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Limitations to carbon assimilation by mild drought in nectarine trees growing under field conditions

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Abstract

The strategies used by nectarine trees (*Prunus persica* L. Batsch, var. Silver King) to cope with high light and high temperature/vapour pressure deficit conditions were evaluated in field-grown plants in central Portugal. Diurnal time courses of gas exchange rates and chlorophyll fluorescence were measured "in situ" in attached leaves of well-watered or mild water-stressed plants under summer conditions. CO_2 assimilation rate (A_n) and stomatal conductance (g_s) of well-watered trees decreased along the day in response to high temperature and vapour pressure deficit. Soil water deficit increased the sensitivity of leaf gas exchange to summer atmospheric conditions; A_n and g_s exhibited important midday depressions under water shortage. During the day, the quantum yield of PSII electron transport in the light (ϕ_e), the electron transport rate (ETR), the intrinsic efficiency of open PSII reaction centers (F'_v/F'_m), the photochemical quenching (q_p) and non-photochemical quenching (NPQ) of chlorophyll fluorescence remained constant in well-watered trees, in spite of some decrease in stomatal conductance in the afternoon. Water stress induced after midday a large, but reversible, decrease of ϕ_e, F'_v/F'_m and ETR, and an increase in NPQ. Simultaneously, an increase in ETR/A_n was observed. Since water stress led to a reduction in the number of PSII centers that remain open after midday, as indicated by the decrease in q_p, the contribution of thermal de-excitation at PSII (given by NPQ) in the protection against photoinhibition became more important in stressed trees. The increase in ETR/A_n suggests that in water stressed plants the excitation energy in the photosynthetic apparatus, that would normally be consumed via CO_2 assimilation, is partially diverted to the photosynthetic reduction of O_2, via photorespiration, Mehler-peroxidase reaction or the water–water cycle. Although electrons not consumed in photosynthetic process may generate active oxygen species, this is not likely to occur in water-stressed nectarine leaves, since chlorophyll concentrations were not decreased (there was no chlorophyll bleaching) and the maximum potential PSII efficiency (estimated through the pre-dawn F_v/F_m ratio) remained high, which are symptoms of no PSII damage.

Keywords: Chlorophyll fluorescence; Electron transport rate; Photoinhibition; Photosynthesis; *Prunus persica*; Stomatal conductance

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1. Introduction

Peach trees are often exposed to drought spells during summer. Even under irrigation, stomatal conductance can substantially restrict CO_2 entry into the leaves, as a result of the interaction of low vapour pressure deficits in the atmosphere with high temperature and irradiance. Because peach is very sensitive to water deficits, negative effects on photosynthesis, growth and production will occur. The nature of the limitations to carbon assimilation under field conditions is still debated (Tezara et al., 1999; Cornic, 2000; Lawlor and Cornic, 2002). It is generally assumed that the decrease in photosynthesis in response to soil and/or atmospheric water deficits is due primarily to stomatal closure, which decreases CO_2 availability in the mesophyll, rather than to a direct effect on the capacity of the photosynthetic apparatus (Chaves, 1991; Cornic and Massacci, 1996; Flexas et al., 2002; Flexas and Medrano, 2002; Chaves et al., 2003). In addition to stomatal conductance, another possible diffusive photosynthetic limitation is the decreased mesophyll conductance to CO_2 that reduces CO_2 concentration at the chloroplasts (Massacci and Loreto, 2001; Flexas et al., 2004). As Flexas et al. (2004) had postulated, it is the sum of the diffusive resistances (stomatal and mesophyll) that sets the limit to photosynthesis rates under drought conditions. Also, there is much evidence (Morales et al., 2004) that water stress "per se" does not cause reductions in primary events of photosynthesis, i.e. PSII efficiency (Cornic et al., 1989; Epron and Dreyer, 1992; Flexas and Medrano, 2002; Morales et al., 2004). Under field conditions, particularly in the Mediterranean regions, water stress is often accompanied by other environmental constraints, such as steep leaf-to-air water vapour gradients, and high light and temperature. It has been demonstrated that the combination of these factors, that pre-disposed plants to photoinhibition or down-regulation process, contributes to the reduction in carbon assimilation. In particular, a CO_2 deprivation at the chloroplast level by stomatal closure during the warmest period of the day could enhance the sensitivity of the photosynthetic apparatus to high irradiance (Faria et al., 1998; Flexas et al., 1998). Protection mechanisms against excess light are, thus, an important strategy under Mediterranean conditions, particularly for water-stressed plants. Such protection may be achieved by the regulated thermal dissipation in light harvesting complexes, somehow involving the xanthophylls cycle (Demmig-Adams and Adams, 1996; Ort, 2001). This photoprotective mechanism competes with photochemistry for the absorbed energy, leading to a decrease in quantum yield of PSII (Genty et al., 1989). Moreover, if the limitation of the rate of CO_2 assimilation is accompanied by the increase in the activity of another sink for the absorbed energy, e.g. photorespiration (Genty et al., 1990; Harbinson et al., 1990) or Mehler-peroxidase reaction (Biehler and Fock, 1996; Cheeseman et al., 1997), the decline in non-cyclic electron transport will be proportionally less than the decrease observed in the rate of CO_2 assimilation. These types of response have been documented mainly in plants native from semi-arid regions. Much less is known on how crop plants respond to excessive light, conditions that may arise even in irrigated field-grown plants during the summer period.

The aim of this study was to investigate the strategies used by peach trees growing under field conditions to cope with high light and high temperature/vapour pressure deficit (VPD) conditions either under irrigation or water deficits. In particular, we quantified the water-stress-related effects on stomata, photosynthetic primary reactions and net carbon assimilation and discussed the implications of the results obtained in relation to peach strategies to mitigate chronic photoinhibition and photon damage under dry/hot environments.

2. Material and methods

2.1. Experimental site and plant material

The experiment was carried out in July 1998, in a nectarine (*Prunus persica* L. Batsch, var. Silver King) orchard near Montijo (central Portugal, 38° North, 9° West), as described in Le Roux et al. (2001). The 4-year-old trees were grown in a 1 ha orchard (5 m × 2 m plantation) with a podzolic sandy soil. Trees were oriented in South–North rows. Drip irrigation and nutrient supplementation ensured non-limiting soil water conditions and a good nutrient supply. Water stress was induced by withholding water supply for trees of four rows, and plant response to water deficits was studied in trees of the central rows 10 days after withholding water supply. The study was conducted