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Photosynthetic performance of soybean plants to water deficit under high and low light intensity

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ABSTRACT

The two major challenges to relay strip intercropping soybean production in Southwest China are drought and low light intensity. This study tests whether the impact of drought on the photosynthetic performance of soybean plants is different between low and high light intensity conditions. To investigate this, soybean plants were grown in pots in a factorial experiment at two irrigation regimes (75 ± 2% and 45 ± 2% of soil field capacity) and two light intensity treatments (100% and 65% light intensity) in 2011. In 2012, soybean plants were grown in two irrigation regimes (75 ± 2% of soil field capacity vs. progressive soil drying) and two light intensity treatments (sole cropping soybean and relay strip intercropping soybean). Photosynthetic performance was assessed by measuring parameters such as net photosynthetic rate (Pn), stomatal conductance (Gs), water use efficiency (WUE), which were decreased significantly in drought stressed plants. We also observed differences in the photosynthetic responses of soybean plants to drought depending on the light intensity treatment the plants were subjected to. Shaded soybean plants in response to drought conditions had increased chlorophyll a (Chl a), chlorophyll b (Chl b), chlorophyll (Chl), carotenoid (Car), ratio of Car/Chl, leaf relative water content (RLWC), leaf area per plant, specific leaf area (SLA), Pn, Gs, intercellular CO_2 concentration (Ci), transpiration rate (Tr), photochemical quenching (qP) and electron transport rate (ETR). The above-mentioned photosynthetic changes may play an important role in determining how shaded soybean plants adjust their photosynthetic rate when experiencing drought conditions.

1. Introduction

As a result of the increasing human population, the demand for food has been growing steadily over the last century (Rosegrant and Cline, 2003; Godfray et al., 2010). Meanwhile, food producers are experiencing greater competition for land, water and energy, while balancing the negative effects of food production (Tilman et al., 2001; Rosegrant and Cline, 2003). Multiple cropping systems using crop rotations or intercropping (two or more crops grown simultaneously) can maximize resource use, and produce greater yield on a given piece of land (Tilman et al., 2002). Some of the benefits of intercropping are increase in yield, improved efficiency different environmental resources, pest and disease suppression and biological nitrogen fixation. As a result, multiple cropping systems such as the legume/non-legume intercropping system (Li et al., 2011), grain multiple cropping (Tong, 1994) and wheat-corn/soybean relay strip intercropping system (Yan et al., 2010), are becoming popular in China. In the multiple cropping systems, plants are typically exposed to several stressors simultaneously. For example, soybean crops grown along maize in a relay strip intercropping system can experience limited light intensity from the shade of maize, and limited water availability.

Physiological responses of evergreen and deciduous tree leaves to various sunlight-drought scenarios have shown that shading could ameliorate, or at least not aggravate, the impact of drought. This is because the performance of leaves under drought stress depends on how much light the leaves receive (Quero et al., 2006). Shade by the tree canopy has indirect effects, such as reducing leaf and air temperatures. Shade can also reduce the understory temperatures, and affect vapor pressure deficits and oxidative stress to alleviate the impact of drought on plants and seedlings in the understory (Holmgren, 2000). Shading conditions can allow olive trees to maintain high

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Abbreviations: Chl a, chlorophyll a; Chl b, chlorophyll b; Car, carotenoid; RLWC, leaf relative water content; Pn, net photosynthetic rate; Gs, stomatal conductance; Ci, intercellular CO_2 concentration; Tr, transpiration rate; WUE, water use efficiency; Fv/Fm, maximum efficiency of PSII photochemical reaction; ΦPSII, quantum yield of PSII; qP, photochemical quenching; NPQ, non-photochemical quenching; ETR, apparent photosynthetic electron transport rate.

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photosynthetic activity at low values of stomatal conductance (Sofo et al., 2009). In contrast, exposed plants can experience reductions in photosynthetic efficiency and intrinsic water efficiency due to difference in the activity of non-stomatal components of photosynthesis. Additionally, the decrease in photosynthetic activity and the increase in photoinhibition during drought are more marked in exposed plants than in shaded plants (Sofo et al., 2009).

In the soybean plant, short-term shading can reduce photosynthesis, leaf temperature, stomatal conductance, transpiration and water use efficiency and increase intercellular CO_2 partial pressure, which leads to carbon gain and water loss (Fay and Knapp, 1995). Photosynthetic rate, stomatal conductance and transpiration rate of soybean plants significantly decline under water stress, while the intercellular CO_2 concentration changes only slightly at the initiation of the stress treatment (Ohashi et al., 2006). Excessive energy in LHC, reaction center of PSII or PSI can cause pigment bleaching in sun leaves, the excessive energy can induce photoinhibition, thereby damaging pigments through oxidative stress (Kim et al., 2011). Shade reduces the chloroplast coupling factor and shifts light-harvesting capacity in soybean plants (Burkey and Wells, 1996). The low level of Chl contents in grapevine leaves at high photosynthetic photon flux density (PPFD) largely results from the decay of Chl that is likely enhanced by chlorophyllase activity (Bertamini and Nedunchezhian, 2003). However, less is known about whether differences in light intensity can influence the impact of drought on photosynthetic performance of the soybean plant. To better understand this, we investigated the impact of temporary shade and water shortage on the photosynthetic performance of soybean plants. We designed our experiments to (1) determine photosynthetic and chlorophyll fluorescence characteristics as affected by drought, low light intensity stresses and their combination; and (2) elucidate the relationships between them.

2. Materials and methods

2.1. Plant material and growth conditions

Soybean cultivar Gongxuan No. 1, a major component of southwestern indeterminate soybean cultivars was tested in the experiments performed in 2011 and 2012. Each seed was weighed individually and sown in cylindrical pots of 14-L volume (23 cm high × 28 cm diameter). The pots contained 13 kg soil composed of 50% sand, 47.5% clay and 2.5% organic matter. The soil was mixed with fertilizer consisting of N = 0.355 g, P_2O_5 = 0.556 g and K_2O = 0.406 g. Fertilizers were applied after emergence, with 3 g single super phosphate, 1 g potassium sulfate and 1.5 g of urea per pot. The experiment was carried out in a glasshouse of the Sichuan Agricultural University (29°59′N, 103°00′E; at an altitude of 500 m), and the greenhouse had an upper ceiling automatic closure system that was utilized when it rained.

Soybean plants were subjected to two light intensity levels: (1) high light intensity treatment (HI), where the soybean plants received normal light intensity from the sun when it was sunny, with additional light intensity inside the glasshouse when it was rainy (2011, 2012); (2) low light intensity treatment (LI), where the soybean plants were covered by a shade cloth (YaanNongzhi Co., China, 2011) or were under the shade of corn (2012). These experimental light intensity treatments were used to simulate field conditions in the relay strip intercropping system, distinguishing two types of microhabitats: sole cropping soybean (HI) and relay strip intercropping soybean (LI). In the experiment conducted in 2011, the light intensity that penetrated through the shade cloth to the soybean plants was 65%. In 2012, the light intensity that penetrated through the maize canopy to the soybean plants was 80% when the soybean was sown, 65% at the vegetative stage (V_5), 72% at the reproductive stage (R_1) and 70% when the soybean plant was in the reproductive stage (R_2) and the maize was at maturity. Maize (var. Chuandan 418) is 2.6 m in height, and the whole growth period is around 109 days. Each of the watering treatments were set up within each shade frame and replicated four times, each by one plant in a single pot.

Pots were watered every two days during the first stage of the experiment. Once the soybean seedlings reached V_5 stage (at the end of July 2011/2012), two months after sowing, two separate water treatments were applied. Half of the pots were kept continuously moist (high-water treatment, HW, 75 ± 2% of the field water capacity, FWC), and the other half were maintained at moderate drought conditions (low-water treatment, LW, 45 ± 2% of FWC) in 2011. In 2012, half of the pots were not watered (LW), while the other half was kept continuously moist (HW, 75 ± 2% of FWC). The 2012, LW treatment simulated a typical climate situation of seasonal drought in Southwestern China, as compared to a continuously moist treatment (HW) (Table 1). During the experiment, we measured soil moisture in volumetric water content (VWC) along the first 20 cm depth with a TRIME-PICO (German) on a daily basis, in a subsample of five pots under different light intensity and water treatments. We did this because the water content changes were different in pots under LW treatments for the two light intensity treatments (Zhang et al., 2011).

2.2. Microenvironment measurements

A micro-meteorological machine that included sensors for air temperature, relative humidity and light intensity (Hobo, Onset, Pocasset, MA) was used to measure microenvironmental parameters. Readings from each sensor were recorded every 6°min with a Hobo data logger. Two additional data loggers were installed to record air temperature measured with sensors attached to the abaxial side of leaves of four plants in each light intensity treatment. From the data, we could see that the light intensity and air temperature of the LI soybean group were lower than the HI soybean group, while relative humidity was opposite (Fig. 1).

2.3. Relative water content

RLWC of leaves was calculated using the standard formula [(FW − DW)/HydW − DW)°×°100] (Farrant, 2000). FW, HydW and DW stand for the leaf fresh weight, hydrated (full turgor) and dry weights, respectively. The hydrated weight was determined by weighing the leaf after 24 h of immersion in distilled water in a sealed flask at room temperature. Dry weight was determined gravimetrically after drying to steady weight at 70 °C in an oven. Soybean leaves were harvested daily during the V_5 stage (at the end of July 2011/2012). Five plants were randomly chosen, and one of the most recently expanded leaves was selected from each plant. The beginning point of the non-hydraulic root signals (nHRS) were determined depending on when there was a significant lowering of leaf stomatal conductance (Gs) without change in leaf RWC (compared with Gs in 75 ± 2% FWC). The hydraulic root signal (HRS) was judged to begin when there were significant differences for both of the above leaf parameters (Gowing et al., 1990).

Table 1
Soil water content (measured with TDR) at the beginning of progressive drying and hydraulic root signals (mean ± SE) in a subsample of pots under different light intensity and water combinations in 2012.

Treatments	Date of the commencement of signal point (*d*)	Soil relative water content (% of FWC)	
		HI	LI
HW	1	80 ± 1.2	80 ± 1.1
LW	9	53.7 ± 2.1	53.3 ± 0.3

HI represents high light intensity; LI represents low light intensity, under the shade of maize. LW represents low-water treatment; HW represents high-water treatment.