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Effect of Plant Hormones on Sucrose Uptake by Sugar Beet Root Tissue Discs[1]

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ABSTRACT

Abscisic acid (ABA), auxins, cytokinins, gibberellic acid, alone or in combination were tested for their effects on short-term sucrose uptake in sugar beet (*Beta vulgaris* cv USH-20) roots. The effect of ABA on active sucrose uptake varied from no effect to the more generally observed 1.4- to 3.0-fold stimulation. A racemic mixture of ABA and its *trans* isomer were more stimulatory than ABA alone. Pretreating and/or simultaneously treating the tissue with K^+ or IAA prevented the ABA response while cytokinins and gibberellic acid did not. While the variable sensitivities of beet root to ABA may somehow be related to the auxin and alkali cation status of the tissue, tissue sensitivity to ABA was not correlated with ABA uptake, accumulation, or metabolic patterns. In contrast to ABA, indoleacetic acid (IAA) and other auxins strongly inhibited active sucrose uptake in beet roots. Cytokinins enhanced the auxin-induced inhibition of sucrose uptake but ABA and gibberellic acid did not modify or counteract the auxin effect. *Trans*-zeatin, benzyladenine, kinetin, and gibberellins had no effect on active sucrose uptake. None of the hormones or hormone mixtures tested had any significant effect on passive sucrose uptake. The effects of IAA and ABA on sucrose uptake were detectable within 1 h suggesting a rather close relationship between the physiological activities of IAA and ABA and the operation of the active transport system.

Phytohormones play an important role in the transport and allocation of photosynthates (see references 7, 13, 17, and references therein). While the mechanism for this so-called hormone-directed transport remains obscure, the effects of phytohormones on photosynthate transport have tentatively been dissociated from hormone-induced growth (15), senescence-delaying and transpirational effects (16 and references therein). Additionally, hormone-directed photosynthate transport studies have been conducted over time periods where the hormonal effect on transport is greater than the hormonal influences on growth, respiration, senescence, and/or other possible rate-limiting physiological processes. Relying on the differential effects of phytohormones on photosynthate transport and other physiological, rate-limiting processes, it has been suggested that phytohormones may directly affect phloem loading (9, 10, 25), translocation (9, 14, and references therein), and sugar uptake by sink tissues (8, 12, 15, 23). All major classes of phytohormones have been shown to influence photosynthate transport and combinations of phytohormones can have additive, synergistic, or inhibitory effects (7 and references therein). The available evidence implicating hormone-directed transport is still tentative due to the multitude of hormonal effects in plant tissue, but is nevertheless sufficient to justify further research.

In sugar beet, large quantities of photosynthate (sucrose) are translocated and stored in the vacuole of parenchymal cells in the root sink without hydrolysis (26). In this paper, we report the effects of auxins, ABA, gibberellins, cytokinins, and their interactions on short-term membrane transport of sucrose into root discs of sugar beet.

MATERIALS AND METHODS

Preparation of Plants. Seeds of *Beta vulgaris* L. (sugar beet) cv USH-20 were obtained from Dr. Gerald Coe, USDA sugar beet breeder, Beltsville, Maryland. Cultivar USH-20 were grown both in the field and in the greenhouse as previously described (18). Individual plants between 3 and 7 months old were harvested on the morning experiments were conducted. While sucrose uptake patterns were similar in the root sink tissue of greenhouse and field-grown sugar beets, active sucrose uptake rates were generally higher and less responsive to ABA and auxins in field-grown beets than in greenhouse-grown beets. Root tissue discs were prepared and then equilibrated in sorbitol solutions of appropriate osmolality for 90 min as previously described (18).

Sucrose Uptake Measurements. The procedure for measuring sucrose uptake rates was essentially the same as that previously described (18). Sets of 30 osmotically equilibrated discs were incubated for 4 h at room temperature and 3 ml of an aerated sucrose solution (40 mM sucrose, sufficient sorbitol to maintain osmolality of sucrose solutions uniform at 0.26 molal and 10 milliosmolal MOPS[2] adjusted to pH 6.5 with 1.0 M KOH) either with or without 5 μM CCCP. The specific radioactivity of the solutions was 23 nCi/μmol provided through appropriate dilution of uniformly labeled [^{14}C]sucrose (6.7 μCi/μmol). The specific radioactivity did not significantly change during the incubation period. At the end of the incubation, each set of discs was washed five times for 2 min each in 10 ml of 250 mM sorbitol to remove labeled sucrose from the cut cells at the surface and over 90% of the sucrose in the free space of the cell wall. Each set of discs was then prepared for liquid scintillation counting as previously described (19).

Sucrose uptake from sucrose solutions containing 5 μM CCCP is considered passive transport and may involve [^{14}C]sucrose

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[2] Abbreviations: MOPS: 3-(*N*-Morpholino) propanesulfonic acid; CCCP: Carbonyl cyanide *m*-chlorophenylhydrazone; KIDA: potassium iminodiacetic acid.

uptake in exchange for unlabeled tissue sucrose (18). In an operational but not necessarily rigorous sense, metabolically dependent or active sucrose uptake is calculated by subtracting passive sucrose uptake from total sucrose uptake in the absence of CCCP (18). All uptake experiments were run at least twice and the data analyzed using a factorial design. In some experiments, ABA or IAA uptake rates were determined in addition to sucrose uptake rates using a dual label counting procedure. In such cases, tritiated ABA or IAA (2.3 nCi/pmol for hormone solutions less than 10^{-5} M and 0.23 nCi/pmol for 10^{-5} M solutions) were added to the incubation medium.

Purification and HPLC Analysis of Tritiated IAA and ABA from Plant Tissue. One-gram samples of beet tissue incubated in sucrose uptake solution containing either tritiated IAA or ABA and subsequently rinsed with sorbitol as per sucrose uptake measurements were extracted and the IAA or ABA purified using the procedure of Shindy and Smith (21). The acidic ethyl acetate fraction containing the tritiated hormone was evaporated *in vacuo* to a small volume, stored at −25°C and then analyzed for tritiated IAA or ABA using HPLC and liquid scintillation counting within 1 d after extraction. The incubation solution containing tritiated IAA or ABA was purified in the same manner as the plant tissue.

The HPLC used included a Waters Model 6000A[3] pump and a U6K injector, coupled to a Model 730 data module and a Model 720 systems controller. A Beckman-Altex 5μ ODS ultrasphere column (4.6 mm × 25 cm) was guarded by a Beckman-Altex ODS precolumn. Solvent flow (55:45 for 0.2 N CH_3COOH:CH_3OH) was 1 ml min^{-1}. Aliquots of 1 ml fractions collected from the HPLC were prepared for liquid scintillation counting as previously described (19).

RESULTS AND DISCUSSION

Introductory Comments. During the 4-h tissue incubations with [^{14}C]sucrose performed as described above, the size of and the sucrose concentration in the metabolic and storage compartments of beet discs were not significantly altered (19). In addition, 80% ethanolic extracts of tissue discs incubated with [^{14}C]sucrose for 4 h showed that over 95% of the label was retained as sucrose (19). Since sucrose metabolism was relatively low in this tissue system, sucrose metabolism *per se*, as well as hormonal and CCCP-induced changes in sucrose metabolism, probably did not significantly interfere with the uptake kinetics. However, the rates given for sucrose uptake, particularly active sucrose uptake into the vacuole (19), must be considered relative until the influence of internal sucrose on the specific activity of sucrose at the site for uptake into the vacuole is established.

The use of the term 'active' to describe CCCP-inhibited transport is justified because this transport is against its chemical potential gradient, and is strongly or completely inhibited by anaerobiosis, ATPase inhibitors, and ionophores (see references 18 and 19 for specific details). Passive sucrose uptake is not affected by CCCP, ATPase inhibitors, or ionophores and results in no detectable accumulation of sucrose within beet discs. Additionally, CCCP does not cause a general perturbation of membrane integrity (19).

Effect of Auxins on Sucrose Uptake. Auxins affect both the direction and rate of photosynthate transport in intact plants and isolated plant materials (7, 13, 16, 22 and references therein). While the mechanism by which auxins mediate these effects are not understood, several studies (14, 22 and references therein) indicate that auxins rather directly affect membrane transport of sugars.

In sugar beet root discs concentrations of IAA above 10^{-8} M inhibited active sucrose uptake in a typical log dose-linear response manner but had no significant effect on passive sucrose uptake (Fig. 1). The lack of an IAA effect on passive sucrose transport indicates that IAA was not having a deleterious physical effect on membrane integrity. [^{3}H]IAA is rapidly taken into sugar beet tissue and the uptake rate was linear with IAA concentration (Fig. 1, inset). [^{3}H]IAA in the medium was verified by HPLC to remain as IAA during the incubation. The inhibitory effect of IAA on active sucrose uptake was always observed despite the rapid metabolism of the influxing IAA. More than 98% of the radioactivity recovered from extracts of [^{3}H]IAA-incubated tissue did not partition or coelute from HPLC columns with IAA. To what extent the IAA-induced change in sucrose transport in beet root discs is dependent upon the level of IAA within the tissue or within specific cellular compartments or upon IAA turnover rates and IAA metabolism in general is not known. Nevertheless, during the course of this study, a 10^{-6} M concentration of IAA inhibited active sucrose uptake 52% to 96%. Tissue incubations with IAA from 15 to 180 min all showed IAA inhibition of active sucrose uptake (Fig. 2A), the effect being significant within 1 h. The rapidity of the response indicates a rather close relationship between the physiological activities of IAA and the operation of the active transport system. Other auxins also inhibited active sucrose uptake with the presumed slowly metabolizing 2,4-D and the presumed rapidly penetrating ethyl ester of IAA being more effective than IAA itself (Table I). This inhibitory effect of auxins on active sucrose uptake is supported by findings of reduced photosynthate movement toward sites of IAA application in certain plant materials (see Reference 17 for details). However, auxins have also been reported to promote sucrose uptake in leaf tissue (10, 22) and sucrose transport through stem tissue (14). While the cause for the opposing effects of auxins on sucrose transport in various shoot tissues *versus* sugar beet root tissue is not understood, it is interesting to note that present evidence supports a proton/sucrose co-transport mechanism in shoot tissues (2) and a proton/sucrose antiport system in sugar beet root tissue (19). A better understanding of the formation and maintenance of electrochemical potential gradients for H^+ and other ions across the membrane(s) that actively transport sucrose and the effects of auxins thereon is needed for a better understanding of how auxins affect sucrose transport in sugar beet.

To gain insights into the physiological importance of auxin inhibition of active sucrose uptake, various substances were tested that might interact or otherwise modify auxin levels and/or activities within sugar beet tissues. The auxin antagonists, *p*-chlorophenoxyisobutyric acid (4), and 2,4,5,-trichlorophenoxypropionic acid (1) at concentrations of 10^{-4} M, stimulated active sucrose uptake 7% to 32%. When added at the same time as 10^{-6} M IAA, the auxin antagonists reduced the IAA-induced inhibition of active sucrose uptake by as much as 63%. Optimal concentrations of two substances known to stimulate active sucrose uptake in beet roots, 100 mM K^+ (19) and 10^{-5} M ABA (see below) were not able to overcome the inhibitory effect of 10^{-6} M IAA. High concentrations (10^{-5} M) of *trans*-zeatin, BA, and kinetin which do not significantly affect active sucrose uptake by themselves (see below), each increased the inhibitory effect of a suboptimal concentration (10^{-7} M) of IAA by at least 20%. Whether or not these cytokinins increase endogenous IAA levels and/or reduce auxin metabolism as has been reported for cytokinins in other plant materials (11, 20) is not known. Zeatin riboside, GA_3, and a mixture of GA_4 and GA_7 had no apparent effect on auxin-induced inhibitions of active sucrose uptake. Thus, auxin antagonists and cytokinins, but not ABA, GA's, or K^+ ions interact with the auxin/sucrose transport processes. The

[3] Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by the United States Department of Agriculture and does not imply its approval to the exclusion of other products which may also be available.

physiological basis of these interactions is not known.

ABA Effect on Sucrose Uptake. Numerous reports indicate that ABA affects the accumulation of sucrose and other assimilates in certain tissues (8–10, 23, and references therein). In sugar beet root discs, ABA stimulated active sucrose uptake in a log dose-linear response manner over the concentration range 10^{-8} to 10^{-5} M but had no significant effect on passive sucrose uptake (Fig. 3). The lack of an ABA effect on passive sucrose uptake indicates that ABA, like IAA, was not having a deleterious physical effect on membrane integrity. The optimal ABA concentration for stimulating active sucrose uptake was between 10^{-6} and 10^{-5} M. Higher concentrations were generally less stimulatory (Fig. 3). The ABA-enhanced active uptake was 1.4- to 3.0-fold of control. In 28% of the ABA experiments, ABA had no significant effect on active sucrose uptake. ABA stimulation of active sucrose uptake was significant in tissue incubations of 1 h and could be observed in incubations of even shorter durations (Fig. 2B). To our knowledge, this is the earliest observed effect of applied ABA on active transport of sucrose. The rapid effect of ABA on sucrose transport indicates a relatively close association between the physiological activities of ABA and the operation of the active transport system. ABA stimulation of

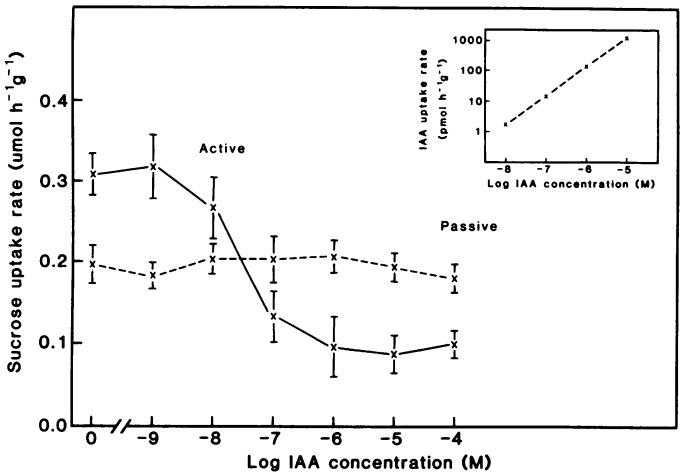

FIG. 1. Effect of indole-3-acetic acid on sucrose uptake in sugar beet root. Inset, indole-3-acetic acid uptake in sugar beet root during sucrose uptake studies in the absence of CCCP. Bars indicate three replications of a single experiment.

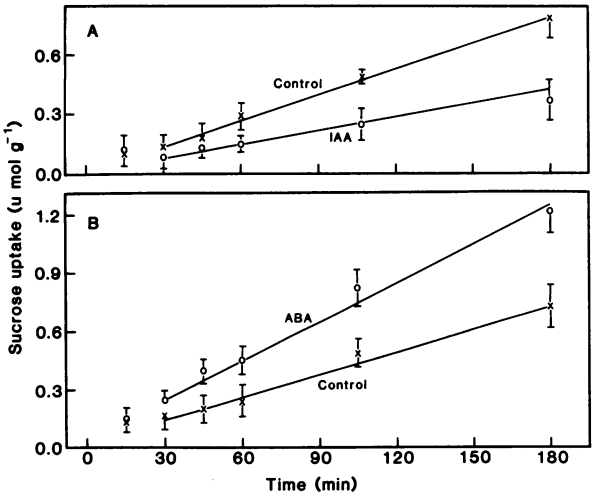

FIG. 2. Relationship between tissue incubation time and the effects of indole-3-acetic acid and abscisic acid on the active sucrose uptake rate in sugar beet root. Bars represent three replications of a single experiment.

Table I. *Effect of Auxins on Rate of Sucrose Uptake in Sugar Beet Roots*

Auxin Treatment (1.0 μM)	Sucrose Uptake		Inhibition of Active Uptake
	Active	Passive	
	nmol h⁻¹ g⁻¹		%
Control	322 ± 33	216 ± 16	
IAA	138 ± 35	221 ± 11	57
2,4-D	43 ± 13	226 ± 17	87
IAA—methyl ester	81 ± 29	225 ± 10	75

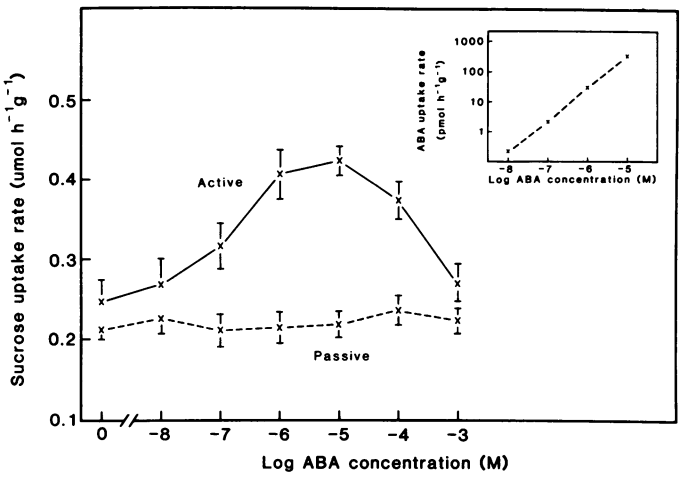

FIG. 3. Effect of abscisic acid on sucrose uptake in sugar beet root. Inset, abscisic acid uptake in sugar beet root during sucrose uptake studies in the absence of CCCP.

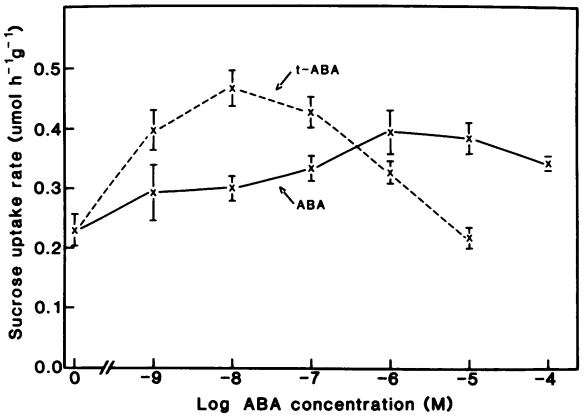

FIG. 4. Effect of abscisic acid and a racemic mixture of abscisic acid and its *trans* isomer on active sucrose uptake in sugar beet root. Bars indicate three replications of a single experiment.

Table II. *Effect of K⁺ on ABA-induced Stimulation of the Active Sucrose Uptake in Sugar Beet Tissue Discs*

The ABA treatment was 10^{-5} M ABA in basal uptake solution containing 200 mM sorbitol. K^+ treatments, with and without 10^{-5} ABA, had 100 mM KIDA in a basal uptake solution containing 20 mM sorbitol. The osmotic concentration of all solutions was about 260 milliosmolal.

K^+ Concentration	Active Sucrose Uptake Rate		ABA Effect
	−ABA	+ABA	
mM	*nmol h⁻¹ g⁻¹*		%
0	233 ± 30	430 ± 20	+84
100	479 ± 39	440 ± 33	0

Table III. *Effect of Various Hormones on ABA-induced Stimulation of the Active Sucrose Uptake Rate in Sugar Beet Root*

Hormone Addition (10^{-5} M)	Active Sucrose Uptake Rate	
	−ABA	+ABA (10^{-5} M)
	nmol h^{-1} g^{-1}	
None	341 ± 26	555 ± 33
IAA	73 ± 4	65 ± 9
trans-zeatin	333 ± 30	510 ± 40
BA	322 ± 31	539 ± 38
GA_3	326 ± 19	540 ± 25

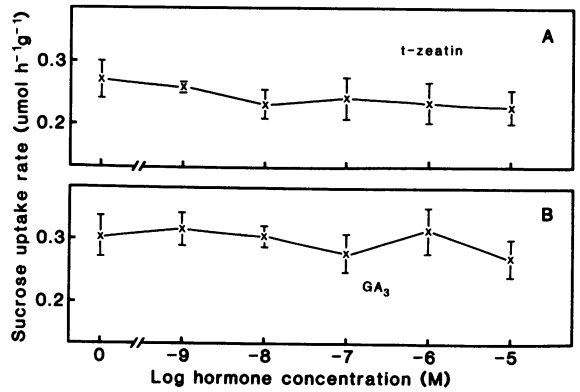

FIG. 5. Effect of gibberellic acid and *trans*-zeatin on active sucrose uptake in sugar beet root. Bars indicate three replications of a single experiment.

sucrose uptake may explain both the observed correlation between dry matter accumulation and endogenous ABA level in the sink region of a number of other angiosperms (6, 23, and references therein) and the ABA-enhanced assimilate transport to sink regions (6, 9, 23, and references therein).

Tissue Sensitivity to ABA; ABA Uptake, Accumulation, and Turnover. Experiments were conducted to better understand the erratic tissue response to ABA. Lowering the pH of the incubation solution from 6.5 to 6.0, a process which increases ABA uptake into the tissue (5), increased tissue sensitivity to ABA. However, increasing the external ABA concentration to 10^{-3} M, a process which also increases ABA uptake into the tissue (Fig. 3, inset) did not result in higher sucrose uptake rates. Apparently, lowering the external pH induces changes in cell physiology other than increasing ABA uptake which results in increased tissue sensitivity to ABA. ABA responsive and nonresponsive tissues exhibited similar rates of ABA uptake, indicating that tissue sensitivity to ABA is not related to the ABA uptake capacity of the tissue.

Despite the high uptake of ABA (Fig. 3, inset), less than 1% of the radioactivity recovered during extraction of [^{3}H]ABA-incubated tissue cochromatographed on HPLC with ABA, regardless of the degree to which the tissue was responsible to ABA. Small differences in net accumulation of ABA in tissues of varying sensitivity to ABA cannot be ruled out. However, Daie and Wyse (5) have shown that in sugar beet root tissue, exogenously applied ABA is quickly metabolized in what appears to be a 'detoxification' reaction since ABA uptake rates are directly correlated to rates of ABA-metabolite accumulation. The above information indicates that ABA stimulates active sucrose uptake in a tissue that does not accumulate ABA and which has a high capacity to metabolize exogenously supplied ABA.

Surprisingly, we found that a racemic mixture of ABA and its *trans* isomer stimulated active sucrose uptake to a greater degree and at lower concentrations than ABA alone (Fig. 4). While this finding was not further investigated, the presumably inactive *trans*-ABA might be gradually converted to its active *cis* isomer as has been observed in other plant material (3). Such a sequence of metabolic steps would provide a continuous intracellular supply of physiologically active ABA.

Tissue Sensitivity to ABA; K^+ ion Effect on ABA-Stimulated Sucrose Uptake. In an earlier investigation, we found that active sucrose uptake rates in sugar beet root discs could be increased 2- to 4-fold by treating the tissue with alkali cations and suggested a working model for sucrose uptake in beet roots involving an alkali cation/sucrose co-transport, H^+ antiport system (19). ABA is known to affect K^+ transport in other plant systems (24 and references therein). If alkali cations and ABA interact in the active sucrose uptake system in sugar beet root tissue, tissue sensitivity to ABA may be dependent, in part, upon the K^+ status of the tissue. Table II shows that an optimal concentration of K^+ stimulated active sucrose uptake to a slightly greater degree than an optimal concentration of ABA. The ABA and K^+ ion effects were neither synergistic nor additive. Table II also shows that ABA-responsive tissue could be made nonresponsive by treating the tissue with K^+. These results indicate that the alkali cation (K^+) status of the tissue could play a major role in the sensitivity of beet roots to ABA.

Tissue Sensitivity to ABA; Hormonal Effects on ABA-Stimulated Sucrose Uptake. ABA was tested by itself and in combination with t-zeatin, BA, IAA, and GA_3 for their effect on active sucrose uptake. Only 10^{-5} M IAA significantly modified the ABA-induced stimulation of active sucrose uptake (Table III). Cytokinins and GA had no effect on the ABA-enhanced sucrose uptake. Therefore, ABA may stimulate active sucrose uptake only in tissues having relatively low endogenous concentrations of auxins. High concentrations of endogenous ABA may also decrease tissue sensitivity to applied ABA. Tietz *et al.* (23) found that sucrose transport from flag leaves to ears in barley was stimulated by ABA applications to the ears, but only at growth stages in which endogenous ABA levels in the ears were relatively low. At present, the sensitivity of sugar beet root tissue to ABA appears to be a complex matter involving the alkali cation status, hormonal interactions within the tissue and probably other rate-modifying sucrose transport factors.

Cytokinin and Gibberellin Effects on Sucrose Uptake. Although not as intensively studied as ABA and auxins, a few reports (see references within 17) indicate that gibberellins and cytokinins directly influence photosynthate transport. Figure 5 shows that GA_3 and *trans*-zeatin between 10^{-9} and 10^{-5} M did not significantly affect active sucrose uptake. The slight inhibition by GA_3 and *trans*-zeatin were consistently observed but never exceeded 20%. BA and a mixture of GA_4 and GA_7 also inhibited active sucrose uptake. None of these hormones had a consistent or significant effect on passive sucrose uptake. Cytokinins and gibberellins are generally reported to interact with auxins to affect photosynthate transport (see reference 17 for details). While cytokinins were found to enhance the auxin effect on sucrose transport, no interactions between gibberellins and IAA could be found. However, all of our studies are rather short term in nature and intended to reveal only relatively close associations between the physiological activities of the hormone and the membrane transport of sucrose. While gibberellins may not affect short-term membrane transport of sucrose, GA_3 has been reported in long-term sucrose transport studies to stimulate hormone-directed photosynthate transport.

Concluding Comment. The control of assimilate allocation among competing sinks is not well understood but current research suggests factors regulating sink metabolism play a dominant role. Relevant sink metabolism involves phloem unloading, cell wall invertase activity, plasma membrane and tonoplast membrane transport, and conversion of assimilates to storage

products. These metabolic activities all influence the steepness of the osmotic gradient for sucrose within the phloem which is the factor controlling assimilate flux from source to sink (7). Although hormones have been implicated as potential regulators of sink activity, and thus of sink mobilizing ability, little direct evidence is available to explain their role. Our results suggest a relatively close association between the physiological activities of ABA and IAA on the transport of sucrose into sugar beet taproot tissue. However, the nature of the effect, whether exerted on the sucrose carrier, membrane potential, ΔpH, or physical characteristics of the membrane is still unclear.

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