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RESEARCH ARTICLE

## Effects of progressive drought on photosynthesis and partitioning of absorbed light in apple trees



MA Ping, BAI Tuan-hui and MA Feng-wang

College of Horticulture, Northwest A&F University/State Key Laboratory of Crop Stress Biology for Arid Areas, Yangling 712100, P.R.China

### Abstract

To understand how drought stress affects CO<sub>2</sub> assimilation and energy partitioning in apple (*Malus domestica* Borkh.), we investigated photosynthesis and photo-protective mechanisms when irrigation was withheld from potted Fuji trees. As the drought progressing, soil relative water content (SRWC) decreased from 87 to 24% in 15 d; this combined the decreasing in leaf relative water content (LRWC), net photosynthesis rate ( $P_n$ ) and stomatal conductance ( $G_s$ ). However, the concentrations of chlorophylls (Chl) remained unchanged while  $P_n$  values were declining. Photochemistry reactions were slightly down-regulated only under severe drought. Rubisco activity was significantly decreased as drought conditions became more severe. The actual efficiency of photosystem II ( $\Phi_{PSII}$ ) was diminished as drought became more intense. Consequently, xanthophyll-regulated dissipation of thermal energy was greatly enhanced. Simultaneously, the ratio of  $\Phi_{PSII}$  to the quantum yield of carbon metabolism, which is measured under non-photorespiratory conditions, increased in parallel with drought severity. Our results indicate that, under progressive drought stress, the reduction in photosynthesis in apple leaves can be attributed primarily to stomatal limitations and the inhibited capacity for CO<sub>2</sub> fixation. Xanthophyll cycle-dependent thermal dissipation and the Mehler reaction are the most important pathways for dispersing excess energy from apple leaves during periods of drought stress.

**Keywords:** apple, drought stress, energy dissipation, photosynthesis

### 1. Introduction

Drought stress is an important environmental factor that strongly limits plant growth and yield worldwide (Chaves 1991). Global change is expected to exacerbate water deficits in semiarid areas (IPCC 2001). Inhibition of photo-

synthesis is a primary physiological consequence of drought stress (Cornic and Massacci 1994; Lawlor 1995; Zhang *et al.* 2013). Under such conditions, stomatal closure is the main factor. However, as drought becomes more severe, the greatest impact is due to photosystem damage from excess light or impairments to photophosphorylation, Rubisco activity, and the regeneration of ribulose-bisphosphate (Parry *et al.* 2002; Bota *et al.* 2004; Xu *et al.* 2013).

During drought periods, the utilization and consumption of absorbed light energy is out of balance. When the rate of photosynthesis decreases, excess excited energy cannot be consumed *via* CO<sub>2</sub> assimilation (Reddy *et al.* 2004; Farooq *et al.* 2009). Although such excess energy can be partially dissipated through non-photochemical quenching (NPQ), photorespiration, the Mehler reaction, and other

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Correspondence MA Feng-wang, Tel/Fax: +86-29-87082648,  
E-mail: [fwm64@sina.com](mailto:fwm64@sina.com), [fwm64@nwsuaf.edu.cn](mailto:fwm64@nwsuaf.edu.cn)

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processes, plant leaves often undergo photo-oxidative stress that results in an accumulation of reactive oxygen species (ROS) (Demmig and Björkman 1987; Yordanov et al. 2000; Paul and Foyer 2001; Flexas and Medrano 2002). If these accumulated ROS cannot be detoxified quickly by the antioxidant systems, photo-oxidative damage will occur (Krause and Weis 1991; Foyer and Noctor 2005; Dietz and Pfannschmidt 2011; Murchie and Niyogi 2011; Li and Ma 2012). Under such conditions, plants protect the photosynthetic apparatus through various mechanisms, e.g., conversion of the state in the xanthophyll-cycle pigments to dissipate excess light, a means that is considered the most efficient (Müller et al. 2001; Sircelj et al. 2007; Duan et al. 2009). Other mechanisms might include enhanced activity by antioxidative systems (Munne and Penuelas 2004; Pompelli et al. 2010; Noctor et al. 2014) or an increase in photorespiration (Wingler et al. 1999). However, the latter remains controversial (Asada 1999; Lima et al. 2002; Ort and Baker 2002; Sofo et al. 2005; Aganchich et al. 2009). These photosynthesis and photo-protective mechanisms differ among plant species and according to the severity of drought (Beis and Patakas 2012). Such mechanisms are still not well understood for apple trees (*Malus domestica* Borkh.) during progressive drought.

Our study evaluated the effects of drought on Fuji apple, the most commonly planted cultivar worldwide. Its fruit production is significantly restricted in regions where water shortage occurs, especially in northwestern China. To determine how this stress influences those mechanisms in Fuji leaves, we compared values for water status, gas exchange, chlorophyll (Chl) fluorescence, antioxidase activity, and levels of Rubisco activity between stressed and well-watered (control) plants.

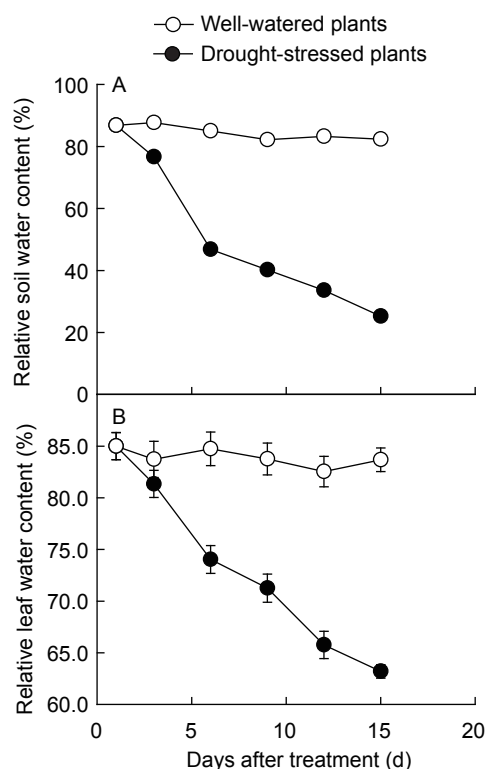
## 2. Results

### 2.1. Progression of drought stress

After irrigation was withheld from selected apple plants for 15 d, their soil relative water content (SRWC) decreased from 87 to 24% (Fig. 1-A), meanwhile, the leaf relative water content (LRWC) decreased from 85 to 62% (Fig. 1-B).

### 2.2. Gas exchange

In response to progressive drought, as shown in Fig. 2-A–C, values for net photosynthetic rate ( $P_n$ ), stomatal conductance ( $G_s$ ), and internal  $CO_2$  ( $C_i$ ) decreased gradually as conditions intensified. A sharp decrease was observed in  $G_s$  from d 9 to 12 when SRWC was below to 40%.



**Fig. 1** Changes in soil relative water content (A) and leaf relative water content (B) over time. Values are means $\pm$ SE from five trees. The same as below.

### 2.3. Photosynthetic electron transport chain

The maximum quantum yield of photosystem II ( $F_v/F_m$ ) remained constant in leaves from drought-stressed plants for the first 9 d, but then decreased from 0.83 to 0.76 as treatment was prolonged (Fig. 3-A). Meanwhile, the delayed fluorescence intensity at 7 ms ( $DF_{7ms}$ ) began to decline in stressed leaves on d 6 (Fig. 3-B). Although the efficiency with which a trapped exciton can move an electron into the electron transport chain further than  $Q_A(\Psi_o)$  was not significantly altered over time by the treatment (Fig. 3-C), and the efficiency with which an electron from the intersystem electron carriers moves to reduce end-electron acceptors at the PSI acceptor side ( $\delta R_o$ ) decreased slightly after 9 d of water deficit (Fig. 3-D).

### 2.4. Photosystem II (PSII) photochemistry and partitioning of excitation energy

As the drought became more intense, values for capture efficiency of excitation energy ( $F_v'/F_m'$ ), coefficient for photochemical quenching ( $q_p$ ), and actual PSII efficiency under irradiance ( $\Phi_{PSII}$ ) remained relatively constant during the first 6 d before declining (Fig. 4-A, C, E). By contrast, the xanthophyll-regulated thermal energy dissipation

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