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Effects of enhanced UV-B radiation on seed growth characteristics and yield components in soybean

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ABSTRACT

In order to understand the effects of enhanced ultraviolet-B (UV-B) radiation on soybean yield components and seed growth characteristics, three determinate soybean cultivars, Hai339 (H339), Heinong35 (HN35) and Kennong18 (KN18) were grown for 2 years in a field experiment exposed to enhanced UV-B radiation. Enhanced UV-B radiation decreased plant height, dry weight of individual stem and yield per plant of three soybean cultivars on average by 15.5%, 16.9% and 43.7%, respectively. Pod number per plant was the most responsible component for yield change under UV-B radiation in the 2-year study. Seed number per pod was less affected by change in light treatment in our experiment, compared with the pod number per plant. UV-B radiation had no significant effect on effective filling period, however, seed size was negatively impacted by UV-B radiation and it decreased 12.3% for three soybean cultivars. Reduction of seed size was mainly due to the decrease of cotyledon cell number. Enhanced UV-B radiation had no significant effect on cotyledon cell volume, cell growth rate or cell weight. Our results suggested that the reduction of seed ABA concentration was directly responsible for lower cotyledon cell number under enhanced UV-B radiation.

1. Introduction

During the past decades the thinning of the stratospheric ozone had led to the enhanced ultraviolet-B (UV-B) radiation on the earth surface (McKenzie et al., 1999). Numerous studies have shown that enhanced UV-B radiation can affect physiological and biochemical processes of many plant species, including altered plant photosynthesis (Reddy et al., 2004; Sunita and Guruprasad, 2012), changes in the carbon partitioning from growth pools to secondary metabolic pathways (Bassman, 2004), and thus changes in crop morphology, crop reproductive organ abortion and yield reduction (Mohammed and Tarpley, 2010, 2009).

Soybean, a main crop in China, has 94% of its planting region exposure to enhanced UV-B radiation (Peng and Zhou, 2010). For the past 10 plus years, the effect of enhanced UV-B radiation on soybean yield has been extensively studied because of the importance of intensity and quality of solar radiation intercepted by the canopy in determining soybean yield and yield components (Teramura, 1983; Board and Harville, 1996; Liu et al., 2009). Barnes et al. (1990) suggested enhanced UV-B radiation makes the soybean plant dwarf by shortening the internode length. Feng et al. (2001a) indicated enhanced UV-B radiation changed flowering time in some soybean cultivars and decreased contents of chlorophyll a/b, total leaf number and total leaf area in all cultivars. Enhanced UV-B radiation decreased total biomass and seed yield of 10 soybean cultivars averaged by 24.2% and 23.3% respectively, and different responses of seed size to enhanced UV-B radiation were observed (Feng et al., 2001b). Recent studies found that elevated ultraviolet-B radiation reduced concentrations of isoflavones and phenolic compounds in soybean seeds (Kim et al., 2011).

Endogenous plant growth substances have been implicated in controlling many developmental processes of plants (Wilkinson and Davies, 2002; Yang et al., 2004; Zhang et al., 2007). Liu et al. (2010) reported that ABA concentration in seed was positively correlated with seed-filling rate. Similarly, a decrease in the rate of dry weight accumulation was associated with a sharp decline in ABA concentration. ABA may be involved in the stimulation of rapid unloading of sucrose into the testa of soybean and the ABA in cotyledons may enhance sucrose uptake by the cotyledons (Schussler et al., 1984).

The effect of enhanced UV-B radiation on soybean physiology and yield has been extensively studied. However, the effects of enhanced UV-B radiation on seed growth characteristics of soybean has not been investigated, and little information is available concerning the UV-B radiation effects on the relationship among seed endogenous hormone and developing seeds in soybeans.

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The objective of this study was to examine the effect of enhanced UV-B radiation on soybean yield components, with an emphasis on responses of seed growth characteristics and endogenous abscisic acid (ABA) concentration to enhanced UV-B radiation. Plant morphology change and reproductive organs abortion might be two main reasons for soybean yield reduction.

2. Materials and methods

2.1. Site description

A 2-year filed study was conducted in 2011 and 2012 in Agricultural experiment station of Jilin Normal University, China. The research site is in the north temperate zone and continental monsoon area (cold and arid in winter, hot and rainy in summer), has an average annual precipitation of 573 mm, and an average annual temperature of 5.9 °C. Annual sunshine is around 2679 h, total annual solar radiation is 124 MJ cm^{-2} and annual average available accumulated temperature (≥10 °C) is 3079 °C. The area is the typical Mollisol (Black soil) region and the textural class of the Black soil is silty clay loam.

2.2. Cultural practice

Three determinate soybean cultivars differing in seed size were used in the experiment. They were Hai339 (H339), Heinong35 (HN35), and Kennong18 (KN18). Their seed weight was average 276, 198, and 165 mg at physiological maturity, representing a large-seeded, a moderate-seeded and small-seeded cultivar respectively. Seeds were sown on 6th May 2011 and 8th May 2012. Soybean cultivars Hai339, Heinong35 and Kennong18 were planted and precision drilling, ridge tillage was used. The ridge distance is 67 cm. Carbamide of 50 kg ha^{-1}(N 46%), and diammonium phosphate of 50 kg ha^{-1}(N 18%, P_2O_5 46%), and composite fertilizer of 150 kg ha^{-1}(N 18%, P_2O_5 16%, K_2O 16%) were applied before seeding. The weeds were controlled by hand. Usual field management was followed.

2.3. Enhanced UV-B treatment

Enhanced UV-B treatment was performed using 40 W UV-B lamps (produced by Nanjing Lamp Factory, China) hanging horizontally 1 m above the soybean plants. The UV-B lamps were installed on wooden posts at early flowering R1 stage (Fehr and Caviness, 1977), and were left in place for the remainder of the growing season. Strength of UV-B radiation employed in this study represented 21% of ozone depletion which corresponds to the 13 kJ m^{-2} d^{-1} UV-B radiation. The soybeans were irradiated for 7 h, from 10:00 to 17:00 each day except rainy days.

2.4. Agronomic traits and yield component

The soybean agronomic traits measured at maturity were taken on 10 plants, cut at ground level, bulked and determined by normal methods. The detailed yield components were separated and processed from 10 plants by hand. Mass of a 100-seed subsample was used to determine the mass of an individual seed. Among the data recorded were pod numbers per plant, seed number per plant, seed number per pod and seed size for further calculation of yield components. The volume of soybean seed was determined by a water displacement method.

2.5. Plant hormone (ABA) quantification

Seed samples were collected every 10 days from 20 days after flowering (DAF) at middle nodes (beginning of the linear seed filling period) to 60 DAF (physiological maturity) for analysis of endogenous plant hormone (ABA) in seed. Seed samples were taken from 10 pods. Harvested seed samples were immediately frozen on dry ice and stored at approximately −18 °C until analysis with an HPLC. The endogenous plant hormone analysis was carried out using the HPLC procedure outlined previously (Hein et al., 1984; Zhang et al., 1999; Liu et al., 2010). Briefly, samples were initially weighed then about 1 g was homogenized with a Polytron homogenizer for 3 min in 10 mL of 80% cold methanol (4 °C) containing 10 mg/L BHT (chilled to −80 °C before use). After extraction for 4 h at 4 °C, the homogenates were centrifuged at 10,000 × g for 15 min and then the supernatant was decanted. The residues were further extracted twice with 10 mL of 80% cold methanol and then the supernatants were combined. These combined extracts were reduced to the aqueous phase in salinized glass tubes under reduced pressure at 30 °C. The combined extracts were brought to a volume of 4.0 mL with distilled deionized H_2O, and then sonicated, and microfiltered (1.2 μm cellulose nitrate, Micro Filtration System). Samples were injected onto a stainless steel column packed with PRP-1 (10 μm particle size) and subjected to a 15-min linear solvent gradient from 0.01 M NaH_2PO_4 in 10% ethanol to 0.01 M NaH_2PO_4 in 50% ethanol (2.0 mL min^{-1}). The fraction in which authentic standards of plant hormones eluted from the PRP-1 column was diverted to a preparative C_{18} column (7 μm particle diameter, 10 mm × 15 cm column) with a high pressure valve. The fractions were eluted from the C_{18} column with a 30-min linear gradient from 0.1 N acetic acid (pH 2.8) to 0.1 N acetic acid in 50% ethanol (2.5 mL min^{-1}). Fractions containing plant hormones were reduced to 1.0 mL of aqueous eluent under reduced pressure (30 °C). For ABA, the fractions were injected (50 μL, Waters Associates) onto a strong anion exchange column (7 μm particle diameter, Wilmington, DE, 4.2 mm × 15 cm column) and eluted with a mobile phase of 30% CH_3OH, 10% CH_3CN, 60% H_2O (adjusted to pH 3.5 with H_3PO_4). The velocity of flow was 0.8 mL min^{-1}. The measurement apparatus worked at UV 254 nm. Plant hormone (ABA) in samples was quantified by external standardization to authenticate the standard swatch using peak height measurements. The lowest sensitivity was 10^{-8} g/L.

2.6. Seed growth rate and effective seed filling period

Pods and seed samples were collected from the same plants used for ABA quantification every 10 d during the linear growth phase. Three seeded pods from middle node positions were collected to minimize bias from position of the seed in the pod. After the sample collection, seed fresh mass was determined and seed volume was estimated by a water displacement method. Seeds were dried at approximately 70 °C for 24 h and seed moisture content was calculated. Linear regression was used to estimate seed growth rates (SGR) for each treatment, after eliminating non-linear points from the initial and final stages of seed development. At maturity, plants were sampled to determine final seed size. The effective filling period (EFP) was estimated by dividing final seed size by the seed growth rate during the linear filling period.

2.7. Cotyledon cell characteristics

The number of cotyledon cells was estimated by the improved method of Wang et al. (2009) (Patent Number: ZL200910072894.4) compared to Swank et al. (1987). Seeds were allowed to imbibe water for 8–10 h in a beaker and then the testa and embryo axis were carefully removed. Seeds were dried for 24 h (30–35 °C) and were then weighed using a balance with 0.0001 g precision. Seeds were then ground to fine powder in a mortar. A small amount (approximately 50 mg) of seed powder was weighed and then put into a 50 mL beaker. Then 10 mL chromic acid solution (concentration 10–20%) was added to the beaker for 48 h. A further 10 mL

chromic acid solution was added for another 24 h, and then the third 10 mL chromic acid solution was added for another 12 h to completely dissolve the powder. The solution was constantly stirred by a vortex device. After a uniform cell suspension was obtained by glass rod stirring, a 5 μL suspension was transferred to a hemacytometer with a pipettor and the cells were counted under a 100× magnification microscope. Fifteen replicates were made for the counting. Given the known counting chamber volume in the blood count plate and the total cell suspension volume, the cotyledon cell number in total cell suspension was calculated as follows, $W{:}W1 = X{:}A$, then $X = A^*(W/W1)$, where W is the dry soybean seed weight, X is cotyledon cell number, $W1$ is the dry weight of a small amount of seed powder, and A is the cotyledon cell number in total cell suspension from this known weight. Cotyledon cell volume was obtained by dividing seed volume by number of cotyledon cells. Cell weight was obtained by dividing seed size by cotyledon cell number.

Statistical analysis of data was performed by using the PROC ANOVA of SAS, and mean comparison was made according to the Duncan's multiple range tests (SAS Institute, 1996). Experimental figures were drawn by Sigma plot 2000 software.

3. Results

3.1. Seed growth and cotyledon cell characteristics response

Seed growth characteristics under UV-B radiation and natural light conditions obtained from the two experimental years were summarized in Table 1. UV-B radiation decreased seed volume and seed growth rate compared with that of the natural light. UV-B radiation decreased H339 seed volume and seed growth rate by 10.5% and 12.8%; that of HN35 by 14.4% and 13.1% and that of KN18 by 12.1% and 11.1%, respectively. UV-B radiation had no significant effect on effective filling period.

Cotyledon cell characteristics under UV-B radiation and natural light conditions obtained from the two experimental years were summarized in Table 2. UV-B radiation decreased cotyledon cell number compared with that of the natural light. UV-B radiation decreased Hai339 (H339) cotyledon cell number by 11.1%; that of Heinong35 (HN35) by 13.3% and that of Kennong18 (KN18) by 12.5% respectively. UV-B radiation had no significant effect on cotyledon cell volume, cell growth rate and cell weight.

3.2. Effect of enhanced UV-B radiation on seed endogenous ABA level

Compared to natural light condition, UV-B radiation decreased seed ABA concentration of H339 by 64%; that of HN35 by 37% and that of KN18 by 32% throughout seed growth period. Regardless of cultivars and light conditions, the concentrations of ABA in seed showed a one-peak curve, i.e. highest values were observed at 30 DAF at 10,000–20,000 ng/g fresh weight, depending on cultivar, and then declined to 200–4000 ng/g fresh weight at physiological maturity (Fig. 1). The peak of ABA concentration in the large-seeded cultivar was greater than that of the moderate-seeded and small-seeded cultivars. Under natural light condition, the ABA concentration in the large-seeded cultivar seed was 23% greater than the average ABA concentration of middle- and small-seeded cultivars at 30 DAF. As is shown in the Fig. 1, seed ABA concentration of large-seeded cultivar was more affected by UV-B radiation compared to moderate-seeded and small-seeded cultivars.

3.3. Soybean agronomic traits response

Soybean agronomic traits under UV-B radiation and ambient light conditions obtained from the two experimental years were summarized in Table 3. UV-B radiation consistently decreased plant height compared to ambient light. UV-B radiation decreased H339 plant height by 21.7%; that of HN35 by 10.0% and that of KN18 by 14.8%. Average number of nodes of HN35 was decreased by UV-B radiation, however those of H339 and KN18 by UV-B radiation was not significantly decreased (Table 3). UV-B radiation decreased diameter of basal node compared to ambient light. UV-B radiation decreased H339 diameter of basal node by 23.2%; that of HN35 by 22.8% and that of KN18 by 23.7%. UV-B radiation decreased dry weight of individual stem compared to natural light. The decrease for H339 dry weight of individual stem was 17.9%; that of HN35 14.3% and that of KN18 18.6%. Harvest index was decreased slightly by UV-B radiation, but this effect was not significant (Table 3).

3.4. Soybean yield and yield components response

Soybean yield and yield components under UV-B radiation and ambient light conditions obtained from the two experimental years were summarized in Table 4. UV-B radiation decreased yield per

Table 1
Effects of enhanced UV-B treatment on seed growth characteristics.

Cultivars	Light treatment	Seed size (mg)	Seed volume (μl)	Seed growth rate (mg/seed/day)	Effective filling period (days)
H339	UV-B	256b	212b	7.5b	34.1a
	CK	289a	237a	8.6a	33.6a
HN35	UV-B	175b	143b	5.3b	33.0a
	CK	202a	167a	6.1a	33.1a
KN18	UV-B	132b	109b	4.0b	33.0a
	CK	150a	124a	4.5a	33.3a

CK and UV-B mean ambient light and UV-B radiation. Different letter mean significant difference in same soybean cultivar under different light treatments at the 0.05 probability level.

Table 2
Effects of enhanced UV-B treatment on cotyledon cell characteristics.

Cultivars	Light treatment	Cell number ($\times 10^6$)	Cell volume ($\mu l \times 10^{-6}$)	Cell growth rate (ng/day)	Cell weight (ng)
H339	UV-B	9.6b	22.1a	0.78a	26.7a
	CK	10.8a	21.9a	0.80a	26.8a
HN35	UV-B	6.5b	22.0a	0.82a	26.9a
	CK	7.5a	22.3a	0.81a	26.9a
KN18	UV-B	4.9b	22.2a	0.82a	26.9a
	CK	5.6a	22.1a	0.80a	26.8a

CK and UV-B mean ambient light and UV-B radiation. Different letter mean significant difference in same soybean cultivar under different light treatments at the 0.05 probability level.

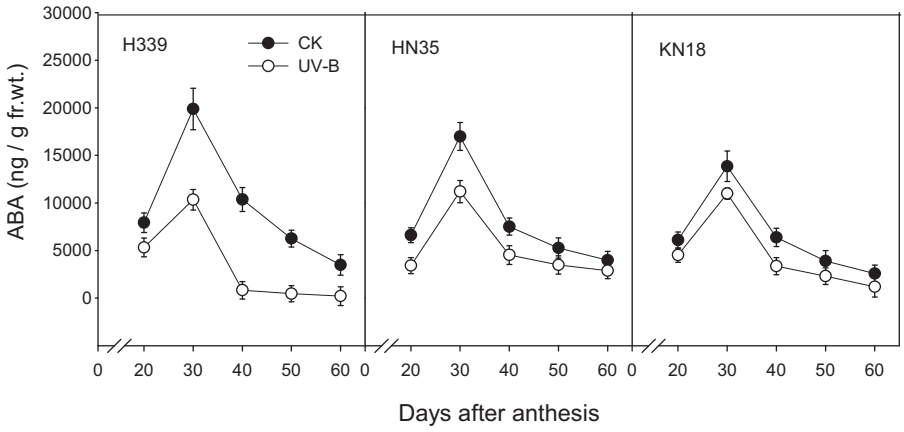

Fig. 1. Seed ABA concentration of three soybean cultivars under ambient light and UV-B radiation.

Table 3
Effect of enhanced UV-B treatment on soybean agronomic traits.

Cultivars	Light treatment	Plant height (cm)	Average number of nodes	Diameter of basal node (mm)	Dry weight of individual stem (g)	Harvest index
H339	UV-B	59.7**	15.8	6.3**	10.1**	0.41
	CK	76.2	16.1	8.2	12.3	0.46
HN35	UV-B	56.1**	10.5*	6.1**	7.8**	0.45
	CK	62.3	13.8	7.9	9.1	0.51
KN18	UV-B	62.4**	14.8	5.8**	8.3**	0.42
	CK	73.2	15.6	7.6	10.2	0.48

CK and UV-B mean ambient light and UV-B radiation.
* Mean significant difference in same soybean cultivar under different light treatments at the 0.05 probability level.
** Mean significant difference in same soybean cultivar under different light treatments at the 0.01 probability level.

plant compared to natural light. The decrease for H339 yield per plant was 39.1%; that of HN35 41.4% and that of KN18 50.6%. UV-B radiation decreased pod number per plant of three soybean cultivars by 29.6% for H339, 30.4% for HN35, 43.5% for KN18 (Table 4). UV-B radiation decreased seed number per plant of three soybean cultivars by 31.4% for H339, 33.3% for HN35, 44.2% for KN18 (Table 4). Pod number per plant was the most responsible component for yield change under UV-B radiation in the 2-year study. This suggests that UV-B radiation imposed during early flowering stage would change assimilates availability to the developing reproductive structures, influence flowering, and flower and pod abscission number with a resultant change in final pod number at harvest. Pod number per plant as the yield component was previously shown to be the most influenced by change in cultural and environmental conditions (Herbert and Litchfield, 1982; Board et al., 1992).

Seed number per pod was less affected by change in light regime in our experiment, compared with the pod number per plant (Table 4). There was a small tendency of decreased seed number per pod under UV-B radiation. Since seed number per pod was not significantly decreased by UV-B radiation (Table 4), the significantly decreased seed number per plant under UV-B radiation was mainly caused by decrease in pod number per plant.

Seed size was negatively impacted by UV-B radiation. UV-B radiation decreased H339 seed size by 11.4%; that of HN35 by 13.4% and that of KN18 by 12.0% respectively.

4. Discussion

The attenuation of the stratospheric ozone has led to the enhanced UV-B radiation on the surface of land in recent decades (Schrope, 2000). Enhanced UV-B radiation can alter plant photosynthesis (Reddy et al., 2004), water metabolism (Fuhrer and Booker, 2003) and the carbon partitioning from growth pools to secondary metabolic pathways (Bassman, 2004). Moreover, it can damage plant cell membrane structure (Tanyolac et al., 2007). The present study confirmed previous reports (Barnes et al., 1990; Qiang et al., 2004) that UV-B radiation in the canopy changed soybean agronomic traits and decreased yield per plant.

Feng et al. (2002) reported that UV-B radiation decreased plant height of two soybean cultivars 9.7% and 15.2%, and decreased dry weight of individual stem by 44.4% and 28.1%. In our study, average plant height and average dry weight of individual stem in three soybean cultivars were decreased 15.5% and 16.9% by UV-B radiation. Feng et al. (2001b) indicated UV-B radiation decreased

Table 4
Effect of enhanced UV-B treatment on soybean yield and yield components.

Cultivars	Light treatments	Yield per plant (g)	Pod number per plant	Seed number per plant	Seed number per pod	Seed size (mg)
H339	UV-B	12.3**	23.1**	48**	2.06	256**
	CK	20.2	32.8	70	2.12	289
HN35	UV-B	8.9**	26.5**	50**	1.89	175**
	CK	15.2	38.1	75	1.98	202
KN18	UV-B	7.7**	27.3**	58**	2.11	132**
	CK	15.6	48.3	104	2.16	150

CK and UV-B mean ambient light and UV-B radiation. * Mean significant difference in same soybean cultivar under different light treatments at the 0.05 probability level.
** Mean significant difference in same soybean cultivar under different light treatments at the 0.01 probability level.

total biomass and yield per plant by 24.2% and 23.3% respectively. Our previous research founded that UV-B radiation significantly decreased soybean yield per plant (Liu et al., 2009). Our research also reported that yield per plant of three soybean cultivars averagely decreased 43.7% by UV-B radiation.

Yield reduction was the mainly attributable to change of pod number per plant under UV-B radiation in the 2-year study. UV-B radiation decreased average pod number of per plant of three soybean cultivars by 34.5%. This suggests that UV-B radiation imposed during early flowering stage would change assimilates availability to the developing reproductive structures, influence flowering, and flower and pod abscission number with a resultant change in final pod number at harvest. Pod number per plant was the yield component most influenced by change in cultural and environmental conditions (Mathew et al., 2000).

In our study, UV-B radiation had no significant effect on seed number per pod (Table 4). Herbert and Litchfield (1982) reported that seed number per pod is a minor component determining the yield of soybean. However, the small tendency of decreased seed number per pod under UV-B radiation indicated that seed number per pod is strongly determined by the internal genetic mechanism, and is less influenced by environment condition.

Seed size was negatively impacted by UV-B radiation in our experiment. UV-B radiation averagely decreased seed size of three soybean cultivars 12.3%. Chen et al. (2004) reported that seed weight of 20 soybean cultivars showed different sensitivity to UV-B radiation. The seed weight of the 15 soybean cultivars decreased quite significantly while the seed weight of five other soybean cultivars had no significant changes. Seed size was a function of the rate of seed growth and the duration of dry weight accumulation in the seed fraction and thereby the dry weight. Genetic differences in seed growth rate are controlled by the cotyledon cell number (Egli et al., 1981). In our study, UV-B radiation decreased seed growth rate of three soybean cultivars on average by 12.5%. Seed growth rate was shown to be a function of the cotyledon cell number and the supply of assimilates to the developing cotyledons (Egli et al., 1989).

Cotyledon cell number and cotyledon cell volume are two main components determining seed size (Mathew et al., 2000). Our experiment suggested that reduction of cotyledon cell number is main reason for seed size decreased induced by UV-B radiation. UV-B radiation decreased cotyledon cell number of three soybean cultivars by 12.3% in our experiment. Since there were no significant differences in cotyledon cell volume, cell growth rate and cell weight, we propose that only the difference in cotyledon cell number, caused by UV-B radiation, was responsible for the observed variations in seed size within the three genotypes tested. However, Hirshfield et al. (1992) reported that seed size may be influenced more by cotyledon cell size than by cell number. There was a possible reason that different soybean cultivars showed different cotyledon cell sensitivity to environment change. It seems clear that the effects of cotyledon cell number on seed growth rate cannot be separated from possible effects of assimilate supply during seed growth period.

In soybean ABA is reported to be synthesized in the leaves and is exported in substantial quantities via the phloem (Hein et al., 1984). The lowering of the seed endogenous ABA level, through the seed filling, by UV-B radiation in our experiment indicates that most of the ABA in plants originates in leaf tissue and that any interference with the photosynthesizing leaves will reduce ABA level in developing soybean seeds. Liu et al. (2010) associated rapid increases in the rate of dry weight accumulation of the soybean seed with a high level of endogenous ABA in the seed. High concentration of ABA in the cotyledons of soybean genotypes was found to coincide with rapid uptake of sucrose, while lower rates of sucrose uptake, later during seed filling, were paired with lower ABA concentrations in the cotyledons (Schussler et al., 1984).

Our results also showed that UV-B radiation decreased seed ABA level that was correlated with seed growth rate, resulting in smaller seed size. This indicates that seed ABA concentration is involved in the control of the rate of dry matter accumulation. Morandi et al. (1990) suggested that ABA may increase the assimilate availability during the critical cell division period, and thus may regulate cotyledon cell number and seed growth rates. Ackerson (1984) also found that ABA could regulate cell division during early embryo development, thus influencing potential cell storage capacity. During the soybean seed filling stage, 2 mechanisms existed for photosynthate transfer: phloem unloading in the seed coat to regulate sucrose efflux, and sucrose uptake by cotyledon cells (Liu et al., 2010). Since all photosynthate entering the soybean cotyledon must enter through the seed coat, ABA might offer a driving force for photosynthate phloem unloading in the seed coat. Of course, ABA may also stimulate phloem assimilate unloading in controlling cotyledon enlargement during the seed growth period. This is because higher ABA concentration decreases the ATPase proton extrusion from the sieve tube elements, thus enhancing the efflux of sucrose into the apoplast by H^+-sucrose co-transport (Tanner, 1980). As is well known, ABA is synthesized in leaf tissue and is transported via the phloem to filling seed (Setter et al., 1981). The present study found that with lower the concentration of ABA in seed, the smaller was the seed size. This suggests a parallel relationship between seed growth and the ABA concentration in the cotyledon, although the relationship of ABA transport from the leaf to the seed and assimilate transfer is still unclear. Our experiments provide evidence for a promotive role of ABA in photoassimilate accumulation in soybean seeds. ABA may stimulate rapid unloading of sucrose into the seed coat apoplast and may enhance movement of sucrose into cotyledons during the seed filling stage.

It has been suggested that the progression through cell division and cell enlargement to seed maturity is coordinated by the interactions of stage-specific developmental regulators such as ABA, GAs, and ethylene (Nagel et al., 2001; Brocard-Gifford et al., 2003). Thus, more data is needed to build a solid case for a regulatory role of endogenous hormone control in seed growth.

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