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Influence of Growth Regulator Treatments on Dry Matter Production, Fruit Abscission, and ^{14}C-Assimilate Partitioning in Citrus

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Abstract. Experiments were performed to monitor (1) uptake and translocation of foliar-applied microdroplets of ^{14}C hormones and (2) effects of multiple growth regulator sprays on foliar and fruit growth variables and photosynthate partitioning in Valencia orange trees (*Citrus sinensis* (L.) Osbeck). The uptake of ^{14}C-sucrose, ^{14}C-paclobutrazol (PP333), and ^{14}C-napthaleneacetic acid (NAA) in 6-month-old greenhouse-grown trees exceeded that of ^{14}C-abscisic acid (ABA) and ^{14}C-benzyladenine (BA) 48 h after microdroplet application. ^{14}C-sucrose transport from the application site was much greater than any other source, especially ^{14}C-BA. In a second study, 2-year-old Valencia orange trees were maintained under field conditions and were sprayed to foliar runoff (3×/week for 3 weeks) with BA, NAA, ABA, PP333, and gibberellic acid (GA_3) at 100 μM during flowering and early fruit set. Select branches were then briefly exposed to $^{14}CO_2$ and harvested 24 h later. Both GA_3 and BA sprays promoted foliar growth. BA also stimulated fruit growth, whereas GA_3 sharply increased fruit dry weight while fruit number decreased. BA and GA_3 enhanced ^{14}C assimilate export by the foliage to the developing fruit, and GA_3 was especially active in promoting fruit sink intensity (^{14}C/dry wt). The other compounds (NAA, ABA, PP333) restricted foliar and fruit growth. They also inhibited transport of ^{14}C assimilate from the leaves to the fruit. Results indicate that foliar-applied growth regulators can influence source-sink relations in citrus early in reproductive development by manipulating photoassimilate production and partitioning.

Growth regulators have been exogenously applied to citrus foliage and fruit to reduce premature fruit drop and enhance total yield (Cooper and Henry 1973,

Krezdorn and Cohen 1962). Growth regulators such as 2,4-dichlorophenoxyacetic acid (2,4-D) alone or in combination with gibberellic acid (GA_3), for example, have reduced fruit drop in oranges (Lima and Davies 1984). Floral dips of GA_3 have also been especially promotive in this regard (Brown 1974). Success in general, however, has been limited because of the uncertainty of rate, timing, and frequency of application.

The use of growth regulator sprays is based on the premise that they will be absorbed and act as chemical stimuli in a manner similar to endogenous hormonal pools. The mode of action of externally applied growth regulators and their interaction with the internal factors in citrus have received only slight attention (Bausher and Yelenosky 1986, Monselise and Goren 1978, Wang et al. 1985). More information is needed to link growth regulators with internal physiological processes vital for foliar functioning and reproductive growth.

The reduction of photosynthate production and distribution during the early reproductive period has resulted in abscission and reduced yield (Brun and Betts 1984, Herzog 1982, Mauk and Breen 1986, Pate and Farrington 1981). Assimilate distribution has been studied in citrus (Guy et al. 1981, Koch 1984a,b, Kriedeman 1970), but rarely during the critical period of flowering and fruit set. Early studies involving the exogenous application of kinetin (Kriedemann 1968) and gibberellin, GA_3 (Brown 1974), to citrus fruit showed that these growth regulators enhanced ^{14}C assimilate exportation by the foliage to developing reproductive structures. Therefore, a study was initiated (1) to examine the uptake and translocation of foliar-applied ^{14}C growth regulators, and (2) to evaluate further the influence of growth regulator sprays on reproductive organ abscission and photosynthate distribution between the foliage and fruit during flowering and early fruit set in citrus.

Materials and Methods

Foliar Application of ^{14}C Growth Regulators

Uniformly sized 2.5-month-old, greenhouse-grown Valencia orange trees (*Citrus sinensis* (L.) Osbeck) budded onto 1-year-old rough lemon rootstock were selected. Each plant consisted of 10–12 fully expanded leaves. The fifth and sixth leaves (numbered acropetally) were positioned abaxially on styrofoam boards so that they remained flat, which prevented the droplets of material from running off. Leaves were then briefly cleaned with 70% ethanol to remove any pesticide spray residue. Greenhouse conditions during treatment were 30/21°C day/night with a light intensity of 1700 $\mu E/m^2/sec$ at the time of application (midmorning). Treatments consisted of benzyl(8-^{14}C)adenine (57 $\mu Ci/\mu mol$; Amersham Corp., Arlington Hts, IL, USA), napthaleneacetic (carboxyl-^{14}C) acid (6.6 $\mu Ci/\mu mol$; California Bionuclear Corp., Sun Valley, CA, USA), DL-cis-trans-(2-^{14}C) abscisic acid (10 $\mu Ci/\mu mol$; Amersham Corp.), paclobutrazol [(2RS,3RS)-1-(4-chlorophenyl)-4,4-dimethyl-2-1,2,4-(3,5-^{14}C)-triazol-1-yl-pentan-3-ol) (3.5 $\mu Ci/\mu mol$; Imperial Chemical Industries, Goldsboro, NC, USA), and sucrose [^{14}C-(U)], (673 $\mu Ci/\mu mol$; New England Nuclear, Boston, MA, USA). Each ^{14}C solution was adjusted to a final concentration of 40% methanol and pH 6.5. The methanol concentration was chosen on the basis of previous research with foliar sprays in citrus (Krezdorn and Cohen

1962, and unpublished results) in which 40% methanol was used and showed no phytotoxic effect on the foliage and aided in compound penetration through the heavy cuticle characteristic of citrus species. This concentration was also necessary to completely solubilize 100 μm paclobutrazol and was thus used as the standardized base solution for all treatments. This facilitated comparison between ^{14}C droplet-uptake experiments and multiple, foliar growth regulator sprays.

Two leaves per plant were utilized with two different treatments applied per leaf. Each treatment was repeated four times. A 20-μl droplet of each ^{14}C growth regulator (30,000–60,000 disintegrations/min (DPM)) was applied midway between the leaf margin and midrib at the widest portion of the blade. Under the greenhouse conditions, the droplets took approximately 20–25 min to dry. The actual exposure sites (75-mm^2 disks) were removed at 12, 24, and 48 h after droplet application. The disks were floated upside down in distilled water for 1 h to remove the nonabsorbed ^{14}C compound, and an aliquot of the wash was assayed for ^{14}C activity to determine quantitatively the amount of nonabsorbed ^{14}C. Each disk was then dried for 24 h at 50°C prior to combustion in a sample oxidizer (Packard Instruments, model 306). ^{14}C activity per disk was measured in a liquid scintillation counter (LKB Instruments, model 1217) equipped with chemiluminescence correction. This served as a measurement of ^{14}C activity that was absorbed but not translocated from the application site. The remainder of each leaf (minus the application site) was also combusted to determine the percentage of total applied ^{14}C activity that was exported from the exposure area. Quench correction curves were prepared for each tissue type, and all values of ^{14}C activity were represented in DPM. Previous experiments revealed that there was no significant interchange of ^{14}C between leaves during the 48-h exposure period that could confound results. The entire stem and root systems were also assayed for ^{14}C activity via the sample combustion method and failed to exhibit any significant activity even on pooling all the sample (500–700 mg) aliquots of dried tissue.

Exogenous Spray Treatments

Foliar spray treatments consisted of benzyladenine (BA), gibberellic acid (GA_3), abscisic acid (ABA), napthaleneacetic acid (NAA), and paclobutrazol (PP333), each at 100 μM in 40% methanol and 0.1% Triton X-100. Foliar sprays were applied 3×/week for 3 weeks to 2-year-old Valencia orange trees originally budded onto Milam rootstock. Abaxial and adaxial surfaces were sprayed until runoff occurred. Trees were grown outdoors in 14-L pots of soil:sand (1:2, v/v) and drip-irrigated. Foliar treatments were applied from flowering through early fruit development to branches selected for uniformity. Dry weight of individual plant parts and abscission data were taken at harvest 3 weeks later.

$^{14}CO_2$ Pulsing

After 3 weeks of foliar sprays, four uniform branches from each spray treatment were selected for $^{14}CO_2$ exposure. Four branch units were placed in a

14-L airtight Plexiglas assimilation cell equipped with electric fans (for cooling and $^{14}CO_2$ circulation) and modified injection ports for facilitating $^{14}CO_2$ generation. The cell was sealed and $^{14}CO_2$ generated by injection of 1.5 ml 6 N HCl into two vessels, each containing 25 μCi of BA $^{14}CO_3$ (55 μCi/μmol; ICN Radiochemicals, Irvine, CA, USA). After 30 min of exposure to $^{14}CO_2$, the air in the cell was exhausted through a $^{14}CO_2$ trap to remove nonabsorbed $^{14}CO_2$. The cell was then opened and plants were removed. Approximately 24 h later the ^{14}C-exposed tissue was subdivided by nodes (lower, middle, and upper branch position) into leaves, fruitlets, and stem. Leaf area was measured, and all plant parts were dried at 50°C for 48 h prior to dry weight determination. ^{14}C activity was assayed after sample oxidation as previously described. There was no appreciable ^{14}C (less than 0.5%) found in any tissue below the $^{14}CO_2$-pulsed branch 24 h after exposure.

Results

^{14}C Hormonal Uptake and Translocation (Microdroplet Application)

Foliar absorption of ^{14}C-PP333 and ^{14}C-sucrose was more rapid than any other source 12 h after application (Fig. 1). Their uptake reached a maximum (62–65%) and then remained relatively constant, whereas the absorption of ^{14}C-NAA and ^{14}C-ABA continued to increase during the entire exposure period. Absorption of ^{14}C-BA also increased, but noticeably less than the other treatments.

Transport of ^{14}C-sucrose from the site of application was much higher than that of the other ^{14}C compounds, reaching a maximum at 12 h (Fig. 2). Translocation of ^{14}C-ABA and ^{14}C-NAA steadily increased throughout the exposure period but was less than that of ^{14}C-sucrose. ^{14}C-PP333 transport was fairly constant from 12 to 48 h (10–12%), and ^{14}C-BA exhibited very little translocation (2–5%).

Spray Treatment Effects

Response of Vegetative Parts

Foliage dry weight was increased 200% and 85% for BA- and NAA-treated branches, respectively, compared to the control (Fig. 3A). Sink intensity (^{14}C/dry wt) of the foliage was not as noticeably influenced by hormonal treatment as the other foliar parameters. Stem dry weight was increased 3.5× that of the control for the GA treatment (Fig. 3B). Stem sink intensity was very similar among treatments except for the marked decline (45%) associated with NAA spray.

Effects on Reproductive Tissue

BA and GA_3 treatments produced nearly 2× the total fruit dry weight of the control (Fig. 4). GA_3 resulted in a 2.4× increase in ^{14}C fruit activity (data

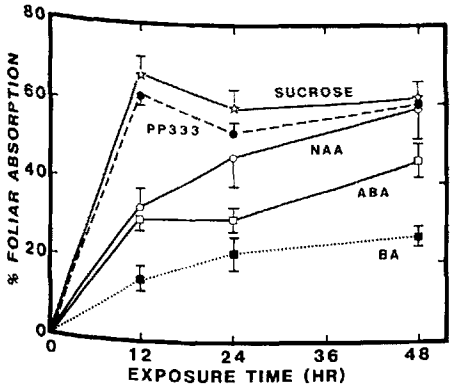

Fig. 1. Uptake of ^{14}C-labeled sources (^{14}C-sucrose, abscisic acid (ABA), napthaleneacetic acid (NAA), benzyladenine (BA), and paclobutrazol (PP333)) from 0 to 48 h after application to fully expanded Valencia orange foliage. The ^{14}C compounds were applied as 20-μl droplets in 40% methanol with 0.1% Triton X-100 added as a surfactant. Each data point is the mean ± SE of four replicates.

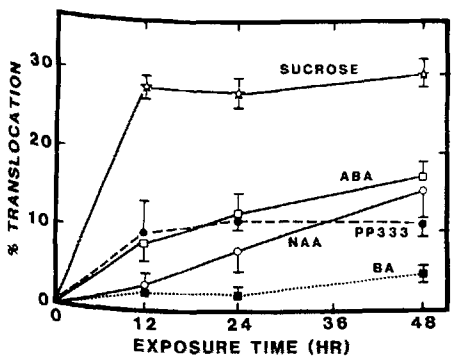

Fig. 2. Translocation of ^{14}C-labeled sources (same designations as Fig. 1) over a 48-h exposure period following their application to fully expanded leaves of Valencia orange. The ^{14}C compounds were applied as 20-μl droplets in 40% methanol with 0.1% Triton X-100. Translocation was expressed as the percentage of the total applied ^{14}C activity that was exported from the original application site (75-mm^2 leaf disk). Each data point is the mean ± SE of four replicates.

unpublished) and a 41% rise in fruitlet sink intensity (Fig. 4). The other growth regulators (NAA, ABA, PP333) led to a sharp decline in fruit growth and in levels of ^{14}C found in fruit tissue.

Total number of flowers produced per branch was consistently greater for those treatments that previously inhibited vegetative plant growth and ^{14}C levels (Table 1). Although PP333 and NAA substantially increased flowering (68% and 59%, respectively), the only treatments that appreciably reduced abscission were BA (52%) and ABA (63%) compared to the control (80%).

Partitioning of ^{14}C Activity

The foliage of the control contained the largest fraction of ^{14}C activity (65%) followed by the fruit (24%), and then stem tissue (11%) 24 h after $^{14}CO_2$ exposure (Fig. 5). The ^{14}C distribution pattern between the control and BA treatment was very similar; however, fruit and stem tissue of the GA_3 treatment had considerably higher values (10 and 9 percentage units, respectively) than the control. A greater percentage of the ^{14}C resided in the foliage and less in the fruit of the PP333, NAA, and ABA treatments. The fruit of the NAA- and

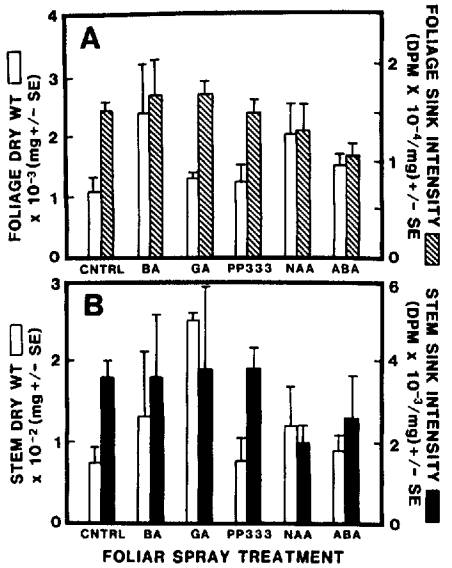

Fig. 3. Response of Valencia orange foliage (A) and stem (B) dry weight and sink intensity (^{14}C activity/mg dry wt) to foliar-applied growth regulator sprays (100 μm in 40% methanol with 0.1% Triton X-100). Plants were sprayed 3×/week for 3 weeks prior to brief exposure of selected branch units to $^{14}CO_2$ during early fruiting. Data are means ± SE of five replicates.

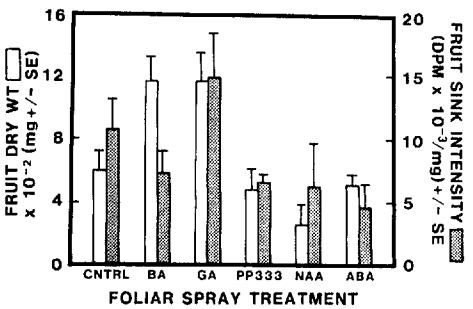

Fig. 4. Effect of foliar-applied growth regulator sprays (100 μm in 40% methanol with 0.1% Triton X-100) on Valencia orange fruit dry weight and sink intensity (^{14}C activity/mg dry wt). Plants were sprayed 3×/week for 3 weeks prior to brief exposure of selected branch units to $^{14}CO_2$ during early fruiting. Data are means ± SE of five replicates.

ABA-treated plants, for example, comprised only 3% and 10%, respectively, of the total recovered ^{14}C activity.

Partitioning of ^{14}C assimilate between the foliage and fruit was affected by both hormonal treatment and leaf canopy position within the branch (Fig. 6). Levels of ^{14}C were evenly distributed among leaves in most of the treatments; however, the values obtained for the GA_3 and BA treatments were noticeably higher. NAA treatment was the exception in which an acropetal decline in ^{14}C actually occurred.

The uppermost portion of the branch accounted for over 96% of the total ^{14}C recovered in fruit of the control (Fig. 6). This value fell to 70% and 74% in the BA and GA_3 treatments, respectively, as a greater proportion of the total fruit ^{14}C activity was found in those fruit residing in the lowermost portion of the branch. This was most evident in the GA_3 treatment. Partitioning of ^{14}C among the fruited nodes of the growth inhibitor treatments was severely restricted by the reduction in average fruit dry weight and sink intensity (Fig. 2, Table 1).

Table 1. Influence of foliar-applied hormonal sprays (100 μM in 40% methanol with 0.1% Triton X-100) on flower and fruit number and abscission in Valencia orange[a]

Treatment	No. of flowers	No. of fruit	Percent abscission
Control	22.2 ± 2.8	4.8 ± 1.5	79.8 ± 4.2
Benzyladenine	25.0 ± 2.7	12.0 ± 3.5	52.0 ± 11.6
Gibberellic acid	26.7 ± 5.2	2.3 ± 1.3	89.7 ± 6.8
Paclobutrazol	37.2 ± 2.6	10.4 ± 3.7	73.2 ± 7.9
Napthaleneacetic acid	35.2 ± 5.2	8.6 ± 1.6	74.9 ± 5.1
Abscisic acid	30.5 ± 4.9	11.3 ± 2.3	62.7 ± 6.8

[a] Plants were sprayed 3×/week for 3 weeks prior to brief exposure of selected branch units to $^{14}CO_2$ during early fruiting. Data are means ± SE of 5 replicates.

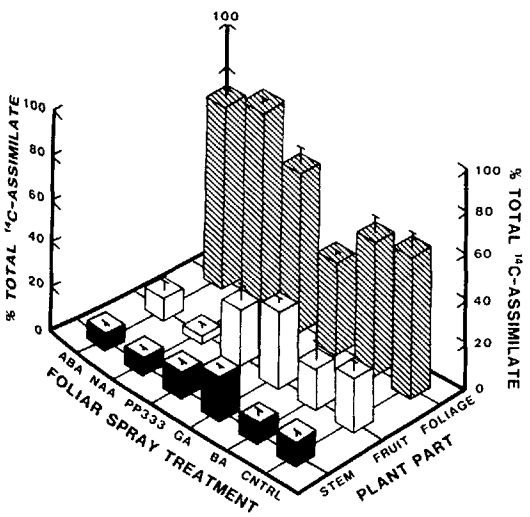

Fig. 5. Influence of growth regulator spray treatments on distribution of ^{14}C photosynthate among the foliage, fruit, and stem tissue of 1-year-old Valencia orange trees 24 h after 30-min exposure of selected branches to $^{14}CO_2$. Spray treatments of BA, GA_3, NAA, PP333, and ABA (100 μM in 40% methanol and 0.1% Triton X-100) were applied 3×/week for 3 weeks prior to $^{14}CO_2$ pulsing.

Discussion

Benzyladenine (BA) and gibberellic acid (GA_3) enhanced the growth of foliage and fruit in Valencia orange when applied at an early reproductive stage. Higher endogenous cytokinin levels have previously been associated with increased vigor and yield in oranges (Saidha et al. 1983). Branches of BA-treated plants showed an increase in leaf, fruit, and stem dry weight (Figs. 3, 4). There was also a concomitant rise in levels of ^{14}C photosynthate in these plant parts (Fig. 5). This demonstrates that multiple BA sprays enhance foliar $^{14}CO_2$ uptake and its subsequent export to developing fruitlets (Fig. 6). Previous work (Kriedemann 1968) showed that kinetin applied to citrus fruit enhanced their ^{14}C-assimilate importing capacity. External application of BA could be mobilizing starch reserves and stimulating sugar movement from the foliage to the fruit in a manner similar to that reported for BA-treated grape vines (Skene

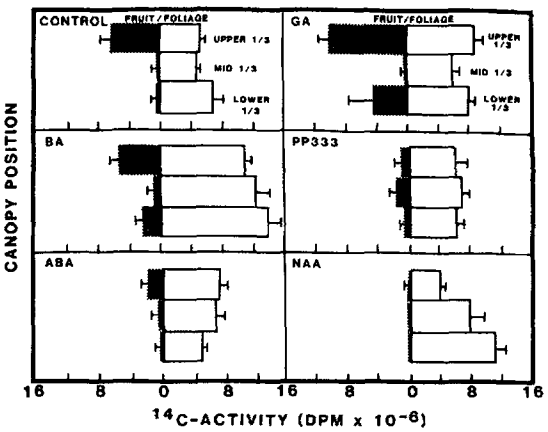

Fig. 6. Effect of growth regulator spray treatments (same as in Fig. 3) on the partitioning of ^{14}C photosynthate between the foliage and fruit of 2-year-old Valencia orange trees at three canopy levels (upper, middle, lower). Selected branch units from each treatment were harvested 24 h after a 30-min $^{14}CO_2$ pulse that followed 3 weeks of foliar sprays (3 x/ week). Each value is the mean ± SE of five replicates.

1971). Since the individual fruitlets were not isolated from $^{14}CO_2$ exposure, there could have been a partial enhancement of $^{14}CO_2$ directly by the fruit in addition to their acquisition of ^{14}C assimilate via foliar export. Tissue from flower buds and small fruitlets of Valencia orange has previously been shown to actively fix $^{14}CO_2$ (Vu et al. 1985).

Treatment with BA markedly reduced fruit abscission over the 3-week period from flowering through fruit set (Table 1). Therefore, BA treatment can augment the total number of fruit retained, which could potentially translate into higher yields. The BA-induced increase in fruit number occurred throughout the branch, especially at nodes in the lower regions of the branch which were usually devoid of fruit in most other treatments, including the control (Fig. 6). Not only were these fruit retained, but they also sequestered a nominal share of foliar-exported ^{14}C assimilate. Other studies with fruit abscission have stressed the importance of assimilate acquisition by the fruit at an early stage of reproductive development (Brun and Betts 1984, Mauk and Breen 1986, Pate and Farrington 1981).

Foliage of BA-treated branches exhibited the highest levels of ^{14}C compared to the other treatments at each respective canopy position, especially the lowermost level (Fig. 6). This is particularly important because fruit lower in the canopy must depend heavily on adjacent, older leaves for their primary source of photoassimilate (Koch 1984a, Kriedemann 1970). In contrast, terminally located fruit are not as restricted in their source-sink relations and can import photosynthate from foliage in the mid to the upper region of the branch. Therefore, cytokinin application can affect source-sink activity as shown in other crops (Herzog 1982) to benefit fruit at all canopy levels.

Gibberellic acid responded similarly to BA in its effects on the foliage and fruit. The increase in foliage dry weight was not as pronounced as that in BA-treated branches; however, the foliage sink intensity was greater with GA_3 (Fig. 3A). The most dramatic effect of GA_3 on vegetative tissue was the rise in stem dry weight. This stem-thickening phenomenon has been described in earlier research with GA_3 sprays in citrus (Krezdorn and Cohen 1962) and may be related to GA_3-induced enhancement of sugar movement throughout the vascular transport system (Skene 1971).

Fruitlet import of ^{14}C photosynthate was greatest in GA_3-treated branches (Figs. 5, 6), demonstrating the ability of GA_3 to enhance translocation of assimilate to the fruit at an early reproductive stage. The same effect has been reported with GA_3 floral dip treatments (Brown 1974), where increased movement of ^{14}C assimilate into fruits from this treatment greatly exceeded the control and also GA_3 foliar sprays. This transport enhancement effect by GA_3 was even more pronounced than in the case of BA, where foliage-sink intensity was increased more so than that of the fruit (Figs. 3, 4). The result of GA_3 sprays on ^{14}C assimilate partitioning by branch position, however, was very similar to that of BA treatment (Fig. 6). The increase in ^{14}C activity in fruit at the lower branch position may serve to potentially increase yield for the same reasoning as previously discussed for BA. Sprays of GA_3 have been shown to enhance yield in citrus through increased individual fruit size (Krezdorn and Cohen 1962) and/or reduced fruit abscission (Lima and Davies 1984). High levels of endogenous GA_3 have also been found throughout development in fruit retained throughout the season (Goren and Goldschmidt 1970), which could be related to the reported GA_3 inhibition of ethylene production (Cooper and Henry 1973). Gibberellin activity was also much greater in the tracheal sap of alternate-bearing citrus trees in fruiting shoots during the more productive, bearing year (Saidha et al. 1983). Sprays of GA_3 on Valencia orange reduced fruit number (Table 1) through a slight increase in fruitlet abscission. Monselise and Goren (1978) reported that GA_3 reduced flowering and levels of total protein in flower buds. To increase fruit size, GA_3 sprays may be more beneficial later in the season.

The other treatments (NAA, ABA, PP333) generally inhibited fruit but not foliar growth (Table 1, Fig. 3). The increase in flowering associated with these treatments, especially PP333, may be due to their antigibberellin action (Dalziel and Lawrence 1984). The fruit resulting from the increased flower number were quite undersize. The ^{14}C partitioning profiles showed that NAA, PP333, and ABA greatly reduced the foliar export of ^{14}C (Figs. 5, 6), which in turn limited fruit growth. This effect could be due to the inhibition of phloem loading and therefore increased assimilate retention in the foliage (During and Alleweldt 1980).

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