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Responses in gas exchange and water status between drought-tolerant and -susceptible soybean genotypes with ABA application

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ABSTRACT

The purpose of this study was to investigate the physiological responses of drought-tolerant and drought-susceptible soybean genotypes to exogenous abscisic acid (ABA) application during progressive soil drying at seedling stages. Five-day old soybean seedlings were transplanted into PVC tubes filled with soil mixture. Seedlings were watered daily with similar water volumes until second trifoliate leaves emerged, and thereafter soil drying with or without exogenous ABA application was imposed. Half of the seedlings of each genotype were left for regular watering as control plants. Soil water status declined significantly over seven days of withholding water supply for both genotypes. Leaf expansion rate, stomatal conductance (g_s), leaf water potential (ψ_w), and relative water content of leaves (%RWC) declined significantly under soil drying as well as soil drying with ABA application, compared to their values for well-watered soybean genotypes. However, a drought-tolerant genotype (C12) responded more rapidly than a drought-susceptible genotype (C08) after imposition of soil drying and soil drying with exogenous ABA. In addition, application of exogenous ABA to water-restricted soybeans resulted in higher %RWC and ψ_w in the drought-tolerant than in the drought-susceptible genotype. Compared to the drought-susceptible genotype, the drought-tolerant genotype was more responsive to exogenous ABA application, resulting in a higher root-to-shoot ratio.

1. Introduction

Drought stress is a key environmental constraint to productivity in world agriculture. Water stress impairs numerous physiological as well as biochemical processes of crop plants. Photosynthesis is a major process affected by water deficit, via decreased CO_2 diffusion to the chloroplast and metabolic constraints [1]. Water-restricted plants show immediate low stomatal conductance without alteration of shoot water potential. The reason for this response is that leaf stomata cannot open because plants can

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Abbreviations: ABA, abscisic acid; g_s, stomatal conductance; LA, leaf area; LL, leaf length; LW, leaf width; RWC, relative water content; ψ_w, leaf water potential.

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sense the availability of water in the soil and regulate stomatal behavior accordingly, whatever the water status of their leaves [2]. The consequences of water stress to crop plants are thus a reduction in leaf expansion rate, accelerated leaf senescence, and reduction in production and partitioning of photo assimilates to the plants.

Drought tolerance is thus a key trait for increasing and stabilizing crop production [3,4]. Abscisic acid (ABA) accumulates in response to low-temperature and water stress [5,6], and is now known to be involved in several developmental processes as well as acclimation to environmental stresses (cold, salt, and drought) [7,8]. ABA is produced in plant roots and transported to leaves via xylem flow under water-limiting conditions [9]. It triggers stomatal closure in response to drought stress, thereby reducing photosynthetic CO_2 assimilation [10]. The influence of plant hormones such as ABA in plants under drought stress is thus important in determining physiological responses that may ultimately lead to adaptation to unfavorable environmental conditions [11].

Exogenous ABA application reduced photosynthetic rate, stomatal conductance, and transpiration rate in cotton [12]. Liu et al. [13] found that exogenous ABA application decreased photosynthetic rate and pod set in well-watered soybean plants but that those parameters were increased when ABA was applied to drought-stressed plants. Lam [14] genomically evaluated 31 soybean accessions at the Chinese University of Hong Kong for developing drought-tolerant soybean varieties, and identified promising genotypes in a hydroponic culture system using polyethylene glycol (PEG) and salts. Field performance of two drought-tolerant and susceptible genotypes (C12 and C08) has been partially tested in Dunhuang, China.

Given that drought-stressed plants produce ABA in leaves and regulate their stomata by maintaining higher water status in leaves, we hypothesized that the application of exogenous ABA to leaves of soil drying soybean plants would encourage earlier stomatal closure and reduce water loss from plants, thereby leading to higher relative water content and water potential in leaves. This study was accordingly undertaken to investigate the differences in physiological response to exogenous ABA application of drought-tolerant and drought-susceptible soybean genotypes during progressive soil drying.

2. Materials and methods

2.1. Plant materials and exogenous ABA application

The drought-tolerant Jindou 21 (C12) and drought-susceptible Union (C08) soybean genotypes were used for this study. Seedlings were grown in a plastic tray containing soil mixture (soil and peat moss) in the greenhouse. Five-day old seedlings were transplanted into PVC tubes (50 cm length × 5 cm inner diameter) filled with soil mixture (soil and peat moss in a 1:1 volume ratio, with the addition of NPK at 14:14:14). Fertilizer granules were mixed at 5 g L^{-1} of soil mixture. Plants were grown under natural sunlight in the greenhouse with average daytime temperature 28 ± 2 °C and relative humidity 60–70%. Plants were watered daily with similar water volumes until second trifoliate leaves emerged, after which soil drying treatment was imposed. One third of the seedlings of each genotype were kept for regular watering as control plants, another third subjected to soil drying, and the remaining third subjected to soil drying + exogenous ABA treatment. At the time of beginning soil drying, 50 mol L^{-1} solution of ABA with 0.05% Tween-20 was sprayed on soil drying plants twice daily (at 1000 h and 1400 h) for two days on both adaxial and abaxial surface of leaves and measurement was started 3 h after the first spray.

2.2. Measurement of stomatal conductance

After the onset of soil drying along with spraying of exogenous ABA on leaves, the stomatal conductance (g_s) of fully expanded leaves was measured 3 h after ABA application. Thereafter, g_s was measured daily with a leaf porometer (Decagon Devices, Inc. USA) until a week of soil drying.

2.3. Measurement of leaf area expansion

Leaf area (LA) was measured with a portable leaf area meter (LI-3100; Li-COR, Inc. USA). After imposition of soil drying followed by application of exogenous ABA newly emerged leaves (center leaflet of second trifoliate leaf) were tagged for measuring LA each day. Leaf length (LL) and width (LW) were measured daily with a measuring ruler and the relationship between the product LL × LW and LA was determined for each genotype from individual leaf measurements of 15 leaves. The regression of LA on LL × LW was fitted as $LA = k \times LL \times LW$, where k is the slope of the linear function.

2.4. Measurement of relative water content

Relative water content (%RWC) of fully expanded youngest mature leaves was measured on both soil drying and soil drying + ABA-treated plants 0, 1, 3, and 7 days after imposition of treatments. To minimize solute leakage and cut surface effect, the entire leaf was used. Leaf petioles were carefully detached from plants, fresh weights were recorded, and then kept in water holding plastic tube in a closed container in an atmosphere saturated by means of wet tissue paper around the inner wall of the container. Turgid weight was measured after 24 h and dry weight was measured after oven-drying for 48 h at 65 °C. Leaf relative water content was calculated by the following equation:

$$\text{Relative water content } (\%\text{RWC}) = \frac{\text{Fresh weight–dry weight}}{\text{Turgid weight–dry weight}} \times 100$$

2.5. Measurement of leaf water potential

Leaf water potential (ψ_w) was measured at 0, 1, 3, and 7 days after soil drying and soil drying + exogenous ABA application using a pressure chamber (Soilmoisture Equipment Corp, Santa Barbara, California, USA). The leaf petiole was sealed into a pressure chamber and the chamber was gradually pressurized until the meniscus of the xylem sap become