Plant Physiol. (1989) 91, 980–985
0032-0889/89/91/0980/06/$01.00/0

Received for publication March 30, 1989
and in revised form July 14, 1989

Effect of Water Deficits on Seed Development in Soybean[1]

II. Conservation of Seed Growth Rate

Mark E. Westgate*, J. R. Schussler, D. C. Reicosky, and M. L. Brenner

U.S. Department of Agriculture-Agricultural Research Service-MWA, North Central Soil Conservation Research Laboratory, Morris, Minnesota 56267 (M.E.W., J.R.S., D.C.R.); *and University of Minnesota, St. Paul, Minnesota 54108* (M.L.B.)

ABSTRACT

Water deficits during seed filling decrease seed size in soybean (*Glycine max* L.). This may result from a reduction in the supply of assimilates from the maternal plant and/or an inhibition of seed metabolism. To determine whether maternal or zygotic factors limited seed growth, we examined the effects of a plant water deficit on the supply of sucrose to and its utilization by developing embryos. Plants were grown in the greenhouse, and water deficits were imposed by withholding water for a period of 6 days during linear seed fill. When water was withheld, leaf water potential decreased rapidly, inhibiting canopy photosynthesis completely within 3 days. However, seed dry weight (nodes 7–11) continued to increase at or near the control rate. The level of total extractable carbohydrates in leaf, stem, and pericarp tissue decreased by 70, 50, and 45%, respectively, indicating that reserves were mobilized to support seed growth. Cotyledon sucrose content decreased from about 60 milligrams per gram dry weight to 30 milligrams per gram dry weight. Similarly, the concentration of sucrose in the interfacial apoplast of the cotyledons decreased from approximately 100 millimolar to 50 millimolar. However, the rate of sucrose accumulation by excised embryos, measured in a short-term *in vitro* assay, increased in response to the water deficit. These results indicate that both source and sink activity in soybean are altered by water deficits to maintain the flux of assimilates to the developing embryos. This may explain why seed growth is maintained, albeit for a shorter duration, when soybean is exposed to water deficits during the seed filling period.

Water deficits during seed filling decrease seed size in soybean (*Glycine max* L.) (9, 20, 21). Recent evidence indicates that the reduction in seed size is due primarily to a shortening of the filling period rather than an inhibition of seed growth rate (12, 18). Since seed growth is dependent upon the supply of assimilates from the maternal plant (source activity) as well as the demand for assimilates within the zygotic tissue (sink activity), both maternal and zygotic factors may contribute to the maintenance of seed growth in water-deficient plants.

Normally, concurrent photosynthesis is the predominant source of photoassimilates for seed growth (3, 30). When photosynthesis is inhibited during seed fill, reserves in the maternal tissues can be mobilized to maintain assimilate supply to the seed (5, 12, 27). Whether this alternate source of assimilates represents a limitation to seed development under dry conditions is uncertain. However, seed growth has been shown to continue in water-deficient plants until reserves are nearly depleted (27).

We observed that the water status (Ψ_w, Ψ_s, and turgor)[2] of soybean embryos was buffered from low Ψ_w that developed in the maternal tissue (28). This finding, coupled with continued seed growth under dry conditions (12, 18) suggests that sink activity may not be inhibited by water deficits during the seed filling period. Schussler (18) recently reported that several cycles of water deficit increased the rate of sucrose accumulation by excised embryos relative to the controls. Whether such a shift in sink activity could contribute to the maintenance of seed growth in water-deficient plants is not known.

To determine whether source or sink activity might limit seed growth at low Ψ_w, we made simultaneous measurements on maternal and zygotic tissues of plants experiencing a severe water deficit during linear seed fill. The effects of low Ψ_w on source activity were assessed by measuring leaf Ψ_w, canopy photosynthesis, and reserve carbohydrate status. The effects of this treatment on sink activity were assessed by measuring seed growth rate, cotyledon sucrose content, apoplast sucrose concentration, and rate of sucrose accumulation by excised embryos. It was hypothesized that a rapid depletion of sucrose in and around the embryos would indicate a source limitation, whereas a reduction in sucrose uptake would implicate a sink limitation.

MATERIALS AND METHODS

Culture Conditions

Soybeans (*Glycine max* L. cv Evans) were grown in a greenhouse in soil mix as previously described (28), receiving adequate water and nutrients throughout vegetative and early reproductive growth. Under these conditions, plants typically set at least 80 fruits. At anthesis (node 7), 27 plants (3 in each of nine pots) were selected at random to receive the water-

[1] Contribution of the USDA-Agricultural Research Service, North Central Soil Conservation Research Laboratory, in cooperation with the University of Minnesota West Central Experiment Station, Journal Series No. 16,974.

[2] Abbreviations: Ψ_w, water potential; Ψ_s, osmotic potential; CER, carbon exchange rate; TEC, total extractable carbohydrates; BTP, 1,3-bis-tris-(hydroxymethyl)methylamino propane; CI, confidence interval; Mes, 2-(*N*-morphonina)-ethanesulfonic acid.

deficit treatment; an additional 27 plants were selected to serve as controls. Control and treatment pots were arranged randomly and rotated weekly to minimize shading effects. On 0, 3, and 6 d after water was withheld, three pots were selected from each group for analysis. Plants were sampled only once to avoid potential compensation effects due to removal of fruits and leaves.

Water Deficit Treatments

Water deficits were imposed for 6 d during the linear filling period (approximately 30 d after anthesis) by withholding water from the soil. The progress of the water deficit was monitored by measuring leaf Ψ_w using a pressure chamber (Soil Moisture, Santa Barbara, CA)[3] as previously described (28). Leaves were collected between 1200 and 1400 h after measuring canopy photosynthesis.

Canopy Photosynthesis

Apparent net photosynthesis (CER) was measured *in situ* by CO_2 depletion on a canopy of nine plants placed in a transparent Lexan (General Electric, Inc.) chamber (area: 0.593 m^2, vol: 808.2 L, air circulation: 76 L s^{-1}) similar to that described by Reicosky and Peters (17). Ambient light was supplemented with two HID sodium vapor lamps providing a total of 850 to 1300 $\mu Em^{-2}\ s^{-1}$ (PAR) at canopy level during the CER measurement. Chamber air was delivered at 0.033 L s^{-1} to a Binos (model Bin 4.2T, Leybold-Heraeus Co.) infrared gas analyzer operating in the differential mode using ambient air as a reference (approximately 360 $\mu L\ L^{-1}$ CO_2). Data were collected by an HP85A computer controlling an HP3054A data acquisition unit (Hewlett-Packard, St. Paul, MN). Upon chamber closure, measurements were made every 2 s for 60 s providing a typical ΔCO_2 of approximately 20 $\mu L\ L^{-1}$ for control plants. CER was calculated by linear regression on a 30 s measurement interval initiated after a lag time of 16 s. CER measurements were replicated four times on each sampling date. For estimates of CER on a leaf-area basis, canopy leaf area was determined directly on harvested plants using a LI-COR 3100 leaf area meter (LI-COR, Lincoln, NE).

In Vitro Sucrose Uptake

On each sampling date, approximately 30 three-seeded fruits (3 or 4 per plant) were collected from nodes 7 to 11 of plants in each treatment group, placed immediately in an air-tight plastic bag, and transferred to a humid chamber (maintained at saturating vapor pressure) in the laboratory. All subsequent dissections and tissue manipulations were performed within this humid chamber. Nine fruits were visually selected as most representative of each sample and used for sucrose uptake measurements. The remaining fruits were used for water status measurements (28) or sucrose analysis (see below). Two seeds were selected from each fruit, and testa were surgically removed. The paired embryos were incubated in 50 mL of either 20 or 200 mM sucrose buffered with 5 mM Mes (adjusted to pH 5.5 with BTP) containing approximately 1 μCi[U-^{14}C]sucrose (specific activity 5000 dpm μmol^{-1}) for 1 h in a gyrating water bath at 25°C and 170 rpm. After incubation, embryos were sequentially rinsed for 4 and 3 min in nonlabeled incubation media at 4°C to remove free-space label, frozen on dry ice, and freeze-dried. Total ^{14}C taken up by the embryos was recovered by oxidation in a Packard Tri-Carb oxidizer (90–95% recovery) and measured by liquid scintillation spectroscopy on a Beckman LS3801 (counting efficiency 70–90%). Data are expressed on a dry weight basis, determined on the freeze-dried embryos prior to oxidation.

Apoplast Sucrose Concentration

The concentration of sucrose in the interfacial apoplast surrounding the cotyledons was estimated using the null-balance technique of Gifford and Thorne (7). On each sampling date, 25 embryos were isolated as described above. After surgical removal of the seed coat, one cotyledon from each embryo was immediately frozen on dry ice. The remaining paired cotyledon was incubated in one of five sucrose solutions (50–250 mM sucrose, pH 5.5) for 2 h at 23.5°C. Five replicate cotyledons were incubated in each solution. After incubation, the cotyledons were rinsed for 10 s in ice-cold water, freeze-dried, and analyzed for total sucrose. Interfacial apoplastic sucrose concentration was calculated by linear regression analysis as the media concentration at which no change in endogenous sucrose content within the cotyledons occurred during incubation. Data are presented as the balance concentration ± 95% CI for the regression analysis.

Endogenous Sucrose Content

Freeze-dried cotyledons were rehydrated overnight in 80% ethanol at 4°C, then extracted 3 × 1.5 h in 80% ethanol at 70°C. The combined extracts were reduced to dryness and redissolved in a 4 mL H_2O. Total sucrose was determined using the NADH-linked enzymatic assay of Birnberg and Brenner (1). Data are presented as the mean ± SE of five replicates of five cotyledons each.

Carbohydrate Status

TEC were determined on 50 mg samples prepared and analyzed according to Westgate and Boyer (27). Each sample was analyzed in duplicate and data are represented as the mean ± SE of nine replicates.

RESULTS

Figure 1 shows that midday leaf Ψ_w varied from −0.7 to −1.1 MPa in control plants during this study. When water was withheld, leaf Ψ_w decreased rapidly, reaching −2.8 MPa within 3 d. Leaves at nodes 7 to 11 senesced as the water deficit progressed so that no leaf Ψ_w measurements were possible on day 6. Canopy CER of well-watered plants was about 25 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (Fig. 1B). This is equivalent to approximately 5.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ on a leaf area basis and is similar to rates measured in the field (3). CER followed the rapid decline in leaf Ψ_w and was completely inhibited by day 3. However, seed dry weight (nodes 7–11) continued to increase at or near the control rate despite low leaf Ψ_w and the

[3] Names of products are provided for the benefit of the reader and do not imply endorsement or preferential treatment by the USDA or the University of Minnesota.

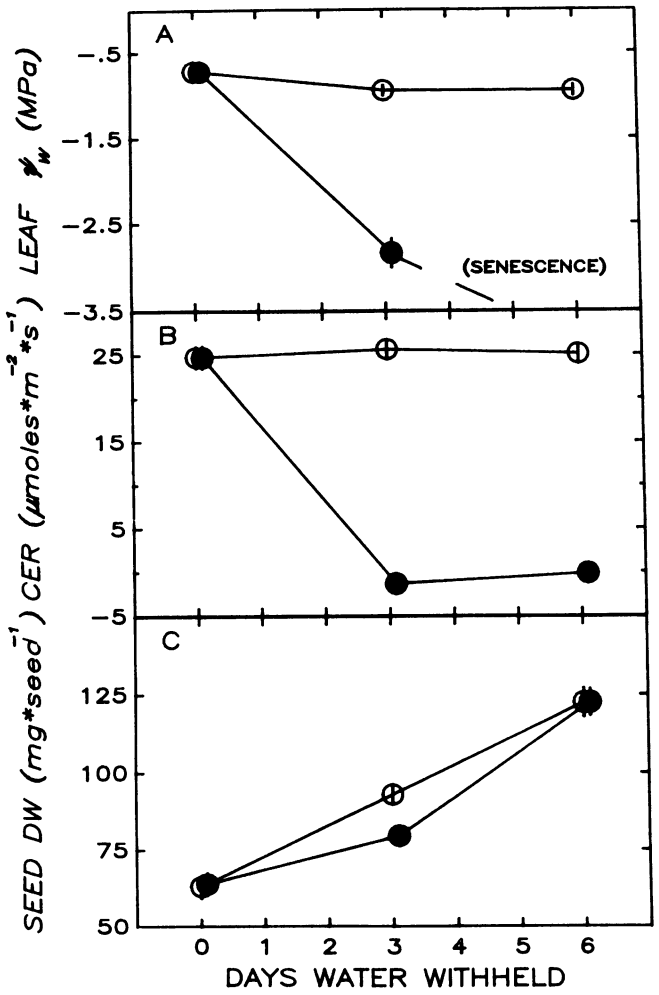

Figure 1. Leaf Ψ_w (A), canopy CER (B), and seed dry weight (C) of well-watered (open symbols) and water-deficient (closed symbols) plants. Leaves and seeds from nodes 7 to 11. CER expressed on a ground-area basis. Vertical bars indicate standard error of the mean.

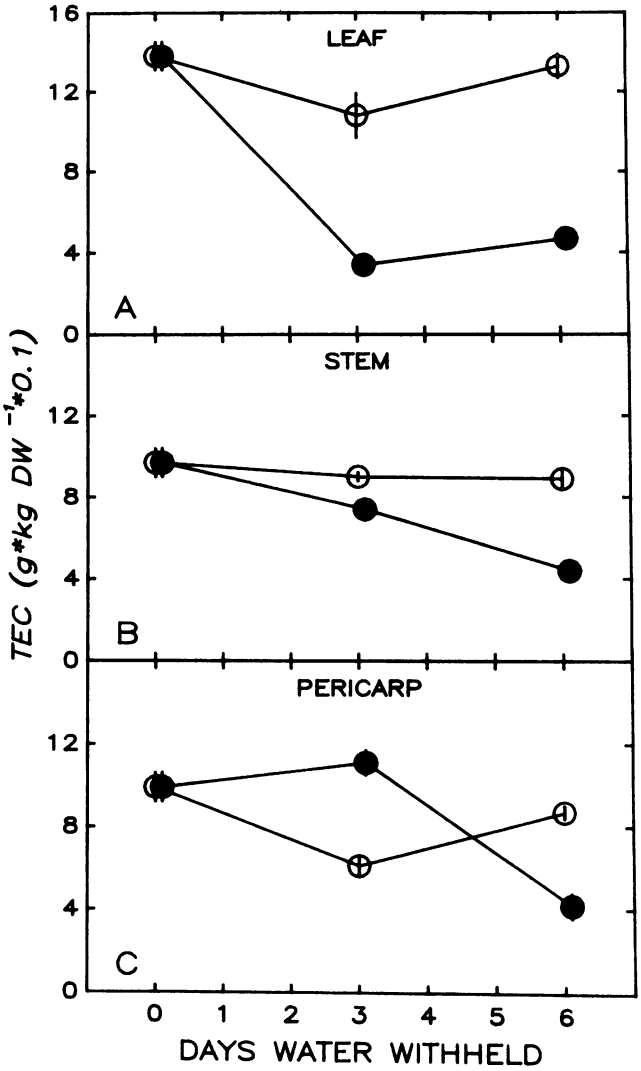

Figure 2. Total extractable carbohydrates in leaf (A), stem (B), and pericarp (C) tissue of well-watered (open symbols) and water deficient (closed symbols) plants. Data are the mean ± SE for nine plants.

complete inhibition of photosynthesis (Fig. 1C). Continued seed growth also has been observed in soybeans exposed to water deficits in both field (12; ME Westgate, unpublished data) and controlled environments (18).

The maintenance of seed growth in the absence of concurrent photosynthesis implied that reserves were mobilized from the maternal tissues at low Ψ_w. Figure 2 shows that, indeed, TEC in leaf, stem, and pericarp tissue decreased as the water deficit progressed. Reserves were mobilized rapidly from the leaves, and more slowly from the stems. Apparently, sugars accumulated temporarily in the pericarp but eventually were mobilized as TEC in leaf and stem tissue was depleted (Fig. 2). The pattern of mobilization in the water-deficient plants is similar to that observed in well-watered plants during the later stages of seed filling (4, 22).

Measurements of seed water status indicated that this short-term water deficit had little, if any, effect on seed Ψ_w, Ψ_s, or turgor (28). However, such measurements do not necessarily reflect net changes in assimilate supply or seed metabolism that might be caused by low Ψ_w in the maternal tissue. Since sucrose represents the predominant form of reduced carbon supplied to the seed (23, 24), we measured the level of endogenous sucrose in the cotyledon tissue and estimated the concentration of sucrose within the interfacial apoplast between the testa and cotyledon symplasm. Figure 3 shows that endogenous sucrose in the controls was about 60 to 70 mg·g dry weight^{-1} in agreement with previous estimates (7, 18). The water deficit caused nearly a 50% reduction in this level within 3 d (Fig. 3). Previous workers noted a decrease in sucrose of cotyledons from growth chamber plants in response to defoliation (7) or water deficits (18). However, Meckel *et al.* (12) observed a slight increase in the level of cotyledon sucrose (on a fresh weight basis) of plants exposed to water deficits in the field.

The concentration of sucrose in the apoplast of cotyledons from control plants was about 100 mM (Fig. 4), which is similar to previous estimates using the null-balance technique (7, 18). As with the endogenous levels of sucrose in the cotyledon, the water deficit caused a large reduction (about 50%) in the concentration of the sucrose in the apoplast (Fig.

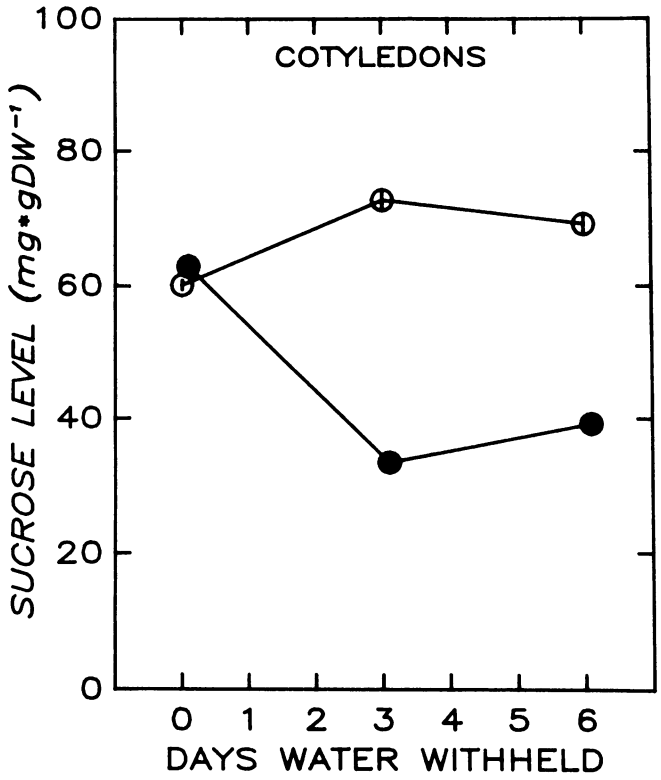

Figure 3. Endogenous sucrose in cotyledons from well-watered (open symbols) and water-deficient (closed symbols) plants. Data are the mean ± SE of five replicates of five cotyledons each.

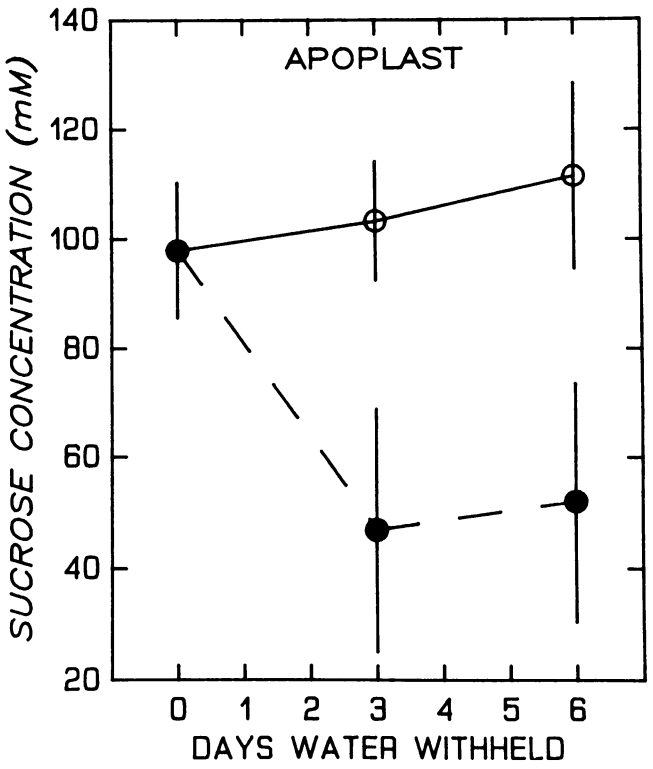

Figure 4. Concentration of sucrose in the interfacial apoplast of cotyledons from well-watered (open symbols) and water-deficient (closed symbols) plants. Concentrations were estimated using the null-balance technique described in "Materials and Methods." Data are presented as predicted values ± 95% CI for the regression analysis.

4). Thus, the water deficit had a dramatic effect on the steady state level of sucrose supplied to the outer layer of cotyledonary cells as well as the total pool of sucrose within the cotyledons.

An important component of assimilate transport to the developing seed is the rate at which sucrose supplied by the plant is taken up by the embryo. This has been described as sink sucrose mobilizing ability by Wyse and Saftner (29). In soybean, the uptake system has both a saturable and nonsaturable component, the former being the dominant mode of uptake below 25 mM sucrose in the apoplast (11, 25). Since water deficits might affect the saturable and nonsaturable components of sucrose uptake differently, embryos excised from the control and water-deficient plants were incubated in either 20 or 200 mM sucrose. Figure 5 shows that low plant Ψ_w did not reduce the rate of sucrose uptake at either concentration. Rather, the rate of sucrose accumulation via the saturable and nonsaturable component increased within the first 3 d after water was withheld (Fig. 5). A similar increase in the rate of sucrose uptake was reported by Schussler (18) for soybeans exposed to 1 to 3 cycles of water deficit.

DISCUSSION

In this study, we compared the relative effects of a short-term water deficit on assimilate supply to and assimilate uptake by developing seeds of soybean. Our results show that water deficits severe enough to completely inhibit photosynthesis decreased endogenous sucrose content and sucrose concentration in cotyledon apoplast by approximately 50%. However, seeds continued to accumulate dry matter at or near the control rate for at least 6 d. Reserve carbohydrates were mobilized at low Ψ_w from leaf, stem, and pericarp tissue to support continued seed growth. In addition, embryos from water-deficient plants exhibited an increased rate of sucrose uptake relative to their well-watered counterparts. These data indicate that both the maternal and zygotic tissues in soybean are affected directly by plant water deficits during linear filling. Both the mobilization of reserves from vegetative tissues and rapid uptake of assimilates by the reproductive tissues at low Ψ_w acted in concert to maintain seed growth. These results may explain why seed growth rate is conserved in soybean under adverse environmental conditions (5, 12, 18).

Westgate and Thomson Grant (28) observed that the water status of soybean seeds was largely unaffected by severe water deficits that develop in the maternal plant. The maintenance of a favorable water status within the developing embryos may be an important prerequisite for continued seed growth observed here and by others investigating the effects of water deficits on seed growth (2, 10, 15).

Seed growth rate in the water-deficient plants was similar to the controls despite a 50% reduction in the level of sucrose in the cotyledons (Fig. 3). The continued accumulation of dry matter observed here suggests that seed growth rate may not be tightly coupled to the level of sucrose in the cotyledons. If metabolism were saturated for sucrose, large changes in concentration could occur without affecting growth rate. A sim-

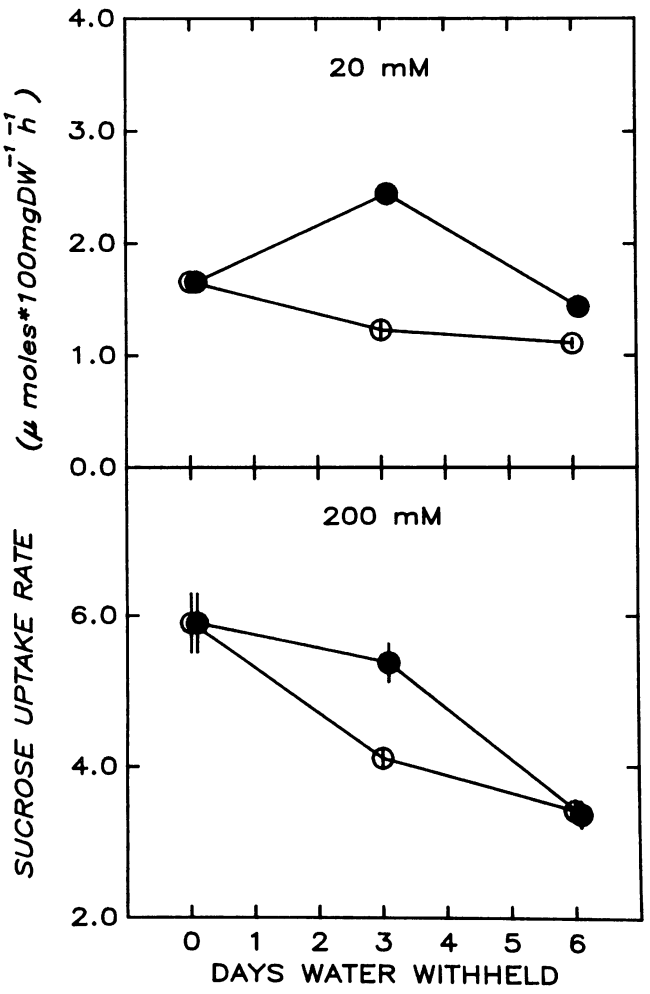

Figure 5. *In vitro* sucrose uptake embryos sampled from well-watered (open symbols) or water-deficient (closed symbols) plants during linear seed fill. Embryos were incubated in 20 mM (A) or 200 mM (B) sucrose, 5 mM MeS (pH 5.5) for 1 h at 25°C and 170 rpm. Data are the mean ± SE of nine embryos.

ilar conclusion was reached by Fader and Koller (6), who observed that seed growth rate was independent of cotyledon sucrose concentration at growth rates above 4 mg d^{-1}. Seeds examined in this study were growing at approximately 10 mg·day^{-1} (Fig. 1C).

The concentration of sucrose in the interfacial apoplast, as estimated using the null-balanced technique, also decreased about 50% in response to the water deficit (Fig. 4). Since the concentration in the apoplast is determined both by the rate of assimilate supply and utilization, the observed decrease suggests that reserve assimilates mobilized from leaf, stem, and pericarp tissue (Fig. 2) may be supplied more slowly than concurrent photosynthate. Alternatively, the higher rates of sucrose uptake by embryos from water-deficient plants (Fig. 5) at low sucrose concentrations in the apoplast (Fig. 4) may have depleted the apoplastic pool of sucrose until a new steady state level was attained, again reflecting the balance between assimilate supply and demand. In either case, the similarity in seed growth rate between control and water-deficient seeds despite the large change in apoplast sucrose concentration indicates that the magnitude of the sucrose pool in the apoplast is not a reliable indicator of assimilate flux to the developing seed.

It is significant that rate of *in vitro* sucrose uptake of excised embryos was altered by the water deficit. In the controls, the rate of sucrose uptake at 20 mM sucrose would be equivalent to a dry weight gain of 3 to 5 mg d^{-1}, assuming 5 mg dry weight d^{-1} lost to respiration (8, 13). At 200 mM, the equivalent weight gain would have been about 17 mg d^{-1}. These estimates suggest that an apoplast concentration of about 80 to 100 mM sucrose would be sufficient to support the measured growth rate of 10 mg d^{-1} in agreement with our estimates (Fig. 4) and previous reports (18). Embryos from water-deficient plants accumulated sucrose nearly twice as fast as the controls when supplied with 20 mM sucrose (d 3, Fig. 5). Again, assuming similar respiratory losses, this would translate to a dry weight gain of about 9 to 11 mg d^{-1}, approximately that observed for embryos sampled from the water-deficient plants. Apparently, the decrease in apoplast sucrose concentration from 100 to 50 mM within the first 3 d after water was withheld (Fig. 4) had little effect on seed growth rate because the embryos continued to accumulate sucrose rapidly even at the lower apoplast concentrations. Seed dry weight continued to increase at or near the control rate through d 6 despite a return of sucrose uptake rates to control levels (Fig. 4). This continued growth may reflect, in part, the rapid accumulation of N compounds mobilized from senescing leaves. Ver Nooy *et al.* (26) reported an enhanced capacity for uptake of amino acids late in cotyledon development, which would serve to maintain the accumulation of C and N compounds as well as dry weight beyond the cessation of sucrose import.

These results indicate that the rate of assimilate uptake by developing embryos is not a static process but can be altered by environmental conditions. At present, the specific effector(s) is (are) not known. However, the rate of sucrose uptake can be increased by ABA (19), lower cotyledon sucrose levels (18), and osmotica (S Stombaugh, ML Brenner, unpublished data). Our measurements of seed water status (28) indicate that no significant change in the osmotic environment occurred in seeds of the water-deficient plants. However, the lower levels of cotyledon sucrose (Fig. 3) could have contributed to the increase in uptake rate observed here. ABA was not measured in this study. However, Schussler (18) observed that water deficits can increase the level of ABA in embryos and testa of soybean by as much as 120%. He proposed that under water stress, ABA is rapidly synthesized in the leaves and transported to the filling seeds, increasing endogenous levels. The increased ABA could improve the sucrose mobilizing ability (29) of the seed by enhancing sucrose unloading from testa (14, 16) or sucrose uptake by the embryos (19). It is important to point out that the response observed was variable, depending on genotype, developmental stage, and environmental conditions. Higher levels of endogenous ABA were associated with an increase in the rate of sucrose uptake by the saturable component (at 10 mM sucrose), but this response also was variable. In some cases, uptake was inversely related to sucrose concentration in the cotyledons; in other cases, uptake was responsive to ABA. In preliminary studies (data not shown), we observed only a modest increase in uptake rate in response to water-deficit treatments in seeds

having low growth rates of about 4 mg d^{-1}. Thus, while it has been possible to demonstrate that sucrose uptake by soybean embryos can be altered by water deficits, the physiological basis for this response must await further investigation. Whatever the cause, an elevated rate of uptake would serve to maintain the flux of assimilates to the cotyledonary cells when concentrations in the apoplast are diminished.

In well-watered plants, estimates of interfacial apoplast sucrose concentration between 35 and 150 mM (7, 11, 18) have led most investigators to conclude that nonsaturable uptake is the physiologically relevant component of the system. However, our measurements indicate that sucrose uptake via the saturable component (20 mM sucrose) was nearly sufficient to account for the observed growth rate of water-deficient embryos. This suggests that the saturable component of sucrose uptake could be more important in maintaining embryo growth rate than previously assumed (7, 11). A similar phenomenon also may occur near the center of the cotyledon where apoplast concentrations of sucrose could be well below that estimated for the interfacial apoplast.

It seems unlikely that seed growth in the water-deficient plants would have continued much beyond the time course of this experiment. Reserves were mobilized rapidly and soon would have been depleted in the absence of concurrent photosynthesis (Fig. 2). Also, the increase in sucrose uptake rate appeared to be a transient phenomenon returning to near the control rate by d 6 (Fig. 5). Taken together, these observations suggest that a shorter filling period due to water deficits reflects primarily the premature demise of source activity. Apparently, this demise can be compensated for only temporarily by altered sink activity. Thus, while seed growth rate is maintained, it may occur only at the expense of the duration of seed fill.

ACKNOWLEDGMENTS

The authors gratefully acknowledge the technical assistance of S. W. Wagner, L. Staples, and D. Thomson Grant.

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