



Water-deficit priming of papaya reduces high-light stress through oxidation avoidance rather than anti-oxidant activity



Christopher Vincent^{a,*}, Bruce Schaffer^b, Diane Rowland^c

^a Horticultural Sciences Department, Citrus Research and Education Center, University of Florida, 700 Experiment Station, Lake Alfred, FL, 33850, USA

^b Horticultural Sciences Department, Tropical Research and Education Center, University of Florida, 18905 S.W. 280 Street, Homestead, FL, 33031, USA

^c Agronomy Department, University of Florida, P.O. Box 110500, Gainesville, FL, 32611, USA

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ABSTRACT

The mechanisms for tolerance of various abiotic stresses in plants are often considered to be similar, but there are also specific traits responsible for acclimation that differ according to the type and extent of stress. Water-deficit priming is the imposition of a period of moderate drought stress to induce tolerance to a subsequent stress. We hypothesized that priming improves papaya (*Carica papaya* L.) response to high light intensity. We tested the effects of water-deficit priming on photoinhibition upon shade removal. We assessed morphological and physiological variables associated with priming responses. Priming reduced the intensity and duration of photoinhibition upon shade removal and increased mean leaf area compared to non-primed plants. Photochemical responses to priming included reduced absorption and increased efficiencies of electron transfer from plastoquinone through photosystem I. Photosynthetic responses included upregulation of Rubisco and Ribulose 1,5-bisphosphate regeneration. Morphological responses included increased stomatal density and size. Anti-oxidant capacity was not affected by priming or prior shade treatment. We conclude that water-deficit priming improves papaya response to high light by different physiological mechanisms than shade-to-light acclimation itself. Rather than anti-oxidant upregulation, priming reduces energetic bottlenecks, thereby reducing oxidative stress during shade-to-high-light transitions.

1. Introduction

Abiotic stresses of plants caused by different environmental factors have long been noted to have common mechanisms of damage and tolerance. For example, in response to different stresses, reactive oxygen species (ROS) elicit plant “stress” signals and cause oxidative damage to various cellular components (Apel and Hirt, 2004; Gill and Tuteja, 2010). Likewise, anti-oxidant capacity has been associated with tolerance of various types of abiotic and biotic stresses (Gill and Tuteja, 2010). Osmoprotective compounds, such as proline, are associated with dehydration, salinity, and cold stresses (Huang et al., 2011). However, other studies have noted traits that confer benefits under certain environmental conditions and not in others (Tardieu, 2011). Thus, there are two general hypotheses regarding plant environmental acclimation. The first holds that plants tolerate stresses by universal mechanisms of cell-level protection (universal). The second focuses on mechanisms that are specific to the conditions and sometimes to the plant species (specific). These hypotheses are not mutually exclusive: they may compete or act synergistically in any given circumstance.

Priming is both a concept and an applied practice of managing plant stresses. The concept describes a beneficial physiological state in which a plant has elicited (primed) defense responses that improve fitness upon subsequent stress exposures (Conrath et al., 2002). Most studies of priming have assumed some type of cross-tolerance based on the universal tolerance mechanism hypothesis (Savvides et al., 2016). For example, priming agents induced *Citrus* spp. resistance to pathogenic infection (Sharifi-Sirchi et al., 2011; Llorens et al., 2013) and increased tolerance to abiotic stresses (Ziogas et al., 2015; Molassiotis et al., 2016). Additionally, mild forms of stress can prime plants for subsequent stress exposure, as has been demonstrated primarily using water deficits in agronomic crops, in which a period of regulated deficit irrigation to may improve subsequent stress tolerance. For, example, in wheat (*Triticum* spp. L.) exposure to a brief period of water deficit during the early vegetative stage has been found to improve tolerance to cold, drought, and heat during pollination (Li et al., 2015; Abid et al., 2016; Liu et al., 2017), indicating cross-tolerance induced by water-deficit priming.

Not all types of stress are created equal, and differences in the type

* Corresponding author.

E-mail address: civince@ufl.edu (C. Vincent).

and severity of stress have been attributed to variability in fitness among plants with contrasting stress tolerance traits. In an elegant demonstration of the phenotypic tradeoffs between varying degrees of stress, Skirycz et al. (2011) found no correlation between the growth of *Arabidopsis* genotypes exposed to moderate drought stress and their ability to survive severe drought stress. This is true for priming responses as well as inherited traits, where water-deficit priming treatments have produced responses that would be expected to be either of no utility or even deleterious for tolerance to certain other types of stress. For example, deeper roots of peanut (*Arachis hypogaea* L.; Rowland et al., 2012) or increased water use of potato (*Solanum tuberosum* L.; Byrd et al., 2014) in response to priming are not expected to enhance tolerance to salinity or cold.

Studies of water-deficit priming have primarily addressed annual crop species. However, recent studies of priming in papaya (*Carica papaya* L.) indicated that different mechanisms may be at play in this tropical perennial species than have been reported in annual species. Although priming induced increases in stomatal conductance (g_s) and net photosynthesis (A) in papaya, the effect was transitory and did not increase tolerance to subsequent severe water deficit (Vincent et al., 2015, 2017a). Thus, water-deficit priming of papaya may result in changes that produce benefits under different environmental conditions than those for which it benefits previously studied annual crops. For example, photochemical attributes of papaya plants subjected to priming treatments included decreased absorption and dissipation and increased electron transport through photosystem I (PSI), which resulted in increased driving force of photochemistry (Vincent et al., 2015). Thus, we hypothesized that priming-induced physiological responses can improve perennial plant response to high-light stress by increasing the energy fluxes in the photosynthetic pathway (specific tolerance), not through detoxification of reactive oxygen species (ROS; universal tolerance). This hypothesis was in contrast to observation of increased stress tolerance of several species due to priming in association with increased detoxification of ROS (Savvides et al., 2016). Papaya was an ideal species to test this because our previous results demonstrated that this species can acclimate to a wide range of light regimes, including acclimation of morphological, physiological, and biochemical traits (Buisson and Lee, 1993; Vincent et al., 2017b), and because we had observed a photosynthetic priming response in this species. We tested this first by assessing the degree of shade acclimation and photoinhibition upon shade removal across a range of shade levels. We subsequently assessed the physiological and morphological responses of papaya to an abrupt shade-to-high-light transition with and without water-deficit priming.

2. Materials and methods

2.1. Experiment 1

2.1.1. Experimental conditions

This study was performed outdoors in Homestead, FL, USA, at the University of Florida Tropical Research and Education Center (latitude 25°30'24" N, longitude 80°29'57"N). 'Red Lady' papaya seeds were sown in trays of ProMix® potting medium (Premier Tech, Quebec, Canada) and allowed to germinate in a greenhouse. After germination, seedlings were transplanted into 8-L pots with ProMix®. Seedlings were allowed to grow in the greenhouse for 8 weeks after transplanting, irrigated as needed with a water-soluble 20-20-20 (N-P-K) fertilizer applied at a rate of 1 g N plant⁻¹ month⁻¹. Plants were then relocated to an outdoor location with individual shade structures per plant. Shade treatments were 0% (full sun), 40, 70, or 90% shade reduction of light intensity from full sun. Light intensity reduction was achieved with spectrum neutral shade cloths, which had been tested for percent photosynthetically active radiation (PAR) reduction using LI-190 PAR sensors (Li-Cor, Inc., Lincoln, NE, USA) at midday. The experiment was arranged as a randomized complete block design with 4 replicates, blocking by row in the outdoor location. Each plant was placed on a

cement paver in an area covered in weed cloth, and provided with drip irrigation, irrigating with 1 L plant⁻¹ twice each day, which was previously observed to achieve soil water content above field capacity with minimal drainage. The plants were allowed to grow in these conditions for 8 weeks (longer than the average leaf lifespan) before shade structures were removed to expose shade-acclimated plants to full sun.

2.1.2. Measurements

Measurements were made on the first fully expanded leaf (usually the 5th leaf from the apex) using a portable leaf chlorophyll fluorometer (model OS-30, Opti-Sciences, Hudson, NH, USA). To measure the degree of photoinhibition, pre-dawn chlorophyll fluorescence variables F_m and F_o were measured, from which F_v/F_m was calculated. Chlorophyll fluorescence was measured one day before shade removal, and on days 1, 2, 4, 5, and 8 after shade removal. To quantify morphological shade acclimation, on the date of shade removal, 1 lobe was removed from the measured leaf, the area was measured, then the lobe was dried at 60 °C for 72 h and dry weight was measured.

2.2. Experiment 2

2.2.1. Experimental conditions

This experiment was performed in the same location as Experiment 1. Plants were propagated, transplanted, and relocated in the same manner as Experiment 1. Experiment 2 was arranged as a randomized complete block design, with row as the blocking factor with 8 blocks (Fig. 1B). Treatments were: 1. Full sun control, 2. Shade control, 3. Shaded-primed (See Fig. 1A for a timeline of treatment applications). Based on the results of Experiment 1, 90% shade cloth was used. Because a previous study had compared primed and non-primed papaya plants in full sunlight, we did not include a primed-full sun treatment (Vincent et al., 2015). Priming water deficit was imposed by daily measurement of gravimetric water loss. As reported in previous studies, a gravimetric versus tensiometric water potential curve was developed before implementing the study (Vincent et al., 2015, 2016). To impose the priming treatment, the pots were weighed daily, and upon weighing, they were irrigated with the precise volume required to bring the medium to -20 kPa, which was previously determined to reduce g_s with minimal effects on A , indicating a "mild stress" that induced a plant response without greatly reducing growth (Vincent et al., 2015). Plants in the non-primed treatments continued to be irrigated at a rate of 2 L plant⁻¹ day⁻¹, as described above. The priming treatment lasted for three weeks, and full irrigation was resumed (the same scheduled irrigation program as the other treatments) 4 days before shade removal. Shade removal occurred eight weeks after plants were relocated to the outdoor location.

2.2.2. Measurements

2.2.2.1. Leaf morphology. On one fully mature leaf per plant, a single lobe was excised, and immediately taken for imaging with a high powered digital scope (VHX 5000, Keyence Corp, Itasca, IL, USA) at 700x magnification with light from above and from below the sample. For each lobe, three images were taken of the distal side of the leaf because papaya leaves are primarily hypostomatal. Using these images, the numbers of stomata and non-stomatal epidermal cells were counted. From these counts both stomatal density (stomata mm⁻²) and differentiation rate (stomatal cells/total epidermal cell number; Sack and Buckley, 2016) were calculated. Using ImageJ open-source software, the length and width of each stoma was measured, which were used to calculate stomatal size as an ellipse ($width/2 \times length/2 \times \pi = area$).

Whole-leaf morphological measurements were collected destructively at the end of the study. To estimate leaf longevity and rate of production of new leaves, the first fully mature leaf on the date of shade removal on each plant was marked, and at the end of the study, the total number of leaves and the total number of new leaves were

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