



Research article

Understanding abiotic stress tolerance mechanisms in soybean: A comparative evaluation of soybean response to drought and flooding stress



Raymond N. Mutava^{a,1}, Silvas Jebakumar K. Prince^{a,1}, Naeem Hasan Syed^{b,1}, Li Song^a, Babu Valliyodan^a, Wei Chen^a, Henry T. Nguyen^{a,*}

^a National Center for Soybean Biotechnology and Division of Plant Sciences, University of Missouri, Columbia, MO 65211, USA

^b School of Human and Life Sciences, Canterbury Christ Church University, Canterbury, CT1 1QU, United Kingdom

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ABSTRACT

Many sources of drought and flooding tolerance have been identified in soybean, however underlying molecular and physiological mechanisms are poorly understood. Therefore, it is important to illuminate different plant responses to these abiotic stresses and understand the mechanisms that confer tolerance. Towards this goal we used four contrasting soybean (*Glycine max*) genotypes (PI 567690 – drought tolerant, Pana – drought susceptible, PI 408105A – flooding tolerant, S99-2281 – flooding susceptible) grown under greenhouse conditions and compared genotypic responses to drought and flooding at the physiological, biochemical, and cellular level. We also quantified these variations and tried to infer their role in drought and flooding tolerance in soybean. Our results revealed that different mechanisms contribute to reduction in net photosynthesis under drought and flooding stress. Under drought stress, ABA and stomatal conductance are responsible for reduced photosynthetic rate; while under flooding stress, accumulation of starch granules played a major role. Drought tolerant genotypes PI 567690 and PI 408105A had higher plastoglobule numbers than the susceptible Pana and S99-2281. Drought stress increased the number and size of plastoglobules in most of the genotypes pointing to a possible role in stress tolerance. Interestingly, there were seven fibrillin proteins localized within the plastoglobules that were up-regulated in the drought and flooding tolerant genotypes PI 567690 and PI 408105A, respectively, but down-regulated in the drought susceptible genotype Pana. These results suggest a potential role of Fibrillin proteins, FBN1a, 1b and 7a in soybean response to drought and flooding stress.

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1. Introduction

Drought, flooding, high temperature, cold, salinity, and nutrient availability are abiotic factors that have a huge impact on world agriculture and account for more than 50% reduction in average potential yields for most major crops (Wang et al., 2003). As climate prediction models show increased occurrences of drought, flooding, and high temperature spells during the crop growing periods (IPCC, 2008; Mittler and Blumwald, 2010), global food production will continue to be challenged. The demand for food and oil crops will continue to rise with the increase in global population;

therefore improving productivity to ensure sustainable yields under changing environmental conditions is essential. To achieve global food security there is a need to increase our understanding of plant responses to abiotic stress with an aim of breeding crops that can maintain higher photosynthetic rates, better growth, and improved yield under stress conditions (Condon et al., 2004; Morison et al., 2008). Some level of success has been achieved in crop breeding for tolerance to abiotic stresses through genetic manipulation of transcription factors (TFs), late embryogenesis abundant (LEA) proteins, and antioxidant proteins (Umezawa et al., 2006; Bhatnagar-Mathur et al., 2008). However, research programs aimed at developing tolerance to a particular stress do not necessarily test susceptibility to other abiotic stresses and this can have unforeseen consequences.

Although irrigation can be used as a strategy to overcome the effects of drought stress on crop yields, the available water

* Corresponding author.

E-mail address: nguyenhenry@missouri.edu (H.T. Nguyen).

¹ Contributed equally.

resources continue to decline. Therefore, adapting crops to water-limited environments and improving their water use efficiency will be crucial for developing climate-resilient cultivars that are capable of producing more food per unit of water used. Drought stress causes tissue dehydration which is characterized by fundamental changes in water relations, physiological and biochemical processes, membrane structure, as well as ultrastructure of sub-cellular organelles (Sarafis, 1998; Yordanov et al., 2003). At the whole-plant level, drought stress leads to a progressive suppression of photosynthesis caused by stomatal and non-stomatal limitations (Wise et al., 1992; Yordanov et al., 2003). Tolerant genotypes should not only be able to retain sufficient water under drought, but also have a highly active system for protection against oxidative stress injury.

Flooding affects about 10% of the global land area (Setter and Waters, 2003). In the USA alone 16% of soils are affected by waterlogging and the economic losses for crop production are estimated to be the second largest after drought (Zhou, 2010). Yield losses resulting from flooding depend on the plant species and age, soil type, and duration of flooding. Despite knowledge of adaptive mechanisms and regulation at the molecular level, understanding of the mechanisms behind plant response to flooding is very limited. Studies with *Arabidopsis* (*Arabidopsis thaliana*) (Gonzali et al., 2005) and rice (*Oryza sativa*) (Hattori et al., 2009; Xu et al., 2006; Singh et al., 2010) have shown that there are many genes associated with flooding responses suggesting that the regulation of flooding tolerance in plants is complex. Many studies have looked into the mechanisms underlying the responses to flooding stress using model plants (Vashisht et al., 2011) as well as crop species (Setter and Water, 2003; Zaidi et al., 2004; Rhine et al., 2010) however very few studies have looked at this at the whole plant and cellular level.

Plastoglobules are lipoprotein bodies attached to the thylakoids (Austin et al., 2006) that store lipids and antioxidants such as tocopherols, carotenes, and plastoquinones (Steinmuller and Tevini, 1985) and also contain tocopherol cyclase, which is involved in α -tocopherol synthesis (Austin et al., 2006; Vidi et al., 2006). Plastoglobules contain fibrillins, which are ubiquitous proteins that maintain plastoglobule structural integrity (Langenkamper et al., 2001; Vidi et al., 2006; Brehelin et al., 2007) and stabilize the photosynthetic apparatus during photo-oxidative stress (Yang et al., 2006; Youssef et al., 2010), osmotic stress (Gillet et al., 1998), drought (Rey et al., 2000), and low temperature (Rorat et al., 2001). Even though some studies have been conducted to dissect the role of plastoglobules in model (Ytterberg et al., 2006; Giacomelli et al., 2006) and some horticultural plants (Chen et al., 1998; Gillet et al., 1998), no information on major crops such as soybean is available for drought and flooding conditions.

Soybean is the world's most widely grown seed legume, providing an inexpensive source of protein and vegetable oil for human consumption. This important legume crop is adapted to grow in a wide range of climatic conditions; however, soybean growth, development, and yield are greatly affected by several abiotic stressors, such as; flooding (Komatsu et al., 2012; Khatoon et al., 2012), drought (Mohammadi et al., 2012), and salinity (Sobhanian et al., 2010). As in other major crops, breeding for drought tolerance in soybean has been a challenge because of the inherent complexity of breeding for drought tolerance combined with a lack of physiological perspective in the dissection of traits (Sadok and Sinclair, 2011) and limited drought tolerant germplasm resources (Carter et al., 1999, 2004). Traits that have been targeted for drought tolerance in soybean include deeper rooting system, sustained nitrogen fixation (Sinclair et al., 2007), slow canopy wilting (Sloane et al., 1990; Hufstetler et al., 2007; King et al., 2009) and water use efficiency. The slow wilting trait in soybean suggests

a conservative water use strategy by some genotypes and has been used in breeding for drought tolerance. Even though there has been some success in breeding for abiotic stress tolerance in soybean, the underlying molecular and physiological mechanisms involved in drought and flooding tolerance are still poorly understood. Previous studies explored some morphological (Benjamin and Nielsen, 2006; Wang et al., 2012), physiological and biochemical (Sloane et al., 1990; Agarwal et al., 2005; Manavalan et al., 2009) and molecular (Ahuja et al., 2010; Stolf-Moreira et al., 2010; Manavalan et al., 2009) aspects in an effort to understand drought tolerance mechanisms in soybean; however, there is still limited information at the cellular and biochemical levels. Photosynthetic efficiency which is crucial for maximum yields is negatively affected by abiotic stress. In this study we looked at the role of some of the processes that will affect photosynthesis under drought and flooding stress. Using contrasting genotypes we compared soybean responses to drought and flooding stress at the physiological, biochemical, and cellular level, quantified these responses and tried to infer their role in soybean drought and flooding tolerance.

2. Materials and methods

2.1. Growing conditions

Four contrasting soybean (*Glycine max*) genotypes were used in this experiment: PI 567690 – drought tolerant (DT), Pana (PI 597387) – drought susceptible (DS) (Pathan et al., 2014), PI 408105A – flooding tolerant (FT) and S99-2281 (PI 654356) – flooding susceptible (FS). The plants were grown under a 14 h photoperiod and optimum temperature 28/18 °C day/night at the Division of Plant Sciences greenhouses, University of Missouri, Columbia. A mixture of soil and sand (2:1) was used in 26.5-L pots (top and bottom diameter were 30 cm and 27 cm, respectively, and 37 cm in height). Four seeds were sown per pot and Osmocote (slow release fertilizer – 14:14:14 – N:P₂O₅:K₂O; Scotts Co., Marysville, OH, USA) was used as a nutrient source at a rate of 20 g per pot. Pots were kept well-watered and thinning done to one plant per pot when the plants had two sets of unfolded trifoliolate leaves (V2 stage). At the V5 stage (five unfolded trifoliolate leaves), drought stress was imposed by withdrawing water and flooding stress was imposed by placing the pot with the plant into a 56.8-L pot (top and bottom diameter were 38 cm and 34 cm, respectively, and 46 cm in height) containing trash can liner. The 56.8-L pots were then filled with water to flood the 26.5-L pot. After 21 days of drought stress the plants were re-watered and allowed to recover. Flooding was done for 15 days and on day 16, the trash can liners were punctured to drain all water and the plants were allowed to recover. This experiment was set up as a randomized complete design with four replications.

2.2. Relative water content, chlorophyll content and gas exchange

Leaf relative water content (RWC) was determined using the equation: (Weatherley, 1950; Barr and Weatherley, 1962)

$$\text{RWC} = \frac{(\text{FW} - \text{DW})}{(\text{TW} - \text{DW})} \times 100$$

Where FW – leaf fresh weight, DW – leaf dry weight and TW – leaf turgid weight. Full leaves were used in the determination of RWC. To quantify variation in physiological traits (chlorophyll content and gas exchange) data were collected from an attached leaflet of the fourth trifoliolate leaf from the main-stem apex at midday (11:00–13:30 h) at mild and severe stress. We used a self-calibrating chlorophyll meter (SPAD 502, Spectrum Technologies,

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