Plant Cell Physiol. 27(5): 853–860 (1986)

Effect of Ethylene on Sucrose Uptake in Root Discs of Sugar Beet

Robert A. Saftner

United States Department of Agriculture, Agricultural Research Service, Plant Hormone Laboratory, Beltsville, Maryland 20705, U.S.A.

Exogenously-added ethylene stimulated active sucrose uptake in root discs of sugar beet (*Beta vulgaris* L.) in a log dose-linear response manner. The ethylene precursor, 1-aminocyclopropane-1-carboxylic acid (ACC) stimulated both endogenous ethylene production and sucrose uptake. Conversely, an inhibitor of ACC synthesis, aminoethoxyvinylglycine (AVG) inhibited both endogenous ethylene production and sucrose uptake. Exogenously-added ethylene can overcome the AVG effect on sucrose uptake. Root tissue from freshly-harvested sugar beet plants contain gas-phase ethylene levels slightly below that required to stimulate active sucrose uptake. No differences were found in gas-phase ethylene levels in the root tissue of sugar beet cultivars having different concentrations of sucrose. The root tissue has an inherent capacity to synthesize ACC and ethylene at high rates.

Like ethylene, propylene can stimulate active sucrose uptake in beet root discs, but it is not detected in the gas phase of the tissue. Acetylene, propane, and ethane had no effect on sucrose uptake. Exogenously-added IAA and ABA each make ethylene-sensitive tissue insensitive to ethylene stimulation of sucrose uptake. Other plant hormones have no apparent effect on the ethylene response. The role that ethylene may play on sucrose uptake in root tissue of sugar beet is discussed.

Key words: *Beta vulgaris* — Ethylene — Root (disc) — Sucrose uptake.

Phytohormones play an important role in the transport and allocation of photosynthates (Gifford and Evans 1981, Patrick 1976, Phillips 1975). It has been suggested that phytohormones affect phloem loading, interorgan transport, phloem unloading, and sink tissue accumulation of photosynthates (see Saftner and Wyse 1984). Of the major classes of phytohormones, ethylene has been studied the least for its ability to "direct" sugar transport even though ethylene or ethylene-releasing substances can alter sugar transport and accumulation patterns in a variety of plants (Abeles 1973, Hirai 1982, Veen and Kwakkenlos 1984). Furthermore, ethylene is very soluble in lipids (Eger and Larson 1964) and would partition into cell membranes (Abeles 1973). Exogenously-applied ethylene has been shown to increase membrane permeability in a variety of plants (Abeles 1973, Parups 1977). However, in a few plant systems, ethylene has no apparent effect on membrane permeability (Abeles 1973, Sacher and Salminen 1969). Ethylene certainly does not disrupt cell membranes (Lieberman et al. 1983). Despite all these observations, no one has specifically studied short-term effects of ethylene on photosynthate transport.

Abbreviations: ACC, 1-aminocyclopropane-1-carboxylic acid; AVG, 2-amino-4-(2 aminoethoxy)-*trans*-3-butenoic acid; MOPS, 3-(*N*-morpholino)propanesulfonic acid; CCCP, carbonyl cyanide *m*-chlorophenylhydrazone.

Recently, Saftner and Wyse (1984) showed that auxins inhibit and ABA stimulates active sucrose uptake in beet root discs i.e., the hormones alter the rate of sucrose uptake against its electrochemical potential gradient. They also showed that cytokinins enhance the auxin-induced inhibition of sucrose uptake but that neither cytokinins nor gibberellins alone have any noticeable effect on short-term sucrose uptake. In this paper, I report that exogenously-added ethylene stimulates active sucrose uptake in beet root discs.

Materials and Methods

Plant material and equilibration—Seeds of *Beta vulgaris* L. (sugar beet) cv. USH-20 were obtained from Dr. Gerald Coe, USDA sugar beet breeder Beltsville, Maryland while cvs. D2 and L53XL19 were obtained from Dr. Roger Wyse, USDA plant physiologist, Beltsville, Maryland. Cultivars USH-20 (moderate sucrose containing line), L53XL19 (experimental high sucrose line) and D2 (low sucrose line) were grown both in the field and in the greenhouse as previously described (Saftner et al. 1983). Cultivar L53XL19 and D2 plants were used only for endogenous gas-phase ethylene measurements. Individual plants of cultivar USH-20 between 4 and 8 months old were harvested between 8 and 9 AM on the morning that experiments were conducted. Root discs were prepared and then equilibrated for 180 min in aerated 250 mM sorbitol (pH 6.5) containing 1.0 mM $CaCl_2$ as previously described (Saftner et al. 1983). The solution was replaced after 15, 30, 60, 90, 120, and 150 min to remove from the tissue unidentified substances that inhibit sucrose uptake.

Sucrose uptake measurements—Sets of 30 equilibrated discs were submerged and incubated in 3.0 ml of a solution containing 40 mM sucrose, 200 mM sorbitol, 10 mM MOPS adjusted to pH 6.5 with 1.0 M KOH either with or without 10 μM CCCP and with or without various treatments being tested for their effect on sucrose uptake as indicated. Calcium did not affect sucrose transport and thus was not added to the sucrose uptake solution. The specific activity of the solution was about 25 nCi μmol^{-1} sucrose obtained by dilution of uniformly labelled [^{14}C]-sucrose (6.7 μCi μmol^{-1}). Unless otherwise stated, incubations were done at room temperature for 3 h during which time uptake remained linear. Humidified, hydrocarbon-purged air (Eastwell et al. 1978, method 2) with and without added hydrocarbons was passed through teflon tubings and bubbled through the sucrose uptake solution at a rate of about 20 ml/min. Besides supplying the hydrocarbons, this treatment also kept the tissue from becoming anaerobic. During the incubation, the specific activity of the sucrose in the incubation solution did not change. At the end of the incubation, each set of discs was washed five times for 2 min each with 9 ml of 250 mM sorbitol. This removed [^{14}C]-sucrose from the cut cells at the tissue surface and over 95% of the [^{14}C]-sucrose from within the free space of the cell wall (Saftner et al. 1983). Finally, each set of discs was prepared for liquid scintillation counting as previously described (Saftner and Wyse 1980).

Sucrose uptake from sucrose solutions containing 10 μM CCCP is considered passive uptake. It may represent an exchange between [^{14}C]-sucrose moving into the tissue and unlabelled endogenous sucrose moving out of the tissue. Certainly, CCCP affects sucrose uptake in the same way as does N_2 gassing of the root discs. Further, CCCP does not change the sucrose compartmentation pattern in beet root discs (Saftner and Wyse 1983) which indicates that CCCP is probably not having a deleterious effect on sucrose transport and compartmentation patterns in beet root discs. 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 (Saftner and Wyse 1980). Active sucrose uptake primarily represents sucrose uptake into the vacuole against the chemical potential gradient for sucrose (Saftner et al. 1983).

Measurement of endogenous gas-phase ethylene—The concentration of ethylene in the gas phase of beet root tissue was determined according to the vacuum extraction method of Beyer and Morgan (1970). Briefly a vacuum of 120 mm Hg was applied to beet root tissue completely immersed under a stoppered funnel in a saturating (0.41 g ml^{-1}) solution of $(NH_4)_2SO_4$ for 2 min. This caused gases within the tissue to expand, escape, and collect over the liquid inside the stoppered funnel. The collected gas samples were analyzed with a gas chromatograph equipped with an activated alumina column and a flame ionization detector. The beet root tissue used in these extractions was from freshly harvested roots cut into about 3 cm thick blocks with a sharp knife. The time from harvesting the root to the time of gas sample collection was less than 10 min.

Measurement of ethylene production rates—Ethylene production rates were determined in root discs at various times before and during sucrose uptake measurements. At each point, sets of root discs totaling 0.75 g fr wt were transferred to separate jars lined with sorbitol-wetted Kimwipes[1] and the jars stoppered so that each jar had a volume of 60 ml. At various times after stoppering the jars, air samples were withdrawn with a hypodermic syringe for analysis of ethylene as already mentioned. At the same times tissue samples were collected for ethylene analysis during sucrose uptake experiments, other sets of root discs again totaling 0.75 g fr wt were transferred to liquid nitrogen, frozen, stored in a deep freezer at −90°C for 2 to 5 days, then extracted and analyzed for ACC.

ACC extraction and analysis—Sets of root discs collected during sucrose uptake experiments were extracted and analyzed for ACC content. Frozen root discs (0.75 g) were homogenized with a 10× volume of ice-cold 80% (v/v) aqueous ethanol in a Kimematica Polytron homogenizer at half speed for 30 sec. To follow recovery, [2,3 ^{14}C]-ACC (specific activity of 50 μCi μmol^{-1}) prepared enzymatically by Dr. Shiow Ying Wang, USDA investigator, Beltsville, Maryland, was added to the tissue homogenate. The tissue homogenate was purified and analyzed for ACC using the methods of Lizada and Yang (1979). Occasionally, tissue homogenates were chromatographed on paper (Lizada and Yang 1979) to verify that the ethylene evolved during the ACC assay originated from a substance that co-chromatographed with ACC.

Results

Effect of ethylene and related hydrocarbons on sucrose transport—The effect of ethylene and related hydrocarbons on active sucrose uptake in beet root discs is shown in Figure 1. Ethylene stimulated active sucrose uptake in a log dose-linear response manner over the concentration range 0.1 to about 1 μl $liter^{-1}$. A saturating dose occurred between 1.0 and 3.0 μl $liter^{-1}$. After a maximum response to ethylene is observed, higher concentrations have no additional effect, i.e., dose-response curves are asymptotic and do not show reversed or secondary effects at high concentrations. Ethylene usually stimulated sucrose uptake 1.4 to 1.7 fold above control rates but occasionally stimulations as high as 3.1 fold were observed. However, in about 20% of the experiments, no ethylene response or sucrose uptake could be observed.

Propylene also stimulated active sucrose uptake in beet root discs but threshold, half-maximal, and saturating doses were about 10 fold higher than those needed for ethylene (Figure 1). Acetylene, propane, and ethane had no effect on active sucrose uptake (Figure 1). None of the hydrocarbons treatments shown in Figure 1 had any noticeable effect on passive sucrose uptake (data not shown).

[1] 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.

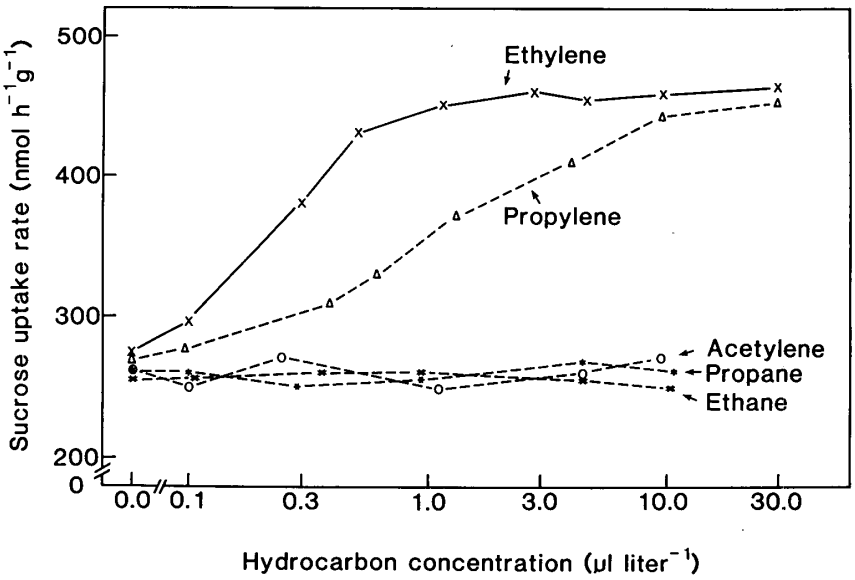

Fig. 1 Effect of ethylene and related hydrocarbon gases on active sucrose uptake in beet root discs. Equilibrated sets of beet root discs were incubated in sucrose uptake solution containing [^{14}C]-sucrose (55,000 dpm μmol^{-1}) for 3 h. During the incubation, air or air containing various indicated levels of ethylene or other hydrocarbon gases was bubbled continuously through the incubation solution. Results are the summation of 10 experiments using 10 sugar beet roots each of which displayed a 53 to 64% stimulation of active sucrose uptake when treated with 1.15 μl liter^{-1} ethylene in air. For clarity, standard deviation bars are not shown. The standard deviation did not exceed 7% of the mean value shown for the sucrose uptake rate.

Effect of ACC and AVG on sucrose uptake and ethylene production—Since ethylene stimulates active sucrose uptake in beet root discs, other substances that affect ethylene production should have a similar effect on active sucrose uptake. ACC, the immediate precursor of ethylene, stimulated ethylene production by 66% and active sucrose uptake by 24% (Table 1). On the other hand AVG, an inhibitor of ACC synthesis, inhibited both ethylene production by 45% and active sucrose uptake by 21% (Table 1). Table 1 also shows that ethylene can overcome the inhibitory effect of AVG on sucrose uptake.

Effect of plant hormones alone and in combination with ethylene on active sucrose uptake—Previously Saftner and Wyse (1984) showed that exogenous applications of ABA stimulated active sucrose uptake in beet root discs whereas IAA inhibited uptake and gibberellins and cytokinins alone had no effect on uptake. As such, the sensitivity of beet root discs to ethylene enhancement of sucrose uptake may change in the presence of other plant hormones. Table 2 shows how ethylene affects

Table 1 Effect of ethylene, ACC and AVG on active sucrose uptake and ethylene production rates in beet root discs

Treatment	Active sucrose uptake rate	Ethylene production rate
	(nmol h^{-1} g^{-1})	(nmol h^{-1} g^{-1})
Control	302±20	0.018±0.002
0.78 μl liter^{-1} ethylene	480±23	—
0.1 mM ACC	374±18	0.030±0.004
0.1 mM AVG	238±27	0.010±0.002
0.1 mM AVG+0.78 μl liter^{-1} ethylene	487± 9	—

Table 2 Effect of plant hormones alone and in combination with ethylene on active sucrose uptake rates in beet root discs

Hormone addition (10^{-5} M)	Active sucrose uptake rate	
	$-C_2H_4$	$+C_2H_4$ (0.92 μl liter^{-1})
	(nmol h^{-1} g^{-1})	
None	295± 9	430±29
ABA	445±22	432±11
IAA	75±12	82±25
t-Zeatin	282±17	406±25
GA_3	286±22	441±20

sucrose uptake when applied alone and in combination with other plant hormones. ABA stimulated sucrose uptake to a slightly greater degree than ethylene. The ABA and ethylene effects are neither additive nor synergistic. Table 2 also shows that ethylene-responsive tissue can be made insensitive to ethylene treatment by applying ABA to the tissue. Ethylene responsive tissue can also be made nonresponsive by treating the tissue with IAA (Table 2), a strong inhibitor of active sucrose uptake in beet root discs (Saftner and Wyse 1984). Neither t-zeatin nor GA_3 had any significant effect on ethylene-enhanced sucrose uptake (Table 2).

Gas-phase ethylene content of beet root tissue—In the hope of better understanding the physiological importance of ethylene on sucrose uptake, the gas-phase level of ethylene in root tissue from freshly-harvested sugar beet plants was determined. Three cultivars of sugar beet plants were used. Cultivars D2, USH-20, and L53XL19 contained about 8, 14, and 19% fr wt sucrose respectively. Despite the large variations in sucrose content, the gas-phase ethylene levels in the three cultivars were similar, being 0.05±0.01 μl liter^{-1} in the low sugar D2 cultivar and 0.07±0.01 in the two higher sugar cultivars. Besides ethylene, the only other hydrocarbon detected in the gas phase of beet root tissue was CO_2.

Endogenous ACC content and ethylene production rate—To add to these findings, the endogenous

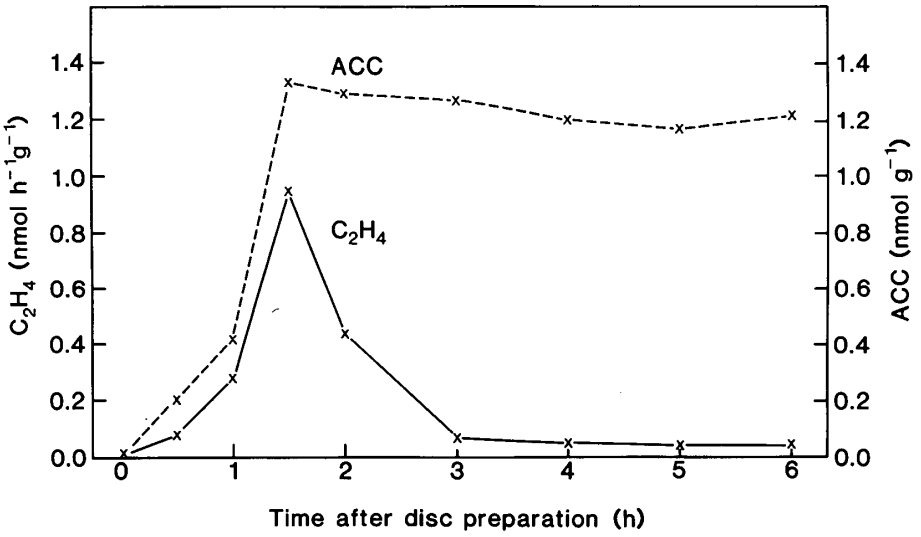

Fig. 2 Time course of ACC content and ethylene production in beet root tissue. Ethylene production rates and the ACC level in the beet root discs were determined after various incubation periods. The standard deviation did not exceed 10% of the mean values shown for ACC content and ethylene production.

ACC content and ethylene production rate were analyzed in beet root discs. Figure 2 shows that the ACC content in root discs increased at least 20 fold during the first 1.5 h of tissue incubation and paralled a similar rise in ethylene production. Subsequently, the ACC level tended to level off with time while ethylene production declined to a rate similar to that of freshly-prepared discs (Figure 2). Sucrose uptake measurements were done between 3 and 6 h after disc preparation when ethylene production rates are low and relatively stable (Figure 2).

Discussion

Ethylene stimulated active sucrose uptake in root discs of sugar beet (Figure 1). The central question that arises from this finding is whether or not ethylene plays a role on sucrose uptake under natural conditions. Certainly the concentration of ethylene required for threshold, half maximal, and maximal stimulation of sucrose uptake are typical for a number of ethylene-mediated processes (Figure 1 and Abeles 1973). Similar to other ethylene-mediated processes, ethylene concentrations higher than optimal have no additional effects (Figure 1). In other words, the dose-response relationship for ethylene-mediated sucrose uptake is typical of most other ethylene-mediated processes. For externally supplied ethylene to have any effect on a plant tissue, it must be supplied at levels higher than that normally present in the tissue. In beet root discs, externally supplied ethylene stimulated sucrose uptake at concentrations slightly higher (0.03 μl liter^{-1} higher) than the ethylene concentration present in the gas phase of the root tissue. However, despite these consistencies to other ethylene-mediated processes, no connection was found between the sucrose status of the tissue and the ethylene concentration in the gas phase of the tissue. While such a finding argues against an ethylene role on the sucrose transport system, it does not necessarily negate a connection between ethylene and sucrose uptake. There may be localized spaces within the cell where the ethylene concentration differs between cultivars and which are higher than the average gas phase level measured, e.g., in the plasma or tonoplast membranes where active sucrose uptake is thought to occur (Saftner and Wyse 1983). Also, correlations between the ethylene concentrations and the sucrose status of the tissue may have gone undetected because of the difficulty in accurately measuring the low levels of ethylene present in the tissue. On the other hand, the ethylene effect on sucrose uptake in different cultivars of sugar beet may be correlated not with ethylene concentration per se but rather to ethylene turnover rates or to ethylene binding parameters (see Beyer 1979, Sisler and Goren 1981, Goren et al. 1984). In any event, if naturally occurring ethylene does stimulate sucrose uptake, then other substances that affect ethylene production in the tissue should similarly affect sucrose uptake. Table 1 shows that a connection does exist between sucrose uptake and ethylene production rates. ACC, the immediate precursor to ethylene, stimulated both ethylene production and sucrose uptake in root discs. AVG, an inhibitor of ACC synthesis, inhibited both ethylene production and sucrose uptake. AVG is probably not acting as a nonspecific inhibitor because ethylene can still stimulate sucrose uptake in AVG-treated tissue. These findings support but do not prove a role for endogenous ethylene on sucrose uptake. Lastly, ethylene-mediated processes in plant tissues generally show a rather high specificity for ethylene. Figure 1 shows that sucrose uptake is most strongly stimulated by ethylene. Propylene can mimic ethylene action at 10 fold higher concentrations. Since propylene must usually be supplied at 100 fold plus concentrations to mimic ethylene action, sucrose uptake in beet root tissue shows a higher than normal sensitivity to propylene. However, like other ethylene-mediated processes, acetylene, propane, and ethane have no effect. Of the hydrocarbons tested, only ethylene was detected in the gas phase of beet root tissue. None of the hydrocarbons had any significant effect on passive sucrose uptake indicating that they were not having any strong deleterious effects on membrane integrity. Overall, it appears that ethylene-enhanced sucrose uptake strongly

resembles other ethylene-mediated processes in plant tissues but whether or not naturally occurring ethylene has the same effect as applied ethylene is still not clear.

Another matter which needs to be considered is tissue sensitivity to ethylene. During this investigation, in about one experiment in five, ethylene did not stimulate sucrose uptake. In ethylene-sensitive tissue, the control rate of sucrose uptake ranged from 230 to 300 nmol h^{-1} g^{-1} whereas in ethylene-insensitive tissue, the rate of sucrose uptake was either very high (>350 nmol h^{-1} g^{-1}) or very low (<100 nmol h^{-1} g^{-1}). A high sucrose uptake rate may indicate a strongly stimulated uptake system, possibly one working at or near an optimal rate. A low sucrose uptake rate may indicate a generally inactivated or strongly inhibited uptake system. Earlier, Saftner and Wyse (1980, 1984) found that ABA, K^+ and Na^+ ions strongly stimulated active sucrose uptake in beet root discs whereas IAA was strongly inhibitory. It is possible that tissue sensitivity to ethylene on sucrose uptake may change with changes in hormonal and nonhormonal factors that have an effect on sucrose uptake. Table 2 shows that plant hormones affect tissue sensitivity to ethylene. ABA stimulated sucrose uptake to a slightly greater degree than ethylene and made the tissue insensitive to ethylene treatment. [ABA can stimulate ethylene synthesis in beet root tissue incubated on wet Kimwipes in stoppered vials (Saftner, unpublished data) but to what degree, if any, ABA-enhanced ethylene synthesis contributes to ABA-enhanced sucrose uptake in aerated, solution-incubated beet discs is not known. [Gas phase ethylene levels cannot be measured in the small quantity of tissue used in the sucrose uptake experiments]. Like ABA, K^+ and Na^+ ions stimulate sucrose uptake in beet root discs (Saftner and Wyse 1980) and make the tissue insensitive to ethylene (Saftner unpublished data). In contrast to ABA, IAA inhibited sucrose uptake but it too made the tissue insensitive to ethylene (Table 2). As such, the sensitivity of beet root discs to ethylene stimulation of sucrose uptake appears to be a complicated matter involving both hormonal and nonhormonal interactions.

Despite variations in tissue sensitivity to ethylene, ethylene generally had a strong (1.4 to 1.7 fold) stimulatory effect on active sucrose uptake. The high sensitivity is dependent, at least in part, upon the low gas-phase ethylene levels in beet roots and upon the low ethylene production rates in beet root discs during the time that sucrose uptake measurements were made (Figure 2, 3 to 6 h), this despite the inherent capacity of the tissue to produce ethylene at high rates (Figure 2, 0 to 3 h). To my knowledge, this is the earliest observed effect of applied ethylene on active transport of sucrose. The beet root discs used in this study came from mature, nongrowing tissue. Further, the relatively short-term (3 h) ethylene treatments had no significant effect on respiration (Saftner, unpublished data). Prior to this study, when ethylene or ethylene-releasing substances were applied to intact plants or plant parts, the active transport of photosynthates was altered, i.e., photosynthate partitioning and allocation patterns were changed (see Abeles 1973, Dann and Chalmers 1978, Hirai 1982, Robinson 1983, Veen and Kwakkenbos 1984). However, such studies were conducted over time periods where the hormonal effect on transport could not be separated from hormonal influences on growth, respiration, senescence, and/or other possible rate-limiting physiological processes. As such, it is too early to speculate on the suggested ability of ethylene to accelerate sugar accumulation in fruit tissue during ripening (see Abeles 1973, Hirai 1982) or on the potential ability of ethylene to alter photosynthate transport patterns among tissues producing differing amounts of ethylene. Ethylene is also known to increase cellular permeability in a number of plant tissues (see Parups 1977), but what relationship, if any, this has to ethylene-enhanced active sucrose uptake in beet root discs or to ethylene-modified photosynthate transport and allocation patterns in whole plants is not known. Although ethylene has been implicated as a potential regulator of photosynthate transport and allocation patterns, little direct evidence is available to explain its role. My results suggest a relatively close association between the physiological activities of ethylene and the transport of sucrose into sugar beet taproot tissue. However, the nature of the effect,

whether exerted on the sucrose carrier, on membrane-associated electrochemical potential gradients, or on physical characteristics of the membrane is still unclear.

The authors would like to thank Dr. Carl Sams for information and advice on gas mixing procedures and proper handling and analysis of hydrocarbon gases as well as for providing equipment related to the same. The author would also like to thank Sunny Keithley and Delores Sessions for typing related to this manuscript.

References

Abeles, F. B. (1973) *Ethylene in Plant Biology*. Academic Press, New York.

Beyer, E. M., Jr. (1979) Effect of silver ion, carbon dioxide and oxygen on ethylene action and metabolism. *Plant Physiol.* 63: 169–173.

Beyer, E. M., Jr. and P. W. Morgan (1970) A method for determining the concentration of ethylene in the gas phase of vegetative plant tissues. *Plant Physiol.* 46: 352–354.

Dann, I. E. and D. J. Chalmers (1978) Growth of peach fruits after treatment with ethephon during successive periods of fruit development. *Austral. J. Plant Physiol.* 5: 589–595.

Eastwell, K. C., P. K. Bassi and M. E. Spencer (1978) Comparison and evaluation of methods for the removal of ethylene and other hydrocarbons from air for biological studies. *Plant Physiol.* 62: 723–726.

Eger, E. I. and C. P. Larson (1964) Anaesthetic solubility in blood and tissues: Values and significance. *Br. J. Anaesth.* 36: 140–149.

Goren, R., A. K. Mattoo and J. D. Anderson (1984) Ethylene binding during leaf development and senescence and its inhibition by silver nitrate. *J. Plant Physiol.* 117: 243–248.

Hirai, M. (1982) Accelerated sugar accumulation and ripening of loqust fruit by exogenously applied ethylene. *J. Japan Soc. Hort. Sci.* 51: 159–164.

Lieberman, S. J., J. G. Valdovinos and J. E. Jensen (1983) A morphometric study of the effects of ethylene treatment in promoting abscission of tobacco flower pedicels. *Plant Physiol.* 72: 583–585.

Lizada, M. C. C. and S. F. Yang (1979) A simple and sensitive assay for 1-aminocyclopropane-1-carboxylic acid. *Anal. Biochem.* 100: 140–145.

Parups, E. V. (1977) Control of ethylene induced permeability of plant cells by a substituted benzothiazole. *Physiol. Plant.* 39: 290–294.

Robinson, M. (1983) Influence of abscisic acid and ethylene on assimilate distribution in *Gladiolus grandiflorus*. *Ann. Bot.* 51: 779–785.

Sacher, J. A. and S. O. Salminen (1969) Comparative studies of effect of auxin and ethylene on permeability and synthesis of RNA and protein. *Plant Physiol.* 44: 1371–1377.

Saftner, R. A., J. Daie and R. E. Wyse (1983) Sucrose uptake and compartmentation in sugar beet taproot tissue. *Plant Physiol.* 72: 1–6.

Saftner, R. A. and R. E. Wyse (1980) Alkali cation/sucrose co-transport in the root sink of sugar beet. *Plant Physiol.* 66: 884–889.

Saftner, R. A. and R. E. Wyse (1984) Effect of plant hormones on sucrose uptake by sugar beet root tissue discs. *Plant Physiol.* 74: 951–955.

Sisler, E. C. and R. Goren (1981) Ethylene binding—the basis for hormone action in plants. *What's New Plant Physiol.* 12: 37–40.

Veen, M. and A. A. M. Kwakkenbos (1984) Role of ethylene in distribution of assimilates in cut carnations. *J. Plant Physiol.* 115: 389–396.

(Received February 12, 1986; Accepted April 22, 1986)