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The potential for primed acclimation in papaya (*Carica papaya* L.): Determination of critical water deficit thresholds and physiological response variables

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ABSTRACT

Priming is a strategy that potentiates a plant's response to stress. Primed acclimation (PA) in crop irrigation scheduling is the use of a temporary period of regulated deficit irrigation (RDI), imposing mild or moderate deficits, to evoke a primed state, after which full evapotranspiration replacement is resumed. Although little has been reported regarding physiological impacts of PA, the technique has been used to maintain or improve yields in agronomic crops in drought-prone regions. The first objective of this study was to test a plant-based approach to determine the appropriate level of soil water potential needed to evoke a primed response in papaya plants. This was done through a substrate (potting medium) dry-down experiment with one group of plants irrigated to field capacity and a second group of plants for which the soil was allowed to dry gradually. Physiological responses were assessed to determine at what point a mild to moderate level of stress was reached. The second objective was to test the effects of a priming stress (the level set in the first objective) on leaf gas exchange (net photosynthesis [A], stomatal conductance [g_s], transpiration [E]) and chlorophyll fluorescence in papaya as compared to a control treatment in which soil water content was maintained at field capacity. The most sensitive variable in the dry-down experiment was g_s, which was used to select a soil water potential target of −30 kPa for subsequent priming treatments. Priming treatments using this predetermined target resulted in increased A and leaf chlorophyll index (SPAD) during the period when irrigation to field capacity was restored. According to OJIP analysis, primed plants had increased fluorescence performance indices, reduced antennae size per Photosystem II reaction center, and increased fluxes and efficiencies from plastoquinone A through Photosystem I. Thus, increased A as a result of priming had both stomatal and photochemical components. However, increased A due to priming of papaya appeared to be temporary. These results show that papaya has the capacity to reach a primed state and provide the soil water potential levels that could be utilized to achieve the appropriate level of water deficit for priming. This vital information can be used in the development of management techniques to capitalize on papaya's priming ability under commercial irrigation management schemes.

1. Introduction

Improved water use efficiency is vital for sufficient crop production (Godfray et al., 2010), which has led to extensive research in reduced irrigation approaches to crop management. Regulated deficit irrigation (RDI) has long been proposed as a strategy to reduce agricultural water use during non-sensitive periods in crop development (Chalmers et al., 1984). When timed and regulated appropriately, RDI has been found to reduce irrigation water use while maintaining yields of agronomic crops (Chalmers et al., 1983). Also, if RDI incorporates periods of irrigation levels that meet

Abbreviations: RD, regulated deficit irrigation; A, net photosynthesis; g_s, stomatal conductance; VPD, vapor pressure deficit; PI_{ABS}, photosynthetic performance index per photon absorbed; PI_{cs}, photosynthetic performance index per estimated leaf area; PSI, photosystem II; PSI, photosystem I; QA, plastoquinone A; QB, plastoquinone B.

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crop demand, full recovery of physiological processes that were negatively impacted during the deficit period are often achieved (Chalmers et al., 1983; Awal and Ikeda, 2002; Byrd et al., 2014). Although physiological impacts of RDI have been observed, application of RDI treatments have generally been set relative to a percent reduction in replacement of full evapotranspiration (Chalmers et al., 1983; Byrd et al., 2014), rather than based on plant responses or on measures more closely related to plant water uptake capacity, such as soil water potential.

Priming is a treatment that may increase tolerance to subsequent stresses encountered later in an organism's development. The treatment, an elicitor, can be any of a broad range of treatments, and the stresses are from an equally broad range, including biotic and abiotic (Tanou et al., 2012). Elicitors in other studies have included chemical treatments, such as plant hormones or stress signals such as peroxide or nitric oxide, as well as mild levels of stress, such as temporary exposure to high temperatures or ultra-violet radiation (Bruce et al., 2007). Priming necessitates a mild stress level because the goal of priming is to potentiate improved stress response without imposing an elicitor that is severe, which could lead to cellular, tissue, or organismal damage beyond recovery or repair.

Primed acclimation (PA) is a crop management scheme that uses a targeted RDI to elicit a primed state in a crop. Peanut (*Arachis hypogaea* L.), because of its environmental and developmental plasticity, has been used as a model crop for testing this management scheme in an effort to improve water stress tolerance during critical reproductive stages of development. It has also been important for examining the recovery process observed after an RDI period. Awal and Ikeda (2002) found that withholding irrigation for a 12-day period reduced peanut growth, leaf water status, and chlorophyll content, but that these variables recovered upon re-watering. For peanut, withholding water also increased the root:shoot ratio (Awal and Ikeda, 2002). Rowland et al. (2012) tested various levels of reduced irrigation during the vegetative stage of peanut development and found improved yield and leaf greenness, as determined by the normalized difference vegetation index (NDVI), compared to a fully irrigated control when irrigation was reduced by 50% during the vegetative stage followed by full irrigation during the duration of the crop cycle (PA). This was attributed partially to greater rooting depth in the vegetative stage for plants in the PA treatment. Despite results such as increased growth or leaf greenness, there are no reports characterizing the nature of photochemical changes resulting from RDI.

Studies of RDI-induced PA have set the mild reductions in irrigation treatments needed for imposition of priming relative to a reduction of standard or accepted irrigation levels (Rowland et al., 2012; Byrd et al., 2014), and have focused on annual agronomic crops. However, due to the variability in environmental conditions from year to year, the appropriate stress level for achieving priming would likely be better set by direct measures of crop stress or surrogate measures such as soil water potential. The effectiveness of a priming treatment theoretically can be determined, even in the absence of a subsequent stress, by identifying a plant-based variable (i.e., physiological or growth variable) that is stimulated by mild stress (Awal and Ikeda, 2002). The current study aimed to set a plant-based soil water potential target for the appropriate stress level to achieve optimal priming, and test the impacts of such a treatment on papaya (*Carica papaya* L.), a perennial fruit. Papaya was deemed an ideal species because of its environmental plasticity (Clemente and Marler, 1996) and its extreme isohydric capacity (Mahouachi et al., 2006).

Studies of papaya-water relations have included characterization of stomatal and chlorophyll fluorescence responses to water deficits and varying climatic conditions, such as wind and fluctuating light levels (Marler and Mickelbart, 1998; Clemente and Marler, 2001; Marler and Clemente, 2006). Significant reductions in papaya growth and *A* have been observed between soil water tensions of −20 and −60 kPa (Aiyelaagbe et al., 1986; Marler and Clemente, 2006); for example, maintaining soil water tension at −30 kPa reduced *A* and growth relative to irrigating plants to field capacity (Clemente and Marler, 1996). De Lima et al. (2015) tested deficit irrigation and partial root zone drying on papaya, and found that significant reductions in growth occurred by reducing soil water content between 30 and 50%, and that some non-hydraulic effects occurred, as partial root zone drying reduced stomatal conductance. However, 30–50% drying of the root zone did not significantly alter whole-plant growth or carbon partitioning. While water deficit treatments in that study were continuous throughout the growing season and thus did not qualify as RDI or PA, it demonstrated papaya has some degree of yield and growth tolerance to reduced soil water content. Primed acclimation treatments should target this moderate range to produce a physiological response with minimal reduction of photosynthesis during the deficit period.

The objectives of this study were to: (1) determine the most sensitive physiological responses to water deficit in papaya that could serve as indicators for a threshold soil-moisture level at which priming is achieved; and (2) assess the effects of PA on physiological and growth variables associated with papaya water use, vigor, and growth.

2. Materials and methods

2.1. Plant material

Two experiments were conducted outdoors during the summer and fall 2013 in Gainesville, Florida, USA (29.6520° N, 82.3250° W). For both experiments, 'Red Lady' papaya plants were germinated in Pro-Mix® potting medium (Premier Tech Horticulture, Quakertown, PA, USA) in flats in a greenhouse approximately three months before transplanting into 9-L pots in Pro-Mix® potting medium in April. Pots were set on pavers to avoid contact with soil and prevent soil water from entering the potting medium from below. Papaya stems were surrounded with Styrofoam collars to which plastic aprons were attached and spread to cover the top of the pot to prevent entry of rainwater. Plants from the priming experiment were moved into a greenhouse to avoid damage from low temperatures on two nights, and were returned to the field as soon as temperatures exceeded 10 °C.

2.2. Experiment 1: substrate dry-down study

2.2.1. Substrate water-holding capacity

Pro-Mix® potting medium was dried for 72-h in a drying oven at 60 °C. Three 1-kg samples were weighed, thoroughly soaked in water, and allowed to drain for 8 h. After drainage had ceased, the samples were re-weighed to determine the water-holding capacity (WHC) of the potting medium.

2.2.2. Substrate dry-down

The experiment was arranged as a randomized complete block with 10 blocks. Plants were placed in blocks according to size so that initial (pretreatment) means and variances of plant heights were not significantly different between treatments. There were two treatments: (1) fully irrigated, and (2) dry-down. In the fully-irrigated treatment, plants were weighed and re-watered to water holding capacity (WHC) daily. In the dry-down treatment, plants were weighed and re-watered; however on each day during the dry-down period, plants in this treatment were re-watered 7% below that of the fully irrigated treatment, with an additional 7% reduction each day. Thus, plants were re-watered to 100% WHC on Day 1, to 93% on Day 2, to 86% on Day 3, to 79% on Day 4, etc. The