The effects of treeshelters on the growth of *Quercus cocifera* L. seedlings in a semiarid environment. *Forestry* 75 (1), 89–106.
- Bergez, J., 1993. Influence de protections individuelles a effet de serre sur la croissance de jeunes arbres. Interprétations physiologiques et perspectives d'amélioration des protections. Ph.D. Thesis, Université Montpellier II.
- Bergez, J., Dupraz, C., 1997. Transpiration rate of *Prunus avium* seedlings inside an unventilated treeshelter. *Forest Ecol. Manage.* 97, 255–264.
- Bergez, J., Dupraz, C., 2000. Effect of ventilation on growth of *Prunus avium* L. seedlings in treeshelter. *Agric. Forest Meteorol.* 104 (3), 199–214.
- Bergez, J.E., Dupraz, C., 2009. Radiation and thermal microclimate in tree shelter. *Agric. Forest Meteorol.* 149 (1), 179–186.
- Burdett, A.N., 1990. Physiological process in plantation establishment and the development of specifications for forest planting stock. *Can. J. Forest Res.* 20, 415–427.
- Burger, D., Svihra, P., Harris, R., 1992. Treeshelters use in producing container grown trees. *Hort Sci.* 27, 30–32.
- Burger, D., Forister, G.W., Kiehl, P.A., 1996. Height, calliper growth, and biomass response of ten shade tree species to treeshelters. *J. Arboric.* 22 (4), 161–166.
- Cardillo, E., Bernal, C.J., 2005. Morphological response and growth of cork oak (*Quercus suber* L.) seedlings at different shade levels. *Forest Ecol. Manage.* 222 (1–3), 296–301.
- Cowan, I., 1982. Regulation of water use in relation to carbon gain in higher plants. *Ency. Plant Physiol.* 12, 589–612.
- Dupraz, C., Bergez, J., 1999. Carbon dioxide limitation of the photosynthesis of *Prunus avium* L. seedlings inside an unventilated treeshelter. *Forest Ecol. Manage.* 119, 89–97.
- Esteso, J., Valladares, F., Camarero, J.J., Gil-Pelegrín, E., 2006. Crown architecture and leaf habit are associated with intrinsically different light-harvesting efficiencies in *Quercus* seedlings from contrasting environments. *Ann. Forest Sci.* 63, 511–518.
- Fabiao, A., Silva, I., 1996. Effect of individual tree shelters on early survival and growth of a *Quercus faginea* plantation. *Ann. Inst. Sperimentali Selvicoltura* 27, 77–82.
- Falster, D.S., Westoby, M., 2003. Leaf size and angle vary widely across species: what consequences for light interception? *New Phytol.* 158, 509–525.
- Faria, T., Silvério, D., Breia, F., Cabral, R., Abadía, A., Abadía, J., Pereira, J.S., Chaves, M.M., 1998. Differences in the response of carbon assimilation to summer stress (water deficits, high light and temperature) in four Mediterranean tree species. *Physiol. Plant* 102, 419–428.
- Farquhar, G.D., Caemmerer, S., Berry, J.A., 1980. A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C3 species. *Planta* 149, 78–90.
- Frearson, K., Weiss, N.D., 1987. Improved growth rates within treeshelters. *Q. J. For.* 81 (3), 184–187.
- Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J., Baraza, E., 2004. Applying plant positive interactions to reforestation in Mediterranean mountains: a meta-analysis of the use of shrubs as nurse plants. *Ecol. Appl.* 14, 1128–1138.
- Grossnickle, S.C., 2005. Importance of root growth in overcoming planting stress. *New Forests* 30, 273–294.
- King, D.A., 1997. The functional significance of leaf angle in *Eucalyptus*. *Am. J. Bot.* 45, 619–639.
- Kittredge, D.B., Mattew, J.K., Ashton, P.M.S., 1992. The use of treeshelters with northern red oak natural regeneration in southern New England. *NJAF* 9, 141–145.
- Kjelgren, R., Montagne, D., Rupp, L., 1997. Establishment in treeshelters. II. Effects of shelters colour on gas exchange and hardiness. *Hort Sci.* 32 (7), 1284–1287.
- Kjelgren, R., Rupp, L., 1997. Establishment in tree shelters. I. shelters reduce growth, water use and hardiness, but not drought avoidance. *Hort Sci.* 32 (7), 1281–1283.
- Kozłowski, T., Kramer, P.J., Pallardy, S.G., 1991. *The Physiological Ecology of Woody Plants*. Academic Press, San Diego.
- Leroy, C., Caraglio, Y., 2003. Effect of tube shelters on the growth of young Turkish pines (*Pinus brutia* Ten., *Pinaceae*). *Ann. Forest Sci.* 60, 549–556.
- Matesanz, S., Valladares, F., 2007. Improving revegetation of gypsum slopes is not a simple matter of adding native species: insights from a multispecies experiment. *Ecol. Eng.* 30 (1), 67–77.
- Mayhead, J.D., Jones, D., 1991. Carbon dioxide concentrations within tree shelters. *Q. J. For.* 85, 228–232.
- Morales, F., Belkhdja, R., Abadía, A., Abadía, J., 2000. Photosystem II efficiency and mechanisms of energy dissipation in iron-deficient, field-grown pear trees (*Pyrus communis* L.). *Photosynth. Res.* 63 (1), 9–21.
- Navarro Cerrillo, R.M., Fragueiro, B., Ceaceros, C., Del Campo, A., De Prado, R., 2005. Establishment of *Quercus ilex* L. subsp. *ballota* [Desf.] Samp. using different weed control strategies in southern Spain. *Ecol. Eng.* 25, 332–342.
- Ögren, E., Sjöström, M., 1990. Estimation of the effect of photo-inhibition on the carbon gain in leaves of a willow canopy. *Planta* 181, 560–567.
- Oliet, J.A., Navarro Cerrillo, R.M., Contreras, O., 2003. Evaluación de la aplicación de mejoradores y tubos en repoblaciones forestales. *Consejería de Medio Ambiente de la Junta de Andalucía*, 234 pp.
- Oliet, J.A., Jacobs, D.F., 2007. Microclimatic conditions and plant morphophysiological development within a tree shelter environment during establishment of *Quercus ilex* seedlings. *Agric. Forest Met.* 144, 58–72.

- Ortígoza, L., García-Ruiz, J.M., Gil, E., 1990. Land reclamation by reforestation in the Central Pyrenees. *Mt. Res. Dev.* 10, 281–288.
- Palacios, G., Navarro Cerrillo, R.M., Del Campo, A., Toral, M., 2009. Site preparation, stock quality and planning date effect on early establishment of holm oak (*Quercus ilex* L.) seedlings. *Ecol. Eng.* 35 (1), 38–46.
- Pearcy, R.W., Yang, W., 1996. A three-dimensional crown architecture model for assessment of light capture and carbon gain by understory plants. *Oecologia* 108, 1–12.
- Pemán, J., Voltas, J., Gil-Pelegrín, E., 2006. Morphological and functional variability in the root system of *Quercus ilex* L. subject to confinement: consequences for afforestation. *Ann. Forest Sci.* 63, 425–430.
- Pemán, J., Gil-Pelegrín, E., 2008. Sembrar o plantar encinas (*Quercus ilex* subsp. *ballota*)? Implicaciones de la morfología y funcionalidad del sistema radicular. *Cuad. Soc. Esp. Cienc. Forest* 28, 49–54.
- Peguero-Pina, J.J., Sancho-Knapik, D., Morales, F., Flexas, J., Gil-Pelegrín, E., 2009. Differential photosynthetic performance and photoprotection mechanisms of three Mediterranean evergreen oaks under severe drought stress. *Funct. Plant Biol.* 36, 453–462.
- Ponder, F., 1991. Growth of black walnut seedlings protected by treeshelters. In: Annual Report Northern Growers Association, pp. 170–174.
- Potter, M.J., 1991. Tree Shelters. Forestry Commission Handbook no 7. MSO, London.
- Quilhó, T., Lopes, F., Pereira, H., 2003. The effect of tree shelter on the stem anatomy of Cork oak (*Quercus suber*) plants. *IAWA J.* 24 (4), 385–395.
- Retana, J., Espelta, J.M., Gracia, M., Riba, M., 1999. Seedling recruitment: responses of holm oak seedlings to different light and water levels. In: Rodà, F., Retana, J., Gracia, C.A., Belloch, J. (Eds.), *Ecology of Mediterranean Evergreen Oak Forest*. Ecological Studies, 137. Springer Verlag, Berlin, pp. 91–95.
- SAS Institute, 2001. SAS/STAT User's Guide, Version 8. SAS Institute, Inc., Cary, NC.
- Seeley, E.A., Kammereck, R., 1977. Carbon flux in apple trees: the effects of temperature and light intensity on photosynthesis rates. *J. Am. Soc. Hort Sci.* 102 (6), 731–733.
- Sharew, H., Hairston-Strang, A., 2005. A comparison of seedlings growth and light transmission among tree shelters. *NJAF* 22 (2), 102–110.
- Thornley, J.H.M., 1976. *Mathematical Models in Plant Physiology*. Academic Press, New York.
- Tormo, J., Bochet, E., García-Fayos, P., 2006. Is seed availability enough to ensure colonization success? An experimental study in road embankments. *Ecol. Eng.* 26 (3), 224–230.
- Valladares, F., Pearcy, R.W., 1997. Interactions between water stress, sun-shade acclimation, heat tolerance, and photoinhibition in the sclerophyll *Heteromeles arbutifolia*. *Plant Cell Environ.* 20, 25–36.
- Valladares, F., Pearcy, R.W., 1998. The functional ecology of shoot architecture in sun and shade plants of *Heteromeles arbutifolia* M. Roem., a Californian chaparral shrub. *Oecologia* 114, 1–10.
- Valladares, F., Pearcy, R.W., 1999. The geometry of light interception by shoots of *Heteromeles arbutifolia*: morphological and physiological consequences for individual leaves. *Oecologia* 121, 121–171.
- Valladares, F., Martínez-Ferri, E., Balaguer, L., Pérez-Corona, E., Manrique, E., 2000. Low leaf-level response to light and nutrients in Mediterranean evergreen oaks: a conservative resource-use strategy? *New Phytol.* 148 (1), 79–91.
- Valladares, F., Dobarro, I., Sánchez-Gómez, D., Pearcy, R.W., 2005. Photoinhibition and drought in Mediterranean woody saplings: scaling effects and interactions in sun and shade phenotypes. *J. Exp. Bot.* 56 (411), 483–494.
- Van Kooten, O., Snel, J.H.F., 1990. The use of chlorophyll fluorescence in plant stress physiology. *Photosynth. Res.* 25, 147–150.
- Wang, F.X., Wang, Z.Y., Lee, J.H.W., 2007. Acceleration of vegetation succession on eroded land by reforestation in a subtropical zone. *Ecol. Eng.* 31 (4), 232–241.
- Werner, C., Ryel, R.J., Correia, O., Beyschlag, W., 2001. Effects of photoinhibition on whole-plant carbon gain assessed with a photosynthesis model. *Plant Cell Environ.* 24, 27–40.