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MOBILIZATION OF SUCROSE DURING TOMATO FRUIT SET AND DEVELOPMENT

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Douglas David Archbold

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Frank D. Hanson Jr.
Major professor

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MOBILIZATION OF SUCROSE DURING TOMATO FRUIT SET AND DEVELOPMENT

By

Douglas David Archbold

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ABSTRACT

MOBILIZATION OF SUCROSE DURING TOMATO
FRUIT SET AND DEVELOPMENT

By

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Growing fruits act as sinks for photosynthates, and certain plant hormones both induce fruit set and mobilize ^{14}C and ^{32}P to treated portions of plants. This suggests that fruit set may be a mobilization phenomenon. A determinate cherry tomato cultivar (Lycopersicon esculentum cv 'Farthest North') was used to test whether fruit set involved mobilization of ^{14}C-sucrose to the ovary, or whether mobilization occurred only after fruit growth commenced. Ovary growth and accumulation of ^{14}C from treated leaves were evaluated over a 72 hr period following treatment of ovaries with naphthoxyacetic acid (NOA). A statistically significant increase in fresh weight of ovaries was evident 36 hr after NOA treatment. Ethanol-soluble radioactivity from foliar applied ^{14}C-sucrose was not significantly greater in auxin-treated ovaries than in water controls until 48 hr after treatment. Relative import rate (dpm/hr) paralleled growth rate (mg/hr). Pollinated ovaries exhibited similar relationships between growth and mobilization. Thus, tomato fruit set per se does not appear to involve mobilization.

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Guidance Committee:

The journal-article format was adopted for this thesis in accordance with departmental and university requirements. The article was prepared and styled for publication in the Journal of the American Society for Horticultural Science.

INTRODUCTION

Plentiful fruit set is a necessity to insure a profitable harvest. Knowledge of the factors limiting this phenomenon is an essential first step toward the desired goal, regulated cropping. Though exogenous parameters (i.e., temperature, rainfall) are difficult to control some endogenous factors may be manipulated. Seemingly maximum fruit set can occur under ideal conditions. However, the actual capacity of bearing plants is unknown. A 5 to 10% increase in yield while maintaining a balanced vegetative:reproductive system could result in significant economic benefits.

Tomato was selected for this study because plants can be grown year-round, flower profusely, and have been studied extensively. Tomato ovaries respond to both auxin and gibberellin treatment, and their growth rates following auxin treatment generally parallel those following pollination. Sucrose is the major carbohydrate translocated in the tomato plant and patterns of translocation can be studied by ^{14}C-labelling.

Ovaries are weak sinks at anthesis but begin accumulating nutrients soon after fertilization. Little is known as to when accumulation begins or the sink is established. Fruit set is an inductive phase beginning with pollination and culminating in the initiation of fruit growth. Since growth requires an import of nutrients for metabolic needs, a directed accumulation, or mobilization, of nutrients into the ovary may be established prior to or coincidental with growth. Fruit set may

initiate mobilization, and poor set may reflect weak or ineffective mobilization (i.e., weak sink strength). Recent work with Prunus suggests this. Application of a mixture of gibberellin, auxin, and cytokinin to open-pollinated flowers increased final set (Goldwin and Webster, 1978; Webster and Goldwin, 1978; Webster et al, 1979), perhaps by mobilizing nutrients to weak sinks.

The purpose of this thesis is to contribute to an understanding of fruit set. Emphasis centered on (a) investigating sink strength of tomato ovaries in relation to fruit set, (b) establishing when growth begins following auxin treatment or pollination, and (c) determining when mobilization of foliar-applied ^{14}C-sucrose begins in relation to early fruit growth.

LITERATURE REVIEW

Introduction

The purpose of this review is to examine the processes of fruit set and fruit growth with emphasis on tomato, and the evidence for the role of hormones in mobilization of nutrients to the ovary. Fruit set may be defined as an inductive phase beginning at pollination and culminating with the initiation of fruit growth. Accompanying morphological changes include petal and stamen wilting and abscission (Leopold, 1964). Certain plant hormones, synthetic and natural, induce fruit set when exogenously applied (Crane, 1964; 1969). Similar endogenous hormones are believed to control fruit set, and these chemicals may control nutrient movement to the ovary, a phenomenon known as mobilization.

The morphology and physiology of tomato fruit development is well-documented. Development of an unpollinated, unfertilized tomato ovary begins with fruit set. Pollination and fertilization normally induce fruit set, although many species, including some tomato cultivars, exhibit various types of parthenocarpy (Nitsch, 1952), or fruit development without fertilization of the ovules.

Following fertilization, the ovary may continue the cell division processes initiated during flowering for several days (Davies and Cocking, 1965), or may undergo no cell division (Houghtaling, 1935), depending on

the cultivar. Growth of the ovary is due solely to cell enlargement after cell division ends. Within 48 hr of pollination, fresh weight and starch concentration rise dramatically (Marre´ and Murneek, 1953), and growth rate increases rapidly. The sigmoidal curves of fresh weight and dry weight (Gustafson, 1926; El-Beltagy, et al, 1976) are typical of many fruits, including apple (Tukey and Young, 1942) and orange (Bain, 1958).

Effects of applied hormones on fruit set.

Endogenous hormones are believed to play a primary role in fruit set and development. Although correlation between their concentrations and these processes often leave much to be desired, responses to exogenous applications of growth hormones have strongly implicated their essential role.

Gustafson (1937) observed that chloroform extracts of pollen of several species, when applied in lanolin to emasculated flowers, were partially active in setting fruit in a number of species. The results were erratic and growth rates were not normal. Prior to this, Thimann (1934) had noted a high concentration of a growth substance active in the Avena curvature test in a chloroform extract of Sequoia pollen. Also, Laibach (1932) found auxin-like activity in pollen extracts. These investigations implied a role for auxin in fruit set.

Auxins are more effective in setting fruit than other classes of growth regulators in many species. Gustafson (1936) successfully induced parthenocarpy in tomato and several other species with auxins such as 3-Indole-aceticacid (IAA) and indolepropionic acid (IPA). Nitsch (1960a) tested natural and synthetic auxins for their effects in stimulating growth of unpollinated tomato ovaries and found a wide range of effectiveness.

2-Naphthoxyacetic acid (NOA) was highly active at concentrations ranging from 5×10^{-4} to 10^{-3}M. IAA exhibited peak activity, equivalent to NOA, at 4×10^{-4}M with less activity at 5×10^{-4}M and virtually none at 10^{-3}M. Growth rates of tomato fruits induced to grow by auxin application generally paralleled those of pollinated fruit. This suggests that auxin exerts an effect similar to pollination/fertilization. Crane (1964) noted that some fruits, notably the drupes, show little response to auxin application; others (i.e., apple, pear) can be set but do not develop normally.

Luckwill (1948) established a method of evaluating auxin-like activity in extracts via stimulation of tomato fruit development. Activity was compared with that of synthetic auxin standards. The greater the quantity of auxin applied, the greater the subsequent growth rate.

Other classes of growth regulators are active in fruit setting ability. Wittwer et al (1957) and Wittwer and Bukovac (1962) found that gibberellins (GAs) were capable of setting fruit in tomato at lower concentrations than auxins. Set was induced by 3×10^{-5}M GA_3, whereas at least 4×10^{-4}M NOA or IAA was required (Nitsch, 1960). However, the mature GA-set fruit were inferior in size and quality to those induced by auxin. Crane et al (1960) found that applications of GA at full bloom and 8 days thereafter induced parthenocarpy in apricot and almond, while a single application at full bloom induced peach fruit set. Final fruit size was invariably inferior to pollinated controls. This suggests that GAs are involved in fruit set but are less effective in subsequent fruit development.

Cytokinins do not promote set of tomatoes, although they have limited effects on grape (Weaver et al, 1966) and fig (Crane et al, 1965). Fruit growth rate in the responsive species is inferior and final size is reduced compared to pollinated/fertilized fruit.

Role of endogenous hormones in fruit set.

Pollen contains small amounts of auxins (Laibach, 1932; Thimann, 1934) and gibberellins (Coombe, 1960; Sastry and Muir, 1963). The release of these hormones from pollen tubes during their growth through stylar tissue may stimulate the growth increase prior to fertilization that can be detected in some fruit, notably cucumber (Fuller and Leopold, 1975). As determined by stylar excision, which prevents pollen tube growth and subsequent fertilization, fruit set was complete by 18 hr, whereas fertilization required approximately 36 hr. This indicated that pollen tube growth, or pollination itself, could be the initial stimulus to fruit set. Thus, some fruits are capable of growth following pollination only, a condition known as stimulative parthenocarpy (Winkler, 1908)

The endogenous hormones of pollen, which are unable to fully induce set in most species (Gustafson, 1937), or pollen tube growth, may stimulate the production of hormones in the ovary prior to fertilization. Muir (1942) found that pollination increased diffusible auxin in tobacco ovaries within 11 hr, and Sastry and Muir (1963) noted a similar increase in tomato ovaries within 28 hr of pollination or GA_3 treatment. Diffusible auxin in both species at anthesis was nil. Lund (1956) described a wave of auxin-like activity in pollinated tobacco flowers, starting from the apical half of the style and proceeding basipetally to the

ovary, which was correlated with pollen tube growth.

However, hormone production does not occur immediately after pollination in some species. Nitsch et al (1960) noted a general increase in auxin-like activity, as determined by the oat first-internode test, in seeded 'Concord' grape ovaries starting at anthesis. Minimal activity was found in berries at bloom. However, seedless fruit did not exhibit a rise in auxin-like activity for several weeks after anthesis. A lag between pollination and significant hormone production exists in apple (Luckwill, 1953) and currant (Wright, 1956). Wiltbank and Krezdorn (1969) found GA content of navel orange ovaries was highest at full bloom, decreasing thereafter. There is clearly not a trend towards hormone production following pollination in all species.

The elevated levels of hormones in parthenocarpic flowers and fruits suggests that hormone production without pollination or fertilization may be responsible for their ability to set and grow. Floral buds of naturally parthenocarpic orange, lemon, and grape varieties contain higher auxin-like activity than their seeded counterparts (Gustafson, 1939). However, Nitsch et al (1960) did not observe this difference between seeded and seedless 'Concord' grape ovaries at bloom. Coombe (1960) noted that one parthenocarpic and two stenospermocarpic grape cultivars contained higher GA activity preceding and throughout anthesis, whereas seeded varieties did not show such activity. Pathenocarpic fig exhibits a peak in auxin-like activity following anthesis similar to that observed in caprified fig (Crane et al, 1960). Mapelli et al (1978) compared a tomato cultivar and its isogenic parthenocarpic mutant and discovered

some striking differences. From anthesis to 6 days thereafter, auxin concentration and total auxin per ovary were much greater in parthenocarpic ovaries than in seeded ones. Also, GA concentration and total GA per fruit were significantly higher through 4 days post-anthesis in the parthenocarpic fruit. Thereafter, both auxin-like and GA-like activities were higher in the seeded ovaries.

If growth hormones play a role in fruit set, they may act by (a) stimulating metabolite utilization in the ovarian tissue (i.e., sink effect), (b) enhancing the ovary's ability to accumulate nutrients via an effect on phloem loading at the source, phloem unloading at the sink, or longitudinal transfer processes, or (c) a combination of these mechanisms.

Role of endogenous hormones in tomato fruit development. Growth hormones are present in tomato fruit and seed tissue. Gustafson (1939b) found a higher concentration of auxin-like activity in the ovules and surrounding tissues of tomato than in tissues nearer the ovary wall. Cytokinin-like activity was found in tomato juice by Nitsch (1960b)

Recent attempts to quantify auxin-like gibberellin-like, and cytokinin-like activity in developing tomato fruit have yielded differing results. El-Beltagy et al (1976), working with a normal cultivar, found that the growth substances exhibited bimodal concentration curves throughout the period of analysis, anthesis through green mature stage, and a pattern of sequential changes in hormone concentrations was noted. An early (1 to

2 weeks post-anthesis) rapid increase in basic gibberellin (GA_9-like) and neutral auxin concentrations was followed by rises in acidic GA (GA_3-like) and acidic auxin concentrations, the acidic auxin peaks following the acidic GA peaks. After decreasing, late peaks (6 to 7 weeks post-anthesis) of GA and auxin activity coincided. Cytokinin-like components exhibited peak activity midway through the study. Ethylene concentration was high immediately after anthesis and decreased to low levels through the final analysis. Mapelli et al (1978) observed similar hormonal relationships in developing tomato fruit and noted that the early auxin peaks coincided with the end of cell division and beginning of cell enlargement. Abdel-Rahman et al (1975) quantified acidic auxin and acidic GA (GA_3-like) activity as well as free and bound cytokinin activity in cherry tomato from anthesis to maturity. Acidic auxin-like activity increased from 1 to 4 weeks post-anthesis and decreased subsequently, while acidic GA activity increased slowly from anthesis to a peak at 5 weeks (green mature). Cytokinin-like activity in the 'free' fraction was high at an early stage and decreased to a low level within 2 weeks post-anthesis, while the 'bound' fraction exhibited greatest activity at the beginning and end of the sampling period. Though the concentration patterns, single vs dual peaks, contrast, auxin production preceding gibberellin production was a standard feature of these studies. The correlation of cell division cessation and cell elongation initiation with auxin levels implies, with the other noted relationship, that hormones are interacting to control fruit development.

Fruit: A sink for nutrients.

To maintain growth rate, a fruit reguires nutrients such as carbohydrates and inorganic materials. Grape flowers are poor sinks for carbohydrates prior to anthesis, as determined by ^{14}C studies (Hale and Weaver, 1962). However, several days after full bloom, they have become very strong sinks. This increase in sink strength occurs when growth of the berries is rapid. Linck and Swanson (1960) noted that prior to anthesis a pea flower is a poor sink for ^{32}P applied to a subtending leaf. Four days after anthesis, the flower, presumably fertilized, has become a strong sink which accumulates label.

The change from an inactive to a metabolically active sink may occur within hours of fruit set in some species. By 24 hr after pollination or auxin-induced set of watermelon ovaries, Walker and Hawker (1976) noted an increase in reducing sugar concentration. Although the activity of acid invertase, an enzyme which hydrolyzes sucrose to reducing sugars, was high in pollinated, auxin-induced, and non-pollinated ovaries from anthesis through 9 days post-anthesis, only the setting fruit accumulated reducing sugars. The results suggest that a sink was established within 24 hr of set.

At anthesis and during set, flowers (fruit) may be very weak sinks. Tipping and girdling grapevines increases set (Hale and Weaver, 1962); likewise, fruit set in apple can be increased by pruning (Howlett, 1931). Abbott (1960) observed that actively growing shoots may compete with apple fruitlets for nutrients and can reduce set. Single shoots of pot-grown 2-year old apple seedlings were pruned to 2 or 3 flower bud bearing spurs.

A shoot was allowed to grow from one of the spurs, and the flowers on one of the spurs was pollinated. Final fruit set was 0% on the unpruned control shoot and on spurs bearing both flowers and a growing shoot. However, the spurs bearing only pollinated flowers exhibited 20% final fruit set even when a shoot developed on a nearby spur. Quinlan and Preston (1971) also noted a shoot:fruit competition affecting apple fruit set. Shoot removal 5 days after full bloom increased early set, though the subsequent heavy June drop was attributed to the reduced leaf number. However, shoot tip removal resulted in increased initial and final set. Autoradiographic evidence indicated more labelled assimilates moved to the young fruits when shoot tips were removed. The results suggest that young fruits are unable to effectively compete with nearby sites of metabolic activity for available nutrients.

To maintain a high growth rate, carbohydrates must be imported at a high rate. The absolute import rate of a plant organ is termed sink strength (Wilson, 1972), commonly measured as the absolute rate of change of weight. Sink strength is a product of two variables, the sink size, or weight, and sink activity. Sink activity is the import rate per unit weight. Wareing and Patrick (1975) distinguished the sink strength from the mobilizing ability of an organ by equating the former term with potential capacity and the latter with actual rate. Thus, due to the abilities of competing organs, a sink may not realize its sink strength and express a lesser mobilizing ability.

Over a wide range of fruit sizes from 20% to 90% of final size, Walker and Ho (1977) determined that the absolute rate of import of organic materials, predominately sucrose, was highest in the smallest (i.e., youngest)

fruit. Carbon import in mg/h decreased as the fruit approached final size, from 5.87 mg/h at 20% final size to 3.11 mg/h at 90% final size. This is reasonable since a young fruit would be undergoing a higher growth rate than an older fruit according to its sigmoidal curve of growth (Gustafson, 1926; El-Beltagy et al, 1976). McCollum and Skok (1960) noted a greater accumulation of ^{14}C-assimilates in 22 hr by younger (fewer than 19 days post-anthesis) tomato fruits than by older fruits.

Effect of limiting carbohydrate supply on fruit set and development.

A reduction in the supply of carbon compounds can adversely affect growth rate of tomato fruit. Marre and Murneek (1953) found that increases in reducing sugars and starch paralleled increases in fresh weight at 48 hr in pollinated and auxin-set tomato fruit. Competing fruit reduce the fresh weight gain and reducing sugar and starch accumulation of individual fruits. As long as the number of sources (leaves) remains constant or increases slowly, increasing sink number will reduce the absolute amount of organic materials available to an individual fruit. Early-set apples (Howlett, 1931; Beadle, 1937) and tomato (Marre and Murneek, 1953) fruits tend to monopolize a greater proportion of the carbohydrate supply, thereby reducing the growth rate and the weight of later-set fruit. Fisher (1977) found that the yield and mean number of tomato fruit on a truss decreases as the number of distal trusses increase. This suggests that the later-set fruit also reduce the growth of the early-set fruit. As sink number increases, sink size decreases.

Fruit set may also be affected by the supply of carbohydrate. Leopold

and Scott (1952) noted an effect of sucrose concentration on fruit set in tomato. Excised trusses bearing 2 or 3 ovaries, treated with 30 ppm p-chlorophenoxyacetic acid, were cultured in vitro on an agar medium containing increasing concentrations (0-5%) of sucrose, fructose, and glucose. Swelling of the ovaries within 7 days was recorded as an indicator of fruit set. With 0% sugar, no set occurred. A linear increase from 20% to 50% set was noted between 1 and 5% glucose and sucrose. With fructose a linear increase up to 60% set from 1 to 3% sugar was noted, dropping to approximately 40% set at 4 and 5% sugar.

Effect of fruit on photosynthesis and mobilization.

Fruit may stimulate photosynthesis of source leaves. The net assimilation rate of fruiting tomato plants exceeds that of deflorated plants (Hall, 1977), and as fruit load increases, the net assimilation rate increases (Fisher, 1977). Hansen (1967, 1970) and Kazaryan et al (1965) found that apple leaves on fruiting spurs assimilated greater amounts of $^{14}CO_2$ than did those on non-fruiting spurs. Also, more ^{14}C-assimilate was translocated out of source leaves on fruit-bearing spurs than on non-fruiting spurs, which suggests a fruit effect on a translocation mechanism. If the rate of assimilation is controlled by the concentration of sugars in the leaf, the effect of fruit may be to 'unload' the leaves, promoting (or allowing) CO_2 assimilation. Upmeyer and Koller (1973) have observed that as starch accumulation slowed in soybean leaves (i.e., excess starch) soluble sugars increased. Diffusive resistance of the leaves increased significantly at the same time slowing the photosynthetic rate.

More than a single process may be involved in nutrient accumulation by fruit. Williams and Williams (1978) have noted both a sink effect and a direct effect of the pea pods on assimilate transport. The sink effect of intact pods was increased by a 10^{o}C increase in temperature, and decreased by a 10^{o} decrease. Heating increased sugar accumulation. Heating either the upper or lower half of a pod resulted in greater accumulation of labelled assimilates in both halves. If sink effect alone was responsible for the increase, only the heated half (i.e., greater sink effect) should have been affected. The ovules were identified as the primary sinks; 33% of the total ^{14}C recovered was in the ovules. Ovule removal resulted in less total accumulation in the pod and more ^{14}C remaining in the treated leaf. However, pod heating (with ovules removed) increased transport out of the pulsed leaf though the pod itself did not acquire more ^{14}C. The pattern of movement out of the leaves at increasing temperatures suggests that the pod has a remote effect on assimilate translocation, either on phloem loading or longitudinal transfer processes, separate from the sink effect.

Hormones as mobilizing agents

Fruit, and especially immature seeds, are rich sources of growth hormones (Crane, 1964, 1969; Nitsch, 1965), and these compounds may mobilize nutrients to fruit. Auxins can effectively mobilize ^{14}C-labelled assimilates and ^{32}P. IAA applications to the cut surface of decapitated Phaseolus and Malus stems increased accumulation of ^{14}C-sucrose and ^{14}C-sorbitol, respectively, to the site of application (Patrick and Wareing, 1973; Hatch and Powell, 1969). Similarly, application of IAA to a

Phaseolus peduncle after fruit excision stimulated ^{32}P accumulation in the treated region (Seth and Wareing, 1967).

Treatment of a growing fruit with auxin enhances its ability to attract organic materials. Weaver et al (1969) noted that grape berries dipped in 4-chlorophenoxyacetic acid grew more rapidly and imported more ^{14}C-label from a nearby source leaf than did untreated controls. Spraying fruiting tomato trusses with naphthaleneacetic acid or 2,4-dichlorophenoxyacetic acid, synthetic auxins, increased uptake of carbohydrate by the trusses as well as the absolute amount exported from the source leaves (Khan and Sagar, 1966).

Other growth regulators are less effective than auxins. Cytokinins and GAs were unable to mobilize ^{14}C-labelled compounds in Malus (Hatch and Powell, 1969) or ^{32}P in Phaseolus (Seth and Wareing, 1967) when applied to decapitated stems. However, a synergism was observed between IAA, GA and kinetin in Phaseolus. Synergism of benzyladenine (BA) or GA with IAA did not occur in Malus, although GA and BA synergized in stimulating ^{14}C-sorbitol accumulation (Hatch and Powell, 1969). However, Weaver et al noted that GA_3 treatment of whole grape clusters at anthesis increased accumulation of ^{14}C-label within 6 h. A slight increase in dry weight was noted also.

Summary

Growth hormones, especially auxins, induce parthenocarpy in a number of fruits (Gustafson, 1936; Nitsch, 1960; Crane, 1964). The ability of pollen extracts to induce limited fruit set (Gustafson, 1937) and the presence of auxin-like and gibberellin-like activity in the extracts

(Laibach, 1932; Thimann, 1934) suggests that hormones play an integral role in the process of fruit set. Although growth substances are present in growing fruit and seed tissues (Gustafson, 1939b; Nitsch, 1960b; Crane, 1964) their concentrations are often not well correlated with growth (Crane, 1969; El-Beltagy et al, 1976).

The sink strength of fruit such as grape (Hale and Weaver, 1962) and pea (Linck and Swanson, 1960) is firmly established within days of fruit set. The change from a non-active to an active sink may occur within 24 hr of pollination or auxin treatment in watermelon (Walker and Hawker, 1976). Although the sink is established soon after set, its strength may not be significant until after growth begins. Thus, by the time a tomato fruit achieves 20% of its final size, it is a very strong sink (Walker and Ho, 1977).

Growth can be effectively limited by the available nutrient supply, and competition between fruit can decrease growth rates of all fruit (Howlett, 1931; Beadle, 1937; Marfe and Murneek, 1953; Fisher, 1977). Fruit set may also be affected by carbohydrate supply (Leopold and Scott, 1952).

Fruit may stimulate mobilization by means other than the sink effect. Photosynthetic assimilation rates may be increased directly or indirectly by growing fruit (Hall, 1977; Fisher, 1977). In apple (Hansen, 1967) and pea (Williams and Williams, 1978), the growing fruit enhance phloem loading at the source leaves or longitudinal transfer rates of assimilates.

Endogenous hormones may be responsible for mobilizing the nutrient

supply. Exogenously applied growth regulators, auxins in particular, can effectively mobilize ^{14}C-assimilates and ^{32}P in Malus (Hatch and Powell, 1969) and Phaseolus (Patrick and Wareing, 1973). Cytokinins and GAs are less effective.

If it is limited by carbohydrate availability, fruit set may be a mobilization phenomenon. During set the ovary could be mobilizing the carbohydrates it needs to initiate growth. Hormone production or release in the ovary following pollination (Lund, 1956) may be responsible for mobilization, for hormone treatment is effective in stimulating carbohydrate accumulation (Weaver et al, 1969; Khan and Sagar, 1966; Hatch and Powell, 1969). Thus, failure to set fruit could be due to an inability to mobilize. The purpose of this investigation is to determine the sink strength in tomato ovaries in relation to fruit set and exogenous auxin application and to determine when (a) growth and (b) mobilization begin.

MOBILIZATION OF SUCROSE DURING TOMATO FRUIT SET AND INITIAL DEVELOPMENT

Abstract. A determinate cherry tomato cultivar (Lycopersicon esculentum Mill. cv Farthest North) was used to test whether fruit set involves mobilization of ^{14}C-sucrose to the ovary, or whether mobilization occurs only after fruit growth commences. Following auxin treatment, average ovary fresh weight increased 0.4 mg (statistically non-significant) and 3.6 mg (statistically significant, 5% level) during the first 24 and 36 hr, respectively. Ethanol-soluble radioactivity from foliar-applied ^{14}C-sucrose was not significantly greater in auxin-treated ovaries than in water controls until 48 hr after treatment. Relative import rate (dpm/h) paralleled growth rate (mg/h). Pollinated ovaries exhibited similar relationships between growth and mobilization. Thus, tomato fruit set per se does not appear to involve mobilization.

Fruit set is a critical factor in determining yield and resulting financial returns. To achieve regulated cropping, the limitations to set must be understood. Fruit set may be defined as an inductive phase beginning with pollination and culminating in the initiation of fruit growth. Accompanying morphological changes may include petal and stamen wilting and abscission (Leopold, 1964).

Endogenously produced growth hormones may control fruit set and fruit development. Exogenous applications of hormones, especially auxins and gibberellins, induce parthenocarpy in a number of species (Gustafson, 1936;

Wittwer et al, 1957). Pollen extracts contain auxin-like and gibberellin-like activity (Thimann, 1934, Coombe, 1960) and can stimulate limited fruit set in some species (Gustafson, 1937). Pollen germination and tube growth stimulate auxin production in tobacco flowers (Muir, 1942), although not all species exhibit increased hormone production following pollination (Luckwill, 1953; Nitsch et al, 1960; Wiltbank and Krezdorn, 1969).

Prior to anthesis, flowers are poor sinks for nutrients (Hale and Weaver, 1962, Linck and Swanson, 1960). Within a few days of fertilization, ovaries become strong sinks. Competition among fruit (Marfe and Murneek, 1953) and between fruit and shoots (Abbott, 1960) can reduce fruit growth rates and percent set. Fruit set of auxin-induced tomato ovaries on trusses cultured in vitro increases linearly with increasing media sugar concentration (Leopold and Scott, 1952).

Fruit exert control over translocation of materials to them. Growing fruit may stimulate net photosynthesis rates directly (Fisher, 1977; Hall, 1977) or indirectly via stimulation of leaf export rates (Williams and Williams, 1978). Although the effect on leaf export rates may be due to the sink effect of the fruit, phloem loading at the sources and/or longitudinal transfer processes may be stimulated also.

Hormones may mediate the mobilization effect. Auxins and gibberellins mobilize carbohydrates to hormone-treated region of fruit in several species (Hatch and Powell, 1969; Weaver et al, 1969; Patrick and Wareing, 1973) and stimulate leaf export rates (Khan and Sagar, 1966). Synergism between auxins, GAs, and cytokinins has been observed also. The presence of hormones during fruit set and early fruit development and their apparent

effectiveness in mobilization when exogenously applied suggest a similar endogenous role. The purpose of this research was to investigate the mobilizing ability of auxin-treated tomato ovaries in relation to fruit set, and to determine when mobilization begins in relation to early growth.

MATERIALS AND METHODS

General Procedures

Plant material. Determinate dwarf tomato plants (Lycopersicon esculentum Mill. cv Farthest North) were greenhouse-grown (temperature range 22 $\pm$ 3°C with extremes of 18° and 35°) without supplemental lighting at East Lansing, MI., between May and September, 1978, unless otherwise noted. Plants were selected for uniformity of vegetative and reproductive development, and prepared by removing a) axillary and terminal apices and lateral stems, b) post-anthesis flowers and c) trusses bearing growing fruit. Two neighboring trusses with a mutually subtending mature leaf served as the basic experimental unit. Two flowers which had not reached anthesis were left on each truss.

Induction of fruit set. Two flowers per truss were emasculated by removing petals, stamens, and style. Ten µl of distilled water was applied to one ovary per truss, and 10 µl of a solution of naphthoxyacetic acid (NOA) was applied to the other. In the first experiment 10^{-2}M NOA in 50% ethanol was used; subsequent experiments employed 10^{-3}M NOA in 5% ethanol Some ovaries treated with the higher concentration exhibited some tissue browning at the stylar scar and sepals due to the ethanol concentration, though fruit growth rates and percent set were similar for both. Six Ovaries were used per treatment per experiment, and both trusses of an individual plant were treated alike. Thus, ovaries from three plants were sampled at each time interval.

In experiments involving pollination, flowers were selected when the petals had reflexed and the stigma was visible at the tip of the fused stamens. Preliminary work indicated that the stigma was most receptive at that time. The flowers were emasculated with care to avoid damage to the style. The upper half of the style of one ovary of each pair was removed to prevent pollination, while fresh pollen was applied to the stigma of the second.

Treatments were applied on a schedule which allowed ^{14}C-scurose labelling and sample collection of all ovaries within an experiment between 7:00 and 9:00 a.m.

Labelling with ^{14}C-sucrose. ^{14}C-sucrose was used to monitor the translocation of photosynthate between source (leaf) and sink (ovary). To the upper surface of the basal leaflet of the subtending leaf, 0.75 µCi ^{14}C-sucrose (sp. act. 48 mCi/mM; source, Cal Atomic and Schwarz/Mann; purity, >99%) in 5 µl 5% ethanol was applied in drops spread over a small area of the leaf surface to one side of the midvein. Preliminary work indicated that absorption averaged 10% or more, though factors such as leaf age, cuticle characteristics, temperature, and relative humidity (Vickery and Mercer, 1964; Greene and Bukovac, 1971) probably have caused some variation.

Sample collection and analysis. The ovaries were excised 24 hr after ^{14}C-sucrose application, except as otherwise noted. Fresh weights were immediatley obtained using preweighed, capped vials. Sucrose was extracted by macerating in 1 ml hot 80% ethanol. Ethanol solutions were analyzed by adding 19 ml dioxane:naphthalene:PPO cocktail and counting each sample for 5 min in a LS-100 Beckman Liquid Scintillation counter. Activities

were corrected for efficiency, background, and quenching, and data are expressed as dpm.

Procedures for specific experiments.

Exp. 1 and 2. To determine when a) growth and b) mobilization of sucrose to the ovary were first detectable, ovaries were treated in Exp. 1 with either distilled water or NOA at 10^{-2}M and harvested 0, 24, 36, 48, 60, and 72 hr after treatment. ^{14}C-Sucrose was applied 24 hr prior to ovary collection. Fresh weight was compared with radioactivity to evaluate whether the two increased simultaneously or one preceded the other. The experiment was repeated (Exp. 2), except that a sample was taken at 12 hr to evaluate early response. The weight measurements from 0 - 36 hr in Exp. 2 were high due to humid conditions in the greenhouse.

Exp. 3. Since the results of experiments 1 and 2 indicated that both growth and mobilization were evident at 48 hr, ovaries were sampled more frequently in a third experiment (Exp. 3). Ovaries were treated with either distilled water or 10^{-3}M NOA and samples were collected 24, 27, 30, 33, 36, 42, and 48 hr after treatment. ^{14}C-Sucrose was again applied 24 hr prior to ovary collection.

Exp. 4. Previous experiments had indicated that NOA-treated ovaries did not accumulate significantly more labelled sucrose from a subtending leaf within 12 hr of NOA-treatment than did control ovaries. However, this might have been due to slow absorption of sucrose by the leaf rather than failure of the ovary to attract sucrose. In all previous experiments sucrose had been applied 24 hr prior to sample collection, regardless of the time of NOA application. Diffusion through the cuticle and through epidermal and mesophyll cells into the apoplast and uptake by the

parenchymous phloem-loading cells might have taken several hours. This could have reduced the time during which a significant quantity of ^{14}C-sucrose would have been available for translocation.

To determine if earlier application of ^{14}C-sucrose would increase the ^{14}C content of NOA-treated ovaries relative to controls, sucrose was applied 24 hr prior to treatment with water or NOA, and ovaries were sampled 0, 12, and 24 hr after treatment. The experiment was repeated.

Exp. 5. To ascertain whether growth and mobilization in auxin-treated ovaries paralled those in pollinated ovaries, the following experiment was performed. Tomato plants used here were winter-grown in the greenhouse with supplemental lighting, and subsequently moved to a growth chamber with a 16 hr light period and a day/night temperature of 23/26^{o}C. Because of low light levels and temperatures in the greenhouse, floral development was not normal on a large number of trusses; fasciated pistils were common though care was taken to avoid using them.

Flowers were pollinated or styles were cut, and ovaries were harvested 24, 48, and 72 hr after treatment.

As described above ^{14}C-sucrose was applied 24 hr prior to sample collection, and the tissues were extracted in 80% EtOH. The experiment was repeated, and additional ovaries were treated with NOA to compare growth patterns.

Effect of pooling data from several experiments. To increase the possiblity of detecting real differences in growth and sucrose accumulation, the data from the preceding experiments and several similar ones were pooled. Plants from separate experiments were of different ages and experienced

different environmental conditions during ^{14}C-sucrose absorption and translocation and ovary growth. These differences were factored out by using plants as blocks.

RESULTS AND DISCUSSION

Exp. 1 and 2. Forty-eight hours after auxin treatment ovaries had increased 3- to 5-fold in fresh weight (Table 1; Figures 1 and 2). Fresh weight increases were statistically significant (5% level) after 48, 60, and 72 hr, whereas the small increases observed in control ovaries were not. The dramatic weight increase between 36 and 48 hr implied that growth had begun earlier than 48 hr. Marre and Murneek (1953) also observed an increase in fresh and dry weight of tomato ovaries by 48 hr after auxin treatment.

Total ethanol-soluble radioactivity (dpm) per ovary paralleled fresh weight, although differences due to auxin treatment were not significant until 60 (Exp. 1) or 72 hr (Exp. 2) after treatment. A marked increase in activity was observed at 24 hr in Exp. 1. However, the increase was not statistically significant, did not occur in Exp. 2 (or in preliminary work), and hence must be discounted. Increases in activity at 48 hr might have been significant had more replications been used (see Table 4).

When radioactivity was corrected for ovary size by dividing dpm per ovary by weight per ovary to give a relative value for sink activity (Wareing and Patrick, 1975), only two sample values were significantly greater than those for untreated ovaries at 0 hr, and values for NOA-treated ovaries were consistently greater than those for control ovaries only in

Table I. Effects of auxin treatment (0 hr) on tomato ovary growth and mobilization of ^{14}C from leaf treated with ^{14}C sucrose 24 hr prior to sample collection. Exp. 1 and 2. All values are means for 6 ovaries.

Time after Tmt (hr)	Activity (dpm)		Fresh Wt. (mg)		dpm/mg		dpm/mg incr.[z]
Tmt	Water	NOA	Water	NOA	Water	NOA	
Exp. 1							
0	17.3 a[y]		2.33 a		10.2 a		--
24	127.3 a	533.3 a	1.48 a	1.33 a	110.7 a	326.8 ab	-533.0
36	35.0 a	68.2 a	1.05 a	2.92 a	37.6 a	24.9 a	42.7
48	168.8 a	454.7 a	1.95 a	8.42 b	105.7 a	90.9 a	82.7
60	164.0 a	1193.7 b	3.55 ab	15.90 c	47.0 a	98.0 a	159.6
72	41.2 a	1363.0 b	4.20 ab	17.90 c	10.4 a	66.0 a	681.5
Exp. 2							
0	9.7 a		2.83 a		3.1 a		--
12	11.0 a	47.8 a	4.80 a	4.92 a	1.5 a	12.5 a	--
24	0.0 a	7.5 a	6.08 a	5.63 a	0.0 a	1.0 a	2.5
36	45.0 a	120.3 a	6.93 a	5.72 a	5.8 a	16.5 ab	1333.3
48	0.0 a	405.7 ab	6.40 a	16.40 b	0.0 a	19.1 ab	38.0
60	0.0 a	466.0 ab	6.12 a	24.43 b	0.0 a	15.5 ab	58.0
72	0.0 a	740.0 b	5.45 a	38.02 b	0.0 a	24.4 b	54.4

[z]Calculated as total dpm over the difference in fresh weight from the preceding measurement.

[y]Mean separation among treatments within experiments by Duncan's Multiple Range Test, 5% level.

Figure 1. Effect of auxin treatment of tomato ovaries on ovary growth and mobilization of ^{14}C from leaf treated with ^{14}C-sucrose. A. Average fresh weight (mg) of tomato ovaries treated with distilled water or 10^{-2}M NOA at intervals from 0 to 72 hrs after treatment. B. Average ethanol-soluble radioactivity (dpm) per ovary accumulated in 24 hr prior to sample collection. All values are averages for 6 samples.

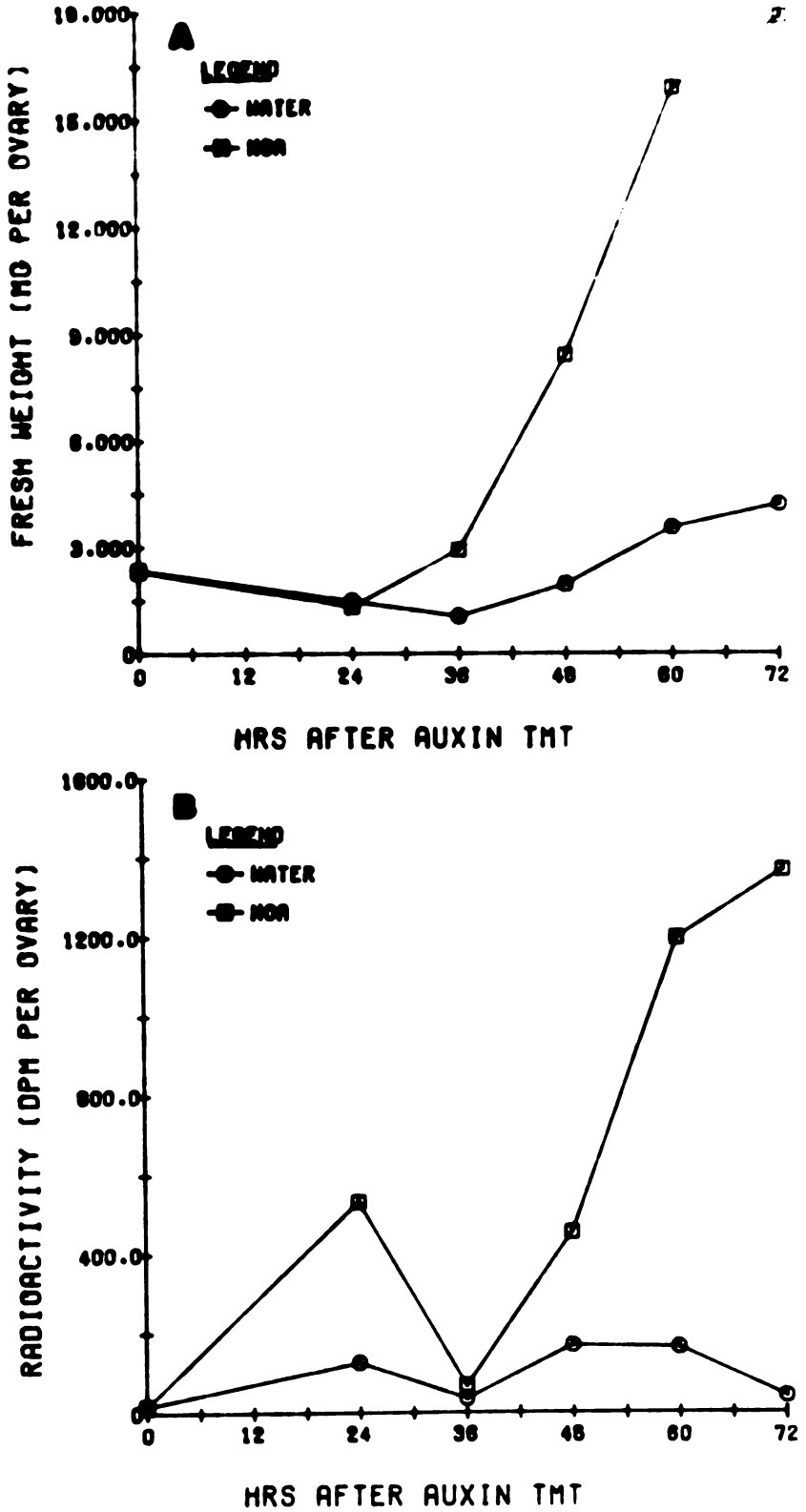
A
LEGEND
WATER
NAA
FRESH WEIGHT (MG PER OVARY)
18.000
15.000
12.000
9.000
6.000
3.000
0
0
12
24
36
48
60
72
HRS AFTER AUXIN TMT
B
LEGEND
WATER
NAA
RADIOACTIVITY (DPM PER OVARY)
1600.0
1200.0
800.0
400.0
0
0
12
24
36
48
60
72
HRS AFTER AUXIN TMT

FIGURE 1

Figure 2. Effect of auxin treatment of tomato ovaries on ovary growth and on mobilization of ^{14}C from leaf treated with ^{14}C-sucrose. A. Average fresh weight (mg) of tomato ovaries treated with distilled water or 10^{-3}M NOA at intervals from 0 to 72 hr after treatment. B. Average ethanol-soluble radioactivity (dpm) per ovary accumulated in 24 hr prior to sample collection. All values are averages of 6 samples.

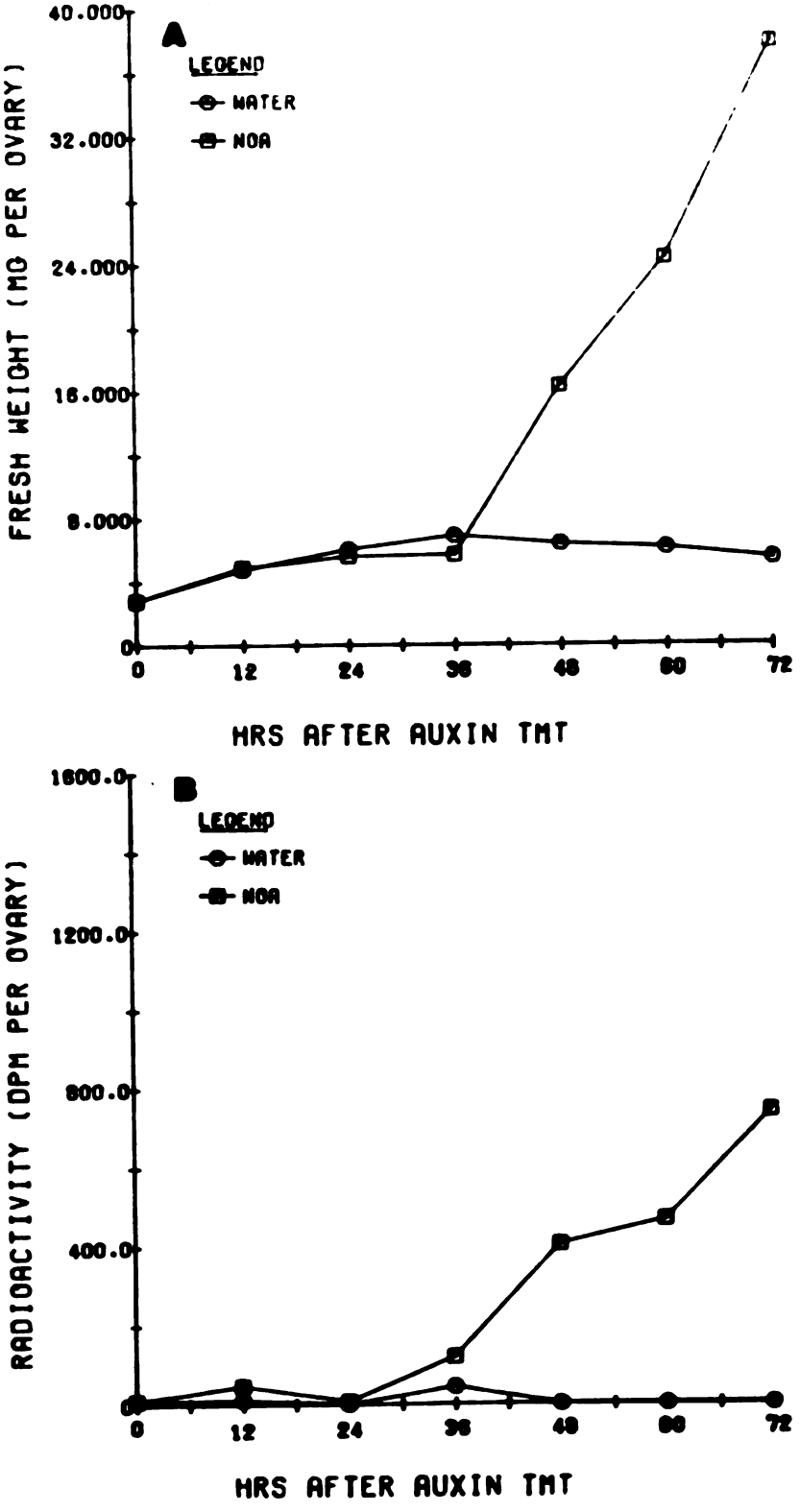
A
LEGEND
WATER
NOA
FRESH WEIGHT (MG PER OVARY)
40.000
32.000
24.000
16.000
8.000
0
0
12
24
36
48
60
72
HRS AFTER AUXIN TMT
B
LEGEND
WATER
NOA
RADIOACTIVITY (DPM PER OVARY)
1600.0
1200.0
800.0
400.0
0
0
12
24
36
48
60
72
HRS AFTER AUXIN TMT

FIGURE 2

Exp. 2. If the results are evaluated as dpm per ovary per mg increase in weight, basing mobilizing ability on the increase in weight, a different picture emerges. In Exp. 1, increasing values were observed for each 12 hr period from 24 to 72 hr. A different pattern was noted in Exp. 2, though early weights were not reliable (note Materials and Methods). The results, of Exp. 1 at least, suggest that mobilizing ability increases as sink size increases and is weak or nil until growth begins.

Exp. 3. Evaluation of growth and ^{14}C-sucrose accumulation at 3 to 6 hr intervals between 24 and 48 hr after treatment with water or NOA indicated that both total radioactivity per ovary and fresh weight gain were significant at 30 hr after NOA treatment, although increases were evident by 24 and 27 hr (Table 2, Figure 3). Values for neither radioactivity nor fresh weight were significant at 36 or 42 hr, though both increased significantly by 48 hr. Radioactivity per mg ovary tissue was significantly affected only once (30 hr), even though values for NOA-treated ovaries were consistently greater than control ovaries. The results, calculated as dpm per ovary per mg increase in weight per ovary, exhibited nearly the same pattern as observed in Exp. 1, a sequential increase at each time from 24 to 36 hr and 48 hr.Together with the results of Exp.1 and 2., these data suggest that sucrose is not being mobilized prior to growth, and that mobilizing ability exhibits change only after growth begins.

Exp. 4. Allowing a 24 hr period for sucrose uptake by the treated leaf prior to ovary treatment did not alter the response (Table 3). Activity at 12 or 24 hr was not greater than that at 0 hr regardless of treatment. Auxin-treated ovaries exhibited a slight but statistically non-significant

Table 2. Effects of auxin treatment (0 hr) on tomato ovary growth and mobilization of ^{14}C from leaf treated with ^{14}C-sucrose 24 hr prior to sample collection Exp. 3. All values are means for 6 ovaries.

Time (hr)	Tmt	Activity (dpm)	Fresh Wt. (mg)	dpm/mg	dpm/ mg incr.[z]
24	water	18.5 a[y]	2.75 a	5.0 a	--
24	NOA	156.5 a	4.00 a	41.7 ab	110.4
27	water	51.5 a	3.22 a	15.8 a	--
27	NOA	321.3 ab	4.58 a	71.0 ab	465.0
30	water	62.5 a	3.32 a	18.2 a	--
30	NOA	930.8 bc	5.90 bc	165.9 b	650.0
33	water	48.8 a	3.60 a	13.6 a	--
33	NOA	875.7 bc	5.98 bc	134.6 ab	10337.5
36	water	53.2 a	3.53 a	14.4 a	--
36	NOA	323.0 ab	9.57 d	36.9 ab	75.2
42	water	9.0 a	3.57 a	2.5 a	--
42	NOA	453.3 abc	6.58 c	60.1 ab	-151.5
48	water	56.7 ab	4.30 ab	15.3 a	--
48	NOA	1088.3 c	8.50 d	123.3 ab	495.8

[z]Calculated as total dpm measured over the difference in fresh weight from the preceding measurement.

[y]Mean separation within columns by Duncan's Multiple Range Test, 5% level.

Figure 3. Effect of auxin treatment of tomato ovaries on ovary growth and mobilization of ^{14}C from leaf treated with ^{14}C-sucrose. A. Average fresh weight (mg) of tomato ovaries treated with distilled water or 10^{-3}M NOA, sampled at intervals from 24 to 48 hrs after treatment. B. Average ethanol-soluble radioactivity (dpm) per ovary accumulated in 24 hr prior to sample collection. All values are averages for 6 samples.

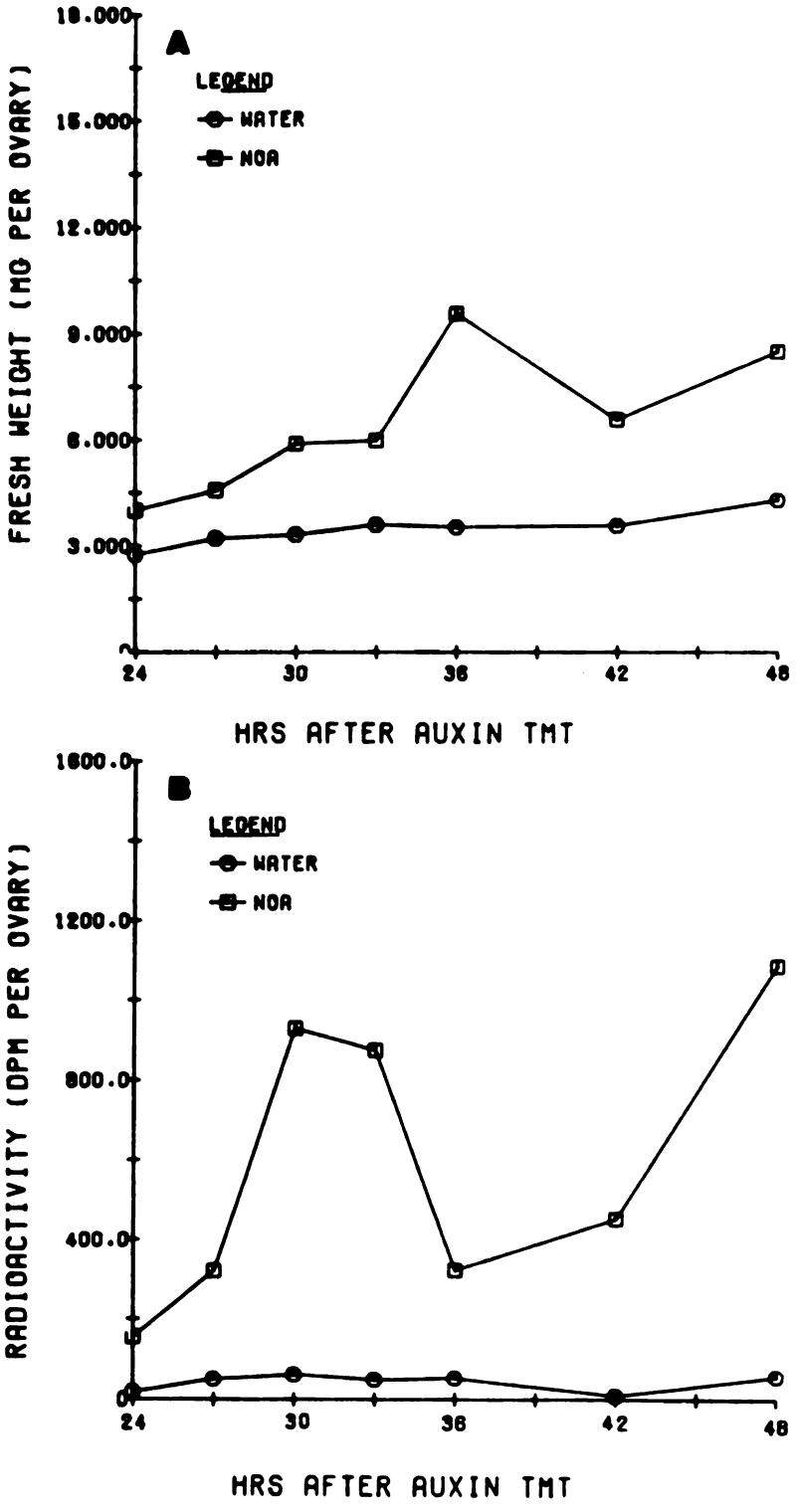
A
LEGEND
WATER
NOA
FRESH WEIGHT (MG PER OVARY)
18.000
15.000
12.000
9.000
6.000
3.000
24
30
36
42
48
HRS AFTER AUXIN TMT
B
LEGEND
WATER
NOA
RADIOACTIVITY (DPM PER OVARY)
1600.0
1200.0
800.0
400.0
0
24
30
36
42
48
HRS AFTER AUXIN TMT

FIGURE 3

Table 3. Effects of auxin treatment on tomato ovary growth and mobilization of ^{14}C from leaf treated with ^{14}C-sucrose 24 hr prior to auxin treatment. Expt. 4. All values are means for 12 ovaries.

Hrs after NOA Tmt.	Tmt	Fresh Wt. (mg)	Activity (dpm)	dpm/mg
0	--	1.86 a[z]	82.0 a	44.1 a
12	water	2.48 a	79.0 a	31.8 a
12	NOA	2.18 a	27.3 a	12.5 a
24	water	2.22 a	35.8 a	16.1 a
24	NOA	2.40 a	36.5 a	15.2 a

[z]Mean separation within columns by Duncan's Multiple Range Test, 5% level.

increase in fresh weight at 24 hr. Morris and Thomas (1968) observed that foliar applied ^{14}C-sucrose was well distributed within pea plants 24 hr after application.

Effect of pooling data from several experiments. Data for 24, 36 and 48 hr (Table 4) indicate that the effects of NOA on ovary weight are significant (5%) level) at 36 hr whereas its effect on mobilization does not become significant until 48 hr after treatment. Although activity increases at 24 and 36 hr, lack of a sequential increase with time indicates that mobilization is not occurring.

Exp. 5. Forty-eight hours after pollination, a significant 3-fold increase in ovary fresh weight was observed (Table 5, Figure 4). A difference between pollinated and control ovaries was noted as early as 24 hr, and this difference was greater than between control and auxin-treated ovaries observed in previous experiments. The growth rate of the pollinated ovaries also was much greater over the 72 hr period of analysis and fresh weights of control ovaries were greater than observed previously. Growth of NOA-treated and pollinated ovaries was compared, and the results indicated that growth rates were parallel (data not shown).

Total radioactivity per ovary appeared to parallel fresh weight increase but rose more slowly. Activity in pollinated ovaries differed significantly (5% level) from that in controls of 72 hr only, though a small difference was evident at 48 hr. Analysis of activity either per unit weight or per unit weight increase resulted in non-significant differences between pollinated and control ovaries for all sampling times.

Table 4. Effects of auxin treatment (0 hr) on tomato ovary growth and mobilization of ^{14}C from leaf treated with ^{14}C-sucrose 24 hr prior to sample collection. Pooled data for several experiments.

Observation	Tmt	Time (Hr after NOA treatment) 24	36[z]	48[y]
dpm/ovary	water	129[x]	44	53
	NOA	210[x] n.s.	171 n.s.	505*
Weight/ovary (mg)	water	2.16[y]	2.59	4.34
	NOA	2.54[y]	6.24**	11.11***

[z]Mean of 18 ovaries
[y]Mean of 23 ovaries
[x]Mean of 41 ovaries
*Significantly different from water treatment at the 5(*). 1 (**), or 0.1 (***) % level.

Table 5. Effects of pollination (0 hr) on tomato ovary growth and mobilization of ^{14}C from leaf treated with ^{14}C-sucrose 24 hr prior to sample collection. Exp. 5. All values are means for 12 ovaries.

Time (hr)	Tmt	Activity (dpm)	Fresh Wt. (mg)	dpm/mg	dpm/ mg incr.[z]
24	Style cut	58 a[y]	4.2 a	17.6 a	--
24	Pollinated	72 a	7.4 ab	9.8 a	4.4
48	Style cut	63 a	3.4 a	20.4 a	--
48	Pollinated	138 a	14.8 b	12.2 a	10.1
72	Style cut	82 a	5.0 a	15.2 a	--
72	Pollinated	553 b	46.3 c	11.6 a	15.0

[z]Calculated as total dpm measured over the difference in fresh weight from the preceding measurement.

[y]Mean separation within columns by Duncan's Multiple Range Test, 5% level.

Figure 4. Effect of pollination on tomato ovary growth and mobilization of ^{14}C from leaf treated with ^{14}C-sucrose. A. Average fresh weight (mg) of pollinated or control (style cut) ovaries sampled at intervals from 24 to 72 hrs after treatment. B. Average ethanol-soluble radioactivity (dpm) per ovary accumulated in 24 hr prior to sample collection. All values are averages of 12 samples.

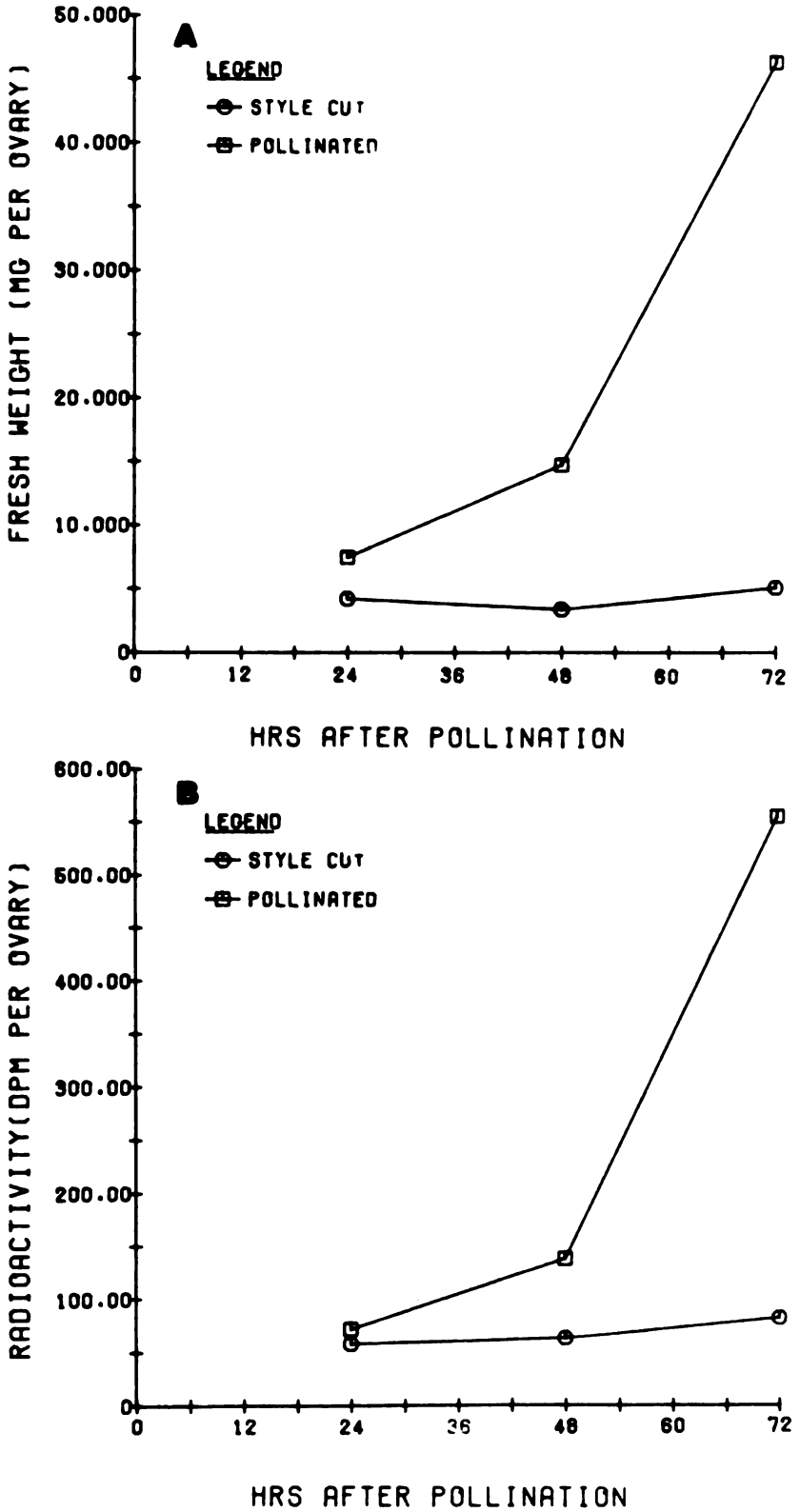
A
LEGEND
STYLE CUT
POLLINATED
FRESH WEIGHT (MG PER OVARY)
50.000
40.000
30.000
20.000
10.000
0
0
12
24
36
48
60
72
HRS AFTER POLLINATION
B
LEGEND
STYLE CUT
POLLINATED
RADIOACTIVITY(DPM PER OVARY)
600.00
500.00
400.00
300.00
200.00
100.00
0
0
12
24
36
48
60
72
HRS AFTER POLLINATION

FIGURE 4

Comparison of the results of Exp. 5 with those of Exp. 1 - 3 suggests that patterns of growth and accumulation in pollinated and NOA-treated ovaries are similar. Fresh weight increases in both were statistically significant at 48 hr, though increases as early as 24 hr were evident. Accumulation of ^{14}C tended to follow the same pattern. As sink size increased the relative quantity of imported sucrose increased. This is not surprising since the quantity of reducing sugars, hydrolytic products of sucrose, increase with increasing fruit size in tomato (Marre and Murneck, 1953) and watermelon and pepper (Walker and Hawker, 1976).

Wilson (1970) suggests that sink strength can be equated with import rate. The data from Exp. 1 - 3, using ^{14}C-sucrose import as a relative value for import rate indicate that import rate remains constant through 36 hr and increases between 36 and 48 hr, while growth rate increases over each interval until it assumes a constant value (Figure 5). Thus, sink strength does not appear to increase following auxin treatment until growth is apparent.

Barring the possibility that the sepals of the fruit itself may provide sufficient photosynthate for fruit set, the data indicate that mobilization of ^{14}C-sucrose from a subtending leaf to a treated ovary is not significant during fruit set and therefore is not a crucial aspect of the phenomenon. Translocation of the labelled sugar from the source leaf was more closely associated with fruit growth than with fruit set.

Figure 5. Rate of ^{14}C import (dpm/hr) and growth (mg/hr) of tomato ovaries during sequential time intervals from 0 to 72 hrs after auxin treatment. Data from Exps. 1-3.

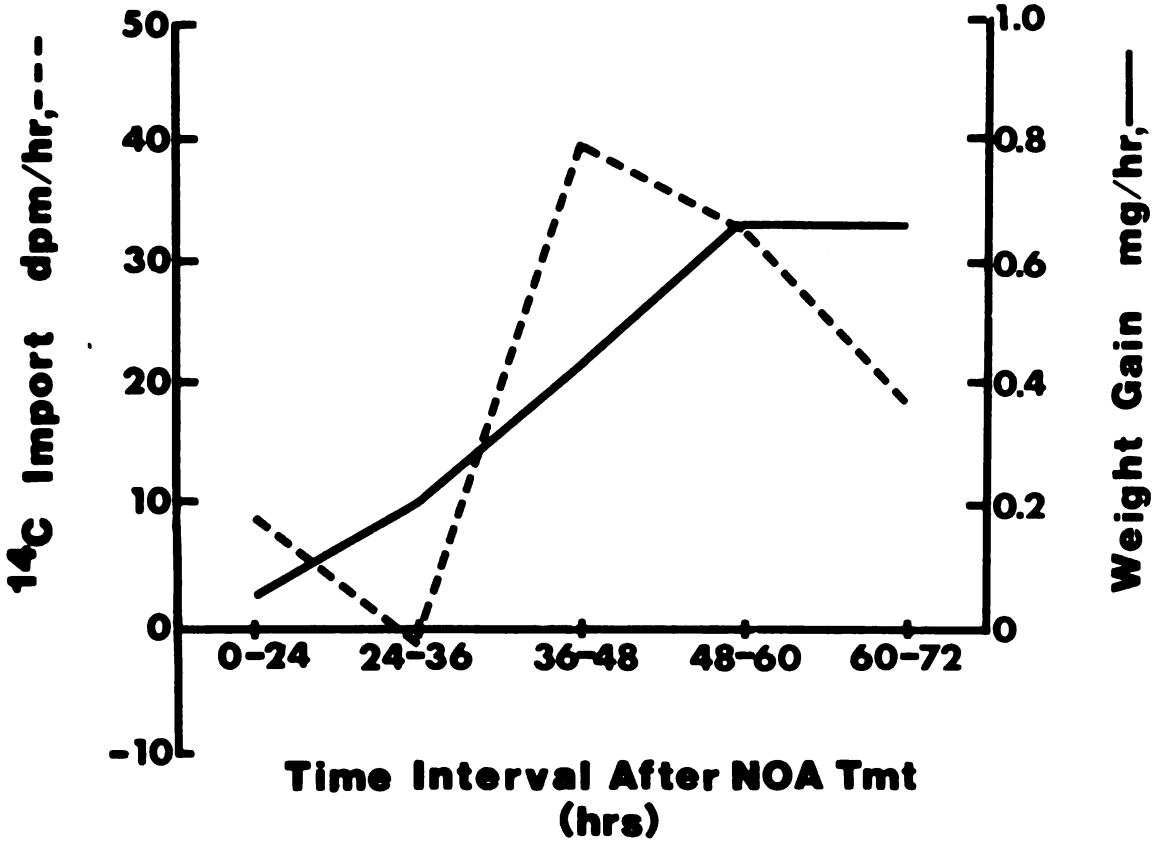
50
40
30
20
10
0
-10
1.0
0.8
0.6
0.4
0.2
0
0-24
24-36
36-48
48-60
60-72
14C Import dpm/hr,---
Weight Gain mg/hr,——
Time Interval After NOA Tmt
(hrs)

FIGURE 5

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APPENDIX A

DETERMINATION OF PERCENTAGE OF ABSORPTION OF FOLIAR APPLIED SUCROSE

DETERMINATION OF PERCENTAGE OF ABSORPTION OF FOLIAR APPLIED SUCROSF

Foliar application of ^{14}C-sucrose has been utilized by a number of workers to label the photosynthate pool. Sovonick et al (1974) and Housely et al (1977) applied ^{14}C-sucrose to abraded surfaces of leaves of sugar beet and soybean, respectively, to study translocation patterns. Both groups compared the movement of assimilates of $^{14}CO_2$ vs ^{14}C-sucrose and found identical patterns of distribution. Morris and Thomas (1968) applied ^{14}C-sucrose to the unabraded surface of pea leaves to study distribution within the plant. Although the total amounts of ^{14}C recovered from the untreated plant regions varied, consistent patterns of distribution were observed. A variety of factors, including leaf, cuticle characteristics, air temperature, relative humidity, and solute concentration (Vickery and Mercer, 1964; Franke, 1967; Greene and Bukovac, 1971; Adedipe and Ormrod, 1975), can influence absorption of foliar-applied compounds. To determine the amount of ^{14}C-sucrose absorbed by the foliar application method, the following experiment was performed.

Greenhouse-grown cherry tomato plants (Lycopersicon esculentum Mill. cv Farthest North) were used. To the adaxial surface of a fully-expanded leaflet, 5 µl of ^{14}C-sucrose (sp. act. 48 mCi/mM) in 5% EtOH was applied in microdroplets in an area approx. 1 cm in diameter, avoiding prominent veins. Concentrations used were: 3.3×10^5, 5.1×10^5, 6.8×10^5, 1.2×10^6, and 1.7×10^6 dpm in 5 µl. Immediately following drying of the droplets, the treated tissue was excised from the leaflet and rinsed

with 2 ml 80% EtOH dripped slowly across the surface to remove unabsorbed sucrose. Aliquots of the rinses were analyzed via liquid scintillation. The leaflet sections were ground in 2 ml 80% EtOH and aliquots were taken from the macerates for liquid scintillation analysis. Results were corrected on background, quenching, and efficiency. Each application was replicated 3 times and some concentrations were used for a second experiment.

Total recovery varied considerably (Table A). The total applied was calculated from an average of three 2 µl samples of the test solutions. The variability emphasizes the difficulty in obtaining homogenous solutions and applying exact amounts with a microsyringe.

Absorption, expressed as either percent of recovered or applied amounts, was less variable. Absorption as a percent of the total recovered increased with concentration applied, ranging from 9 to 17%, with but one exception. Vickery and Mercer (1964) observed the same phenomenon in bean leaves. Assuming complete recovery of the unabsorbed sucrose, 10% or more of the total applied (or recovered) was absorbed. The foliar application method therefore should have sufficiently labelled the photosynthate pool.

Table A. Effect of concentration of ^{14}C-sucrose in 5% EtOH on absorption by tomato leaflets.[z]

^{14}C applied as ^{14}C-sucrose in 5µl (dpm)	^{14}C Recovered		
	Total (%)	Absorbed (% of recovered)	Absorbed (% of applied)
3.3×10^{5}[y]	108.3 ± 13.8	9.3 ± 2.7	10.3 ± 4.5
5.1×10^{5}[x]	115.0 ± 33.0	10.5 ± 3.0	12.4 ± 7.0
6.8×10^{5}[y]	121.6 ± 49.0	11.7 ± 3.3	14.6 ± 9.0
1.2×10^{6}[x]	78.2 ± 33.3	10.2 ± 5.6	7.0 ± 3.2
1.7×10^{6}[x]	84.7 ± 13.4	17.4 ± 10.4	14.6 ± 9.0

[z]Means and standard deviations

[y]3 replicates

[x]2 experiments x 3 replicates

APPENDIX B

COMPARISON OF $^{14}CO_2$ vs ^{14}C-SUCROSE AS A SOURCE OF ^{14}C TO STUDY PHOTOSYNTHATE MOVEMENT DURING FRUIT SET

COMPARISON OF $^{14}CO_2$ vs ^{14}C-SUCROSE AS A SOURCE OF ^{14}C TO STUDY PHOTOSYNTHATE MOVEMENT DURING FRUIT SET

Preliminary work indicated tomato ovaries accumulated minimal amounts of radioactivity within 24 hr of auxin treatment. This raised the possibility that sucrose was not a good source of ^{14}C in spite of its successful use by others (Sovonick et al, 1974; Housley et al, 1977; Morris and Thomas, 1968). To test whether $^{14}CO_2$ was a better source of ^{14}C, the following experiment was performed.

Cherry tomato plants (Lycopersicon esculentum Mill. cv Farthest North) were prepared as in Exp. 1-4 (p. 22). Ovaries were treated at 0 hr with 10 µl of 10^{-3}M NOA or distilled H_2O. Also at 0 hr, to the source leaf either 0.75 µCi of ^{14}C-sucrose (sp. act. 48 mCi/mM) in 5 µl of 5% EtOH was applied, or $^{14}CO_2$ (sp. act. 10µCi/l) was supplied for 2 min to a 1 cm^2 area of the leaflet enclosed in a flow-through chamber. Three plants were used for each method. Analysis of $^{14}CO_2$-treated leaflets showed approx. 46,000 dpm was fixed during the 2 min. Twenty-four hours after labelling and ovary treatment (0 hr), ovaries were excised, macerated in hot 80% EtOH, and the macerates analyzed via liquid scintillation. Results are means of 6 ovaries.

Within 24 hr of labelling and auxin treatment, radioactivity was detected in the ovaries, both $^{14}CO_2$ and ^{14}C-sucrose giving similar values (Table B). Water controls appeared to accumulate as much or more label as NOA-treated ovaries, although differences were non-significant. Mobilization was not occurring to a significant degree by 24 hr. However, ^{14}C-sucrose appears to be useful for studying photosynthate distribution.

Table B. Effect of treating source leaf with $^{14}CO_2$ vs. ^{14}C-sucrose on accumulation of activity by tomato ovaries 24 hr after auxin treatment of ovaries and treating source leaf. All values are means of 6 ovaries.

Source of ^{14}C	Ovary Tmt	Activity
$^{14}CO_2$	Water	268 a
	NOA	368 a
^{14}C-sucrose	Water	344 a
	NOA	67 a

[z]Mean separation within column by Duncan's Multiple Range Test, 5% level.

APPENDIX C

MOBILIZING ABILITY OF TOMATO APICES, FLORAL BUDS, AND AUXIN-TREATED OVARIES

MOBILIZING ABILITY OF TOMATO APICES, FLORAL BUDS, AND AUXIN-TREATED OVARIES

Preliminary work indicated that 24 hr after auxin treatment, tomato ovaries were accumulating no more ^{14}C-sucrose from a subtending leaf than were control ovaries. To determine if other sinks could effectively mobilize ^{14}C-sucrose, the mobilizing abilities of several sinks were compared. Khan and Sagar (1966) concluded that vegetative apices of tomato plants were weak sinks in comparison with fruit bearing trusses, considered strong sinks. Apices did mobilize ^{14}C-assimilates, however. Hale and Weaver (1962) found that ^{14}C-assimilate accumulation by developing grape inflorescences was significant. Therefore, the mobilizing abilities of vegetative apices and floral buds of tomato were compared with those of auxin-treated and control ovaries.

Six unpruned cherry tomato plants were included in Exp. 1 (see p. 22). Only axillary shoots and growing fruit were removed from the plants. To the adaxial surface of the basal leaflet of the uppermost fully-expanded leaf (corresponding to the treated leaflet in Exp. 1), 0.75 µCi of ^{14}C-sucrose (sp. act 48 mCi/mM) in 5 µl of 5% EtOH was applied. Twenty-four hours later, the apical of 4 cm of each plant and one floral bud was excised. Each sample was macerated in 2 ml of hot 80% EtOH, and the macerates were analyzed via liquid scintillation. Results are means of 6 samples, and mean values of activity of auxin and water treated ovaries are included for comparison (see Table 1).

Apices and floral buds were strong sinks, accumulating 3 to 5 times the activity of auxin-treated ovaries (Table C). Lack of statistical significance

probably reflects the small number of replications. The response of ovaries at 24 hr is unusual; preliminary experiments indicated they were ineffective sinks at this time. The opposite of Khan and Sagar's (1966) findings appears to be true when fruit are recently set; young fruits were weak sinks compared to vegetative apices, although different results might have been obtained had ovaries been allowed to compete with apices and floral buds on the same plants. These results conclusively established that ^{14}C-sucrose is transported from the source leaf to potential sinks.

Table C. Comparative ability of tomato plant apices, floral buds, and auxin-treated ovaries to mobilize ^{14}C during 24 hr following application of ^{14}C-sucrose to mature apical leaflet. All values are means for 6 samples.

Sink	Tmt	Activity dpm[z]
Apex	--	2481 a
Floral bud	--	1497 a
Ovary, 24 hr after tmt	water	127 a
	NOA	533 a
Ovary, 48 hr after tmt	water	126 a
	NOA	411 a

[z]Mean separation within column by Duncan's Multiple Range Test, 5% level.

APPENDIX D

EVALUATION OF THE SEPALS AS A SOURCE OF PHOTOSYNTHATE FOR AN OVARY

EVALUATION OF THE SEPALS AS A SOURCE OF PHOTOSYNTHATE FOR AN OVARY

The available evidence indicates that no mobilization from a source leaf to a treated ovary occurs prior to growth (i.e., during fruit set). However, the effectiveness of other sources in exporting sugars has not been fully investigated. As tomato fruit grow, the sepals expand also (personal observation). This suggests some role for the sepals in fruit development, either passive or active. Since sepals are the most proximal tissues to an ovary and are undoubtedly capable of photosynthesis, they may contribute carbohydrates to an ovary during fruit set. This experiment examined sepal export of photosynthate during the 24 hr following auxin treatment of tomato ovaries.

Several greenhouse-grown cherry tomato plants (Lycopersicon esculentum cv Farthest North) were moved to a growth chamber (16 hr daylength, $23^{o}/26^{o}C$ day/night temp.) for this experiment. Fully-developed, pre-anthesis flowers were tagged and emasculated. The emasculated flowers were treated with 10 µl distilled H_2O or 10^{-3}M NOA 6, 12, and 24 hr prior to sample collection. Six hours before collection, 3 µl of ^{14}C-sucrose (sp. act. 48 mCi/mM) containing 0.1 µCi in 5 % ethanol was applied to the outer surface of the sepals. Ovaries were collected, and were extracted in 2 ml 80% ethanol, and the extracts were analyzed via liquid scintillation. In the first experiment, each treatment was replicated 4 times; in the second, each was replicated 8 times.

Within the first 6 hr, auxin treatment significantly increased (5% level) the amount of label imported from the sepals (Table D). Subsequent

differences were not significant, although the 6 and 24 hr water controls and 24 hr NOA-treated ovaries did acquire a notable amount of radioactivity. Sucrose moves from a region of high concentration within a plant to one of lower concentration (Hartt and Korschak, 1965). Since sucrose is the main mobile assimilate in tomato plants (Walker and Ho, 1977) and applications to the sepals raise its concentration, the label might have been exported with endogenous sucrose without mobilization having occurred. However, the treated ovaries failed to acquire a significant amount at 12 or 24 hr. These results indicated that the auxin-treated ovaries did not mobilize sucrose from the sepals consistently prior to growth, and suggest that the early response (6 hr) was an artifact. Therefore the experiment provides no evidence that the sepals furnish sufficient photosynthate for fruit set.

Table D. Effect of auxin treatment (0 hr) of tomato ovaries on accumulation of ^{14}C from sepals treated with ^{14}C-sucrose 6 hr before sampling. All values are means of 12 ovaries.

Time after ovary tmt	Tmt	dpm/ovary[z]
6 hr	water	692 a
6 hr	NOA	1311 b
12 hr	water	137 a
12 hr	NOA	117 a
24 hr	water	266 a
24 hr	NOA	432 a

[z]Mean separation within columns by Duncan's Multiple Range Test, 5% level.

SUMMARY AND CONCLUSIONS

The foliar-application method of labelling the photosynthate pool was successful. Both growing fruit and apices mobilized significant quantities of ^{14}C. Ethanol extraction removed the soluble sugars, though the amount of ^{14}C in the insoluble fraction was not determined. Analysis of the ethanol-soluble sugars should give a relative indication of the mobilizing ability of tomato ovaries, because the quantities of both reducing sugars and starch increase in growing fruit (Marfe and Murneek, 1953).

Though variability was marked, the general patterns of growth in relation to mobilization were quite similar. Mobilization of ^{14}C-sucrose from a source leaf to a treated ovary did not begin until growth was occurring. Uptake of ^{14}C-sucrose at the source leaf was not limiting, thus an immediate response would be possible if fruit set were a mobilization phenomenon. Movement of ^{14}C from sepals to treated ovaries was not siginficant (except at 6 hr) indicating that they do not function as a consistent source during fruit set. Thus, fruit set does not appear to involve mobilization.

The labelled sucrose appeared to move into the ovaries in response to demand. As growth rate increased, sink demand, as judged from ^{14}C-sucrose import, increased. Wardlaw (1974) concludes that the available evidence indicates hormones do not actively stimulate phloem transport. Movement of sugars occurs down a gradient as a result

of sink demand. A growing ovary would steepen the gradient with time. Thus, greater amounts of ^{14}C would accumulate in the growing fruit at sequential intervals following set, as observed.

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