Elevated atmospheric CO$_2$ does not modify osmotic adjustment to light and drought in the Mediterranean oak *Quercus suber* L.

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Abstract

The current ongoing increase in the atmospheric CO$_2$ concentration is an unquestionable fact. Thus, plants are bound to live in a more enriched CO$_2$ world in a not far-off future. In this new framework, regeneration of forest tree species may be modified as a consequence of the change in the current patterns of seedling response to other environmental resources, such as water or light. We studied the impact of an elevated CO$_2$ concentration on the interaction of drought and light upon the water relations of cork oak (*Quercus suber* L.) seedlings. In a complete factorial design of contrasting light (HL vs LL), water (WW vs S) and CO$_2$ levels (800 ppm vs 370 ppm), we analysed the influence of each factor and its interaction in the modification of different leaf water parameters in potted seedlings after a 6 months experimental period. These parameters were derived from the construction, with leaf materials, of the P-V curves: osmotic potential at full turgor (Ψ$_{π100}$), osmotic potential at zero turgor (Ψ$_{π0}$), modulus of elasticity at full turgor (ε$_{max}$), and the ratio dry/turgor weight (DW/TW).

Doubling of the CO$_2$ levels over the current concentration (380 ppm) did not change any of the studied leaf water parameters, while light and water availabilities had a significant influence. This result does not exclude changes in other basic physiological parameters that could modify the pattern of cork oak regeneration responding to a CO$_2$ enriched atmosphere in the future, and under climatic conditions different to the current ones.

Key words: cork oak, CO$_2$ enrichment, water availability, shade, PV curves.

Resumen

Niveles elevados de CO$_2$ no modifican el ajuste osmótico en respuesta a la luz y la sequía en *Quercus ruber*

El continuo aumento actual en la concentración de CO$_2$ en la atmósfera es un hecho incuestionable. Así, las plantas se verán abocadas a vivir en un mundo más enriquecido en CO$_2$ que el actual en un futuro no muy lejano. En este nuevo marco, la regeneración de las especies arbóreas puede modificarse como consecuencia del cambio en los patrones actuales de respuesta a otros recursos del medio como el agua o la luz. En relación con esto, se realizó un estudio para investigar el impacto de una concentración de CO$_2$ elevada sobre la interacción de la sequía y la luz en las relaciones hídricas de hojas de brinzales de alcornoque (*Quercus suber* L.). En un diseño factorial completo, y considerando niveles altos y bajos de: luz (HL-alto, respecto a LL-bajo), agua (WW-bien regadas, respecto a S-estresadas) y CO$_2$ (800 ppm respecto a 370 ppm), se analizó la influencia de cada factor individual, y su interacción, en la modificación de distintos parámetros hídricos en hojas tras un periodo experimental de 6 meses. Los diferentes parámetros se estimaron a partir de la construcción de curvas P-V en hojas: potencial osmótico a plena turgencia (Ψ$_{π100}$), potencial osmótico en el punto de marchitez (Ψ$_{π0}$), módulo de elasticidad a máxima turgencia (ε$_{max}$), y la relación entre el peso seco y el peso turgente (DW/TW).

Una duplicación de los niveles de CO$_2$ por encima de la concentración actual (380 ppm) no cambió ninguno de los parámetros hídricos estudiados, mientras que las disponibilidades de luz y de agua tuvieron una influencia significativa. Esto no excluye posibles modificaciones de otros procesos fisiológicos básicos que puedan alterar los actuales patrones de regulación en el alcornoque en respuesta a una atmósfera más enriquecida en CO$_2$ en el futuro, y en marcos climáticos diferentes al actual.

Palabras clave: alcornoque, enriquecimiento en CO$_2$, disponibilidad de agua, sombra, curvas P-V.

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Introduction

In Mediterranean forests, water stress and light may be considered as the main climatic limiting factors that control regeneration success of forest tree species. Both factors may act in a non-coordinate manner rendering a segregation in species regeneration niches (Sack and Grubb, 2002; Sack et al., 2003). However, a new environmental factor must currently be taken into account, the progressive increase in the levels of the atmospheric carbon dioxide concentration (IPCC, 2007). Such increase, in conjunction with other greenhouse gases, is considered to be responsible for climatic change. One of the effects predicted in the future is the likely increase in the occurrence and intensity of drought in the Mediterranean basin (Pastor and Post, 1988; Peñuelas et al., 1998). Whether these changes may induce displacements in the actual recruitment of seedlings in the understory of forest ecosystems and the patterns of segregation in the regeneration niches is an important issue that needs to be unravelled (Bazzaz and Miao, 1993; Hättenschwiler and Körner, 2000). Indeed, the issue is much more complex when considering the interaction between shade and drought on performance of seedlings (Valladares and Pearcy, 2002; Aranda et al., 2005; Pardos et al., 2005; Sack et al., 2003). How the interaction of both factors, co-occurring in nature, will be modified in the future enriched CO2 world is uncertain, as are the changes promoted in forest composition.

Under this change in the future climatic scenario, tolerance to drought must be analysed taking into account its interaction with light availability (Abrams and Knapp, 1986; Augé et al., 1990; Tschaplinski et al., 1998), along with the increase in the atmospheric CO2 concentration. Whereas a lot of information is available on the change in water relations of forest tree species responding to drought under current environmental conditions (Aranda et al., 1996; Bahari et al., 1985; Davis and Mooney, 1986; Tschaplinski et al., 1998), and for variable levels of CO2 (Tognetti et al., 2002; Tschaplinski et al., 1995), the interaction of both factors with light availability has been assessed to a lesser extent (Hättenschwiler and Körner, 2000).

The increase of atmospheric CO2 concentration during the next few decades will have a direct impact on the physiology of tree species in environments with complex interactions with other resources. Different changes in basic physiological processes such as photosynthetic capacity or stomatal conductance to water vapour have been described to respond to increasing CO2 (Wullschleger et al., 2002). Furthermore, an enhancement in the ability of plants to face water stress by increasing, for example, water use efficiency has been frequently observed (Tyree and Alexander, 1993; Eamus and Jarvis, 1989; Osborne et al., 2000). Thus, it is also expected that an increase in CO2 levels might enhance the ability to develop mechanisms of dehydration tolerance such as osmotic adjustment (Morgan, 1984; Picon et al., 1997). In this sense, the lower osmotic capacity observed in shade conditions under actual atmospheric CO2 concentration (Vance and Zaerr, 1991; Tschaplinski et al., 1998; Aranda et al., 2001), may be compensated in part by the increase in the CO2 concentration in the air. This would render a higher accumulation of osmotic solutes such as soluble carbohydrates by increasing carbon uptake, thereby lowering the osmotic potential at full and zero turgor. In the short-term, the enhancement in carbon fixing would provide a mechanism of increasing the tolerance of seedlings that experience the effects of drought under shade environments (Aranda et al., 2005; Tschaplinski et al., 1998; Tschaplinski and Gebre, 2003). However, no clear trends have been found in this respect. Indeed, even a decrease in osmotic potential at full turgor has been observed when growing under high CO2 environments (Tschaplinski et al., 1993). This result was probably explained by a stimulation of growth, which brought about a depletion in the concentration of osmotically-active organic solutes (Tschaplinski et al., 1995). In other cases, no changes were observed in the osmotic adjustment ability responding to a CO2 enrichment of the atmosphere (Polley et al., 1999).

In the present study, the influence of CO2 levels on osmotic adjustment and other leaf water parameters of cork oak seedlings in response to water stress under different light environments was analysed. A factorial design was established to assess the interaction of the three environmental factors: light, water and atmospheric CO2. These three factors sum up the main environmental constraints in the future regeneration of Mediterranean forest tree species. Two hypotheses were tested: (i) an increase in CO2 may ameliorate the drought response of cork oak seedlings by enhancing osmotic adjustment, and (ii) the effect will be dependent on the light environment. Both questions may be important in the context of the climatic change and its impact on Mediterranean forest regeneration. The niches of regeneration may be altered in the future, not only by a change in the main
climatic variables, but by a differential effect of the increasing CO₂ on the physiological response of forest tree species at the seedling state (Hättenschwiler and Körner, 2000, 2003).

**Material and Methods**

Acorns of cork oak (*Quercus suber* L.) from a population at the center of the Iberian Peninsula (39°58’N, 5°6’W) were collected in the 2003 fall and kept in moist plastic bags at 4°C. Two hundred acorns were seeded in a seedbed inside a climatic chamber at 25°C. Two weeks after seeding, and when seed radicules had emerged 2 cm, 120 acorns were selected and transplanted to 3 L pots containing a mixture of peat and sand (3:1, v:v). A six-months controlled release fertilizer (N:P:K, 20:10:20 +micronutrients) was added to the growing medium (3 g l⁻¹). Seedlings were randomly assigned to each of two climatic chambers containing either ambient air (370 µmol mol⁻¹) or ambient air enriched with CO₂ to a target level of 800 µmol mol⁻¹. CO₂ concentration into the climatic chambers was checked regularly at two weeks intervals. Temperature (25-20°C day/night) and vapour pressure deficit (1.5-1 KPa day/night) were maintained constant during the experiment.

Seedlings were divided in two groups inside each chamber. One group was maintained under low light (LL: 3 mol m⁻² d⁻¹ –60 µmol m⁻² s⁻¹) during the experiment, and the other was grown under high light (HL: 27 mol m⁻² d⁻¹ 600 µmol m⁻² s⁻¹). Low light levels were achieved by growing the seedlings under a neutral shade-cloth. Light was provided by lamps of high vapour pressure and fluorescent tubes as light sources, without observing differences on both climatic chambers in daily irradiance, temperature and vapour pressure deficit during the experiment. To avoid position effects, seedlings were rotated once a week inside the growing chamber.

Within each light treatment, watering was withdrawn on half of the seedlings (S), maintaining the rest well-watered (WW) during all the experiment. Because weekly water consumption in HL seedlings was slightly higher than in LL, additional water was added to HL seedlings to reach the same weekly target average soil moisture content as in LL. This watering regime was applied to well-watered and to water stressed seedlings. The protocol was followed until the minimum soil water content in the pots of stressed seedlings (LLS and HLS) reached a mean gravimetric soil moisture content of 34%. Afterwards, this target level of water stress was maintained until the end of the experiment. Average soil water content on well-watered seedlings was around 84% during the experiment. Water content in the pots was controlled by gravimetric estimation weighing the pots twice per week.

Five seedlings per treatment combination were harvested at three dates, selecting one leaf per seedling from the upper third of the plant. For construction of P-V curves, one fully expanded leaf was sealed with parafilm and the base of the petiole was placed in distilled water in a beaker after re-cutting under water. Leaves were allowed to re-hydrate for an hour at room temperature. Special care was taken to prevent over-saturation of apoplasmic and intercellular spaces in leaves because of immersion. Over-saturation during the first steps of dehydration causes the shift in leaf saturation deficit due to water losses without changes in measured water potential (Dreyer et al., 1990; Abrams and Menges, 1992). The repeat pressurization technique (Robichaux, 1984) was used to construct PV curves from a series of parallel fresh weight and pressure chamber Ψ measurements. After each Ψ measurement, leave samples were removed from the chamber, weighed immediately, and allowed to air dry between consecutive Ψ determinations. When approximately 7-8 data points on the apparent linear portion of the PV curves were obtained, samples were oven dried at 70°C for 48h to obtain leaf dry weight (DW). Sample relative water content (RWC) was calculated as (fresh weight – dry weight) / (weight at full turgor – dry weight). Weight at turgor was derived from the relationship between fresh weight and water potential. Data points above loss of turgor were identified and weight at full turgor determined by linear regression (r² > 0.98) (27).

For the derivation of PV parameters, paired observations of Ψ and RWC were plotted using (1/Ψ) transformations to identify data points to be included in simple regression analysis of the linear portion of PV curves. For the regression analysis, 1/Ψ and RWC were used as the dependent and independent variables, respectively. The x- and y- intercepts yielded estimates of the water content in the apoplast at full turgor (RWCₐ) and inverse of osmotic potential at full turgor (Ψπₐ). The x- and y- coordinates of the first data point of the linear portion of the PV curve corresponded to relative water content at the turgor-loss point (RWCₜ₀₀), and inverse of osmotic potential at the turgor-loss point (Ψπₜ₀₀). From the relationship between 1/Ψ and RWC, the relationship between turgor pressure (P) and RWC
was calculated. Values for the bulk tissue elastic modulus (\(\varepsilon\)) were calculated from this latter relationship. The bulk tissue elastic modulus is defined as the change in tissue turgor pressure for a given fractional change in symplastic content \([\varepsilon = dP/dRWC (RWC-RWC_\text{d})]\).

Osmotic and elastic adjustments, defined as the decrease in osmotic potential at full turgor or in \(\varepsilon\), respectively, in response to water deficits were calculated. Estimates of \(\Psi_{\text{π100}}\) and \(\varepsilon\) were used to characterize osmotic and elastic adjustments.

Water stress was assessed through the measurement of predawn water potential on leaves from the same seedlings sampled for P-V curves construction. The first harvest was made 45 days after reaching the target soil moisture content on stressed seedlings. The following harvests were carried out in two 45-days intervals following the first one.

Data were analysed by ANOVA, with CO2, watering and light as main fixed effects. Comparison of mean treatment differences was done by LSD test. Linear regressions of osmotic potential at full turgor (\(\Psi_{\text{π100}}\)) and at the turgor-loss point (\(\Psi_{\text{π0}}\)) with predawn water potential (\(\Psi_{\text{pd}}\)), as surrogate of water stress, were made considering only the effect of light and watering.

### Results

No differences on water parameters between the three harvests were observed, although in the first harvest, \(\Psi_{\text{pd}}\) was slightly lower for water stressed seedlings compared to the second and third harvests (Fig. 1). Water availability, in terms of \(\Psi_{\text{pd}}\), was linked to watering regime without differences in \(\Psi_{\text{pd}}\) related to the light environment or the CO2 level (Table 1). The water stress experienced by seedlings, in terms of water availability, was the same across the light environments. Harvest date was not significant in the ANOVA analysis, so data were pooled for subsequent analysis.

CO2 was not significant in promoting any change on the different water parameters studied. Thus, only light environment and watering were significant (Table 1). \(\Psi_{\text{π0}}\) and \(\Psi_{\text{π100}}\) decreased in response to water stress in HL, as well as in LL seedlings (Table 2). However, the decrease was steeper in HL seedlings, since the slopes and intercepts from the relationships between \(\Psi_{\text{pd}}\) and \(\Psi_{\text{π0}}\) or \(\Psi_{\text{pd}}\) and \(\Psi_{\text{π100}}\) were higher for HL (Fig. 2). The significance of the interaction L × W in the ANOVA analysis (\(P < 0.01\)) reinforces this result (Table 1).

The relative water content at zero turgor (RWC\(^0\)) decreased only in response to drought. The modulus of elasticity at maximum turgor (\(\varepsilon_{\text{max}}\)) changed also in response to drought in a similar manner, though

### Table 1. Three-way ANOVA of the different water parameters on leaves from cork oak seedlings growing under high and low light regimes interacting with two levels of water availability and two CO2 atmospheric concentrations

<table>
<thead>
<tr>
<th>Treatment</th>
<th>(\Psi_{\text{pd}})</th>
<th>(\Psi_{\text{π0}})</th>
<th>(\Psi_{\text{π100}})</th>
<th>RWC(^0)</th>
<th>(\varepsilon_{\text{max}})</th>
<th>DW/TW</th>
</tr>
</thead>
<tbody>
<tr>
<td>Light (L)</td>
<td>n.s.</td>
<td>***</td>
<td>***</td>
<td>n.s.</td>
<td>n.s.</td>
<td>***</td>
</tr>
<tr>
<td>Watering (W)</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>n.s.</td>
<td>n.s.</td>
<td>***</td>
</tr>
<tr>
<td>[CO(_2)]</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>L × W</td>
<td>n.s.</td>
<td>***</td>
<td>***</td>
<td>n.s.</td>
<td>n.s.</td>
<td>**</td>
</tr>
<tr>
<td>L × [CO(_2)]</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>W × [CO(_2)]</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
<tr>
<td>L × W × [CO(_2)]</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
<td>n.s.</td>
</tr>
</tbody>
</table>

\(\Psi_{\text{pd}}\): predawn water potential. \(\Psi_{\text{π0}}\): osmotic potential at zero turgor. \(\Psi_{\text{π100}}\): osmotic potential at full turgor. CHR\(^0\): relative water content at zero turgor. \(\varepsilon_{\text{max}}\): modulus of elasticity at maximum turgor, leaf dry to turgid weight ratio (DW/TW). Data from different harvests were pooled as no significant differences were related to harvest. n.s.: not significant. \(* P < 0.05. ** P < 0.01. *** P < 0.001.\)
increasing in response to water stress (Table 2). The ratio of leaf dry weight to turgid weight (DW/TW) was affected by watering and light environment. DW/TW increased with light and tended to decline in well watered seedlings. Moreover, as the interaction between both factors was significant ($L \times W$, $P < 0.01$), DW/TW decrease with water stress was steeper in seedlings growing under high light.

**Discussion**

The enhancement of the osmotic adjustment in response to drought under elevated CO$_2$ may be determined by a low demand of solutes by other plant sinks (Wullschleger *et al.*, 2002). However, in the present study, there was no effect of doubling CO$_2$ levels on the water relations of cork oak, including osmotic potential at full ($\Psi_{\pi_{100}}$) and zero turgor ($\Psi_{\pi_{0}}$). This was in accordance with previous results where no clear effect of elevated CO$_2$ was noted in promoting a change in water relations (Tschaplinski *et al.*, 1993; 1995; Polley *et al.*, 1996; 1999; Picon-Cochard and Guehl, 1999; Tognetti *et al.*, 2000). Nevertheless, it must be considered that this was a short-term study about the effects of CO$_2$ enhancement on osmotic adjustment to light and drought, although there is evidence that the slow growth in Mediterranean environments may cancel in the practice the responses to high CO$_2$.

Light and drought were key factors controlling osmotic adjustment in cork oak seedlings, as previously reported (Salleo and Lo Gullo, 1990; Aranda *et al.*, 2005; Pardos *et al.*, 2005). Enhancement in dehydration tolerance in response to a change in light environment is important in order to withstand the more stressful environment achieved by sun leaves (Augé *et al.*, 1990; Aranda *et al.*, 2001; Niinemets, 2001). Under these conditions, leaves must withstand lower water potentials as a consequence of higher heating and higher water losses by transpiration (Ellsworth and Reich, 1992; Groom and Lamont, 1997; Niinemets, 2001).

**Table 2.** Mean values (± SE) of different water parameters derived from P-V curves

<table>
<thead>
<tr>
<th>Light</th>
<th>Watering</th>
<th>$\Psi_{\pi_{0}}$</th>
<th>$\Psi_{\pi_{100}}$</th>
<th>RWC$^6$</th>
<th>$\varepsilon_{\text{max}}$</th>
<th>DW/TW</th>
</tr>
</thead>
<tbody>
<tr>
<td>[CO$_2$]-370 ppm</td>
<td>HL WW</td>
<td>$-2.29 \pm 0.04$ b</td>
<td>$-1.74 \pm 0.03$ b</td>
<td>82.75 ± 0.66 b</td>
<td>6.58 ± 0.38 a</td>
<td>0.44 ± 0.006 b</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>$-3.20 \pm 0.05$ d</td>
<td>$-2.39 \pm 0.03$ d</td>
<td>81.19 ± 0.76 b</td>
<td>9.71 ± 0.66 c</td>
<td>0.47 ± 0.004 c</td>
</tr>
<tr>
<td>[CO$_2$]-800 ppm</td>
<td>HL WW</td>
<td>$-2.39 \pm 0.06$ b</td>
<td>$-1.79 \pm 0.05$ b</td>
<td>83.17 ± 0.73 b</td>
<td>8.05 ± 0.65 a</td>
<td>0.44 ± 0.007 b</td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>$-3.32 \pm 0.08$ d</td>
<td>$-2.47 \pm 0.08$ d</td>
<td>80.43 ± 0.63 a</td>
<td>9.19 ± 0.89 a</td>
<td>0.48 ± 0.005 c</td>
</tr>
<tr>
<td>LL WW</td>
<td>$-2.68 \pm 0.05$ c</td>
<td>$-1.99 \pm 0.04$ c</td>
<td>80.76 ± 0.70 a</td>
<td>8.49 ± 0.72 bc</td>
<td>0.42 ± 0.005 a</td>
<td></td>
</tr>
<tr>
<td></td>
<td>S</td>
<td>$-2.59 \pm 0.05$ c</td>
<td>$-1.95 \pm 0.05$ c</td>
<td>81.06 ± 0.84 ab</td>
<td>7.74 ± 1.01 a</td>
<td>0.41 ± 0.005 a</td>
</tr>
</tbody>
</table>

Differences between harvests were not significant, so data were pooled ($n = 15$, mean ± s.e.). Different letters indicate significant differences between treatments within each CO$_2$ atmospheric concentration ($P < 0.05$). Symbols refer to water parameters as in the previous table.

![Figure 2. Relationship between osmotic potentials at full ($\Psi_{\pi_{100}}$) and zero turgor ($\Psi_{\pi_{0}}$), and predawn water potential ($\Psi_{pd}$-MPa). HL: seedlings under high light. LL: seedlings under low right. Data from both CO$_2$ treatments were pooled because of absence of differences related to atmospheric CO$_2$ concentrations. The depicted linear regressions are: HL-$\Psi_{\pi_{0}} = -2.07 + 0.88\Psi_{pd}$, $r^2 = 0.60$ $P < 0.001$; LL-$\Psi_{\pi_{0}} = -2.08 + 0.38\Psi_{pd}$, $r^2 = 0.30$ $P < 0.01$, and HL-$\Psi_{\pi_{100}} = -1.60 + 0.61\Psi_{pd}$, $r^2 = 0.53$ $P < 0.001$; LL-$\Psi_{\pi_{100}} = -1.67 + 0.18\Psi_{pd}$, $r^2 = 0.14$ $P = 0.02$.](image)
Low light coupled with a decrease in water availability may limit the capacity of osmotic adjustment by decreasing net carbon assimilation rates (Aranda et al., 2004; Pardos et al., 2005; Aranda et al., 2005). Thus, in extreme climatic years and under intense drought brought about by phenomena such as El Niño (Valladares and Pearcy, 2002), seedlings may be more drought stressed under shady conditions because competence from overstory vegetation may prevail over facilitation (Aranda et al., 2005). Under this scenario, carbon balance may decline, endangering long-term survival of seedlings, not only from a starvation of reserves, but also by a decreased drought tolerance as a consequence of a lesser capacity of the involved mechanisms in it, such as turgor maintenance by osmotic adjustment.

The slope and intercept were significantly different for HL and LL seedlings in the relationships of $\Psi_{\pi_0}$ and $\Psi_{\pi_{100}}$ with $\Psi_{pd}$. In previous works with this species, only the difference on the intercept of these relationships when comparing seedlings growing under low and high light environments was significant (Aranda et al., 2005; Pardos et al., 2005). This was likely a consequence of the shorter span in the water stress experienced by seedlings in terms of $\Psi_{pd}$ in the cited works. Interaction between different environmental resources in modifying the physiological response has long been recognized (Bazzaz and Miao, 1993). Thus, it may be hypothesized the additive character of soil dryness and high sunlight exposure as environmental factors which would bring about the triggering of drought tolerance mechanisms such as the decrease of $\Psi_{\pi_0}$ (Groom and Lamont, 1997). On the other hand, seedlings growing under drought and low light face a greater challenge because both act as stress factors. A physiological trade-off may emerge from the lower capacity of cork oak seedlings to develop mechanisms of tolerance to water stress under shade (Aranda et al., 2001, 2005; Pardos et al., 2005). This fact, jointly with other shortcomings linked to growing under low light, such as a limited capacity for carbon uptake or low water use efficiency (Aranda et al., 2007), might compromise the long-standing of seedlings in the understory of close forests under recurrent dry periods.

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References


