

Lower total soluble sugars in vegetative parts of soybean plants are responsible for reduced pod number under shading conditions

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Abstract

Much of the variation in soybean yield is associated with changes in pod number per plant, however physiological regulation of pod number is not well understood. Three determinate soybean cultivars, Hai339 (H339), Heinong35 (HN35) and Kennong18 (KN18) were grown for 2 years at 27 plants m⁻² in a field experiment and exposed to shading and light enrichment. The data of total soluble sugar (TSS) in leaf, stem and pod wall samples at middle nodes collected every 10 days from 20 days after flowering (DAF) (beginning of the linear seed filling period) to 60 DAF (physiological maturity) were analyzed. The average pod number was reduced by 45% in 2007 and 40% in 2008 with shading, while the average pod number was increased by 49% in 2007 and 70% in 2008 with light enrichment. Shading significantly decreased leaf TSS concentration by 16~39% in 2007 and 14~43% in 2008 and decreased stem TSS concentration by 27% for H339, 19% for HN35, 40% for KN18 across the two years. At 20 DAF, shading decreased the pod wall TSS concentration by 44% for H339, 36% for HN35, 25% for KN18. Shading effect on stem TSS concentration was much greater than leaf and pod wall TSS concentration. The TSS concentration in vegetative parts was not affected by light enrichment. Our results suggested the reduction of TSS concentration was directly responsible for lower pod number under shading conditions, while the increase in pod number by light enrichment is more likely regulated by some other mechanism.

Keywords: Assimilate supply; photosynthesis; Pod abortion; Reproductive success; shade.

Abbreviations: total soluble sugar: TSS; water-soluble carbohydrates: WSC; days after flowering: DAF; DW: dry weight; H339: Hai339; Heinong35: HN35; Kennong18: KN18.

Introduction

Soybean yield is determined, in large part, by the pod numbers that survive to maturity (Egli, 1998). Total reproductive abscission for soybeans ranges from 32 to 82% (Wiebold et al., 1981). Although the abscission process is not fully understood, some studies indicated that change in microenvironment of soybean growth results in the variation in the pod number per plant (Vega et al., 2001; Hassan et al., 2011). A change in the light intensity intercepted by the soybean canopy influenced pod survival number per plant during the reproductive period (Biabani et al., 2008). Light enrichment initiated at late vegetative or early flowering stages increased pod number, resulting in a 144 to 252% increase in seed yield (Mathew et al., 2000). Liu et al. (2006a) found that light enrichment increased pod number per plant for eight glyphosate-resistant soybean cultivars across two years, with some cultivars being more responsive than others. Jiang and Egli (1993) stated that shade reduced pod number per plant and the reductions were due to both increased flower and pod abscission and fewer flowers per plant. Wiebold et al. (1981) reported that abscission is greatest within those regions of soybean canopies where irradiance is lowest and abscission reaches 100% for some nodes in the

bottom one-third canopy. Total soluble sugar (TSS) content is not only the main photosynthate in higher plants, but also the main form of carbohydrate metabolism and temporary storage. Wilcox (2001) indicated that the soluble sugar content plays a very important role in carbohydrate metabolism and has a close relationship with photosynthesis and production. The level of soluble sugar content was a sign of the supply ability of leaves and reflected transformation and ability of grains to use assimilates (Saratha et al., 2001). Wang et al. (2007) reported that the photosynthate exists as a form of water soluble carbohydrate and its main components are soluble sugar, starch and cellulose. Differences in water-soluble carbohydrates among soybean cultivars and fertility levels were relatively small (Egli et al., 1980). Percentages of WSC in leaves increased throughout the growing season, while WSC contents in stems, petioles, and pods decreased as the seeds developed (Ciha and Brun, 1978). This decrease may indicate that soluble metabolically active carbohydrate is a factor involved in seed production during the seed-filling period. However, few published data are available examining the role of carbohydrate in soybean reproductive abscission under varied light regimes.

The objective of this study was to analyze the effect of light enrichment and shading on the concentration of TSS in vegetative parts in soybeans, with a focus on their correlation with reproductive survival.

Results

Reproductive Success across the Main Axis

Total reproductive success or pod number across the main axis in response to light enrichment and shading differed in the two years (Fig 1). Although most main axis pods were produced at the nodes in the middle canopy stratum of the plants, the increase and decrease in pods due to light enrichment and shading occurred relatively consistently across every node in main axis. Thus, light enrichment and shading initiated from early flowering influenced the final pod number through changing flower and pod set and abscission at all nodes. The effect of light condition on pod number per main axis node for KN18 was more pronounced than that for H339 and HN35.

Yield and Yield Components Responses

As shown in Table 1, in 2007, light enrichment increased H339 seed yield per plant by 72%, HN35 by 52%, and KN18 by 28%. In 2008, light enrichment increased H339 seed yield per plant by 95%, HN35 by 38%, and KN18 by 68%. In 2007, shading decreased H339 seed yield per plant by 45%, HN35 by 35%, and KN18 by 50%. In 2008, shading decreased H339 seed yield per plant by 30%, HN35 by 40%, and KN18 by 42%. The effects of light treatments on pod number across the three soybean cultivars were consistent. The average pod number was increased by 49% in 2007 and 70% in 2008 by light enrichment, while the average pod number was reduced by 45% in 2007 and 40% in 2008 by shading (Table 1). Although seed number per pod in response to light regime among cultivars was not consistent, there was a tendency of increased seed number per pod under light enrichment and decreased seed number per pod under shading (Table 1). For instance, light enrichment significantly increased seed number per pod from 1.78 to 2.13 in 2007 for cultivar HN35, and from 1.83 to 2.08 for HN35 and 1.91 to 2.05 for KN18 in 2008 ($P < 0.05$). In 2007 and 2008, shading significantly decreased seed number per pod for cultivar KN18 from 2.11 to 1.78, and 1.91 to 1.78 (Table 1, $P < 0.05$). Seed number per pod for cultivar H339 was not changed with varying light regime. Seed size was negatively impacted by light enrichment in general. Seed size for cultivar H339 was reduced by light enrichment from 287mg to 263 mg (8%), and 287 mg to 265mg (8%) in 2007 and 2008 respectively ($P < 0.05$). For HN35, seed size was decreased by 7% in light enrichment in 2007 and by 8% in light enrichment in 2008 ($P < 0.05$, Table 1). However, shading in 2008 significantly increased H339 seed size by 9%, and KN18 by 7%.

TSS Concentration Responses

Shading greatly reduced TSS concentration in vegetative parts of the soybean plants after flowering regardless of cultivars (Table 2, 3, 4), while the effects of light enrichment varied between days after flowering (DAF) and years. Significant differences of TSS concentration in leaves were found only for H339 and HN35 at 30 DAF in 2008 between light enrichment and ambient light (Table 2). Compared with ambient light, shading significantly decreased leaf TSS concentration for all cultivars by 16~39% in 2007 and 14~43% in 2008. From 20 to 60 DAF, shading significantly reduced stem TSS concentration.

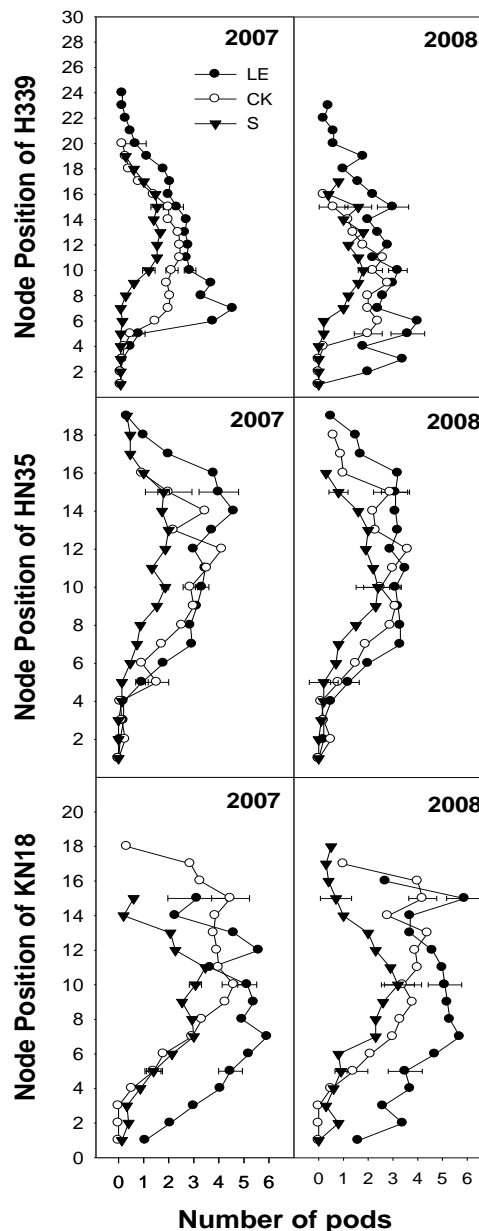


Fig 1. Distribution of pods in main stem of different cultivars treated with light enrichment and shading. H339, HN35 and KN18 are Hai339, Heinong35 and Kennong18, respectively. Bar indicate standard error of the mean. LE, CK and S are light enrichment, natural light and shade treatments respectively.

On average, the reduction in stem TSS concentration by shading was 27% for H339, 19% for HN35, and 40% for KN18 across sample dates and the two years respectively (Table 3). Though light enrichment increased stem TSS concentration, a significant increase was consistently found only at 30 DAF in 2008 compared with ambient light. On average, the stem TSS concentration increase by light enrichment was 8% for H339, 11% for HN35, and 16% for KN18 across sample dates and the two years respectively (Table 3). Shading significantly reduced pod wall TSS concentration by 44% for H339, 36% for HN35,

Table 1. Effects of light enrichment and shading on three soybean yield and yield components in two years

Yield component and light treatments		2007			2008		
		H339	HN35	KN18	H339	HN35	KN18
Yield plant ⁻¹ (g plant ⁻¹)	LE	21.8a	15.4a	19.3a	24.3a	14.4a	21.0a
	CK	12.7b	10.1b	15.1b	12.5b	10.4b	12.5b
	S	7.0c	6.6c	7.6c	8.7c	6.3c	7.2c
Pods plant ⁻¹ (No. plant ⁻¹)	LE	40.2a	41.4a	60.5a	46.8a	39.7a	66.4a
	CK	23.5b	29.3b	45.4b	21.4b	30.0b	41.8b
	S	12.3c	16.7c	25.4c	14.4c	17.0c	23.9c
Seeds pod ⁻¹ (No. pod ⁻¹)	LE	2.05a	2.13a	2.14a	1.96a	2.08a	2.05a
	CK	1.93a	1.78b	2.11a	2.04a	1.83b	1.91b
	S	1.98a	2.07a	1.78b	1.94a	1.88b	1.78c
Seed size (mg seed ⁻¹)	LE	263b	177b	149b	265c	174b	155b
	CK	287a	191a	159ab	287b	189a	157b
	S	292a	185a	166a	313a	196a	168a

Values followed by different letters within the row are significantly different from different light treatments under same cultivar within a year ($P < 0.05$). H339, HN35 and KN18 are Hai339, Heinong35 and Kennong18, respectively. LE, CK and S are light enrichment, natural light and shade treatments, respectively.

and 25% for KN18 at 20 DAF (Table 4). On average the reduction in pod wall TSS concentration by shading was 24% for H339, 23% for HN35, and 17% for KN18 across sample dates and the two years respectively (Table 4). Light enrichment only had significant effect on pod wall TSS concentration for H339 at 40-60 DAF in 2007 and for KN18 at 40 DAF in 2008.

Discussion

The present study confirmed previous reports that light distribution in the soybean canopy is a major limiting factor influencing pod number, and pod number per plant is the yield component most influenced by changes in cultural and environment conditions (Asanome and Ikeda, 1998; Li et al., 2005; Board and Tan, 1995). However, the sensitive light response of pod number per node in the main axis by KN18 indicates genotype differences with varying light regime. Compared with the pod number per plant, seed number per pod was less affected by light treatments, though light enrichment increased (0-19%) seed number per pod and shading decreased (0-16%) seed number per pod. For pod number per plant, light enrichment increased pod number increased 49-70% and with shading decreased pod number 40-45%. This indicated that (1) seed number per pod is strongly determined by the internal genetic mechanism as stated by (Herbert and Litchfield (1982) that seed number per pod is a minor component determining the yield of soybean; (2) seed number per pod is only influenced by an environmental condition to a limited extent. In our study, seed size was negatively impacted by light enrichment. The reduction of seed size in cultivar H339 and HN35 across two years might be due to the greater increase of seed number per plant and less assimilates available to fill the single seeds under the light enrichment condition. Egli (1999) also indicated that increased number of pods and seeds by the plant resulted in less available photosynthate to fill the seeds. Shading in 2008 significantly increased H339 seed size by 9%, and KN18 by 7%, which might be a compensation mechanism to yield loss. Soluble sugar is not only the main photosynthate of higher plants, but the main form of carbohydrate metabolism and temporary storage (Voldeng et al., 1997). Content of soluble sugar in leaves is an important form, and a sign of the supply ability of leaves or a physiological index of leaf status

(Shiraiwa and Ushio, 1995). Soluble sugar is involved in the biochemical process in soybean. Physiological levels of soluble sugars and methyl jasmonate synergistically stimulate accumulation of *vsp* mRNAs and coregulated *vsp* expression and transcription in soybean leaves (Avi et al., 1994). A primary role of sugars depends not only on direct involvement in the synthesis of biochemical compounds and production of energy, but also on the stabilization of membranes (Hoekstra et al., 2001; Behzad et al., 2011), and actions such as regulators of gene expression (Koch, 1996) and signal molecules (Sheen et al., 1999; Smeekens, 2000). Saratha et al. (2001) reported that content of soluble sugar in leaves can reflect transformation and utilization ability of seed grains from assimilates. In the present study, shading significantly decreased leaf TSS concentration by 31% for H339, 20% for HN35 and for 20% KN18 across two years respectively. This further indicates that less photosynthate produced was responsible for the lower pod number. As a result, the average pod number was reduced by 40% for H339, 43% for HN35 and for 44% KN18 across two years respectively. Wiebold et al. (1981) also stated that a decrease in photosynthesis could cause an increase in abscission because of a reduction in the carbohydrate availability. Modification of the environmental conditions to reduce photosynthate supply during reproductive growth caused a reduction in pod number (Egli, 1993; Joachim and Patrick, 2011). However, the increased pod number in each node by light enrichment might not be directly related to leaf TSS concentration. A greater pod number per plant with light enrichment might suggest that the larger sink would continually draw on leaf TSS and therefore a higher leaf TSS concentration might not be evident. However, this phenomenon needs further investigation. Soybean stems are the major sites of stored carbohydrate (Ciha and Brun, 1978). Matthew and Wiebold (1984) reported that soybean stem water soluble sugar and starch concentrations in the lower one-third canopy were less than those in the upper region, resulting in large abscission percentages in bottom main stem nodes. Our data suggest that from 20 to 60 DAF, shading reduced stem TSS concentration in the three cultivars by 28% in 2007, by 30% in 2008. The changes of the soluble sugar concentration have a close relation with photosynthesis and production (Wilcox, 2001). Thus, low stem TSS concentration under shading was associated with the high level of reproductive abscission.

Table 2. Effect of light enrichment and shading on total soluble sugar concentration of soybean leaves in 2007 and 2008 (mg · g⁻¹ DW)

Cultivars and DAF	2007			2008		
	Light enrichment	Ambient light	Shading	Light enrichment	Ambient light	Shading
H339	20	20.7a	19.2a	14.5b	20.8a	20.7a
	30	37.6a	38.3a	25.4b	37.1a	30.9b
	40	20.1a	19.5a	14.9b	22.7a	22.7a
HN35	20	21.0a	18.4ab	15.4b	24.4a	24.3a
	30	26.0a	26.2a	21.7b	28.7a	26.9b
	40	23.5a	22.0a	13.5b	18.5a	18.2a
KN18	20	19.8a	20.1a	15.8b	22.5a	20.5a
	30	27.3a	27.3a	21.2b	23.5a	24.3a
	40	17.6a	16.7a	13.4b	16.9a	17.6a

Values followed by different letters within the row and years are significantly different from three light treatments ($P < 0.05$). H339, HN35 and KN18 are Hai339, Heinong35 and Kennong18, respectively. DAF is days after flowering.

Table 3. Effect of light enrichment and shading on total soluble sugar concentration of soybean stem in 2007 and 2008 (mg · g⁻¹ DW)

Cultivars and DAF	2007			2008		
	Light enrichment	Ambient light	Shading	Light enrichment	Ambient light	Shading
H339	20	22.3a	20.8ab	16.8b	18.9a	22.9a
	30	38.0a	30.4b	20.1c	33.1a	28.7b
	40	26.3a	24.7a	19.9b	22.4a	20.3a
	50	30.6a	28.3a	17.4b	30.4a	26.5b
	60	13.5a	15.1a	14.2a	18.5a	15.6a
HN35	20	21.7a	16.6b	17.3b	27.4a	23.9b
	30	26.6a	28.4a	20.9b	32.5a	22.4b
	40	28.0a	27.4a	17.7b	30.2a	28.2a
	50	17.3a	15.3a	11.2b	22.4a	19.9a
	60	9.8a	10.2a	9.1a	13.5a	13.8a
KN18	20	31.5a	30.9a	15.1b	38.5a	33.4a
	30	38.1a	32.2a	21.4b	43.1a	31.3b
	40	22.2a	19.8a	13.7b	32.2a	26.8b
	50	13.8a	15.3a	6.3b	23.8a	17.5b
	60	8.3a	8.2a	5.4b	10.3a	8.2ab

Values followed by different letters within the row and years are significantly different from three light treatments ($P < 0.05$). H339, HN35 and KN18 are Hai339, Heinong35 and Kennong18, respectively. DAF is days after flowering.

In cereals, water soluble carbohydrates stored in stems have been acknowledged as contributing to maintenance of grain filling rate when photosynthesis declines due to shading (Abbate et al., 1995). In our study, low stem TSS concentration under shading might indicate less TSS in stem is transported to young pods. The essence of soybean yield formation is the process of interactions among source, sink and “flow” (Liu et al., 2010). We propose that the lower leaf and stem TSS concentrations, namely the reduction of source intensity, is one reason for the reduction of reproductive survival under shading. The increased pod number per plant of 49% in 2007 and 70% in 2008 by light treatments adds evidence to this statement. Less information is available concerning the relationship of pod wall TSS concentration and pod survival in soybean. Thorne (1979) reported that pod walls were temporary storage organs for photosynthate and nitrogenous assimilates, and act as catchment and transport link for solutes mobilized from vegetative parts to seeds. In our study, shading significantly decreased soybeans pod wall TSS concentration in the three cultivars by 18% in 2007 and 25% in 2008. The growth of the pod wall appears to depend largely on hormones supplied by the seeds (Eeuwens and Schwabe 1975). Shading significantly decreased endogenous ABA levels in soybean seed (Liu et al., 2006b). Thus, the decreased TSS concentration in pod wall by shading might be due to immediate changes in levels of seed

hormones. Streeter and Jeffers (1979) showed that nonstructural carbohydrate in soybean plants would be redistributed to maintain a larger reproductive load. However, in the present study 2-yrs of research indicated consistent changes in pod wall TSS by light treatments were not found. Although TSS concentration in pod wall was greater for H339 from 40 to 60 DAF in 2007 and for KN18 at 40 DAF in 2008, there were similar TSS ratios between stem and pod wall at 40 DAF were found among the light regimes. This means that the utilization or redistribution of carbohydrate reserve in stem to developing soybean fruit was not affected by both light enrichment and shading. Therefore, the TSS synthesis and production is more important for pod development rather than the allocation or translocation, and lower concentrations of stored carbohydrate are associated with large reproductive abscission percentages.

Materials and methods

Site Description

This study was conducted in National Observation Station of Hailun Agroecosystem, Chinese Academy of Sciences in Northeast China for 2 years from 2007 to 2008. The research site (47°26'N, 126°38'E, altitude 240 m) is in the North

Table 4. Effect of light enrichment and shading on total soluble sugar concentration of soybean pod wall in 2007 and 2008 (mg · g⁻¹ DW)

Cultivars and DAF	2007			2008			
	Light enrichment	Ambient light	Shading	Light enrichment	Ambient light	Shading	
H339	20	18.5a	18.6a	10.2b	19.3a	21.4a	12.2b
	30	16.7a	14.2a	10.8b	21.8a	26.4a	11.6b
	40	22.3a	19.3b	15.5c	23.2a	22.1a	23.4a
	50	36.9a	23.7b	23.3b	35.8a	33.5a	21.3b
	60	28.3a	21.3b	18.4c	23.2a	22.0a	20.8b
HN35	20	22.4a	26.0a	17.4b	27.1a	22.7a	13.8b
	30	19.8a	21.2a	15.2b	26.8a	23.0a	16.2b
	40	28.6a	27.7a	22.3b	28.9a	32.1a	24.5b
	50	15.0a	14.7a	17.6a	22.3a	27.7a	22.6a
	60	12.5a	12.0a	10.1a	15.4a	15.8a	9.9b
KN18	20	20.3a	21.0a	16.4b	25.9a	26.5a	19.3b
	30	30.9a	27.5a	22.3b	33.3a	34.6a	29.1b
	40	22.3a	19.2ab	16.3b	23.4a	18.3b	15.2b
	50	16.5a	18.4a	15.5a	18.9a	17.4ab	14.6b
	60	14.8a	13.1ab	11.8b	13.4a	12.1a	10.3b

Values followed by different letters within the row and years are significantly different from three light treatments ($P < 0.05$). H339, HN35 and KN18 are Hai339, Heinong35 and Kennong18, respectively. DAF is days after flowering.

Temperate Zone and continental monsoon area (cold and arid in winter, hot and rainy in summer). The average annual precipitation is 530 mm with 65% in June–August, and an average annual temperature of 1.5°C. Annual sunshine is around 2600–2800h, total annual solar radiation is 113MJ cm⁻². The soil is the typical Mollisols (Black soil), and textural class i

Experimental plan and field management

The experiments were arranged as split-plot, based on randomized complete block design with three replications. Three soybean cultivars, Hai 339 (H339), Heinong 35 (HN35) and Kennong 18 (KN18), main plots, were planted at 27 plants m⁻² in 2007 and 2008. Each plot consisted of seven rows of 8.5m long with an inter-row spacing of 0.67m. The seeds were sown on May 7, 2007 and May 6, 2008. A total of 50 kg·ha⁻¹ carbamide (46% N), and 50 kg·ha⁻¹ diammonium phosphate (18% N, 46% P₂O₅), and 150 kg ha⁻¹ of composite fertilizer (18% N, 16% P₂O₅, 16% K₂O) were applied before seeding. Weeds were controlled by hand. All other production practices followed standard management procedures. Subplots, consisted of three light levels including ambient light as a check or control treatment.

Light Enrichment Treatment

Light enrichment increased solar radiation available to the center row of each plot by installing 90 cm tall wire mesh fencing (mesh hole size 4-5cm) adjacent to the center row and sloping away at a 45° angle as described previously (Mathew et al., 2000; Liu et al., 2006a). Fences were installed at early flowering R1 stage, and were left in place for the remainder of the growing season. Fences prevented encroachment of plants from neighboring rows into the growing space, and thus increased the radiation intensity to the base of the canopy and thus the interception area of the sample rows. The fences were inspected periodically and all plants in rows bordering the center row were pushed behind the fences to prevent encroachment on the sample row. Light intensity measurements, using a Licor line quantum sensor (LI-188B) placed parallel to, and beside the center row plants, showed that leaves at the base

of the canopy in light-enriched plots were receiving more than 25% ambient light intensity.

Shading Condition

Shading was provided by black polypropylene fabric installed 0.5m above the soybean canopy. Shade cloth was attached to metallic posts, which resulted in 25% light reduction compared to the ambient light. These treatments did not result in large changes for canopy temperature, humidity as well as air circulation.

Measurements

In each subplot, 50 plants were tagged for total soluble sugar (TSS) concentration determination and a further 15 plants were allocated randomly in each treatment for a detailed analysis of seed yield components. For each group of plants for yield components, pod number was recorded according to node position on the main axis and for each branch corresponding to the main axis node from which it arose. Node 1 was the unifoliate node, being the first node above the cotyledons. For TSS determination 10 plants on each sample date were divided into lower, middle and upper one-third canopy strata based on equal node number. The plant material from middle canopy stratum was separated into stem, leaflet and pod wall and dried at 58°C to a constant weight. Dried samples were ground to pass through a 0.5mm screen and stored for analysis. The procedure for the extraction of TSS from stem, leaf, and pod wall was described by Ciha and Brun (1978). TSS was quantified using a modified phenolsulfuric acid assay (Zhang, 1993).

Statistical Analyses

TSS data are expressed as percent of dry weight and are the averages of duplicate determinations. For statistical analysis of variance and mean comparisons, the SPSS software was used. If the ANOVA results were significant ($P < 0.05$), differences among the means were compared using Least Significant Difference test (LSD).

Conclusion

Our results indicate that light regime greatly affected soybean yield and yield components. Pod number per plant was the most critical component for yield formation. The reduction of TSS concentration was directly responsible for lower pod number under shading conditions, while the increase in pod number by light enrichment is more likely regulated by some other mechanism. The selection of shading tolerance cultivars might be an effective approach to increase soybean yield.

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Reference

- Abbate PE, Andrade FH, Culot, JP (1995) The effects of radiation and nitrogen on number of grains in wheat. *J Agric Sci* 124: 351-360.
- Asanome N, Ikeda T (1998) Effect of branch directions arrangement on soybean yield and yield components. *J Agron Crop Sci* 181: 95-102.
- Avi S, Daryll BD, Gregory DM, Willian DP, John EM (1994) Phosphate modulates transcription of soybean *VspB* and other sugar-inducible genes. *The Plant Cell* 6: 737-749.
- Biabani A, Hashemi M, Herbert SJ (2008) Agronomic performance of two intercropped soybean cultivars. *Int J Plant Prod* 2: 215-222.
- Board JE, Tan Q (1995) Assimilatory capacity effects on soybean yield components and pod number. *Crop Sci* 35: 846-851.
- Ciha AJ, Brun WA (1978) Effect of pod removal on nonstructural carbohydrate concentration in soybean tissue. *Crop Sci* 18: 773-776.
- Euwens CJ, Schwabe WW (1975) Seed and pod wall development in *Pisum sativum* L. in relation to extracted and applied hormones. *J Exp Bot* 26: 1-14.
- Egli DB (1993) Cultivar maturity and potential yield of soybean. *Field Crop Res* 32: 147-158.
- Egli DB (1998) Seed biology and the yield of grain crops. CAB international, Wallingford, UK.
- Egli DB (1999) Variation in leaf starch and sink limitations during seed filling in soybean. *Crop Sci* 39: 1361-1368.
- Egli DB, Leggett JE, Cheniae A (1980) Carbohydrate levels in soybean leaves during reproductive growth. *Crop sci* 20: 468-473.
- Herbert SJ, Litchfield GV (1982) Partitioning soybean seed yield components. *Crop Sci* 22: 1074-1079.
- Hoekstra FA, Golovina EA, Buitink J (2001) Mechanisms of plant desiccation tolerance. *Trends Plant Sci* 6: 431-438.
- Jiang H, Egli DB (1993) Shade induced changes in flower and pod number and flower and fruit and abscission in soybean. *Agron J* 85: 221-225.
- Kaviani B, Pourkhalili ST, Sajedi RH, Mosadegh B (2011) Salt treatment can change composition of glycinin and β -conglycinin proteins in soybean seed. *Plant Omics J* 4: 228-235.
- Koch K (1996) Carbohydrate-modulated gene expression in plants. *Ann Rev Plant Physiol Plant Mol Biol* 47: 509-540.
- Li XJ, An P, Inanaga S, Eneji AE, Abdelbagi MA (2005) Mechanisms promoting recovery from defoliation in determinate and indeterminate soybean cultivars. *J Food Agric Environ* 3: 178-183.
- Liu XB, Herbert SJ, Baath K, Hashemi AM (2006b) Soybean (*Glycine max*) seed growth characteristics in response to light enrichment and shading. *Plant Soil Environ* 52: 178-185.
- Liu XB, Herbert SJ, Zhang QY, Hashemi AM (2006a) Yield-density relation of glyphosate-resistant soya beans and their responses to light enrichment in north-eastern USA. *J Agron Crop Sci* 193: 55-62.
- Liu XB, Wang GH, Jin J, Zhang QY (2010) Rhizosphere and Yield Physiology in Crops, Science Press (In Chinese), Beijing
- Makoi JHJR, Ndakidemi PA (2011) Changes in plant growth, nutrient dynamics and accumulation of flavonoids and anthocyanins by manipulating the cropping systems involving legumes and cereals-a review. *Aust J Agric Eng* 2: 56-65.
- Mathew JP, Herbert SJ, Zhang SH, Rautenkranz AAF, Litchfield GV (2000) Differential response of soybean yield components to the timing of light enrichment. *Agron J* 92: 1156-1161.
- Matthew A, Wiebold WJ (1984) Abscission, total soluble sugars, and starch profiles within a soybean canopy. *Agron J* 76: 715-719.
- Saratha K, Hume DJ, Godfrey C (2001) Genetic improvement in short season soybeans: matter accumulation, partitioning, and leaf area duration. *Crop Sci* 41: 391-398.
- Sheen J, Zhou L, Jang JC (1999) Sugar as signaling molecules. *Curr Opin Plant Biol* 2: 410-418.
- Shiraiwa T, Ushio H (1995) Accumulation and partitioning of nitrogen during seed filling in old and modern soybean cultivars in relation to seed production. *Jpn J Crop Sci* 64: 754-759.
- Smeekens S (2000) Sugar-induced signal transduction in plants. *Annu Rev Plant phys* 51: 49-81.
- Streeter JG, Jeffers DL (1979) Distribution of total non-structural carbohydrates in soybean plants having increased reproductive load. *Crop Sci* 19: 729-734.
- Thorne JH (1979) Assimilate redistribution from soybean pod walls during seed development. *Agron J* 71: 812-816.
- Vega CRC, Andrade FH, Sadras VO, Uhart SA, Valentinuz OR (2001) Seed number as a function of growth: A comparative study in soybean, sunflower and maize. *Crop Sci* 41: 748-754.
- Voldeng HD, Cober ER, Hwne D (1997) Fifty-eight year's genetic improvement of short-season soybean cultivars in Canada. *Crop Sci* 37: 428-431.
- Wang XH, Xu KZ, Li DY, Zhang ZA, Wu ZH, Chen ZY, Zhang XR (2007) Variation of soluble sugar content and specific leaf weight during the genetic improvement of soybean cultivars. *Soybean Sci* 26: 879-884. (in Chinese)
- Wiebold WJ, Ashley DA, Boerma HR (1981) Reproductive abscission levels and patterns for eleven determinate soybean cultivars. *Agron J* 73: 43-46.
- Wilcox JR (2001) Sixty years of improvement in publicly developed elite soybean lines. *Crop Sci* 41: 1711-1716.
- Zhang XZ (1993) Crop physiology research method [M]. Beijing: China Agricultural Press, 145-146.