



Short- and long-term responses of pepper seedlings to ABA exposure



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ABSTRACT

Plants perceive environmental stress and use this information to modulate their regular pattern of development. Abscisic acid (ABA) mediates plant responses to many abiotic stresses. This study investigated the efficiency of short- versus long-term ABA exposure on critical morphological and physiological responses linked to functional changes in stomata, stomatal density, plant water status, photosynthetic activity and overall growth in bell pepper (*Capsicum annuum* L.). ABA was applied to pepper seedlings as foliar at 0, 0.1 or 1.0 mM for 5, 10 or 15 consecutive days. A depressive effect of ABA on net photosynthetic rate (A_{CO_2}) and stomatal conductance (g_s) compared to control was found after 5-day ABA-exposure at 1.0 mM, and after 15-day ABA-exposure at 0.1 mM and 1.0 mM ABA. Plants quickly resumed the photosynthetic activity since no effect of ABA was found after a longer recovery. Temporary higher leaf water potential was observed in seedlings treated with ABA compared to control. At 17 days after the beginning of the experiment, the number of stomata at adaxial and abaxial side was reduced at 1.0 mM ABA-rate compared to 0.1 mM ABA for each ABA-day of exposure. ABA-rate at 1.0 mM decreased leaf weight, number and area with a more pronounced effect as ABA-days of exposure increased. Stem dry weight was almost unaffected by ABA-rate at 0.1 mM, but 1.0 mM decreased stem weight by 30% after 15-day ABA-exposure. The increased specific root length at 1.0 mM ABA-rate after 5- or 15-day ABA exposure suggested that ABA induced the growth of thinner roots. The delayed effect of ABA-rate and ABA-days of exposure was measured for plants allowed to recover for 23 days after the last application for the longest treatment. Growth parameters were generally affected by ABA after longer recovery. The effect of ABA on modulation of pepper seedlings growth and physiology was dependent on rate and length of exposure but recovery duration was important as well. These results provide new evidences that application of ABA at a specific rate and length of exposure could eliminate the risk of stressing young seedlings to the point of physiological injury as previously reported for some hardening techniques.

1. Introduction

Abscisic acid (ABA) is a phytohormone that mediates plant responses to abiotic stresses, including water deficit, but it is also important in a non-stress-related regulatory functions (Sharp, 2002). ABA is synthesized in leaves and roots (Thompson et al., 2007). ABA content in roots is well correlated with soil moisture and relative water content in many plant species (Zhang and Davies, 1989; Liang et al., 1997).

The involvement of ABA in mediating drought stress has been extensively researched. A dominant role for ABA in root to shoot signaling under drought is in the control of stomatal aperture (Davies and Zhang, 1991). Increased ABA levels limit transpiration water loss by reducing stomatal aperture, as an adaptation response to alleviate growth inhibition due to a plant water deficit (Leung and Giraudat, 1998).

The increase in ABA concentrations to which stomata respond under

water deficit is the result of synthesis and redistribution of ABA within leaves, and also to the synthesis and export from roots (Davies and Zhang, 1991). The stomatal conductance is negatively correlated with ABA concentration at any given set of environmental conditions (Trejo et al., 1995).

Elevated leaf ABA concentration is generally viewed as a short-term and reversible response since the return of stomatal function to its full potential lasts from a few hours (Trejo et al., 1995) to 1 or 2 days (Ackerson, 1980; Henson, 1981). Repeated applications of exogenous ABA to leaves could induce changes in stomatal size and density in plants under well-watered conditions (Franks and Farquhar, 2001). In plants exposed to frequent or long-term drought stomata reopened more readily upon rewatering than did stomata in plants experiencing a single, brief period of drought (McCree, 1974; Brown et al., 1976). Additionally, a variation in plant water status influences the size and

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performance of stomata. Cutler et al. (1977) and Spence et al. (1986) observed that the stomata in plants grown under water stress were smaller than in well-watered plants. Those observations emphasize an important difference between long-term anatomical and short-term physiological plant reactions to water stress as it was previously proposed by Spence et al. (1986).

Regarding the photosynthetic capacity, Bradford et al. (1983) found that young tomato leaves which were exposed long-term to elevated ABA concentrations had the same photosynthetic capacity as control plants, despite operating at different stomatal conductance, and with distinctive stomatal sizes and density. Exogenous application of ABA to barley seedlings induced changes in photosynthesis by increasing the rate of photorespiration, the activity of the photo-respiratory enzymes, the CO₂-compensation point, and stomatal resistance (Popova et al., 1987; Popova et al., 1996).

ABA has generally been regarded as an inhibitor of shoot growth (Trewavas and Jones, 1991) due to the shoot and root growth modulation when applied to well-watered plants. The root-sourced ABA is at least partly the cause of shoot growth inhibition, although there are studies of ABA-deficient mutants that suggest that endogenous ABA may often function to maintain rather than inhibit shoot growth (Roberts et al., 2002; Sharp and LeNoble, 2002). The regulatory control of shoot inhibition has recently been explored to prevent shoot elongation and increase the quality of containerized pepper and watermelon transplants (Agehara and Leskovar, 2014a, 2014b, 2015, 2017).

The maintenance of root elongation at low water potentials is considered to be an adaptive feature that promotes plant survival under water-limited conditions (Sharp and Davies, 1989; Spollen et al., 1993). In addition to the stimulative role of ABA on primary root elongation (Davies and Bacon, 2003) increasing evidence suggests that ABA has a significant role in root branching by mediating stress response and by functioning as an endogenous developmental signal (De Smet et al., 2006).

Exogenous application of natural s-ABA or its analogues has been reported to improve drought tolerance and reduce transplant shock in various plant species such as maize (*Zea mays* L.) (Bochicchio et al., 1991), pepper (*Capsicum annuum* L.) (Leskovar and Cantliffe, 1992; Goreta et al., 2007; Leskovar et al., 2008), Kentucky bluegrass (Wang et al., 2003), Tradescantia virginiana (Franks and Farquhar, 2001), *Malus* species (Ma et al., 2008), tobacco (Pospíšilová et al., 1998), and tomato (Sharma et al., 2006).

The use of exogenous ABA to chemically stimulate transient drought conditions in well-watered plants enabled investigations of the influence of ABA in modifying stomatal function, plant water status and CO₂ assimilation rate (Franks and Farquhar, 2001). Stomatal closure immediately after single ABA application was repeatedly proved to be a short-term response affecting plant water status (Goreta et al., 2007; Shinohara and Leskovar, 2014), however, the plant response to repeated ABA application and long-term effects are much less known. Some effects of stress conditions could be simulated by exogenous ABA application (Jakab et al., 2005). Therefore, we assume that prolonged exposure of plants to ABA could induce morphological and physiological responses linked to functional changes in stomata, stomata density, plant water status, photosynthetic activity and overall growth in bell pepper seedlings.

It has been reported that pre-exposure to various abiotic stresses or pre-treatment with hormones may alter plants' responses by improving their resistance to a similar stress in future exposures (reviewed in Li and Liu, 2016). These observations have led to the concept of 'stress memory' (Bruce et al., 2007) implying that during subsequent exposures plants provide responses that are different from those during their first encounter with the stress.

The objective of this study was to investigate the efficiency of short-versus long-term exposure of pepper transplants to ABA concentrations on critical morphological and physiological response immediately after the end of ABA application or subsequent recovery. The possibility that

ABA may serve to control developmental processes in specific direction could be useful for acclimation of plants to recurrent stressful events.

2. Materials and methods

2.1. Growth conditions

The greenhouse study was conducted at the Texas A & M AgriLife Research Center in Uvalde (29°1'N, 99°5'W). Maximum photosynthetic photon flux (PPF) within the greenhouse at the canopy level was about 1500 μmol m⁻² s⁻¹ using natural summer photoperiods. Minimum-maximum day/night temperatures during the experiment were 25–40 °C/16–20 °C.

Bell pepper (*Capsicum annuum* L., cv. Brigadier, Novartis Seed Inc., Boise, Idaho) seeds were sown in peat-lite mix (Speedling Peat-lite; Speedling Inc., Sun City, Florida) and covered with a thin layer of medium grade horticultural vermiculite. Seedlings were grown in a commercial greenhouse (South Cross Vegetable Transplants, Mission, Texas) in 338-cell trays with 28 mL of cell volume. At the 5-week old stage, time when seedlings reached the optimum size for transplanting in the field, they were transferred into trays with 108 mL of cell volume giving a plant density of approximately 255 m⁻². The trays were arranged in blocks and during the course of the experiment they were rotated across the greenhouse bench to avoid position effects.

Two days prior to imposing the ABA treatments seedlings were fertilized with a soluble fertilizer 30N-4.4P-8.3 K (Scotts Miracle-Gro Products, Inc., New York) at an N rate of 100 mg L⁻¹. Fertilizations were repeated every 5 days during the experiment. In order to avoid washing off ABA from the leaf surface, plants were irrigated by flotation until near saturation.

2.2. Abscisic acid treatments

Abscisic acid (ABA, Valent BioSciences Co., Libertyville, Illinois) was applied as foliar once a day at 0, 0.1 or 1.0 mM during midday (1200–1300_{HR}) for either 5, 10 or 15 consecutive days. Individual complete trays (replication) were used for each ABA-rate and ABA-repeated exposure. Foliar applications were done with hand-held sprayer until leaves were evenly covered to the dripping point. Control plants (5, 10 and 15 days) and plants for which the ABA exposure treatment was completed (5 and 10 day) were sprayed with tap water.

2.3. Plant growth

Plant height and stem diameter were always measured on the same set of plants during the course of the experiment. Plant height was taken from the substrate level to the shoot apex and stem diameter at the substrate level. For biomass determination, additional plants were harvested and separated into leaves, stems and roots. Leaf area (LA) was measured with a leaf area meter (LI-3100, LI-COR, Lincoln, Nebraska). Stem and leaf components were oven-dried at 70 °C for three days and dry weights were thereafter determined. Roots were carefully washed free of rooting medium and scanned twice. The first scanning consisted of the whole intact root systems, while the second was done after separating root components into basal (coming from the hypocotyl) and lateral roots were separated from the taproot. For both scans, roots were spread out in a transparent tray containing a thin layer of water. Roots were scanned with a digital image analysis system at a resolution of 300 dots per inch (dpi) and total root length and distribution by diameter (≤ 0.25 ; $0.25 > \leq 0.50$; $0.50 > \leq 0.75$; $0.75 > \leq 1.0$; $1.0 > \leq 1.25$ and > 1.25 mm) were measured (WinRhizo LA 1600, Régent Instruments Inc., Québec, Canada). Scanned roots were blotted and oven-dried as was described for stem and leaves. Specific root length (root length/root dry weight) was calculated for all samples.

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