



## Acclimation to heat and drought—Lessons to learn from the date palm (*Phoenix dactylifera*)



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### ABSTRACT

In the present study, we investigated the responses of date palm (*Phoenix dactylifera*) to drought and heat as single stressors and in combination. We tested the hypotheses (i) that heat and drought enhance the capacity of the antioxidative system, and (ii) that due to the high stress tolerance of date palm, the plants' redox state will be widely unaffected, and (iii) that heat but not drought changes the plants' fatty acid composition and biosynthesis of isoprene, both contributing to the stabilization of membrane integrity. Photosynthesis was only weakly affected by both stresses, whereas the levels of the antioxidants ascorbate and glutathione in leaves dropped. This drop was, however, over-compensated by increased activities of glutathione reductase, an important enzyme of the antioxidative system. The plants' redox state was unaffected by stress as indicated by unchanged H<sub>2</sub>O<sub>2</sub> levels. Because we do not know the concentration of isoprene at its site of action, isoprene emission might provide indirect hints on its possible functions. Isoprene emission strongly increased due to heat indicating its possible role as an antioxidant and for stabilization of thylakoid membranes. Fatty acids only reacted in response to drought. We conclude that the high heat and drought tolerance of date palm is the consequence of a concerted action of the antioxidative system, mainly based on enzyme activities and the assumed antioxidative effects of isoprene as well as adjustments in the fatty acid composition.

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### 1. Introduction

Climate change will lead to an increase in global temperatures of at least 2 °C and strongly reduced summer precipitation compared to 1986–2005 levels (IPCC, 2014) in the near future. There is substantial evidence that this climate change also leads to an increase in frequency and intensity of extreme events such as heat waves and summer drought (Perkins et al., 2012). Coumou and Rahmstorf (2012) showed that in the last fifteen years five extreme heat wave events occurred world-wide, four of which were observed in Europe. In order to identify physiological traits

that can reduce the sensitivity of trees to climate change by preventing or scavenging injurious effects of these environmental constraints, analysis of woody plants exposed to extreme climate conditions in their natural environment appears to be a promising approach. In this context, date palms (*Phoenix dactylifera*) are of particular significance, since they can experience both, temperature extremes and prolonged periods of drought under the arid and semi-arid conditions of their natural environment (Shabani et al., 2012). However, the physiological and molecular mechanisms that enable date palms to grow and develop under these conditions have so far not been elucidated.

Both heat and drought can result in enhanced production of reactive oxygen species (ROS) (Rennenberg et al., 2006). However, ROS production is not restricted to stress reactions. Plants have to cope permanently with the formation of ROS, inevitably evolving during metabolism under aerobic conditions in both, autotrophic

Abbreviations: ROS, reactive oxygen species; DW, dry weight; FW, fresh weight.

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and heterotrophic cells. Therefore, plant cells are well equipped with antioxidative systems capable to scavenge ROS. Generation of ROS can increase at potentially harmful rates, if redox disequilibria build up between redox carriers of electron transport chains in thylakoid and mitochondrial membranes (Dietz, 2015). Such imbalances frequently occur as a consequence of fluctuating leaf temperature (Scheibe and Dietz, 2012) and in response to heat and drought stress, in particular when rates of photophosphorylation and NADP<sup>+</sup>-reduction exceed rates of ATP and NADPH-consumption in the Calvin-cycle. This is generally observed at low intracellular CO<sub>2</sub> availability due to stomatal closure (Rennenberg et al., 2006). Reducing the production of ROS as well as highly efficient ROS scavenging may therefore constitute strategies to cope with these environmental constraints (Rennenberg et al., 2006).

Scavenging of ROS is achieved in plant cells mainly by chemical reactions with antioxidants such as ascorbate and glutathione, but also by the enzymatic reactions of the Foyer–Halliwell–Asada pathway using the same metabolites as co-substrates (Munne-Bosch et al., 2014; Noctor et al., 2012). Hence, antioxidative capacity of cells depends on the activity of antioxidative enzymes in different cellular compartments as well as on the pool sizes of antioxidants in these compartments (Tausz et al., 2001). In this context, levels and redox state of ascorbate and glutathione as well as glutathione reductase (GR) and dehydroascorbate reductase (DHAR) activity are thought to be of pivotal importance (Rennenberg et al., 2006).

Plants have developed several additional mechanisms to scavenge ROS, including the accumulation of secondary metabolites (Bartwall et al., 2013). For example, enhanced biosynthesis of isoprene in response to heat can protect the photosynthetic machinery from functional damage (1) by quenching and/or regulating ROS formation (Velikova et al., 2012), and (2) by stabilizing thylakoid membrane structures (Velikova et al., 2011). Even though the exact mechanisms, by which isoprene emission influences ROS and antioxidant levels are still unknown, its emission during heat stress can be substantial for many plant species (Kivimäenpää et al., 2013). Maintaining membrane integrity of plant cells and organelles is thought to be a particular challenge under heat and drought. This may be achieved by modifying the structure of existing membrane components, for example, by integration of isoprene (Velikova et al., 2011, 2012), and/or by changing the level of unsaturated fatty acids in order to adjust membrane fluidity (Zhong et al., 2011). Currently, it is unknown if these or other mechanisms to achieve ROS homeostasis and to maintain membrane integrity have been developed in date palms.

The present study was aimed at elucidating physiological mechanisms that allow date palms to cope with elevated temperatures and water deprivation. For this purpose, we exposed young date palm plants to heat and mild drought, single and in combination. We analyzed central parameters of the antioxidative system including levels and redox states of glutathione and ascorbate as well as the apparent activities of GR and DHAR in leaves and roots. As parameters affecting membrane integrity and fluidity, we further studied the fatty acid composition and isoprene emission in response to heat and drought.

With these approaches, we tested the hypotheses that (i) heat and drought stress in date palm is ameliorated by enhanced capacity of the Foyer–Halliwell–Asada pathway, particularly by increased activities of the responsible enzymes, (ii) the redox state of the palm trees is therefore widely unaffected by heat and drought, and (iii) membrane integrity during heat but not drought stress is maintained by increased isoprene biosynthesis and adjustments in fatty acid composition.

## 2. Materials and methods

### 2.1. Plant material and growth conditions

Two-year old date palm (*Phoenix dactylifera*) seedlings were purchased from a commercial supplier ('Der Palmenmann', Bottrop, Germany). Two months before the start of experiments, plants were repotted (2 L pots; peat–sand–perlite mixture, 20:30:50 (vol%)), and grown under greenhouse conditions (15–25 °C, 60–70% rH). Because of the low nutrient content of peat, 10 g of NPK fertilizer were mixed to the substrate. Plants were irrigated every second day towards the end of the light period (c. 200 mL per pot). After two months, plants were transferred to two climate-controlled chambers (Heraeus, Vötsch, Germany). One chamber was set at 20 °C during the light and 15 °C during the dark period (16 h/8 h; 70 ± 3% rH at day and night), while in the second chamber plants were exposed to enhanced growth temperature during the light period (35 °C at day/15 °C at night; 60 ± 8% rH at day and 70 ± 3% at night). It was taken care that incident light was the same between chambers, reaching a photosynthetic active radiation (PAR) of 200–300 μmol photons m<sup>-2</sup> s<sup>-1</sup> at leaf level. We choose this light intensity to simulate shading conditions in order to exclude light stress in addition to heat and drought stress.

In a first set of experiments, plants continued to be irrigated every second day, including the night before gas exchange measurements ('well-watered' conditions). Plants were given two weeks' time to adjust to different temperature regimes between chambers. Experimental setup ensured that plants were exposed for the same time to different growth temperatures. After two weeks, temperature and light responses of net photosynthesis and isoprene emission were determined. Plants were placed back into the climate-controlled chambers and harvested the following day—always exactly 6 h after onset of light. Plant material was frozen in liquid N<sub>2</sub> and stored at –80 °C until further analysis.

The above experiment was replicated with one modification: after two weeks of acclimation at the two different growth temperatures, the irrigation of the 35 °C-grown plants was stopped for 4–5 days, and that of the 20 °C-grown plants was stopped for 7–8 days prior to gas exchange measurements (mild 'drought' conditions). Because of lower relative humidity in the 35 °C-chamber, the duration of water deprivation was 3 days longer for 20 °C-grown plants. We thereby tested if temperature effects were modified by plant water availability.

### 2.2. Leaf and roots hydration measurements

Leaf and root hydration (H; g H<sub>2</sub>O g<sup>-1</sup> DW) was determined as (FW – DW)/DW, where FW is the fresh mass and DW is the dry mass after drying the samples in an oven at 60 °C for 48 h (Contini et al., 2014).

### 2.3. Determination of total N and total C

Total N and total C contents were determined in leaves and roots according to Dannenmann et al. (2009). Briefly, oven dried (48 h, 60 °C) and ground plant material (aliquots of 0.5–1.0 mg) was transferred into tin capsules (IVA Analysentechnik, Meerbusch, Germany). Samples were analyzed using an elemental analyzer (Vario EL, Elementar Analysensysteme GmbH, Hanau, Germany).

### 2.4. Gas exchange measurements

A portable gas exchange measuring system (GFS 3000, Walz GmbH, Effeltrich, Germany) was used for the determination of leaf gas exchange (net photosynthesis, stomatal conductance) and collection of concomitantly emitted isoprene. Date palm leaves

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