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Effects of the interaction between drought and shade on water relations, gas exchange and morphological traits in cork oak (*Quercus suber* L.) seedlings

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Abstract

The combined effect of drought and light on different physiological and biochemical traits was assessed in cork oak (*Quercus suber* L.) seedlings grown under two levels of light availability and submitted to a long-standing drought. Watering was withdrawn after germination and seedlings were allowed to dry to a water content of ca. 50% of field capacity. At this point, water-stressed seedlings were grown under moderate drought and two light regimes: high light (HL—50%) and low light (LL—2%). Soil water in control plants was kept close to field capacity (90–100%) for both light environments. Water-relations parameters derived from *P*–*V* curves, gas exchange and water status at predawn (Ψ_{pd}) were evaluated at twice during the experiment. Nitrogen and chlorophyll contents were determined in the same leaves used for the gas exchange measurements. In addition, maximum rate of carboxylation (V_{cmax}) and electronic transport (J_{max}) were derived from A–C_i curves in well-watered seedlings.

The variation on moisture availability during the experiment was the same under both light environments. In control plants, Ψ_{pd} was over −0.3 MPa at the two harvests, while stressed seedlings decreased to −0.9 MPa, with no differences between light treatments. Water stress decreased osmotic potentials at full ($\Psi\pi_{100}$) and zero turgor ($\Psi\pi_0$). The regressions between both potentials and Ψ_{pd} showed a higher intercept in shade grown seedlings. This fact will point out the higher osmoregulation capacity in sun seedlings whatever water availability.

Nitrogen investment on a per leaf mass (N_{mass}), chlorophyll content (Chl_{mass}) and SLA tended to show a typical pattern of sun-shade acclimation. Thus, the three parameters increased with shade. Only for N_{mass} there was a significant effect of watering, since water stress increased N_{mass}.

LL plants showed a lower photosynthetic capacity in terms of maximum net photosynthesis at saturating light (A_{max}), which was related to a decrease in V_{cmax} and J_{max}. Both parameters varied with specific leaf area (SLA) in a similar way. The low-light environment brought about a higher nitrogen investment in chlorophyll, while under high-light environment the investment was higher in carboxylation (V_{cmax}) and electronic transport (F_{max}).

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Stomatal conductance to water vapour (g_{wv}) and A_{max} were lower in low-light seedlings independently of watering. In addition, there was a trend to keep higher intrinsic water use efficiency (IWUE) under high light environment. The increase of IWUE under water stress was higher in HL seedlings. This was as consequence of the steeper decline in g_{wv} as Ψ_{pd} decreased. The decrease of A_{max} with Ψ_{pd} occurred in a similar way in LL and HL seedlings. Thus, the HL seedlings tended to sustain a higher ability to increase IWUE than LL seedlings when they were submitted to the same water stress.

Keywords: Cork oak; Drought; Light; Photosynthesis; Osmotic adjustment; Water use efficiency

1. Introduction

The interactive effects of shade and drought in growth and physiology of seedlings have been previously described (Gauhl, 1979; Chapin et al., 1987; Holmgren, 2000; Valladares and Pearcy, 2002). The impact of such interaction is of major interest for understanding regeneration success of forest tree species in Mediterranean ecosystems. Competition for water in stands dominated by mature trees or shrubs may exacerbate drought effects on tree seedlings established in the understory (Burton and Bazzaz, 1995; Valladares and Pearcy, 2002). The ability of regenerated seedlings to respond to drought under shade conditions is also recognized to influence patterns of forest distribution even in relatively aseasonal climatic zones, such as tropical rain forest (Fisher et al., 1991; Newbery et al., 1999; Gibbons and Newbery, 2002). Furthermore, the facilitation of shade by pre-existing vegetation, which favours forest tree species recruitment, seems a general rule, despite the possible interspecific competition for water and other resources (see Callaway, 1995; Callaway et al., 2003).

Although the above-mentioned issue has been profusely studied in terms of changes in biomass allocation and relative growth rate (Burslem et al., 1996; Sack and Grubb, 2002; Sack et al., 2003), there is little information about the physiological response to the interaction of drought and shade (Abrams and Mostoller, 1995; Valladares and Pearcy, 1997, 2002; Aranda et al., 2001). In some cases, patterns shown in the literature are related to the particular conditions of the study. Confuse and sometimes divergent results do not allow us to establish the general role of drought in the performance of seedlings grown under deep shade (Veenendaal et al., 1996; Poorter and Hayashida-Oliver, 2000). Sack and Grubb (2002) have recently summarized five possible hypotheses about the trade-off between shade tolerance and drought tolerance. One of the hypothesis is based on the model developed by Smith and Huston (1989). Furthermore, Holmgren et al. (1997) established a model of facilitation, in which light and water availabilities were taken as main variables in the process. One of the outputs from the model was that facilitation under shade conditions takes place only when water availability overcomes the limitation imposed by shade in seedling's carbon balance.

The interaction of light and water stress may be a compromise between contradictory patterns of seedling's physiological response. For instance, lower osmotic adjustment ability in leaves grown under increasing shade conditions within the canopy has been reported (Uemura et al., 2000; Niinemets, 2001); as well as in seedlings established under low-light environments (Ellsworth and Reich, 1992; Abrams and Mostoller, 1995; Gebre et al., 1998; Tschaplinski et al., 1998; Delpérée et al., 2003). On the other hand, it is widely recognized that osmotic potential at full turgor ($\Psi\pi_{100}$) may decrease because of an active metabolic accumulation of osmolytes when seedlings of drought-tolerant species are exposed to water stress (Collet and Guehl, 1997). Thus, the occurrence of dry periods under shade conditions might comprise an awkward situation between shade- and drought-tolerance. This compromise is shown by the lower ability to develop mechanisms of drought-tolerance, such as osmotic adjustment, under low irradiances (Augé et al., 1990; Abrams and Mostoller, 1995; Aranda et al., 2001). In this sense, it is important to emphasize the ability of seedlings to adjust their physiological response under low light and water-limitant conditions, which in many cases are acting in concert (Mulkey and Pearcy, 1992). These concurrent environmental conditions are usually found in the understory of Mediterranean forests during the summer months. Probably, they are among the main