

Influence of transient shade periods on the effects of drought on photosynthesis, carbohydrate accumulation and lipid peroxidation in sunflower leaves

Maria João Correia^{*}, Maria Leonor Osório, Júlio Osório, Isabel Barrote, Mónica Martins, Maria Manuela David

Faculdade de Engenharia de Recursos Naturais (CDCTPV), Universidade do Algarve, Campus de Gambelas, 8005-139 Faro, Portugal

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Abstract

The effects of a slow-imposing two-week soil drying period, and subsequent re-watering, on leaf water potential (Ψ), gas exchange rates, chlorophyll fluorescence and on the concentrations of malondialdehyde (MDA) and non-structural carbohydrates (starch, hexose and sucrose) were determined in mature leaves of sunflower plants growing under controlled-environmental conditions. To assess how transient shade periods, associated with increased cloud cover, may influence drought-induced effects on carbon assimilation, measurements were carried out both in plants kept under the photosynthetic photon flux density (PPFD) prevailing during the growth period and stress imposition ($750 \mu\text{mol m}^{-2} \text{s}^{-1}$), and in plants subjected to a 5-h long period under a lower PPFD ($200 \mu\text{mol m}^{-2} \text{s}^{-1}$). In plants kept under high PPFD, Ψ , stomatal conductance (g), net CO_2 uptake rate (A), the quantum yield of photosystem II electron transport (Φ_e), the photochemical efficiency of open PSII reaction centres (F'_v/F'_m) and the diurnal accumulation of total non-structural carbohydrates (TNC) were significantly depressed at the end of the soil drying period, whereas non-photochemical quenching (NPQ), the concentrations of MDA and the predawn pools of soluble sugars were found to increase. Under high-light level, drought-induced effects on lipid peroxidation, chlorophyll fluorescence parameters and gas exchange rates were fully reversed upon re-watering. However, the inhibition of diurnal accumulation of TNC still persisted two days following re-watering, suggesting that carbohydrate export rates were enhanced following stress relief. An overall positive effect was found upon transferring water-stressed plants to low light level, as indicated by the increases in Ψ , intrinsic water use efficiency (A/g), Φ_e and F'_v/F'_m , as well as the reversal of drought-induced enhancement of both NPQ and MDA concentration. Despite g being similar in shaded well-watered and re-watered plants, the latter exhibited net CO_2 uptake rates below those found in well-watered leaves under the same light conditions, together with a diurnal decrease in the concentration of TNC that was mainly attributable to the depletion of starch and sucrose. These results indicate that, contrasting with the positive effects of shading on water-stressed plants, low PPFD may negatively affect the recovery of net photosynthesis following stress relief.

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Abbreviations: A , net carbon dioxide uptake rate; C_i , intercellular carbon dioxide concentration; ETR, electron transport rate; F_v/F_m , maximal photochemical efficiency of photosystem II; F'_v/F'_m , photochemical efficiency of open PSII reaction centres; g , stomatal conductance for water vapour diffusion; MDA, malondialdehyde; NPQ, non-photochemical quenching; PPFD, photosynthetic photon flux density; PSII, photosystem II; q_p , photochemical quenching; TNC, total non-structural carbohydrates; Φ_e , quantum yield of photosystem II electron transport; Ψ , leaf water potential

^{*} Corresponding author. Tel.: +351 289800932; fax: +351 289818419.

E-mail address: jcorreia@ualg.pt (M.J. Correia).

1. Introduction

Water deficit is a major constraint to plant growth and productivity, one of the earliest effects of soil drying being the decline in photosynthetic carbon assimilation, resulting from stomatal and mesophyll limitations (Lawlor, 2002; Flexas et al., 2004). However, the extent of drought-induced depression in photosynthesis, and its underlying causes, may be dependent on the superimposition of other environmental stress conditions (Chaves, 1991). As water-stress episodes

in field conditions are often accompanied by strong light, the interaction between high irradiance and drought has been investigated in a number of studies. Ögren and Öquist (1985) found no interaction between drought and irradiance, provided the leaves were properly light-acclimated. However, other studies have shown that water deficits predispose the photosynthetic apparatus to photoinhibition, and drought-induced inhibition of photosynthetic activity is exacerbated when leaves are dehydrated under strong light (Björkman and Powles, 1984; Masojádek et al., 1991; Behera et al., 2002). In contrast, Valladares and Pearcy (2002) recently reported that the capacity of plants to withstand a severe drought might be decreased under shade conditions, rather than being enhanced.

On studies undertaken to assess the influence of light regime on the effects of drought, light level is often kept constant throughout the experimental period. In contrast, the photosynthetic photon flux density varies temporally under field conditions. Cloud cover is one of the major causes of varying sunlight intensity under field conditions, and the incidence of transient shade periods, associated with increased cloud cover, increases during precipitation events. Therefore, re-watering of rain-fed plants is expected to occur under irradiances lower than those prevailing during growth and water deficit development. The impact of those transient decreases in irradiance on carbon assimilation under drought stress and after stress relief has been scarcely addressed. In a study in which sunflower plants were subjected to a days-long shade period during water deficits imposition, Ben et al. (1987) found that the extent of drought-induced reduction in the CO₂-saturated rate of photosynthesis was greater in leaves kept at high-light than in shaded leaves, and no drought-induced changes in photochemistry was detected in the latter. Results obtained in a recent work (Sofo et al., 2004), in which the shading treatment was extended throughout the entire re-watering period, also showed that partial shade alleviates the oxidative load on leaves, and leads to a faster recovery of photosynthesis. Another likely effect of decreased irradiance would be the limitation of drought-induced accumulation of sugars (Munns and Weir, 1981). Carbohydrate build-up in leaves can lead to decreased expression of photosynthetic genes, and hence to a depression in photosynthetic activity (Paul and Foyer, 2001). Therefore, shade-induced limitation in sugar accumulation is expected to alleviate end-product inhibition of photosynthesis, which has been reported to occur under drought conditions (Souza et al., 2004). The above mentioned studies point out to a positive effect of shading on photosynthetic activity under drought conditions, but it is conceivable that the depression in the capacity of the leaves to produce carbohydrates may limit the recovery of growth rate after drought stress relief.

When leaves are subjected to low light, a decreased respiratory rate is essential to allow a positive carbon balance. Because acclimation of leaf respiratory rates to the new light environment may take a few days (Noguchi et al., 2001), tem-

porary carbon imbalance is likely to occur following sudden decreases in irradiance, as respiration continues at high rates typical for high-light grown leaves. This may contribute to explain why switching high-light grown leaves to low irradiance conditions has been found to be associated with a substantial decrease in foliar levels of total non-structural carbohydrates (Veneklaas and den Ouden, 2005), and to negatively affect leaf instantaneous water use efficiency (Fay and Knapp, 1995). However, the relative magnitude of the negative effects of short-term (minutes-long) shade periods on transpiration and photosynthesis, and hence the way water use efficiency is affected, has been found to be dependent on the watering regime (Fay and Knapp, 1998). These results highlight the importance to proceed studies on the influence of sudden decreases in light level on plant responses to drought stress.

The present work was undertaken in order to contribute to a better understanding of the short-term effects of low irradiance on the response of plants to drought. With that purpose, the effects of soil drying, and subsequent re-watering, on water status, gas exchange rates, chlorophyll fluorescence, lipid peroxidation and accumulation of non-structural carbohydrates were determined in mature leaves of sunflower plants, either kept under growth irradiance or subjected to a 5-h long period of partial shade. To our knowledge, the simultaneous effects of temporary shading on leaf gas exchange rates, chloroplast photochemistry, leaf oxidative damage and sugar accumulation in water-stressed leaves has not been assessed so far.

2. Materials and methods

2.1. Plant material and growth conditions

Helianthus annuus L. seeds (cv. Giant) were soaked overnight and allowed to germinate on wet tissue paper, in darkness. They were then placed in 31 pots filled with a mixture of unfertilised peat and vermiculite (1:1, v/v). The plants (one per pot) were grown in a controlled-environment cabinet (Fitoclima 16.000 EHVP, Aralab, Portugal) under a photoperiod of 12 h, with light provided by incandescent and fluorescent lamps, supplying a photosynthetic photon flux density (PPFD) of about 750 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the top of the plants. The temperature was 18 °C/25 °C (night/day) and the relative humidity was 70%/60% (night/day). Watering was done using a complete nutrient solution.

From sowing until the beginning of water deficit imposition, all the pots were regularly brought to field capacity (each two days). The onset of water deficit imposition took place 19 days after sowing, and afterwards the pots were watered on a daily basis. Water-stress was imposed by replacing only about half the water lost by evapotranspiration (determined gravimetrically). After 17 days of soil drying, the water-stressed pots were re-watered to field capacity. In the case

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