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Differences between soybean genotypes in physiological response to sequential soil drying and rewetting

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ABSTRACT

Soybean genotypes show diverse physiological responses to drought, but specific physiological traits that can be used to evaluate drought tolerance have not been identified. In the present study we investigated physiological traits of soybean genotypes under progressive soil drying and rewetting, using a treatment mimicking field conditions. After a preliminary study with eight soybean genotypes, two drought-tolerant genotypes and one susceptible genotype were grown in the greenhouse and subjected to water restriction. Leaf expansion rate, gas exchange, water relation parameters, total chlorophyll (Chl), proline contents of leaves, and root xylem pH were monitored in a time course, and plant growth and root traits were measured at the end of the stress cycle. Drought-tolerant genotypes maintained higher leaf expansion rate, net photosynthetic rate (P_n), Chl content, instantaneous water use efficiency (WUEi), % relative water content (RWC), water potential (ψ_w), and turgor potential (ψ_p) during progressive soil drying and subsequent rewetting than the susceptible genotypes. By contrast, stomatal conductance (g_s) and transpiration rate (T_r) of tolerant genotypes declined faster owing to dehydration and recovered more sharply after rehydration than the same parameters in susceptible ones. Water stress caused a significant increase in leaf proline level and root xylem sap pH of both genotypes but tolerant genotypes recovered to pre-stress levels more quickly after rehydration. Tolerant genotypes also produced longer roots with higher dry mass than susceptible genotypes. We conclude that rapid perception and adjustment in response to soil drying and rewetting as well as the maintenance of relatively high P_n, %RWC, and root growth constitute the mechanisms by which drought-tolerant soybean genotypes cope with water stress.

Abbreviations: Chl, chlorophyll; g_s, stomatal conductance; LA, leaf area; LL, leaf length; LW, leaf width; PPFD, photosynthetic flux density; P_n, net photosynthetic rate; RWC, relative water content; T_r, transpiration rate; wr, water-restricted; ww, well-watered; WUEi, instantaneous water use efficiency; ψ_w, water potential; ψ_s, osmotic potential; ψ_p, turgor.

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1. Introduction

Drought is a critical environmental factor that imposes water stress on crops, and a major constraint on plant growth and productivity [1]. It is the most damaging abiotic stress affecting modern agriculture [2]. Most cultivated crops are comparatively susceptible to even mild water stress. Scarcity of water may become more severe in the future with changing global climate. A lack of sufficient moisture leading to drought stress is a common phenomenon in rainfed areas, brought about by infrequent rain and poor irrigation [3]. Economic yield reduction due to drought stress at various growth stages has been reported in many field crops, such as soybean [4], maize [5], barley [6], rice [7], common bean [8], and potato [9].

The response of drought stress to plants is a highly complex trait involving multiple genetic, morphological, physiological, and biochemical mechanisms [10,11]. Species tolerant to drought generally differ morphologically and/or physiologically and possess mechanisms allowing better production under limited water supply [12]. Drought-tolerance mechanisms involve maximization of water uptake by deep, dense root systems and minimization of water loss by stomatal closure and reduction of leaf area [13].

Plants can sense water shortage around their roots and respond instantaneously by sending chemical signals to shoots to initiate various adaptive responses including reducing leaf expansion and increasing stomatal closure [14,15]. During water shortage, roots produce chemical signals such as increased abscisic acid (ABA) concentration and pH of xylem sap transported to the leaf through the transpiration stream, and regulate stomatal opening and leaf growth [14,16–18]. Even mild water stress may increase xylem sap pH, owing to reduced nitrate uptake causing an increase in apoplastic pH [19,20]. Increased xylem pH has been suggested to act as a drought signal [21]. However, increased pH was observed in some species experiencing water deficit and reduced pH in others [22]. In another study, soil water deficit plants did not show a drought-induced increase in xylem pH [23].

Plants have evolved mechanisms that allow them to perceive external stresses and rapidly regulate their physiology and metabolism to cope with them [2]. Leaf conductance can be reduced in the absence of visible reduction of leaf water potential [24,25]. The net photosynthetic and transpiration rates of water-stressed plants decrease [26–28], and instantaneous water use efficiency (WUEi) reflects the ability of plants to produce biomass per unit of water transpired [29]. In this context, WUEi can be considered as an adaptive indicator of soil drying conditions. The adaptive response of proline accumulation is commonly observed in plants under drought stress [30]. Proline may act in osmotic adjustment [31] and also as an antioxidant [32].

Soybean (*Glycine max* L. Merr.) is one the major sources of protein for human and animal nutrition as well as a key source of vegetable oil. It is considered as a potential crop for production of biodiesel. However, it requires adequate soil moisture throughout its growth period to attain its yield potential [33].

Depending on genotypic characteristics, soybean uses 450–700 mm of water during the growing season [34]. Soybean is considered susceptible to drought stress, especially in the critical period of its ontogeny [35]. It is accordingly desirable to identify drought tolerant soybean genotypes able to grow well with limited water supplies. Different physiological mechanisms in leaves and roots are important in regulating the growth of soybean genotypes under progressive soil drying. A drought-tolerant soybean genotype may escape water stress effects by increasing root depth in soil, reducing leaf area expansion, closing stomata, and maintaining higher relative water content and consequently water potential and turgor pressure.

Unirrigated soybeans showed greater root length than irrigated plants, especially in the subsoil [36]. Significant correlations have been found in soybean between drought resistance and various root traits such as dry weight, total length, and volume and number of lateral roots [37,38]. Rooting depth was greater in drought-tolerant than in drought-susceptible clones of *Coffea canephora* [12]. In *Hibiscus rosa-sinensis*, relative water content, turgor potential, transpiration, stomatal conductance, and water use efficiency decreased under drought stress [39].

However, to our knowledge, leaf expansion rate, gas exchange, water relations, proline, total chlorophyll content, root xylem sap pH, and root traits have not been investigated concomitantly in both drought-tolerant and drought-susceptible soybean genotypes under progressive soil drying followed by rewetting. The present study was designed to improve our understanding of the manner in which drought-tolerant genotypes cope with sequential soil drying, affording a better opportunity to select drought-tolerant soybean genotypes for cultivation in dry areas. In a preliminary experiment, we studied the drought tolerance of eight soybean genotypes under four weeks of water restriction. Two genotypes performed better under water-limited conditions than the others, based on their leaf water status, stomatal conductance, and root length, while one of the genotypes showed markedly poor performance. We focused on these three soybean genotypes for detailed physiological study under progressive water-limited conditions. In the present study, these three genotypes, Jindou 21 (C12), Union (C08), and Mengjin 1 (W05) were used for detailed evaluation of their physiological responses to water restriction and subsequent rewetting.

2. Materials and methods

2.1. Plant materials and growing conditions

Seeds of soybean genotypes were obtained from the Center for Soybean Research of the State Key Laboratory of Agrobiotechnology, The Chinese University of Hong Kong. Seedlings were grown in a plastic tray containing soil mixture (soil and peat moss) in the greenhouse. Five days after germination, seedlings were transplanted into PVC tube (50 cm length and 5 cm inner diameter) filled with soil mixture (sandy loam soil and peat moss at 1:1 volume ratio fertilized with NPK at 14:14:14). Fertilizer granules were added at 5 g L^{-1} of soil mixture. Plants were grown under natural sunlight in the greenhouse with average daytime temperature 25 ± 2 °C and relative humidity 60–70%. The light intensity in the greenhouse was recorded daily at noon and the average was 140–160 μmol m^{-2} s^{-1}. Soybean plants were watered daily