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Changes in leaf characteristics and grain yield of soybean (*Glycine max* L.) in response to shading and water stress

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Abstract

Some leaf characteristics and yield of soybean were investigated under different light interception (25, 65 and 100% of sun light) and irrigation treatments (I_1, I_2, I_3, I_4 for irrigation after 60, 90, 120 and 150 mm evaporation from class A pan, respectively) in 2011. The experiment was arranged as split plot based on randomized complete block design in three replicates. Membrane stability index decreased with increasing shading. However, leaf water potential, relative water content and leaf area index under all irrigation treatments increased as light interception decreased. This trend was improved as water availability decreased. Specific leaf weight significantly decreased with increasing shading under I_1 and I_2, but it was statistically similar for all light interceptions under I_3. In contrast, specific leaf weight was increased as shading increased under I_4. In general, specific leaf weight decreased with increasing water deficit. Increasing shade stress decreased grain yield per unit area under I_1 and I_2, but improved grain yield under I_3 and I_4, which is directly related with changes in leaf water potential, relative water content and leaf area index under these conditions. Therefore, shading can reduce the impact of water stresses on soybean plant performance in the field.

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Introduction

Plants are usually exposed to several stresses simultaneously under field conditions, with limit of light and water availability being the main environmental factors affecting relay strip intercropping soybean. These stresses may cause a variety of plant responses which can be additive, synergistic or antagonistic (Zhang *et al.,* 2011). Water stress causes membrane damage, and stimulates molecular signal transduction and hormone activation (Knight and Knight 2001), leading to a reduction in plant growth and productivity (Saranga *et al.*, 2001; Showler and Moran, 2003). Increasing crop tolerance to water limitation would be the most economical approach to enhance productivity and reduce agricultural use of fresh water resources. To survive against the stress, plants have involved a number of morphological properties and physiological and biochemical responses (Xiong *et al.*, 2006; Gao *et al.*, 2008).

Water stress causes water loss within the plant and therefore a reduction in its relative water content. Leaf water potential (LWP) and relative water content (RWC) are useful means for determining the physiological water status of plants (Gonzales and Gonzales-Vilar, 2001). Maintenance of high LWP is considered to be associated with dehydration avoidance mechanisms (Levitt, 1980). The sensitivity and the tolerance to water stress in plants can be also determined by leaf relative water content (Rampino *et al.*, 2006; Sanchez-Rodriguez *et al.*, 2010). Sanchez-Rodriguez *et al.*, (2010) reported that RWC was one of the best indicators in tomato plant for separating tolerant and sensitive cultivars. It is now clear that there is drought-induced root-to-leaf signaling, which is promoted by soil drying through the transpiration stream, resulting in stomatal closure, which is an important adaptation to limited water supply in the field.

Shading nets structures in semiarid and arid environments can be considered as an intermediate solution for increasing water use efficiency and reducing plant water stress (Nicolas *et al.*, 2008). Some authors reported that shading nets are helping to reduce wind speed within the foliage by about 40% (Tanny and Cohen, 2003), keep lower values of maximum daily shrinkage (Nicolas *et al.*, 2005), maintain high leaf water content and better leaf area index (Cohen *et al.*, 2005), reduce irradiance at the earth surface (Stanhill and Cohen, 2001), decrease crop transpiration by increasing stomatal diffusive resistance in leaves (Muthuchelian *et al.*, 1989) and reduce the daily sap flow (Muthuchelian *et al.*, 1989; Alarcon *et al.*, 2006).

Reduction of solar radiation can influence plants in a number of ways. The main limitation of leaf net photosynthetic carbon assimilation at high photon flux density is the concentration of CO_2. When photon flux density decreases to approximately 40% of that a full sunlight, then carbon assimilation become light-limited (Cohen *et al.*, 2005). This might suggest that leaves would be insensitive to changes in solar radiation at high light, but since plant canopies usually consist of several leaf layers in which radiation decreases exponentially, low light limitation of carbon assimilation is common in canopies and any decrease in solar radiation might be expected to decrease productivity. The extent of this limitation varies with shade tolerance of the species and the nitrogen supply (Wong, 1991). Shade, regardless of its source, reduces PAR and alters spectral quality, affecting plant photosynthesis (Bell *et al.*, 2000). It has been reported (Kobata and Takami, 1986) that inhibition of photosynthesis during the grain filling period, due to environmental stresses like shading, can result in a major reduction in grain yield of rice. Wang *et al.*, (2003) found that applying shade at pre- and post-anthesis on wheat caused a decrease in both photosynthesis and allocation of assimilates to grain. Similarly, Cantallago *et al.*, (2004) reported that shading during the floret growth phase of sunflower prior to anthesis, reduced the unit mass of the resulting grain at physiological maturity.

Plants have considerable ability to acclimate to different light regimes through changes in leaf properties (Syvertsen and Smith, 1984), as well as canopy structure (Syvertsen, 1984). Some plant species adapt to conditions of low light by manifesting such characteristics as an altered leaf angle, larger and thinner leaves with a higher chlorophyll content, altered chloroplast orientation and a decrease in root/shoot ratio, light compensation point and dark respiration rate (Bjorkrnan, 1981; Fails *et al.*, 1982). For several shade-grown species, high net CO_2 assimilation at light saturation has been correlated with increased specific leaf weight (SLW), leaf N content, chlorophyll a/b ratio, and mesophyll cell to leaf surface area (Araus *et al.*, 1986). However, interaction of shade and water stress in crop species was poorly understood. Thus, this research was aimed to evaluate changes in leaf water potential, relative water content, membrane stability, specific leaf weight and grain yield of soybean in response to water limitation and shade stress.

Material and methods

An experiment was conducted at the Research Farm of Tabriz University, Tabriz, Iran (latitude 38.05°N, longitude 46.17°E, Altitude 1360 m above sea level) in 2011. The climate was characterized by mean annual precipitation of 245.75 mm, mean annual temperature of 10˚C, mean annual maximum temperature of 16.6˚C and mean annual minimum temperature of 4.2˚C. The experiment was arranged as split plot on the basis of randomized complete block in three replicates, with irrigation treatments (I_1, I_2, I_3, I_4 for irrigation after 60, 90, 120 and 150 mm evaporation from class A pan, respectively) in main plots and shading treatments (S_1: 0%, S_2: 35% and S_3: 75% shade) in sub plots. Shading nets spread over an iron framework (3 m x 3 m) were placed in the field 1.5 m above the soil to ensure good ventilation and were large enough to fully cover the corresponding shaded plots immediately after seedling establishment up to maturity. Seeds of soybean (cv. Williams) were sown by hand on 6 May 2011 in 4 cm depth of a sandy loam soil. Each plot consisted of 10 rows of 3 m length, spaced 25 cm apart. Seeding rate was 64 seeds m^2. All plots were irrigated immediately after sowing. Subsequent irrigations were carried out on the bases of evaporation from class A pan. Hand weeding of the experimental area was performed as required. All physiological traits were measured during flowering and grain yield per unit area was determined at maturity.

Membrane stability index (MSI) was determined by recording the electrical conductivity of leaf leachates in distilled water at 40 and 100 °C. Leaf samples (0.5 g) were cut into discs of uniform size and taken in test tubes containing 250 ml of distilled water in two sets. One set was kept at 40°C for 30 min and another set at 100 °C in boiling water bath for 15 min and their respective electrical conductivities (C1 and C2, respectively) were measured by a conductivity meter (WTW-LS90).

$$\text{Membrane stability index} = \left[1 - \left(\frac{C1}{C2}\right)\right] 100$$

Measurements of leaf water potential were taken by a portable pressure chamber (Soil Moisture Equipment Crop, Sanata Barbara, CA.). Three leaves from three plants of each plot were randomly selected and then the youngest fully mature leaf of each plant was cut from the petiole and immediately inserted into the leaf chamber of the pressure bomb. Air pressure was introduced and the pressure reading was recorded when sap was first expressed.

Leaves of three plants from each plot were cut before irrigation at 12 pm and were then transferred to the laboratory within an ice box. Subsequently, several discs of the leaves of each plot with 0.5 g fresh weight were taken and immediately weighed. These discs were placed in distilled water for 24 hours at 4°C to saturate. At the end of this stage, the leaf discs were dried by towels papers and were then weighed again (turgid weight). The samples were placed in the oven for about 48 hours at 75°C to dry. The dry weight of leaves was recorded (dry weight). RWC was calculated according to Smart and Bingham (1974), using the following equation:

RWC= [fresh weight- dry weight/ turgid weight – dry weight] × 100

The Sun-Scan canopy analysis system (SS1, Delta-T Devices Ltd) was designed to estimates the leaf area index (LAI) in plant canopies. Sun-Scan probe estimates LAI indirectly from measurements of radiation above and below the canopy, based on a theoretical relationship between leaf area and canopy transmittance.

Fifteen leaf discs were taken from the third leaf of a plant in each plot and specific leaf weight (SLW) was estimated as:

$$\text{SLW} = \frac{DW}{LA}(g/m^2)$$

Where DW= leaf dry weight and LA= leaf area.

At maturity, plants in 1 m^2 of middle part of each plot were harvested to determine grain yield per unit area. Analysis of variance appropriate for a split-plot design was carried of, using General Linear Model (GLM) procedure of SPSS. Means of each trait for different treatments were compared according to Duncan multiple range test at p≤0.05. Excel software was used to draw figures.

Results

Analysis of variance of the data (Table 1) showed that leaf water potential (LWP), relative water content (RWC), leaf area index (LAI) and specific leaf weight (SLW) were significantly affected by irrigation, shade and their interaction. However, membrane stability index (MSI) and grain yield per unit area were significantly affected by shade and shade × irrigation interaction, respectively (Table 1).

Membrane stability index (MSI) decreased with decreasing light interception. However, the difference between S_2 and S_3 was not significant. The highest MSI was obtained in leaves under full sunlight. MSI was not significantly affected by irrigation treatments (Fig. 1).

Table 1. Analysis of variance of the soybean traits affected by irrigation and shading treatments.

Source	d.f	MSI	LWP	RWC	LAI	SLW	Grain yield
Replication	2	38.06	1.56	67.22	0.903	1.65	10320.95
Irrigation (I)	3	53.83	84.58**	1176.89**	4.081**	71.07**	5861.03
E_a	6	39.73	0.87	7.22	0.211	2.45	1541.68
Shading (S)	2	105.99*	32.11**	140.02**	35.55**	17.44**	415.33
I*S	6	32.55	2.86**	37.18*	0.224*	13.68**	1096.88**
E_b	16	25.71	0.49	12.84	0.081	1.18	124.93
CV (%)	-	25.99	8.22	5.12	7.92	11.16	8.44

*, **: significant at p≤0.05 and p≤0.01, respectively

The leaf water potential in all irrigation treatments increased with decreasing light interception. This trend was improved as water availability decreased. Plants with 25% light interception (S_3) showed higher LWP compared with the other light treatments (S_1 and S_2) under all irrigation intervals. The highest LWP (-3.7 bar) was measured in well-watered plants (I_1) at 25% light interception (S_3) and the lowest (-14.42 bar) was observed in plants under severe water deficit (I_4) and full sunlight (S_1). Although, shading improved RWC of leaves under all irrigation treatments, this improvement was only significant under severe water stress. Relative water content of plant leaves under all light treatments decreased with deceasing water availability (Table 2).

Leaf area index (LAI) increased with decreasing light interception under all irrigation treatments. The highest improvement in LAI was observed under the lowest light interception. Leaf area index was generally decreased by increasing water deficit (Table 2).

Specific leaf weight significantly decreased with increasing shading under I_1 and I_2, but SLW was statistically similar for all light interceptions under I_3. In contrast, SLW was increased as light interception decreased under I_4. In general, specific leaf weight decreased with increasing water deficit (Table 2).

Table 2. Means of LWP, RWC, LAI and SLW of soybean under different irrigation and shading treatments

Irrigation	Shading	LWP (bar)	RWC (%)	LAI	SLW (g/m²)
I1	S1	-4.93 a	78.3 ab	3.1 de	14.12 a
	S2	-4.66 a	78.34 ab	4.03 bcd	11.95 b
	S3	-3.7 a	80.5 a	6 a	8.33 cd
I2	S1	-9.53 de	74.91 abc	2.3 e	13.91 a
	S2	-8.15 bc	78.22 ab	3.36 cde	11.58 b
	S3	-7.13 b	78.6 a	6 a	8.29 cd
I3	S1	-11.85 g	66.98 de	2.03 e	11.43 b
	S2	-10.33 ef	71.55 bcd	2.4 de	10.48 b
	S3	-8.13 bc	71.2 cd	5.26 ab	10.08 bc
I4	S1	-14.42 h	45.26 g	1.7 e	4.11 e
	S2	-11.45 fg	54.36 f	2 e	5.29 e
	S3	-8.67 cd	62.18 e	4.9 abc	7.25 d

Different letters at each column indicate significant difference at $p \leq 0.05$

I1, I2, I3 and I4 irrigation after 60, 90, 120 and 150mm evaporation from Class A pan, respectively.

S1, S2 and S3: 0%, 35% and 75% shading, respectively.

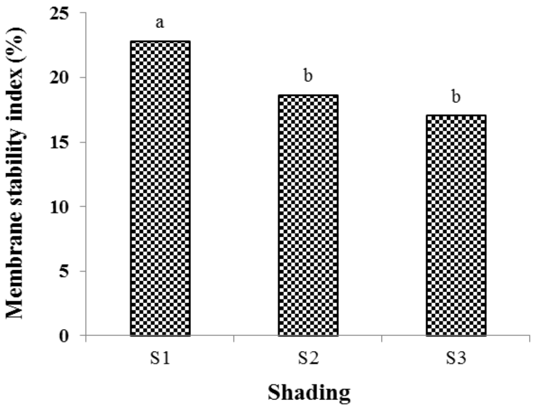

Fig. 1. Effect of light deficit on membrane stability index (MSI) in soybean

S_1, S_2, S_3: 0%, 35% and 75% shading, respectively

Different letters indicate significant difference at $p \leq 0.05$

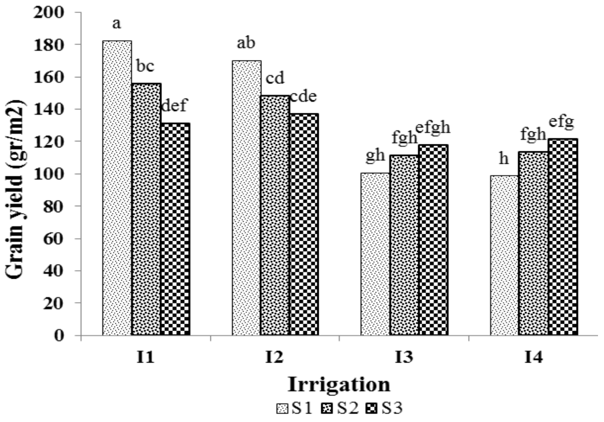

Fig. 2. Effect of water and light deficit on grain yield per unit area in soybean.

I_1, I_2, I_3, I_4 irrigation after 60, 90, 120 and 150 mm evaporation from class A pan, respectively

S_1, S_2, S_3: 0%, 35% and 75% shading, respectively

Different letters indicate significant difference at $p \leq 0.05$

Increasing shade stress decreased grain yield per unit area under I_1 and I_2, but improved grain yield under I_3 and I_4. The highest grain yield was obtained under well watering and full sunlight and the lowest grain yield was produced under severe water deficit (I_4) without shade. Grain yield of soybean under I_3 and I_4 was generally lower than that under I_1 and I_2 (Figure 2).

Discussion

Plant membranes are subject to changes often associated with the increases in permeability and loss of integrity under environmental stresses (Blokhina *et* *al.* 2003). Our results clearly suggest that membrane stability index is more reduced under shade stress than under water stress (Table 1; Fig 1).

Decreasing LWP under water deficit in soybean (Table 2) supports the previous reports on wheat (Siddique *et al.*, 2000) and soybean (Makbul *et al.*, 2011). Siddique *et al.*, (2000) reported that changes in plant water potential might be attributable to a change in osmotic pressure- the osmotic component of water potential. With depletion of water from soil and lack of a substitute for it, water potential in root region decreases and if resistances remain consistent, water potential in plant similarly decreases in order to maintain transpiration rate (Tiyar and Pit, 1994). Under water deficit, cell membrane subjects to changes such as penetrability and decrease in sustainability (Blokhina *et al.*, 2003). Probably, in these conditions, ability to osmotic adjustment is reduced (Meyer and Boyer, 1981). Decreasing RWC due to water limitation (Table 2) is an indication of decrease of swelling pressure in plant cells and causes growth to decrease. These deleterious effects of water deficit on LWP and RWC were considerably reduced as a result of shading, particularly under severe water stress (Table 2). This may be related to decreasing leaf temperature (Zhou *et al.*, 2010) and transpiration under shade (Holmgren, 2000).

Higher LAI in shaded plants particularly under water stress (Table 2) shows that plants in a shady environment invest relatively more of the products of photosynthesis and other resources in leaf area to increase light harvesting and photosynthetic surface (Lambers *et al.*, 2008). Leaf area increment under low light intensities was also reported by (Roussopoulos *et al.*, 1998) in cotton, (Hadi *et al.*, 2006) in common bean and (Nasrullahzadeh *et al.*, 2007) in faba bean. Scuderi *et al.*, (2003) also showed that final leaf area index and canopy volume in shaded Ficus plants was higher than those in unshaded plants. Generally, the increase of leaf area with shading is one of the ways used to photosynthetic surface, ensuring a more efficient yield in low light intensities and consequently, compensating the low photosynthetic rates per leaf area.

Lower specific leaf weights of shaded plants under well watering and moderate water stress (Table 2) suggesting that leaves of shade grown plants are relatively thin. This is associated with relatively few and small palisade mesophyll cells per unit area (Lambers *et al.*, 2008). However, leaf thickness under severe water stress increased with increasing shading as shown by higher SLW (Table 2). Thicker leaves were the result of an increment in the size of palisade cells and also due to a major number of spongy parenchyma layers. The opposite behavior was the result of thinner leaves. Changes in mesophyll thickness as a result of alteration of palisade/spongy parenchyma cells ratio were observed in three ornamental species (Araus *et al.*, 1986).

Decreasing grain yield of soybean under well irrigation and mild water stress and improving it under moderate and severe water deficit as a result of shading (Fig 2) are directly related with changes in leaf water potential, relative water content, leaf area index and specific leaf weight under these conditions (Table 2). According to the facilitation mechanism, shade can reduce leaf and air temperatures, vapor pressure deficit and oxidative stress that would alleviate the drought impact on plants (Holmgren, 2000). This is an advantage for shaded plants to reduce the impact of water limitation on grain yield.

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