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Screening and validation of tomato genotypes under heat stress using F_v/F_m to reveal the physiological mechanism of heat tolerance

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ABSTRACT

Cultivation of tomatoes at high temperatures negatively affects growth and yield. Our aim was to screen tomato genotypes under heat stress for differences in the maximum quantum efficiency of photosystem II (F_v/F_m) and uncover the physiological traits for heat tolerance in a three-step process. Initially, 67 tomato genotypes were ranked according to F_v/F_m. Two genotypes with higher F_v/F_m (heat-tolerant group) and two genotypes with lower F_v/F_m (heat-sensitive group) were selected from the initial screening. Second, the physiological responses of the four genotypes to seven days of heat stress (36/28 °C) were analyzed in detail. Third, pollen germination and fruit set of the four genotypes were investigated at high temperature conditions in the field. The results showed that the heat-tolerant group maintained higher leaf pigment content and higher total phenolic content (TPC) than the heat-sensitive group under heat stress. The heat-tolerant group maintained unaltered stomata and pore area and net photosynthesis rate (P_N) but increased stomatal conductance (g_s) under heat stress compared with the control. Chloroplasts in the heat-tolerant group maintained a normal shape, whereas the chloroplasts in the heat-sensitive group became swollen with decomposed starch grain after heat stress. The heat-tolerant group exhibited a higher pollen germination rate (%), longer pollen tube length and higher fruit set rate compared with the heat-sensitive group at high temperatures in the field. Thus, we concluded that F_v/F_m is an early indicator of heat stress tolerance and that the responses of tomatoes to heat stress were identical in widely different growing conditions. The stay-green trait, improved ability of stomata regulation and higher contents of reactive oxygen species scavengers seemed to be part of the protective mechanisms in heat-tolerant tomatoes.

1. Introduction

The tomato (*Solanum lycopersicum* L.), originating in the Andes mountains of South America, is one of the most important vegetables in the world and is widely grown in both fields and under protected cultivation. The optimal growing temperature for tomato is between 25 °C and 30 °C during the daytime and 20 °C during the night (Camejo et al., 2005). Cultivation of tomatoes under higher temperatures than the optimum has a negative impact on plant growth (Camejo et al., 2006; Zhang et al., 2014) and will decrease productivity (Peet et al., 1998; Sato et al., 2000, 2006). As a consequence of global warming, the impact of high temperatures on field-grown tomatoes has become an urgent issue. Thus, a thorough understanding of physiological responses to heat stress and mechanisms of heat tolerance in tomatoes is imperative to maintain and develop the future production.

Heat susceptibility in plant species varies among genotypes and developmental stages (Camejo et al., 2005; Wahid et al., 2007; Molina-Bravo et al., 2011) and the responses of plants to heat stress involve numerous regulations of physiological processes caused by

Abbreviations: C_i, intracellular CO_2 concentration; CT, cuvette temperature; DPF, decreased proportion of maximum quantum efficiency of photosystem II; *E*, transpiration rate; F_v/F_m, maximum quantum efficiency of photosystem II; g_s, stomatal conductance; LA, leaf area; LT, leaf temperature; ΔT, difference between cuvette temperature and leaf temperature; PN, net photosynthesis rate; PPFD, photosynthetic photon flux density; PSII, photosystem II; RH, relative humidity; TPC, total phenolic content; VPD, vapor pressure deficit.

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changes in organelles (Wahid et al., 2007). Chloroplasts play a vital role in photosynthesis as one of the most heat-sensitive organelles (Krause and Santarius, 1975). Heat stress decreased photosynthesis via perturbations in the photosynthetic apparatus (Ogweno et al., 2008; Abdelmageed and Gruda, 2009). Of the photosynthetic apparatus, photosystem II (PSII) is regarded as the most heat-sensitive component (Čajánek et al., 1998). As the damage to PSII is often the first response, when plants are subjected to heat stress, a study of PSII responses can reveal the primary effects of heat stress on plants (Mathur et al., 2011).

The measurement of the photochemical efficiency of PSII with chlorophyll *a* fluorescence is an effective and non-invasive technique to detect damage in PSII (Baker and Rosenqvist, 2004; Baker, 2008). The ratio between variable fluorescence ($F_v = F_m - F_o$) and maximum fluorescence (F_m) or the maximum potential quantum efficiency of PSII (F_v/F_m) provides an estimate of the maximum quantum efficiency of PSII (Butler, 1978), which is one of the most heat-affected fluorescence parameters. A decrease in F_v/F_m is frequently observed, when plants are subjected to abiotic stresses, including heat stress (Willits and Peet, 2001; Molina-Bravo et al., 2011; Sharma et al., 2012). The reason for the stress-induced reduction in F_v/F_m is an increase in non-photochemical quenching processes leading to a decrease in F_m and subsequent photoinactivation of PSII reaction centers, leading to an increase in F_o (Melis, 1999; Baker, 2008).

F_v/F_m has not yet been applied in mass screenings for heat tolerance in tomato genotypes. In this study, we used F_v/F_m as a criterion for evaluating heat susceptibilities of 67 tomato genotypes, as it is a rapid and non-destructive index to detect stress damage. We hypothesized that genotypes with higher F_v/F_m under heat stress maintain their physiological status compared to genotypes with lower F_v/F_m. To illustrate potential heat-tolerant mechanisms and compare the responses of contrasting tomato genotypes to heat stress, physiological indicators in two selected heat-tolerant and two selected heat-sensitive genotypes were identified. Furthermore, morphological performance with respect to leaves, pollen germination and fruit set rate under long-term high temperatures in the field was investigated to be compared

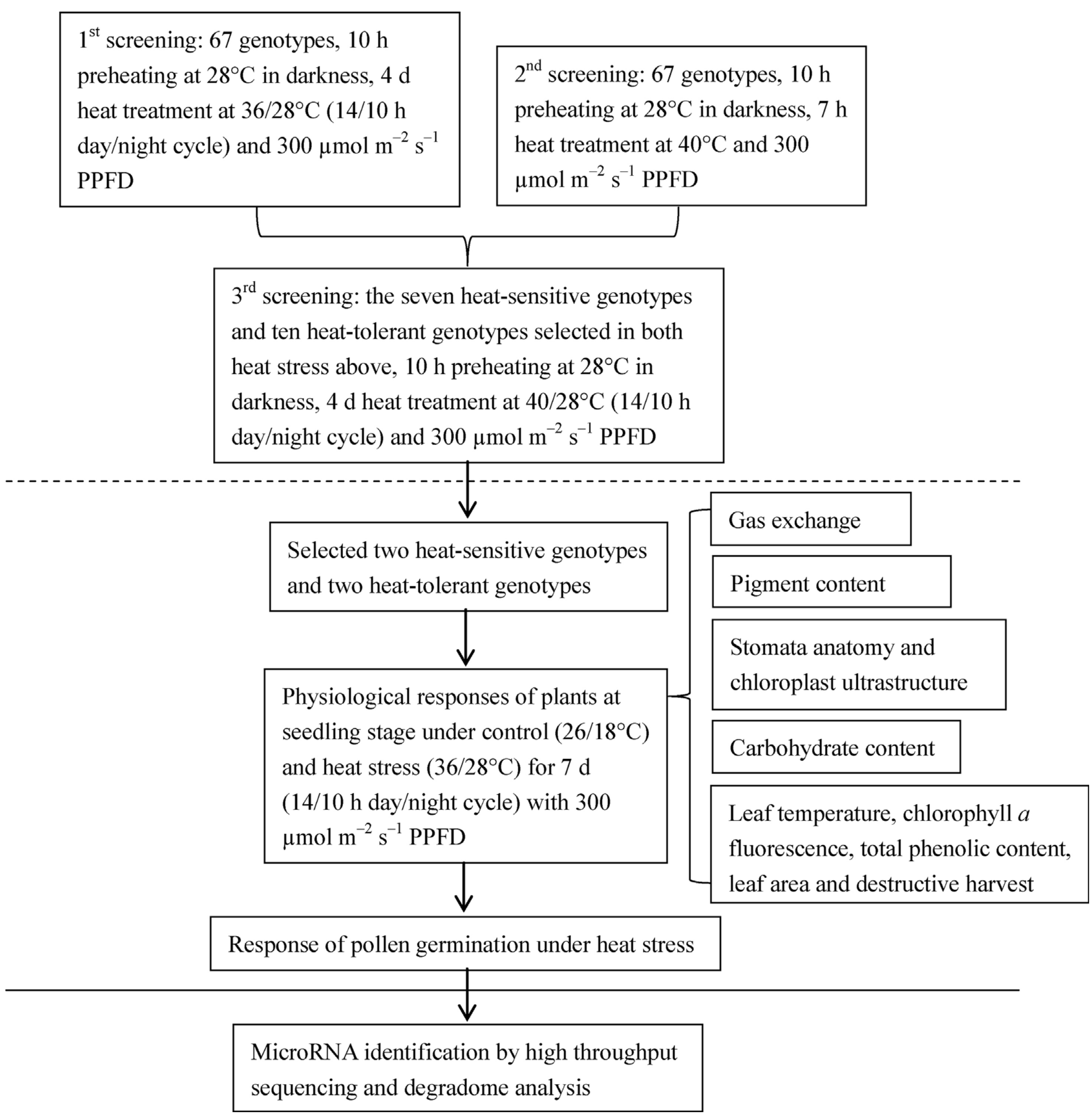

Fig. 1. Work flow of present study including the screening (above the dashed line) and validation (below the dashed line and above solid line). In the first step, the heat tolerance of 67 tomato genotypes was screened by chlorophyll *a* fluorescence and the heat injury index. In the second step, the selected two low-performing genotypes and two top-performing genotypes based on their F_v/F_m were used to validate the heat tolerance in terms of leaf physiology and pollen germination under heat stress. The third part (below the solid line) is the proposed future work.