Relationship of Endogenous Abscisic Acid to Sucrose Level and Seed Growth Rate of Soybeans

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ABSTRACT

It has been proposed that abscisic acid (ABA) may stimulate sucrose transport into filling seeds of legumes, potentially regulating seed growth rate. The objective of this study was to determine whether the rate of dry matter accumulation in seeds of soybeans (Glycine max L.) is correlated with the endogenous levels of ABA and sucrose in those sinks. The levels of ABA and sucrose in seed tissues were compared in nine diverse Plant Introduction lines having seed growth rates ranging from 2.5 to 10.0 milligrams dry weight per seed per day. At 14 days after anthesis (DAA), seeds of all genotypes contained less than 2 micrograms of ABA per gram fresh weight. Levels of ABA increased rapidly, however, reaching maxima at 20 to 30 DAA, depending upon tissue type and genotype. ABA accumulated first in seed coats and then in embryos, and ABA maxima were higher in seed coats (8 to 20 micrograms per gram fresh weight) than in embryos (4 to 9 micrograms per gram fresh weight). From 30 to 50 DAA, ABA levels in both tissues decreased to less than 2 micrograms per gram fresh weight. Levels of sucrose were also low early in development, less than 10 milligrams per gram fresh weight at 14 DAA. However, by 30 DAA, sucrose levels in seed coats had increased to 20 milligrams per gram fresh weight and remained fairly constant for the remainder of the filling period. In contrast, sucrose accumulated in embryos throughout the filling period, reaching levels greater than 40 milligrams per gram fresh weight by 50 DAA. Correlation analyses indicated that the level of ABA in seed coats and embryos was not directly correlated to the level of sucrose measured in those tissues or to the rate of seed dry matter accumulation during the linear filling period. Rather, the ubiquitous pattern of ABA accumulation early in development appeared to coincide with water uptake and the rapid expansion of cotyledons occurring at that time. Whole tissue sucrose levels in embryos and seed coats, as well as sucrose levels in the embryo apoplast, were generally not correlated with the rate of dry matter accumulation. Thus, it appears that, in this set of diverse soybean genotypes, seed growth rate was not limited by endogenous concentrations of ABA or sucrose in reproductive tissues.

In particular, ABA has been shown to stimulate the movement of sugars in sugar beet (30), grape (7), pea (25), bean (6), and soybean (13). In legumes, exogenous ABA has been shown to stimulate assimilate unloading from seed coats (6, 25) and uptake of assimilates by embryos (15, 26), two processes that potentially limit the movement of assimilates to developing seeds (21, 27). Little information is available, however, to determine whether a relationship exists between endogenous levels of ABA in legume seed tissue and assimilate movement to those sinks.

The in vitro uptake of sucrose by soybean embryos is concentration dependent (8, 21, 27), suggesting that higher concentrations of sucrose in seeds in situ would result in higher seed growth rates (8, 10). We hypothesized that endogenous ABA may control sucrose unloading from seed coats and/or sucrose uptake by embryos, thus regulating the concentration of sucrose available for seed growth. Endogenous concentrations of ABA in seed tissues of legumes have been shown to be positively or negatively correlated with seed growth rate, depending upon stage of development and environmental conditions examined (2, 5, 18, 26). However, relationships between the concentrations of ABA and sucrose in these tissues and between the concentrations of sucrose and seed growth rate were not evaluated in these studies because assimilate levels in seed tissues were not measured.

Our objective was to determine whether seed growth rate of soybean is correlated with the concentrations of endogenous ABA and sucrose in reproductive sinks. We evaluated nine PI genotypes with seed growth rates ranging from 2.5 to 10 mg seed d⁻¹. We hypothesized that genotypes with high seed growth rates would be characterized by high concentrations of ABA and sucrose in their seed tissues. In addition, endogenous ABA and sucrose levels were compared with sucrose uptake by isolated embryos in vitro to determine their relationship to sucrose flux into developing seeds.

MATERIALS AND METHODS

Plant Material

Nine soybean (Glycine max L.) PI lines (group 0 maturity, determinate) were grown in four replicates of a randomized complete block design in the field at St. Paul, MN, during the summers of 1983 and 1984. Two weeks after emergence, plants were thinned to a uniform density of 13 plants m⁻¹ in

Abbreviations: PI, plant introduction; DAA, days after anthesis.
rows 76 cm apart. For each genotype, a population of flowers was tagged at anthesis. Samples taken for analysis of endogenous ABA and sucrose, as well as those used for the in vitro sucrose uptake assay and calculation of dry matter accumulation rate, were selected from this population of uniformly aged pods.

**Tissue Sampling**

The study conducted in 1983 was designed to determine the relationship between the levels of ABA in reproductive tissues (pod walls and seeds) early in development (6–22 DAA) and the subsequent rate of dry matter accumulation during the linear period of seed growth. At each sampling date (6, 10, 14, 18, and 22 DAA), previously tagged pods were removed from the center nodes of several plants in each replicate between 0800 and 1000 h. Fifteen pods were pooled in each replicate sample at 6 and 10 DAA. Because the fresh weight of seeds in these pods was <5 mg seed⁻¹, no attempt was made to remove them for separate analysis during these first two sampling dates. Fewer pods were pooled at 14, 18, and 22 DAA, when seeds were removed for separate analysis. At 18 and 22 DAA, seeds were further dissected into seed coats and embryos (cotyledons and embryonic axis combined). Total fresh weight of seed tissue samples ranged from 50 to 100 mg at 14 DAA. After fresh weight was recorded, samples were frozen on solid CO₂ and stored at −20°C.

In 1984, endogenous levels of ABA and sucrose were quantified in seed tissues during the period of linear dry matter accumulation (25–50 DAA). Two uniformly aged pods were sampled in each of the four replicates. One seed was removed from each of the pods for endogenous ABA and sucrose analysis. A second seed from each pod was used to measure in vitro sucrose uptake (26). Additional seeds, sampled during the linear filling period and dried at 60°C, were used to determine the rates of fresh weight and dry weight accumulation for each genotype.

**Quantification of Endogenous ABA and Sucrose Levels**

Tissue samples were initially extracted in 80% methanol as previously described (26). These crude extracts, containing both ABA and sucrose, were purified using a reverse-phase HPLC system (26) in which sucrose was collected in the nonretained fraction (>95% recovery of [U⁻¹⁴C]sucrose), followed by collection of the fraction co-eluting with authentic ABA. ABA and sucrose levels were then quantified using GLC with electron capture detector (26) and an enzymatic assay (3), respectively.

**In Vitro Sucrose Uptake**

In 1984, in vitro sucrose uptake by embryos was measured at three sampling dates during the linear filling period, according to the method of Schussler et al. (26). Briefly, embryos (seed coats surgically removed) were incubated in a buffered (pH 5.5) 10 mM [U⁻¹⁴C]sucrose solution (specific activity 133 Bq μmol⁻¹), for 3 h. ¹⁴C in the free space was removed by rinsing the embryos in ice-cold nonlabeled 10 mM sucrose. Embryos were lyophilized and oxidized with a Packard Tri-Carb oxidizer, and the recovered radioactivity was quantified with liquid scintillation spectroscopy. This in vitro assay, conducted in 10 mM sucrose, primarily measures uptake associated with the saturable component of sucrose uptake (21, 27).

**Estimation of Sucrose Concentrations in the Apoplast of Seed Coats and Cotyledons**

The concentration of sucrose in the apoplastic volume of seed coats and embryos was estimated using the compartmental efflux kinetics technique reported by Hsu et al. (17). These estimates were made between 30 and 35 DAA when seeds were in their linear filling period. Seed coat and embryo apoplastic volumes were estimated in three replicates of two pooled tissues, and endogenous sucrose amounts in apoplastic volumes were estimated in six replicates of five pooled tissues.

**RESULTS**

**Seed Growth Characteristics**

Seed growth rates (mg dry weight seed⁻¹ d⁻¹) during the linear filling period in 1984 were calculated by fitting linear regression equations to the seed dry weight data after discarding obviously nonlinear points at the beginning and end of seed development. All r² values were >0.95. A fourfold difference in seed growth rate, 2.5 to 10.0 mg dry weight seed⁻¹ d⁻¹, was observed, and final seed dry weights ranged from 82.7 to 286.9 mg seed⁻¹ (Table I). Rates of fresh and dry weight accumulation during each 5-d sampling interval are shown in Figure 1. As suggested by the high r² values, dry matter accumulation rates were fairly constant during the linear seed filling period (30–50 DAA). Similarly, fresh weight accumulated at a relatively constant rate in seeds of genotypes 1, 2, and 3. In genotypes with more rapid seed growth rates, however, rates of fresh weight accumulation were higher between 25 and 40 DAA, decreasing thereafter to more constant rates. The negative rates of fresh weight accumulation from 50 to 60 DAA reflect water loss from seeds nearing maturity.

**Table I. Seed Growth Rate during the Linear Seed Filling Period and Final Dry Weight Seed⁻¹ of Nine Soybean Genotypes**

<table>
<thead>
<tr>
<th>Genotype No.</th>
<th>PI Identification</th>
<th>Seed Growth Rate (mg dry wt seed⁻¹ d⁻¹)</th>
<th>Dry Wt Seed⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>361.058</td>
<td>2.5</td>
<td>82.7 ± 1.6</td>
</tr>
<tr>
<td>2</td>
<td>437.198</td>
<td>2.7</td>
<td>78.0 ± 1.7</td>
</tr>
<tr>
<td>3</td>
<td>437.227</td>
<td>3.2</td>
<td>82.2 ± 1.6</td>
</tr>
<tr>
<td>4</td>
<td>445.821</td>
<td>5.4</td>
<td>144.3 ± 3.3</td>
</tr>
<tr>
<td>5</td>
<td>438.319</td>
<td>6.0</td>
<td>167.7 ± 2.2</td>
</tr>
<tr>
<td>6</td>
<td>445.789</td>
<td>6.4</td>
<td>198.7 ± 3.2</td>
</tr>
<tr>
<td>7</td>
<td>317.336</td>
<td>6.6</td>
<td>205.7 ± 3.4</td>
</tr>
<tr>
<td>8</td>
<td>438.279</td>
<td>9.6</td>
<td>266.9 ± 6.5</td>
</tr>
<tr>
<td>9</td>
<td>416.845</td>
<td>10.0</td>
<td>280.0 ± 6.1</td>
</tr>
</tbody>
</table>
**ABA Levels in Reproductive Structures Early in Development**

To determine whether the levels of ABA in pods and/or seeds early in development were related to seed growth rate during the subsequent filling period, we measured ABA in reproductive structures from 6 to 22 DAA in 1983. Typically, the levels of ABA in pods were low (<1 μg g fresh weight⁻¹) and were not related to fresh weight accumulation in seeds early in development or to dry matter accumulation in seeds during the filling period (data not shown). Averaged across all genotypes, the level of ABA in pod tissue was highest at 6 DAA (0.75 μg g fresh weight⁻¹) and declined to 0.25 μg g fresh weight⁻¹ by 22 DAA. This is in agreement with Quebedeaux et al. (24), who found that ABA levels in pod wall tissue decreased from 10 to 20 DAA, but contrasts with the findings of Ackerson (1), who reported that ABA levels increased from 8 to 20 DAA.

Seeds were first removed for separate analysis at 14 DAA when the level of ABA was found to be <2.2 μg g fresh weight⁻¹ in all genotypes (Table II). Subsequently, ABA levels increased first in seed coats (18 DAA) and then in embryos (22 DAA, Table II).

**Sucrose Levels in Seed Tissues Early in Development**

Sucrose levels in seeds ranged from 2.0 to 9.6 mg g fresh weight⁻¹ at 14 DAA (Table II). The levels increased by 18 and 22 DAA, particularly in seed coats of some genotypes. However, sucrose levels in seed coats and embryos did not appear to be coupled with fresh weight accumulation early in development or the subsequent rate of dry matter accumulation during the linear filling period (Table II).

**ABA Levels in Seed Tissues during Linear Filling**

The levels of ABA in seed coats and embryos during the linear filling period in 1984 are shown in Figure 1. In all

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**Figure 1.** Endogenous levels of ABA (closed symbols) and sucrose (open symbols) in embryos (circles) and seed coats (triangles) of nine soybean genotypes. Rates of fresh weight (open bars) and dry weight (hatched bars) accumulation were calculated for each 5-d sampling period. Plants were grown in the field in 1983. ABA and sucrose data are the means of four samples. Pooled SE results for ABA levels in seed coats and embryos averaged 19 and 12% of the mean values, respectively. Pooled SE results for sucrose levels in seed coats and embryos averaged 9 and 7% of the mean values, respectively. SGR = Calculated seed growth rate (mg dry weight seed⁻¹ d⁻¹) throughout the entire linear seed filling period.
genotypes, ABA levels in seed coats and embryos were highest in the 25- to 30-DAA period and declined rapidly thereafter, a pattern similar to that previously reported for various soybean genotypes in different environments (1, 2, 24, 26). For all genotypes, maximum levels of ABA in seed coats were higher than in embryos, particularly in the intermediate- and large-seeded lines. Maximum levels of ABA in embryos were similar in all genotypes (Fig. 1). In contrast, genotypic differences in the maximum levels of ABA in seed coats were observed from 25 to 35 DAA with the highest levels (15–22 \( \mu g \) g fresh weight\(^{-1} \)) found in genotypes with intermediate seed growth rates (genotypes 4, 5, and 6).

### Sucrose Levels in Seed Tissues during Linear Filling

The levels of sucrose in seed coats and embryos sampled during the filling period in 1984 were lowest at 25 DAA and increased rapidly between 25 and 35 DAA (Fig. 1). For all genotypes, maximum levels of sucrose in embryos were higher than those in seed coats. Several distinctions in sucrose accumulation patterns were observed among the various genotypes. The increase in the level of sucrose in embryos of genotypes 1, 2, and 3 was relatively linear throughout the filling period. In most other genotypes, however, the level of sucrose in embryos increased more rapidly between 25 and 35 DAA and remained at relatively high levels. Thus, at least from 25 to 35 DAA, the levels of sucrose in embryos of the three small-seeded genotypes were lower than in the other genotypes.

### Concentration of Sucrose in the Apoplast

Short-term \textit{in vitro} sucrose uptake by isolated soybean embryos (21, 27) and long-term \textit{in vitro} seed growth rate (8) are directly related to the concentration of sucrose in the solution surrounding those tissues. This suggests that the sucrose concentration in the apoplast of seed coats and embryos \textit{in situ} may be higher in genotypes with rapid seed growth rates. Across all genotypes, the concentration of sucrose in the apoplast ranged from 4.4 to 28.4 mmol L\(^{-1} \) in seed coats and from 6.2 to 31.6 mmol L\(^{-1} \) in embryos (data not shown). These values are quite similar to those reported by Hsu \textit{et al}. (17) but much lower than those reported by Gifford and Thorne (14). There was no significant correlation, however, between apoplastic sucrose concentration and seed growth rate in this group of genotypes.

### Correlations among ABA, Sucrose, and Seed Growth Rate

For each sampling date the levels of ABA and sucrose in seed tissues of all genotypes were compared to dry matter accumulation rates during the linear seed filling period to determine whether significant correlations existed. At 14, 18, and 22 DAA, the level of ABA in embryos was negatively correlated (\( r = -0.67, -0.85, \) and \(-0.75, \) respectively; \( P < 0.05 \)) with dry matter accumulation rate. These correlations were due to an earlier accumulation of ABA in seed tissues of the small-seeded genotypes (Table II) rather than higher maximum ABA levels compared with the other genotypes (Fig. 1). During the linear filling period (25–50 DAA), ABA and sucrose levels (Fig. 1) generally were not significantly correlated with seed growth rate in this group of genotypes (data not shown). Similarly, the levels of sucrose and ABA in seed tissues were not significantly correlated with each other during the filling period.

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**Table II. ABA and Sucrose Levels in Seed Tissues of Nine Soybean Genotypes**

Seed growth rate is the rate of dry matter accumulation during the linear seed-filling period. Each data point represents the mean of four samples, with each sample consisting of tissues from eight to 40 seeds, depending upon genotype and stage of development.

<table>
<thead>
<tr>
<th>Genotype No.</th>
<th>Seed Growth Rate</th>
<th>ABA Level 14 DAA Seed</th>
<th>ABA Level 18 DAA Seed</th>
<th>ABA Level 22 DAA Seed</th>
<th>Sucrose Level 14 DAA Seed</th>
<th>Sucrose Level 18 DAA Seed</th>
<th>Sucrose Level 22 DAA Seed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mg dry wt seed(^{-1} ) d(^{-1} )</td>
<td>( \mu g ) fresh wt(^{-1} )</td>
<td>( mg ) g fresh wt(^{-1} )</td>
<td>( mg ) g fresh wt(^{-1} )</td>
<td>( mg ) g fresh wt(^{-1} )</td>
<td>( mg ) g fresh wt(^{-1} )</td>
<td>( mg ) g fresh wt(^{-1} )</td>
</tr>
<tr>
<td>1</td>
<td>2.5</td>
<td>0.8</td>
<td>4.0( ^{a} )</td>
<td>10.5</td>
<td>8.4</td>
<td>7.6</td>
<td>12.0( ^{a} )</td>
</tr>
<tr>
<td>2</td>
<td>2.7</td>
<td>2.1</td>
<td>7.7 4.6</td>
<td>13.3</td>
<td>10.3</td>
<td>8.5</td>
<td>19.8 9.2</td>
</tr>
<tr>
<td>3</td>
<td>3.2</td>
<td>1.3</td>
<td>10.6 7.2</td>
<td>8.3</td>
<td>16.2</td>
<td>9.6</td>
<td>9.3 11.2</td>
</tr>
<tr>
<td>4</td>
<td>5.4</td>
<td>1.0</td>
<td>15.2 4.4</td>
<td>11.9</td>
<td>10.8</td>
<td>3.7</td>
<td>17.5 10.3</td>
</tr>
<tr>
<td>5</td>
<td>6.0</td>
<td>1.1</td>
<td>7.9 2.1</td>
<td>12.4</td>
<td>9.4</td>
<td>3.9</td>
<td>7.9 10.0</td>
</tr>
<tr>
<td>6</td>
<td>6.4</td>
<td>0.5</td>
<td>4.8 1.6</td>
<td>9.6 6.5</td>
<td>3.0</td>
<td>7.9 10.0</td>
<td>30.0 10.2</td>
</tr>
<tr>
<td>7</td>
<td>6.6</td>
<td>0.7</td>
<td>2.8 0.7</td>
<td>8.8 4.8</td>
<td>3.4</td>
<td>11.4 12.9</td>
<td>9.5 11.5</td>
</tr>
<tr>
<td>8</td>
<td>9.6</td>
<td>0.7</td>
<td>3.8( ^{b} )</td>
<td>8.0 5.4</td>
<td>5.0</td>
<td>14.5( ^{b} )</td>
<td>11.2 9.5</td>
</tr>
<tr>
<td>9</td>
<td>10.0</td>
<td>0.4</td>
<td>1.5( ^{c} )</td>
<td>8.4 3.0</td>
<td>2.0</td>
<td>8.6( ^{b} )</td>
<td>8.0 9.5</td>
</tr>
<tr>
<td>Pooled SE</td>
<td>21</td>
<td>9 12 9 6</td>
<td>16 20 7 16 4</td>
<td>( % ) of grand mean</td>
<td>( % ) of grand mean</td>
<td>( % ) of grand mean</td>
<td>( % ) of grand mean</td>
</tr>
</tbody>
</table>

\( ^{a} \) SC, seed coat; \( ^{b} \) embryo; \( ^{c} \) Seeds were not dissected, represents whole seed.
Regulation of in Vitro Sucrose Uptake

To determine whether endogenous ABA and/or sucrose was correlated with assimilate movement into seeds of these diverse genotypes, in vitro sucrose uptake was measured at three times during the filling period in 1984. In agreement with our previous report (26), in vitro sucrose uptake rate of all genotypes was highest early in development, ranging from 1.2 to 3.4 μmol 100 mg dry weight⁻¹ h⁻¹ when measured at 25 DAA (data not shown). By 45 DAA, uptake rates had decreased >50% and ranged from 0.56 to 1.3 μmol 100 mg dry weight⁻¹ h⁻¹. At all three sampling dates, sucrose uptake per unit weight was inversely related to seed size. When the uptake data from all three dates and all genotypes were pooled, in vitro sucrose uptake was found to be negatively correlated with embryo dry weight and endogenous sucrose levels (Table III). Thus, as soybean embryos become larger and accumulate sucrose (Fig. 1), subsequent uptake of incoming sucrose is inhibited. High endogenous sucrose levels have also been shown to inhibit uptake of assimilates in sink tissues of other species including *Beta vulgaris* L. (30) and *Ricinus communis* L. (19).

In contrast, the endogenous level of ABA in embryos was positively correlated with in vitro sucrose uptake rate (r = 0.69), a finding similar to the previous report of Schussler et al. (26).

**DISCUSSION**

Exogenous ABA has been shown to stimulate assimilate unloading from seed coats (6, 25) and uptake of assimilates by embryos (15, 26), two processes that potentially limit the movement of assimilates to developing legume seeds (21, 27). We hypothesized that endogenous ABA may regulate solute transport into seeds and thus the concentration of assimilates available for seed growth. The levels of both ABA and sucrose were low in seed tissues early in development (Table II) and increased rapidly as seeds began to accumulate fresh weight and expand (Table II, Fig. 1). Thus, ABA and sucrose accumulation occurred simultaneously early in seed development. In contrast, from 30 DAA to maturity, ABA levels declined and sucrose levels generally increased (embryos) or remained constant (seed coats) (Fig. 1), suggesting that levels of ABA and sucrose in seed tissues were not closely coupled. These distinct patterns of ABA and sucrose accumulation may have resulted from temporal differences in the supplies of ABA and sucrose delivered to the seed or, alternatively, from different rates of metabolism by the seeds as they matured.

The intermediate- and large-seeded genotypes (4–9) exhibited bursts of fresh weight accumulation during the first half of the filling period, whereas the small-seeded genotypes accumulated fresh weight at a more constant rate throughout filling (Fig. 1). Because dry matter accumulation was relatively constant, these differences must be attributed to water uptake by the seeds. Previous reports have shown a close association between the rate of water uptake by the seed and the rate of dry matter accumulation (9, 10). The higher concentrations of sucrose in embryos of the intermediate- and large-seeded genotypes from 25 to 35 DAA may have enhanced cotyledon expansion by providing the osmotic driving force required for water uptake. Walbot (28) suggested that an elevated level of endogenous ABA in young stage embryos enhances both solute and water uptake, preventing precocious germination while allowing accumulation of the nutrient reserves required for germination. This hypothesis would seem to be correct in the intermediate- and large-seeded genotypes in which the peak in ABA coincided with the periods of most rapid water and sucrose accumulation (Fig. 1). In the small-seeded genotypes, however, ABA levels in embryos early in development were similar to those found in the other genotypes, even though the accumulation of sucrose and water was less rapid. This suggests that factors other than ABA were responsible for the reduced seed growth rate of these genetically diverse genotypes. For example, genotypes with low seed growth rates have fewer cells in the cotyledons (8, 16). This limitation in potential sink size may have precluded any influence of endogenous ABA levels on seed growth rate in these genotypes. Unfortunately, there is always a possibility of such interactions when genetically diverse materials are compared.

Using an alternative approach, Quarrie et al. (23) compared endogenous ABA to seed growth rate in genetically similar wheat genotypes selected for differences in seed size and ABA content. Although these two wheat lines differed 50% in seed growth rate and final seed size, no differences in ABA levels were evident during the filling period. Maximum ABA levels in wheat (23), however, are approximately 100-fold lower than the levels observed in soybeans, suggesting alternative functions for ABA in seed growth of that species as compared to soybeans. Developing near-isogenic lines with differences in seed growth rate or ABA level will be necessary to more critically evaluate the role of endogenous ABA in regulating seed growth in soybeans.

Generally, the levels of sucrose in embryos of the genotypes with intermediate seed growth rates (genotypes 4, 5, and 6) were higher than those in the genotypes with the lowest seed growth rates (genotypes 1, 2, and 3; Fig. 1). The concentrations of sucrose in the genotypes with the highest seed growth rates, however, were similar to those in the intermediate genotypes. Thus, whereas sucrose levels were low in the small-seeded genotypes, seed growth rate of the large-seeded genotypes did not appear to be limited by the concentration of sucrose in seed tissues. These results agree with those of Fader and Koehler (11) who reported that the concentration of carbohydrate pools remained constant in seeds with medium and high seed growth rates, and sucrose pools were low only in seeds with growth rates <4 mg seed⁻¹ d⁻¹. They concluded

**Table III. Correlations among in Vitro Sucrose Uptake, Embryo Dry Weight, and Endogenous ABA and Sucrose Levels**

<table>
<thead>
<tr>
<th>In Vitro Sucrose Uptake (μmol 100 mg dry wt⁻¹ h⁻¹)</th>
<th>Correlation Coefficient*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Versus</td>
<td></td>
</tr>
<tr>
<td>Embryo dry wt</td>
<td>-0.76</td>
</tr>
<tr>
<td>Sucrose level in embryo</td>
<td>-0.86</td>
</tr>
<tr>
<td>ABA level in embryo</td>
<td>0.69</td>
</tr>
</tbody>
</table>

*Correlation significant at P < 0.01.
that high seed growth rates are supported by a rapid flux of sucrose through the sucrose pools in the seeds rather than by a higher concentration in those pools.

The lack of any correlation between the concentration of sucrose in the apoplast of seed tissues and seed growth rate in these soybean genotypes is in agreement with the report of Fischer and Gifford (12) who found no cause and effect relationship between sucrose concentration in the endosperm cavity sap of wheat and seed growth rate. Likewise, Westgate et al. (29) found that 50% reductions in apoplastic sucrose concentrations in water-deficient soybeans did not decrease seed growth rate.

During the filling period, the level of endogenous ABA in embryos was positively correlated with in vitro sucrose uptake rates (Table III), a finding similar to our previous report (26). This correlation was determined in large part, however, by the fact that ABA levels in all genotypes were highest early in filling and decreased during the remainder of the filling period (Fig. 1), concomitantly with the decrease in sucrose uptake associated with dry matter accumulation and increased sucrose concentrations in the embryos (Table III). Thus, no cause and effect relationship between ABA levels and the rate of sucrose uptake by isolated embryos may be inferred from this data. Future evaluations of the effect of endogenous ABA on sucrose uptake must be conducted by altering ABA levels in seeds having similar embryo dry weight and endogenous sucrose levels. This may be addressed by a genetic approach (near-isogenic lines) or, alternatively, by imposing environmental treatments designed to alter ABA levels in developing seeds of a single genotype (22, 29).

In summary, the level of endogenous ABA in reproductive tissues was generally not correlated with the level of sucrose in those tissues or with the rate of dry matter accumulation in the seeds. Rather, there was a ubiquitous accumulation of ABA early in development which coincided with water uptake, sucrose accumulation, and the rapid expansion of cotyledons. Whole tissue sucrose levels in seed tissues, as well as apoplastic concentrations of sucrose, were not significantly correlated with the rate of dry matter accumulation of seeds. Taken together, these data suggest that, in this set of diverse soybean genotypes, seed growth rate was not limited by endogenous concentrations of ABA or sucrose in reproductive tissues.

LITERATURE CITED


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