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The response of contrasting tomato genotypes to combined heat and drought stress



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ABSTRACT

Efforts to maximize yields of food crops can be undermined by abiotic stress factors, particularly those related to climate change. Here, we use a range of physiological methods to detect the individual and combined effects of heat and drought stress on three contrasting varieties of tomato: Hybrid 61, Moskvich, and Nagcarlang. Seedlings were acclimated under the following treatment regimes: CON-TROL (25-36 °C; well-watered), DRY (25-36 °C; 20% field capacity), HOT (25-42 °C; well-watered) and HOT + DRY (25-42 °C; 20% field capacity). In each treatment, stomatal conductance, leaf temperature, chlorophyll content, and several chlorophyll fluorescence variables (both in situ and in vitro following a heat shock treatment) were measured. Plants from the HOT treatment remained statistically similar to the CONTROL plants in most of the measured parameters, while those from the DRY treatment and especially the HOT + DRY treatment showed clear effects of abiotic stress. Hybrid 61 showed considerable resilience to heat and drought stress compared to the other varieties, with significantly cooler leaves (one day after treatments imposed) and significantly higher Fv/Fm values both in situ and in vitro. The genotypic differences in resilience to heat stress were only apparent under water-limited conditions, highlighting the need to consider leaf temperature rather than air temperature when testing for tolerance to heat stress. The most effective parameters for discriminating genotypic variation in heat and drought stress were in vitro Fv/Fm and chlorophyll content.

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1. Introduction

The global human population is currently growing at an unprecedented rate and is expected to remain on this trajectory for at least 35 years (Zargar et al., 2011; Meeks et al., 2013). An increasing population is associated with an increase in demand for food and this is projected to continue until food production has doubled (Howden et al., 2007; Bita and Gerats, 2013). However, efforts to grow and maximize yields of food crops can be undermined by climatic changes, such as increases in atmospheric temperature and decreases in precipitation (Zargar et al., 2011; Meeks et al., 2013; Eitzinger et al., 2015a,b). Changes in these abiotic factors may induce physiological stress such as heat stress and drought stress in agronomically important plants.

Drought stress is considered to be the most damaging abiotic stress to crop productivity (Foolad et al., 2003; Mir et al., 2012). High temperatures can also impact on crop productivity both directly

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http://dx.doi.org/10.1016/j.jplph.2016.07.006 0176-1617/© 2016 Elsevier GmbH. All rights reserved. and by exacerbating the effects of drought by promoting evapotranspiration (Farrell, 2014; Webber et al., 2015; Feller, 2016). These are major challenges in rainfed agriculture, especially in the arid and semi-arid regions of the tropics (Tomar and Kumar, 2004; Kulkarni and Deshpande, 2007). It is, therefore, vital to be able to identify and develop crop varieties that are resilient to abiotic stress so that crop productivity is not unduly affected (Foolad et al., 2003; Camejo et al., 2005; Bita et al., 2011; Feller and Vaseva, 2014).

Tomato (Solanum lycopersicum L.) grows optimally at temperatures ranging from 20 to 30 °C and is sensitive to extreme temperatures (Zhou et al., 2015) as well as water deficits (Petrozza et al., 2014). Tomato cultivation has increased in the tropics and subtropics where there is considerable risk from high temperature and drought periods. Previous studies have demonstrated the drastic impacts of heat on tomato physiology (Sato et al., 2000; Singh et al., 2005; Camejo et al., 2006). Measures of stomatal conductance and leaf surface temperature are useful in determining the effects of stress on plant water relations and on their ability to avoid overheating, while measurements of chlorophyll content and chlorophyll fluorescence help to assess the level of stressinduced damage to photosynthetic structures and so indicate heat

tolerance (Wahid et al., 2007; Farrell, 2014; Feller, 2016). Camejo et al. (2006) compared the response of heat-tolerant (Nagcarlang) and heat-sensitive (Amalia) varieties of tomato to heat stress after exposing seedlings to a heat shock at 45 °C for 3 h. Severe reductions in photosynthesis, stomatal conductance and chlorophyll content were observed in Amalia while Nagcarlang was unaffected. Recently, Zhou et al. (2015) observed similar reductions in these parameters in two heat-sensitive tomato varieties, relative to two heat-tolerant varieties. These same physiological parameters are seen to be impacted when tomato is grown under water deficit (Hayat et al., 2008; Zhang et al., 2011) although, in some cases, stomatal conductance and chlorophyll content have been seen to increase under heat stress while they typically decrease under drought stress (Zhou et al., 2015; Feller, 2016). Thus, there is a need to understand how the interaction between these physiological parameters contribute to genotypic variation in stress tolerance.

Here, we use both *in situ* and *in vitro* physiological parameters measured in control and stress-acclimated tissue. *In vitro* stress testing provides a convenient technique to make uniform comparisons between varieties. In the case of high temperature stress, many studies have used an *in vitro* heat-shock method to estimate the overall thermal tolerance of leaf tissue (Willits and Peet, 2001; Camejo et al., 2005; Camejo et al., 2006). Exposing harvested leaf tissues to high temperatures *in vitro* for a relatively short period of time allows for identification of the lethal temperature, above which there is disruption of metabolic processes and irreversible injury. Prior *in situ* acclimation to abiotic stress is an essential step, as it helps to enhance the ability of tissue to withstand future exposure to heat shock conditions (Mittler et al., 2011; Farrell, 2014).

Mittler (2006) and Feller (2016) highlight the need to develop crops with enhanced resilience to a combination of different stresses and point to the potential negative and complex interaction between drought and high temperature. Drought-tolerant plants may not necessarily be tolerant to heat stress, and vice versa (Jagadish et al., 2011; Feller, 2016). Hence, we aim to examine the response to heat and/or drought in seedlings of three contrasting tomato varieties. Seedling response is evaluated using stomatal conductance, leaf surface temperature, chlorophyll content and chlorophyll fluorescence (measured *in situ* and *in vitro*). In particular, we seek to understand the role of heat avoidance, heat acclimation and heat tolerance processes in enabling resilient varieties to withstand the combined effects of heat and drought as experienced by plants under field conditions.

2. Materials and methods

2.1. Planting materials

The varieties used in our study were Nagcarlang, Hybrid 61 and Moskvich. Nagcarlang is heat-tolerant and is a wildtype, heirloom variety that originated in the Philippines (Camejo et al., 2005). Hybrid 61 is commonly grown in tropical regions and is known to be high-yielding and tolerant to harsh weather conditions, although it is little studied (Ali et al., 2015). In contrast, Moskvich is sensitive to heat and is another heirloom variety with origins in Russia (Kamel et al., 2010).

Tomato seeds were germinated at 22 °C in the laboratory and then transplanted to 16-ounce polystyrene cups with drainage holes, containing a 2:1 mixture of sharp sand and ProMix (Premier Tech Horticultural Inc., Quakertown, PA, USA). The plants were reared in a well-ventilated, full-sun greenhouse at The University of the West Indies in St. Augustine, Trinidad, and were watered daily to field capacity. The daily photoperiod was approximately 12 h and the typical mid-day sunlight within the greenhouse was $600 \,\mu$ mol/m²/s.

2.2. Acclimation

At the 4-leaf stage, the varieties were arranged in a complete randomized block design, with 10 replicates per block and four treatments (CONTROL, HOT, DRY and HOT+DRY). Data loggers (HOBO Pro, Onset Corp., USA) were placed on each bench at canopy height to monitor air temperature and humidity. Each treatment was applied on adjacent benches as follows:

- 1. CONTROL: served as the control and were watered once a day with 150 mL of water.
- 2. HOT: bench was covered in a clear polythene sheet at a height of 1 m, which reduced the ventilation but allowed limited airflow from beneath the bench. Plants were watered once a day with 150 mL of water.
- 3. DRY: plants were partially deprived of water. Each pot received 20 mL of water per day, to maintain soil moisture at approximately 20% of the soil field capacity. Soil volumetric water content was monitored 3 times per week from 6 replicates of each variety prior to re-watering, using a soil moisture meter (Fieldscout TDR 100 Soil Moisture Meter; Spectrum Technologies, Inc., Illinois).
- 4. HOT + DRY: HOT and DRY treatments were combined.

Over the course of the experiment on the uncovered benches (CONTROL and DRY), the mean daily air temperature was 29 °C, with a mean daily range of 25–36 °C, the mean daily relative humidity was 75% with a mean daily range of 39–100%, and the mean daily vapour pressure deficit was 0.9 kPa with a daily range of 0–2.9 kPa. On the covered benches (HOT and HOT+DRY) the mean daily air temperature was 30 °C (range 25–42 °C), the mean daily relative humidity was 73% (range 30–100%) and the mean daily vapour pressure deficit was 1.3 kPa (range 0–4.4 kPa). The different values on the covered benches were due to elevated mid-day temperatures, which were on average 5 °C hotter than the uncovered benches.

During and after acclimation, several physiological parameters were measured as set out in Table 1. All measurements were made mid-way along the leaf, using the first fully expanded leaf. Stomatal conductance was measured immediately after taking leaf temperature. The thermal camera was held at an angle of 45° from the leaf, at a distance of approximately 0.45 m and at an emissivity of 0.98. Chlorophyll content was measured on a per area basis as the ratio of light absorpsion at 660 nm to that at 940 nm (SPAD equivalent ratio units; Zhu et al., 2012).

A modulated chlorophyll fluorometer was used to estimate the steady state quantum yield of photosystem II in the light (at midday; Fq'/Fm') and the maximum quantum yield of photosystem II following dark-adaptation (one hour after nightfall; Fv/Fm) (Baker, 2008).

2.3. Laboratory measurements

After acclimation, the plants were transported from the greenhouse to the laboratory and placed in a dark room for 40 min in order to dark adapt. One leaf was harvested from each plant and rinsed in 20 mL distilled water. *In vitro Fv/Fm* was obtained for each leaf using a pulse modulated chlorophyll fluorometer (Mini-PAM; Walz; Effeltrich, Germany). Each leaf was then placed in a labeled heat-shock vial containing 20 mL de-ionized water and left in a preheated (43 °C) water bath for 1 h, after which fluorescence measurements were repeated. The difference between measurements taken before and after the heat-shock were expressed as a percentage: (fluorescence after heat treatment/fluorescence before heat treatment ×100). A pilot study with control plants showed Download English Version:

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