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Effect of Shading Individual Soybean Reproductive Structures on Their Abscisic Acid Content, Metabolism, and Partitioning[1]

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ABSTRACT

Pod set in soybean is related to carbon partitioning and may be, at least partially, regulated by abscisic acid (ABA) concentrations. The studies reported here examine the relationship between carbon and ABA partitioning, reproductive abscission and ABA metabolism. The partitioning of radiolabeled ABA and photoassimilates from leaves to flowers and endogenous ABA concentrations were determined in shaded and unshaded reproductive structures. Aluminum foil was gently placed over individual soybean reproductive structures for 48 hours at 0, 4, 12, 17, and 22 days after anthesis (DAA). Shading of flowers at 12, 17, and 22 DAA resulted in significantly reduced concentration of ABA. However, shading had no effect on the catabolism of exogenously supplied [^{3}H] ABA. The shading treatment on the first four of the five dates reduced partitioning of photoassimilates and ABA from the subtending leaf to the flower. Shading of reproductive structures also caused a significant reduction in the amount of assimilate exported from the subtending leaf, at 17 DAA. We conclude that shade-induced premature reproductive abscission in soybean is not stimulated by high levels of ABA within reproductive structures, but that ABA may inhibit abscission of reproductive structures by playing a role in preferential assimilate partitioning.

Typically, a large proportion of soybean flowers produced, abscise before reaching maturity. Estimates as high as 57 to 82% abscission have been reported for determinate varieties (23, 27), and 32 to 65% for indeterminate types (23).

Soybean floral abscission may be either stimulated or reduced by environmental factors. Nutrient deficiency (2), high temperatures, (24), long photoperiods (2, 24) and reduced light intensity (9, 15, 24) stimulate abscission, while increasing the available N (2) and CO_2 during flowering (7) reduce it.

Increasing light in the soybean canopy by use of reflective boards (15) or fluorescent lights (9) has been shown to increase pod set. Heindl and Brun (9) showed that supplemental low intensity white or red fluorescent light under the soybean canopy reduced floral abscission, while shading of floral racemes with aluminum foil increased floral abscission. Shading floral structures reduced photoassimilate partitioned to them by as much as 30% and reduced the seed weight per node. It was concluded that light has a direct photomorphogenic effect on floral abscission. Similar conclusions were reached by Mor and Halevy (13) in studies of partitioning to rose shoot buds.

ABA has been reported to be related to abscission of various plant structures (1). However, recent evidence suggests a role of ABA in the partitioning of photoassimilates to developing fruit and seeds. A positive relationship between exogenously applied ABA and sink activity has been shown in both wheat (6) and barley (22). In peas (3) and soybeans (16), a positive relationship was observed between seed growth rate and ABA concentration. ABA stimulated *in vitro* sucrose uptake by isolated soybean cotyledons (16) and sugar beet root discs (14). Decreased reproductive abscission in soybean in response to light was shown to be associated with increased partitioning of recently fixed carbon to the reproductive structures (8); in addition, carbon partitioning was greater in flowers destined to set pods than in flowers destined to abscise (4).

The association of pod set with carbon partitioning (4, 9), and of carbon partitioning with ABA (3, 6, 16), suggests that there may be a positive relationship between pod set and ABA concentration of the flower. The objectives of this study were to determine: (a) if shading of individual reproductive structures has an effect on their endogenous ABA levels, (b) if shading of reproductive structures has an effect on ABA catabolism, and (c) if shading has an effect on partitioning of ABA and photoassimilates from leaves to reproductive structures.

MATERIALS AND METHODS

Plant Material. The semideterminate soybean genotype IX93-100 was grown in four completely randomized blocks in the field at St. Paul, MN in the summer of 1983. This genotype was selected for its relatively long racemes, allowing for easy determination of anthesis date, growth, development, and abscission of individual flowers. Seeds of IX93-100 were donated by C. D. Dybing, USDA-ARS, Brookings, SD.

IX93-100 was selected from crosses made by D. E. Green, Iowa State University, of A71-5558-1 and L61-344, a semideterminate isoline of 'Harosoy.' A71-5558-1 is a genotype derived from crosses of 'Wirth' and PI lines.

Raceme development and abscission patterns of IX93-100 were found to be essentially idential to the E1t isoline of Clark as reported earlier (4, 12). Flowers were numbered sequentially from the most basal flower (position I), to the more distal flowers (position II–position VI). We have observed as many as 12 or more flowers per raceme in IX93-100. Pods usually set at the basal three and sometimes four positions (I–IV), while flowers or young pods more distal tend to abscise.

Flowering was induced at the third trifoliate leaf stage by artifically regulating daylength with black plastic covers for each plot. Anthesis of the first flowers occurred on July 22.

Shading Treatments. Shading was accomplished by placing

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aluminum foil over individual flowers or young pods at positions I, II, and III on five dates during reproductive growth; it has been shown in previous studies (9) that the alumiunum foil shades did not significantly affect the microclimate around the flowers or pods. The treatments were applied between 0800 to 0900, at 0, 4, 12, 17, and 22 DAA.[3] All sampling was done 48 h after shading. Control racemes, without shades, were of the same age.

Endogenous ABA. After shading, racemes were removed from the plant, immediately placed on ice, dipped in an antioxidant solution (consisting of 30 mM EDTA, 30 mM citric acid, and 10 mg/L BHT dissolved in 60% methanol), and quickly frozen in liquid N_2. Subsequently, the various floral positions were separated and stored at −20°C until extraction. The endogenous ABA of floral position III was extracted and quantified as described by Schussler *et al.* (16).

ABA Catabolism. Twenty-four h after application of shade treatments, 1 μCi of ±^{3}H-ABA (39 Ci/mmol; Amersham International) in 5 μl double-distilled H_2O was injected into the petiole of the leaf subtending an axillary raceme in which at least 6 flowers were at or past anthesis. After a 24 h chase period, flowers/pods were collected, weighed, and extracted twice in cold (−80°C) 80% methanol containing 10 mg/L BHT. The homogenate was centrifuged at 20,000 *g* for 40 min and the supernatants combined and dried *in vacuo* at 30°C. Dried residues were stored at −20°C until subjected to HPLC.

Samples were dissolved in 2 ml of water and subjected to HPLC using the method of Daie *et al.* (5), except that the column used was 4.6 mm (i.d.) × 150 mm packed with 5 μm Nucleosil C_{18} particles and the eluent was monitored with a Packard Trace on-line liquid scintillation detector (model No. 7140), packed with CaF_2 crystals. Five fractions were collected that co-eluted with standards of PA-CONJ, DPA, ABA-HE, PA, and ABA. Radioactivity in collected fractions was determined by liquid scintillation spectroscopy. Standards were obtained by introducing ^{14}C-ABA into tomato (for PA and PA-CONJ) or soybean leaves (for DPA and DPA-CONJ) and compounds extracted and purified as above. Identity was verified by GC-mass spectrometry.

Partitioning of ABA and Photoassimilates. One-half μCi of (±)^3 H-ABA (39 Ci/mmol; Amersham Int.) in 5 μl double distilled H_2O was injected into the midvein of a leaf subtending a raceme containing at least 7 flowers at or past anthesis. The same leaf was then exposed to $^{14}CO_2$ released from 20 μCi of $NaH^{14}CO_3$ (57 mCi/mmol; Research Products International) using the method of Heindl and Brun (9). After a 4 h chase period, racemes were collected, frozen in liquid N_2, and separated into raceme positions I to VII, dried at 70°C to constant mass, and combusted using a sample oxidizer (Packard model B-306). The ^{3}H was collected as water condensate, Aqualsol II liquid scintillation cocktail added (New England Nuclear), and counted using liquid scintillation spectroscopy. The ^{14}C was collected as $^{14}CO_2$ in Carbosorb II (Packard Corp.), Permaflour V was added, and radioactivity counted by liquid scintillation spectroscopy. Six to eight replicates were used at each sampling date.

Statistical Analysis. Four randomized complete blocks were used with four to eight samples per analysis. Comparisons between shaded and unshaded treatments were tested by an unpaired *t* test.

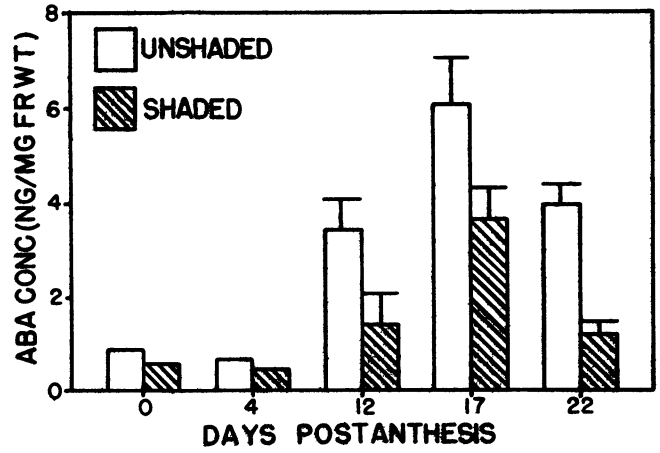

FIG. 1. Concentrations of ABA in shaded and nonshaded reproductive structures of soybean as a function of DAA. Aluminum foil shades were applied for 48 h prior to sampling. Values represent mean ± SE (n = 8). SE bars shown where treatments differ significantly at the 5% level.

[3] Abbreviations: DAA, days after anthesis; PA-CONJ, phaseic acid-conjugate; PA, phaseic acid; DPA, dihydro-phaseic acid; ABA-HE, abscisic acid hexose-ester; BHT, butylated hydroxy-toluene.

RESULTS AND DISCUSSION

The ABA concentrations of shaded flowers (or young pods) were consistently lower than that of control (unshaded) reproductive structures (Fig. 1), although not significantly different until 12 or more DAA. Previous work (4) has shown that the sink intensity for newly assimilated carbon is significantly reduced very soon after anthesis of individual flowers (*i.e.* within 3 or 4 DAA). At 0 and 4 d postanthesis, ABA concentrations were low and no significant differences were found between shaded and unshaded pods.

An apparent maximum ABA concentration was reached at 17 DAA which corresponded to the time of maximum seed growth rate. The timing of the maximum ABA concentration was somewhat earlier than previously reported for developing seeds of different soybean genotypes (16).

The ABA content of pea seedlings (18), grown in the dark for several days have been shown to decrease by several-fold, while the ABA concentration of cotton bolls of plants grown in the dark (25), increased. Shading of soybean plants has reduced the ABA concentration in their pods in a field environment, but had the opposite effect in greenhouse-grown plants (27). The previous studies not only darkened the structures of interest, *i.e.* bolls or pods, but also the remaining plant organs; thus, changes in ABA content of reproductive organs may represent the condition of the whole plant rather than just the reproductive structures.

Three possible mechanisms may account for shade-induced changes in ABA concentration of reproductive structures: (a) increased catabolism of ABA in shaded pods, (b) reduced import of ABA from source leaves to the shaded pods, or (c) reduced synthesis of ABA in shaded pods.

ABA catabolism was examined by injecting ^{3}H-ABA into soybean leaf petioles and allowing it to translocate to and be metabolized by pods/seeds for 24 h. No significant differences in the proportions of ABA or its catabolites were found at any sampling date (Table I).

The majority of the radiolabel was recovered as ABA (64–73%) and DPA (11–19%), with smaller amounts as PA-CONJ, ABA-HE, and PA (Table I). These results are compatible with those previously shown by Setter *et al.* (17) for DPA, PA, and ABA in soybeans.

It is possible that the ^{3}H-ABA-HE was formed predominantly from the unnatural (−) isomer of ABA, while the (+) isomer was converted to PA and DPA, as suggested by studies of Vaughan and Milborrow (26). This may also imply that the recovered ABA was somewhat enriched in the (−) isomer which may not be readily catabolized. Zeevaart (28) has shown that water stressed and rehydrated leaves of *Xanthium* metabolize ABA more readily in the dark than in light. He attributed this to increased concentrations of ethylene in the dark, increasing ABA

Table I. *Relative Amounts of ABA and Four Catabolites Recovered 24 h after Injection of 0.5 μCi of ^{3}H-ABA*

Each value represents mean ± SE (n = 8).

DAA	Treatment	ABA	DPA	PA-CONJ	ABA-HE	PA
		% of ^{3}H recovered				
0	Control	66.16 ± 1.51	19.17 ± 0.62	7.55 ± 0.17	5.06 ± 0.24	2.06 ± 0.02
	Shaded	64.68 ± 3.02	14.96 ± 0.54	10.99 ± 1.55	5.77 ± 0.43	3.61 ± 0.66
4	Control	65.62 ± 2.84	14.12 ± 1.16	7.60 ± 1.12	9.96 ± 3.58	2.70 ± 0.25
	Shaded	67.06 ± 1.22	15.29 ± 0.41	10.11 ± 0.45	5.45 ± 0.15	2.09 ± 0.66
12	Control	72.93 ± 1.69	11.22 ± 1.03	11.48 ± 0.94	3.48 ± 0.25	0.90 ± 1.05
	Shaded	70.74 ± 4.3	13.70 ± 1.57	8.95 ± 0.10	5.79 ± 3.50	0.82 ± 0.03
17	Control	68.53 ± 2.01	10.79 ± 0.91	14.38 ± 1.40	4.34 ± 0.19	2.05 ± 0.04
	Shaded	72.34 ± 0.34	13.70 ± 1.57	13.10 ± 0.55	4.18 ± 0.05	1.78 ± 0.40
22	Control	69.39 ± 2.69	13.51 ± 0.87	11.38 ± 1.35	3.87 ± 0.05	1.85 ± 0.05
	Shaded	64.89 ± 4.39	16.03 ± 2.81	12.93 ± 1.67	4.01 ± 0.53	2.14 ± 0.17

Table II. *Sink Intensities of ^{3}H Label or ^{14}C Label in the Basal Four Floral Positions*

Values represent mean ± SE (n = 4 to 8).

Raceme Position	Label	Treatment	Days after Anthesis				
			0	4	12	17	22
			% dpm/mg dry wt				
I	^{14}C	Control	9.76 + 1.19*	3.73 + 0.36*	1.15 + 0.26*	0.18 + 0.07	0.07 + 0.01
		Shaded	2.99 + 0.15	1.03 + 0.17	0.40 + 0.13	0.08 + 0.01	0.08 + 0.01
	^{3}H	Control	6.97 + 2.30*	3.73 + 0.79*	1.28 + 0.28*	0.18 + 0.08*	0.07 + 0.01
		Shaded	2.78 + 0.15	1.03 + 0.11	0.42 + 0.08	0.08 + 0.01	0.08 + 0.01
II[b]	^{14}C	Control	7.18 + 1.38*	4.07 + 0.54*	0.65 + 0.14*	0.14 + 0.05*	0.09 + 0.01
		Shaded	3.05 + 0.51	0.95 + 0.25	0.28 + 0.09	0.07 + 0.01	0.08 + 0.01
	^{3}H	Control	15.30 + 4.30*	3.69 + 0.68*	0.53 + 0.11	0.15 + 0.06*	0.09 + 0.01
		Shaded	3.01 + 0.59	0.95 + 0.25	0.58 + 0.10	0.06 + 0.01	0.06 + 0.01
III	^{14}C	Control	6.25 + 0.99*	5.75 + 1.59*	0.36 + 0.12	0.18 + 0.01*	0.08 + 0.01
		Shaded	0.75 + 0.29	1.02 + 0.26	0.38 + 0.15	0.06 + 0.02	NA[a]
	^{3}H	Control	0.98 + 0.65*	4.29 + 1.52*	NA	0.17 + 0.02*	0.08 + 0.02
		Shaded	0.31 + 0.13	1.02 + 0.26	0.55 + 0.09	0.06 + 0.02	0.06 + 0.01
IV[b]	^{14}C	Control	10.38 + 0.81*	3.73 + 1.18*	0.88 + 0.32*	0.18 + 0.09	NA
		Shaded	2.10 + 0.70	1.34 + 0.17	0.28 + 0.15	0.08 + 0.02	0.08 + 0.01
	^{3}H	Control	19.92 + 7.78*	2.19 + 0.78*	0.64 + 0.09*	NA	NA
		Shaded	1.94 + 0.53	1.34 + 0.17	0.17 + 0.09	0.08 + 0.02	0.09 + 0.01

* Significant difference between unshaded and shaded at 5% level. [a] Insufficient replication (<4) for adequate computations. [b] Position IV was not shaded; shading only refers to basal three floral positions.

Table III. *Percent of Exogenously Applied Label Exported from Leaves*

Each value represents mean (n = 8) ± SE.

Isotope	% Exported from Leaves Subtending	
	Nonshaded racemes	Shaded Racemes
^{14}C[a]	65 ± 4*	53 ± 5
^{3}H[b]	27 ± 5	12 ± 6

[a] Based on amount of dpms at start of chase period *versus* amount of dpms at end of the chase period. [b] Based on amount of dpms injected into leaf *versus* amount of dpms at end of the chase period. * Significant difference between shaded and nonshaded at the 5% level.

metabolism. In our study, shading pods with aluminum foil apparently did not affect their ability to catabolize ABA and we have no data on ethylene production.

Since it is known that ABA is readily translocated from soybean leaves to developing reproductive structures (17), it is possible that the reduced levels of endogenous ABA present in shaded pods (Fig. 1) was due to reduced export or partitioning of ABA from leaves to developing fruits. Therefore, the partitioning of ^{3}H-ABA and ^{14}C-photoassimilates introduced into the leaf was studied.

As seen in Table II, unshaded pods had greater sink intensities than did shaded pods for both ^{14}C-photoassimilates and ^{3}H-ABA. These differences between shaded and unshaded pods were significant at early sampling dates (0 and 4 DAA) when the differences in endogenous ABA were not significant (Fig. 1). Although this seems to be in conflict, the amount of export from the leaves, indicated by the total amount of label collected, was minute at early dates compared to later dates (data not shown).

At anthesis (0 DAA), sink intensities for both compounds were quite variable at the four raceme positions, but control racemes were consistently and significantly greater than shade treatments (Table II).

At 4 DAA, intensities for both compounds were lower and less variable than at 0 DAA (Table II), and the treatment effect was consistent and significant. Brun and Betts (4) show this as a time at which there is a greater sink intensity of flowers destined to set than of flowers destined to abscise, thus our data is consistent with their observations.

At 12 DAA, the intensities for both compounds were distinctly lower than at 4 DAA, while the endogenous ABA concentrations

of unshaded pods were 3 to 5 times higher (Fig. 1). This is probably indicative of a greater mass of assimilates being exported from the leaves to the young pods as they start to grow, thus diluting the labeled ABA. The pods were also at the linear stage of growth, thus having large increases in weight. By 12 and 17 DAA, significant differences in sink intensity between control and shaded structures had become less frequent (Table II). At 22 DAA, there were no significant differences observed. By this date seeds had almost reached maximum dry weight, thus little import by pods would be expected.

Heindl and Brun (9) reported that shading of whole racemes reduced sink strength (% dpm) by as much as 30%, due to decreased sink intensities (% dpm mg^{-1}). At our early sampling dates, which were earlier in development than in their study, unshaded pods had intensities as much as 5 times higher than shaded pods (Table II). Mor and Halevy (13) found shading of rose shoots reduced relative-specific activity (% dpm/% dry weight) by 13.5-fold. Similarly, Hole and Scott (11) found that shading pea pods reduced growth rates.

Samples of pods at position IV, which was unshaded, taken from racemes with positions I to III shaded, also had lower sink intensities than samples from control racemes (Table II). The mechanism of this response is uncertain. It may simply mean that increased phloem transport, by virtue of stimulated phloem unloading in any part of the sink, may benefit the whole sink (*i.e.* raceme) or it might mean that shading part of the raceme decreases phloem loading in the source, thus decreasing its source activity and thereby reducing assimilates transported to any sink that it serves.

Decreased loading within the source leaf may be the result of reduced amounts of a substance promoting phloem loading being translocated from the shaded reproductive structures to the leaf. In this aspect, Hein (8) has shown that IAA or its precurser tryptophan, is translocated from reproductive sinks to their respective source leaves.

An analysis of leaf tissues at 17 DAA (Table III) showed that significantly less ^{14}C was exported from leaves subtending racemes with shaded pods than from leaves subtending control (nonshaded) racemes. Less ^{3}H was also exported, but the difference was not significant. Without an analysis of sink strengths in other sinks than the subtended raceme, it is not possible to determine if the observed effects of the sink on assimilate export from the source (Table III) are due to events in the sink or source end of the transport pathway.

ABA appears to be a factor in partitioning of photoassimilates (3, 6, 16, 22). It does not seem surprising then that darkening of reproductive structures with subsequent lowering of ABA, and possibly other plant growth substances, results in reduced seed growth rates and final seed size. It is possible that reduced growth rates and increased abscission of seeds/pods could be a result of reduced levels of growth substances in these structures. Pods in the lower canopy of soybean, also have higher abscission and lower seed size (10). Perhaps the reduced light to these structures lowers the concentrations of ABA, and possibly other hormones, thus causing the increased abscission. However, a cause/effect relationship has not been established, and it is possible that the decreased partitioning of ^{3}H-ABA to shaded pods, is a result rather than a cause of decreased sink strength.

ABA has been generally viewed as an abscission inducer in most plant systems (1). However, there is no evidence that high levels of ABA induce abscission of premature soybean reproductive structures from our present study, or from previous studies (GL Yarrow, WA Brun, ML Brenner, unpublished data). We have measured concentrations of endogenous ABA in low and high setting soybean reproductive structures (GL Yarrow, WA Brun, ML Brenner, unpublished data) and found either no differences or higher ABA levels in high setting reproductive structures. In addition, partitioning of radiolabeled ABA and photoassimilates to abscising and nonabscising reproductive structures has shown greater quantities of label partitioning to nonabscising structures (GL Yarrow, WA Brun, ML Brenner, unpublished data). This agrees with data from application of ABA in lanolin to basal pedicel scars of the soybean genotype 'Clark' Elt (12) and also with endogenous ABA analysis in the cultiver 'Williams' (19). In addition, ABA application to pedicel scars in *Phaseolus* (21) and analysis of endogenous ABA in *Phaseolus* (20) has failed to show any clear relationship between ABA and abscission. Results from the present, and previous studies (GL Yarrow, WA Brun, ML Brenner, unpublished data), may indicate that ABA can inhibit abscission of premature soybean reproductive structures by facilitating preferential partitioning of assimilates to reproductive structures containing higher levels of ABA.

From the present study we conclude that shading of reproductive structures at 12 or more DAA decreases their endogenous ABA concentration in a short period of time (48 h) and that this decrease appears not to be caused by ABA catabolism. Shading decreases the partitioning of ABA and photoassimilates from the leaf to the shaded reproductive structures but is not clear whether this response is due to events occurring in the source or in the sink. It is possible that the decreased ABA in the shaded flowers could be a result of reduced *in situ* synthesis of ABA by the reproductive structures; however, no information on *in situ* synthesis of ABA by soybean pods is available.

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