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ABSORPTION AND TRANSLOCATION OF CALCIUM FOLIAR SPRAYS IN RELATION TO THE INCIDENCE OF BLOSSOM-END ROT IN TOMATOES

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SUMMARY

The absorption of calcium from calcium chloride sprays applied to tomato leaves and fruits, and its subsequent movement within the plant, were studied using ^{45}Ca.

Tomato leaves rapidly absorbed foliar-applied calcium but translocation of the element away from the leaves was negligible. Repeated spraying failed to induce translocation.

Absorption of calcium by tomato fruits was inversely related to age. Radioautographs of fruit slices revealed that most of the skin-absorbed calcium is localized in the pericarp around the area of application. Grosse Lisse tomato fruits showed initial development of blossom-end rot only during the period from 9 to 15 days after anthesis. It was estimated from the results that direct absorption from a 0·04M calcium chloride solution applied to fruits in the rot-susceptible stage increased the calcium content of the pericarp at the blossom-end by more than 30% within 48 hr.

Surfactants do not appear to increase the absorption of foliar-applied calcium by tomato leaves and fruits.

Direct absorption of calcium through the skin of tomato fruits may explain the reduction in blossom-end rot achieved with calcium foliar sprays.

I. INTRODUCTION

Blossom-end rot of tomatoes and capsicums appears to be caused by a deficiency of calcium in the developing fruits, but attempts to control the disorder by improving the calcium-supplying capacity of the soil are not always successful (Geraldson 1957; Westerhout 1962). Westerhout believed that, under conditions of moisture stress, calcium transport within the plant is upset, resulting in a fruit deficiency. This could occur even when the plant is well supplied with calcium. A number of workers have reduced the incidence of blossom-end rot by foliar spraying with calcium compounds (Evans and Troxler 1953; Geraldson 1957; Piglionica 1961).

Spurr (1959) found that fruit of the tomato variety San Marzano showed incipient symptoms of internal or external blossom-end rot only during the period from 12 to 15 days after anthesis. The inception of blossom-end rot was associated with an active phase of fruit development. He found that tissues at the distal or blossom-end of tomato fruits had only one-third the calcium content of those at the basal or stem end, even in fruit which appeared perfectly healthy. Internal blossom-end rot symptoms occurred at the distal end of the placenta and the external symptom at the distal end of the pericarp.

Calcium is said to be relatively immobile in the phloem and the quantities translocated away from leaves following a single foliar application are small (Martin 1954; Bukovac and Wittwer 1957; Biddulph, Cory, and Biddulph 1959; Taylor, Moore, and Drinkwater 1961; Norton and Wittwer 1963). These workers used triiodobenzoic acid, diethyl ether, indole-3-acetic acid and a pretreatment with calcium gluconate in an attempt to increase the mobility of calcium in the phloem, but were unsuccessful.

Millikan and Hanger (1965*a*) found that the inclusion of high concentrations of calcium or magnesium, of hydrochloric acid, or of EDTA in the foliar calcium spray caused increased translocation of this calcium throughout the plant. They suggested that exchange phenomena might be involved and that saturation of leaves with calcium would induce its movement in the phloem. Martin (1954) found that the translocation of foliar-applied strontium was not increased by chelation with EDTA. Calcium and strontium are closely related elements and Martin showed that they may replace one another in plants to a certain degree.

Wittwer and Teubner (1959) stated that surfactants seldom increase the absorption and translocation of foliar-applied mineral nutrients, but a number of exceptions to this have been presented (Cook and Boynton 1952; Fisher and Walker 1955; Boroughs and Labarca 1961; Tripathi and Sharma 1963). Dybing and Currier (1959) showed that stomatal penetration by aqueous solutions could be clearly demonstrated only if an efficient surfactant was used at a suitable concentration. However, a number of workers believe that simple mass flow of the spray solution through the stomata is not an important mechanism for the uptake of nutrient ions by leaves (Gustafson 1957; Wittwer and Teubner 1959; Middleton and Sanderson 1963). Currier and Dybing (1959) stated that wettability of leaves is negatively correlated with the amount of surface wax, but Schieferstein and Loomis (1956) did not find surface wax on tomato leaves. Furmidge (1962) concluded that the use of a surfactant nearly always results in a reduced quantity of spray being retained on leaf surfaces.

Barinov and Ratner (1959) distinguished a latent period of 4–6 hr after the application of calcium chloride to tomato leaves during which calcium absorption was very slow. They found that 0·1M calcium chloride sprays did not burn the leaves. Leaf-uptake rates for calcium were greater than for phosphorus and they attributed this partly to the hygroscopicity of calcium chloride. Luckwill and

Lloyd-Jones (1962) found that the rate of drying of the spray deposit was an important factor in the absorption of naphthalene acetic acid by apple leaves, uptake being most rapid while the spray remained moist.

Martin (1954) presented radioautographs demonstrating the penetration of externally applied strontium into tomato fruits. Millikan and Hanger (1965*c*) used direct counting and radioautographs to demonstrate the penetration of skin-applied calcium into apple fruits during storage but did not indicate whether the amount absorbed could cause a significant increase in fruit calcium content. Martin and Lewis (1961, pp. 161-5) found that ^{45}Ca injected into the carpel cavity or painted on the outside of apple fruits appeared in both spur and branch leaves of the same tree after periods of water stress.

The generally reported immobility of calcium in the phloem would suggest that the reduced incidence of blossom-end rot achieved with calcium foliar sprays is not due to movement of this element from the leaves to the fruit. The work of Millikan and Hanger (1965*a*), on the other hand, suggests that such a movement might be significant when large quantities of calcium are applied; for example, with repeated spray application. Geraldson (1959) suggested that calcium sprays applied to the leaves might allow more of the root-absorbed calcium to reach the fruit.

This paper indicates another possibility, namely that direct absorption of calcium by the fruits from the sprays applied to the plants is responsible for the reduction in blossom-end rot.

II. MATERIALS AND METHODS

(a) General

Grosse Lisse tomato plants growing in sand cultures in an evaporatively cooled glasshouse were used for the experiments. A Hoagland-type nutrient solution was applied twice weekly and water every other day. The first fully expanded leaf is defined in this work as the fully expanded leaf closest to the plant apex.

(b) Surfactant Studies

The non-ionic surfactant "Sterox SK" was used to determine the effect of a surfactant in the spray solution on:—(i) the volume of spray solution retained on the leaf or fruit surface at the point of run-off; (ii) the rate of penetration of the spray solution into the leaf; and (iii) the damage caused to the leaf or fruit by a high concentration of calcium chloride in the spray.

(i) *Retention.*—The techniques used were similar to those described by Furmidge (1962). The solutions, containing the fluorescent dye Rhodamine B500 at 0·05%, were sprayed from a clamped Aerograph MP twin fluid

atomizer at a pressure of 15 lb/sq in, from a distance of 80 cm, onto the leaf or fruit surface, and within a draught-proof chamber. Leaflets were inclined at 60° to the horizontal and run-off occurred when the first of the adhering droplets began to move down the leaf surface. Plants were removed from sunlight 1 hr before treatment to allow the leaves to develop full turgor. The spray solutions were washed from the leaf with a known volume of water and the intensity of the colour measured at 550 mμ in a spectrophotometer.

(ii) *Penetration.*—The rate of penetration of the spray solution into the leaf was studied, using the technique of Dybing and Currier (1959). Leaflets still on the plant and with either open or closed stomata were suspended in solutions containing Rhodamine B500 at 0·05%. After a given time, the leaflets were washed with running water and microscopically examined to ensure that the Rhodamine solution had been removed from the leaf surface. The leaflet was then viewed under ultraviolet light. The amount of fluorescence indicates the extent of penetration of the spray solution into the leaflet. Each leaflet was given a penetration rating by comparing it with a set of four leaflets which had been suspended in 0·1% Sterox solution for 1, 5, 15 or 30 min, the ratings of these being standardized at 1, 2, 3 and 4 respectively. The presence of open or closed stomata was determined by viewing the leaflet directly under a microscope, stomatal closure being achieved by placing the plants in the dark for a period before treatment.

(iii) *Damage.*—Various concentrations of calcium chloride, with and without a surfactant, were sprayed onto tomato leaves and fruits to the point of run-off. Damage was visually assessed after 48 hr, using a rating system of 0 to 3.

(c) Isotope Studies

The radioactive isotope ^{45}Ca, as calcium chloride, and with a specific activity 55 mc/g Ca, was used. All isotope solutions were 0·04M with respect to calcium chloride at pH 6·0, and were applied to the surfaces of leaves or fruits dropwise with an Agla micrometer syringe burette.

After the treatment period, unabsorbed and exchangeable calcium was removed by washing the treated leaflet or fruit for 4 min in a solution containing 0·1M calcium chloride plus 0·05% wetting agent, and then applying a jet of the same solution from a wash-bottle. Isotope recovered, after washing, from the leaflet or fruit to which it was applied was classed as absorbed calcium and that recovered from the remainder of the plant as translocated calcium.

Plant material was ashed in a muffle furnace at 550° C, taken up in hydrochloric acid and the extract filtered. Calcium was precipitated as the oxalate by a method of Graf, Comar, and Whitney (1951), filtered under vacuum and mounted on a planchet. Counts were made using a thin-end window G-M counter attached to an Ekco Type N530 scaler. A self-absorption curve was constructed and all counts related to zero thickness.

Radioautography was used to show the distribution of spray calcium after absorption through the skin of tomato fruit. The isotope was applied to specific areas 2 cm square on various parts of the fruit surface. Two or 4½ days later, 0·5-cm slices were removed from the fruits, using a clean knife and cutting towards the area of application. Samples were freeze-dried and exposed to Kodirex X-ray film for various periods. The film was developed using Kodak Type 2 liquid X-ray developer for 3 min at 68°F.

III. RESULTS

(a) Surfactant Studies

Spray retention.—Six different Rhodamine solutions containing Sterox SK at concentrations ranging from 0 to 0·3 % were sprayed onto the upper and lower surfaces of young and old leaves. A young leaf was the first fully expanded one, and an old leaf two below it. Fourfold reductions in the volume of liquid adhering to tomato leaf surfaces at run-off were recorded when various levels of Sterox SK were added to the spray solution (Table 1). The surface tension of the solution appeared to be the main factor affecting retention. Lower leaf surfaces were more retentive of spray solutions than upper surfaces. Surfactants also reduced the volume of spray adhering to tomato fruits at run-off (Table 2). Surfactants caused a greater reduction in spray retention on leaves (76%) than on fruits (64%). The size of the spray droplets applied to the leaf surface was measured by the technique of May (1945) and varied from 7·5 to 174μ, with an average of 45μ.

TABLE 1

RETENTION OF SPRAY SOLUTION ON LEAVES

(μ litres/sq cm)

Sterox SK (%)	Surface Tension Sterox SK in Water (dynes/sq cm)	Old Leaf		Young Leaf		Mean
		Upper Surface	Lower Surface	Upper Surface	Lower Surface	
0	72	20·4	22·3	20·4	21·4	21·1
0·0125	32	5·2	6·7	5·2	6·2	5·8
0·025	31	3·8	4·4	4·3	4·2	4·2
0·05	31	4·6	5·0	4·1	4·8	4·6
0·1	31	5·7	5·6	5·5	5·2	5·5
0·3	31	4·1	4·2	3·9	4·0	4·0

Necessary differences for significance	Marginal	Individual
5%	1·13	2·26
1%	1·50	3·00

The results are for 5 replicates.

TABLE 2

RETENTION OF SPRAY SOLUTION ON FRUIT

(μ litres/sq cm)

Sterox SK (%)	Age of Fruit—Days From Anthesis			Mean
	22	32	44	
0	21·6	18·4	18·4	19·5
0·05	7·5	7·0	6·4	7·0

Necessary differences for significance	Marginal	Individual
5%	1·08	1·88
1%	1·47	2·54

The results are for 6 replicates.

Spray penetration.—The rate of penetration of eight different Rhodamine solutions containing Sterox SK at concentrations ranging from 0 to 0·3% was studied, using the first fully expanded leaf. Sterox SK accelerated the penetration of the solution into tomato lower leaf surfaces when the stomata were open and to a lesser extent when they were closed (Figure 1). Surfactant-free solutions appeared to penetrate at the same rate whether the stomata were open or closed. Penetration of solution into the interveinal areas of the upper leaf surfaces was not observed with any treatments. The solutions penetrated veins on the upper surface but more slowly than those of the lower surface. Stomatal counts for the upper and lower leaf surfaces were 10,000 and 24,500 per sq cm respectively.

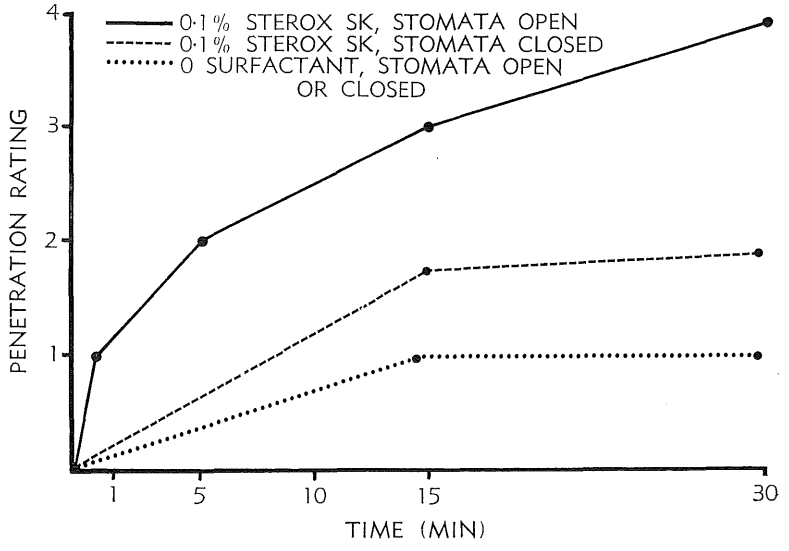

Fig. 1.—Rate of penetration of solutions into interveinal areas of tomato lower leaf surface.

Spray damage.—Five concentrations of a calcium chloride solution were applied with and without Sterox SK to fruits and to both surfaces of the first fully expanded leaf of tomato plants. Calcium chloride spray solutions caused less visual damage to the leaves when a surfactant was included, the maximum concentrations which could be applied with safety being 0·04 and 0·05M for the nil and plus surfactant treatments respectively. Lower leaf surfaces were the more susceptible to spray burn. Fruits were most easily damaged when they were young. Concentrations of calcium chloride which could be safely applied to fruits 9–15 days from anthesis were 0·04 and 0·06M for the nil and plus surfactant treatments respectively.

Symptoms of calcium chloride spray damage on tomato leaves were as follows:—margins and leaf tips scorched with tips hooked; leaves puckered with slight chlorosis; hairs on upper surface poorly developed; necrotic spots on veins and in interveinal areas; complete necrosis of the smaller veins in more severe cases. On the fruits, spray injury appeared as slightly depressed, dark-green areas on the fruit surface, often with one or more necrotic spots.

(b) Isotope Studies

Leaf absorption.—$^{45}Ca\ Cl_2$ was applied to the upper surface of a leaflet from the first fully expanded leaf, and after periods ranging from $5\frac{1}{2}$ to 98 hr the amount of ^{45}Ca absorbed and translocated was determined. Each leaflet received 2 μc of ^{45}Ca in 20 droplets each 0·005 ml, the droplets being applied on a grid system which avoided the main vein. All applications were made between 6.30 and 7.30 a.m. Figure 2 shows the absorption of applied calcium after various intervals of time. Significant counts above background could not be obtained for the samples used to measure translocation of ^{45}Ca away from the treated leaf.

To test the efficiency of the washing technique, droplets applied to the leaves were dried, using an infrared lamp (375W) at a distance which did not appear to injure the tissues (40 cm), and then washed. Droplets took approximately 20 min to dry under these conditions. Isotopic calcium not removed by this washing was considered to be adsorbed onto the leaf surface. This technique may over-estimate the error due to adsorption, as some isotope could have been absorbed into the leaf during the drying period. Errors due to adsorption of ^{45}Ca onto the leaf surface were estimated by this technique to be less than 1%.

Attempts to increase translocation.—An application of 15 μc of ^{45}Ca was made to leaves which had received 0, 2 or 5 previous sprays of 0·04M calcium chloride at 3-day intervals. Applications were made to the fourth leaf from the base, excluding the cotyledons. After 110 hr, the amount of isotope translocated away from the treated leaf was extremely small, and no treatment differences were observed. It was estimated that on the average 0·009 μc ^{45}Ca was present in plant parts external to the treated leaf; this represents 0·06% of the amount applied. The calcium content of the leaves which had not been sprayed was 1·29 m-equiv./g. Three sprays of calcium chloride increased this to 1·54.

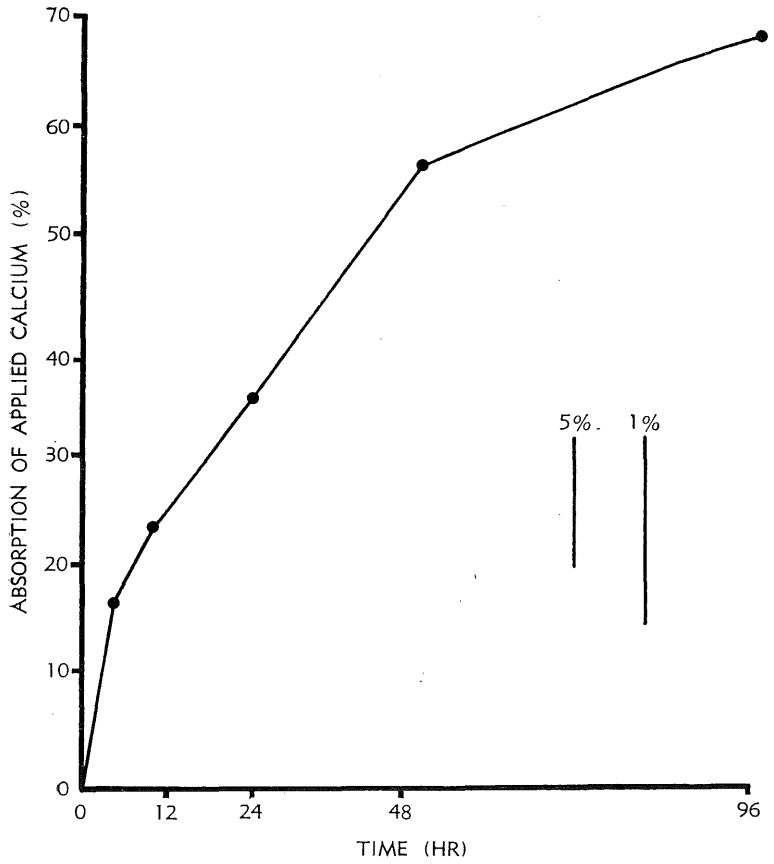

Fig. 2.—Absorption of foliar-applied calcium by tomato upper leaf surfaces.

Fruit absorption.—Applications of 2 μc ^{45}Ca in twelve 0·005-ml droplets were applied to the surface of fruits of three different ages. The droplets were placed evenly over a section of the fruit from the shoulder to the blossom-end. All fruits treated had developed a glossy cuticle.

After 48 hr, the fruit were harvested and the amount of ^{45}Ca absorbed and translocated determined. Adsorption errors were estimated, using a similar technique to that described under leaf absorption, at less than 1%. In the first experiment, the fruit of three ages was selected from different trusses on the same plant, each plant thus representing a block. In the second experiment, fruits in similar positions on plants of different ages were used. Total fruit calcium levels were determined in both experiments.

Absorption of surface-applied calcium by tomato fruits was inversely related to age (Figure 3).

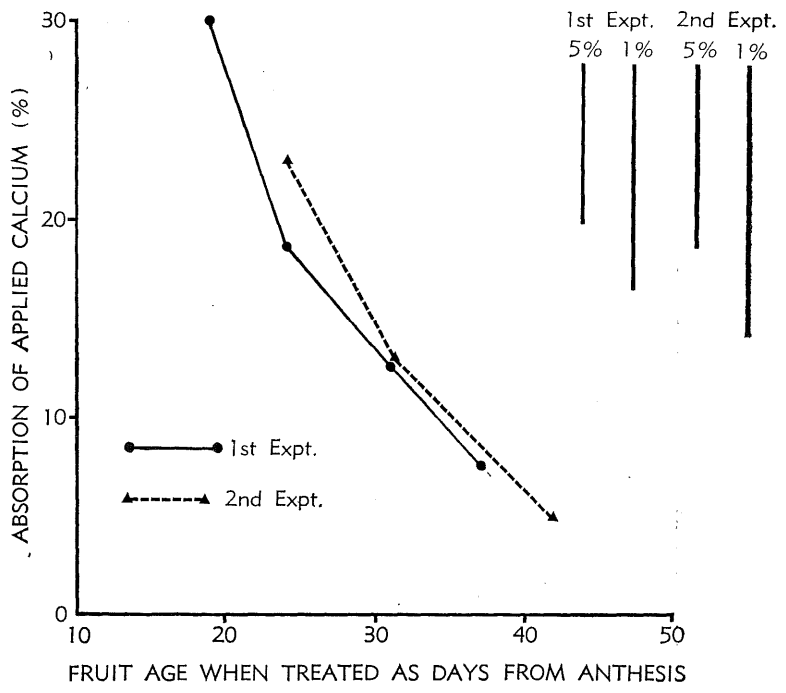

Fig. 3.—Regression lines for absorption of foliar-applied calcium by fruits over a 48-hr period.

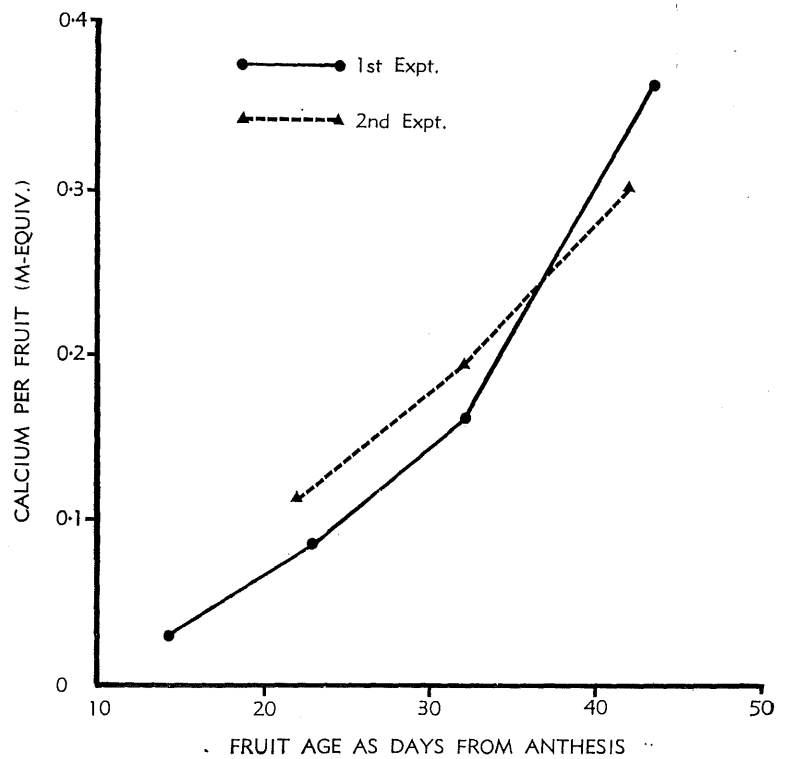

Fig. 4.—Regression lines for total calcium content of tomato fruits as a function of age.

Total calcium content of fruit.—Determinations of the total calcium content of fruits used in the two absorption experiments revealed that, as the fruit aged, the total calcium increased but concentration expressed as milliequivalents per gram decreased (Figures 4 and 5).

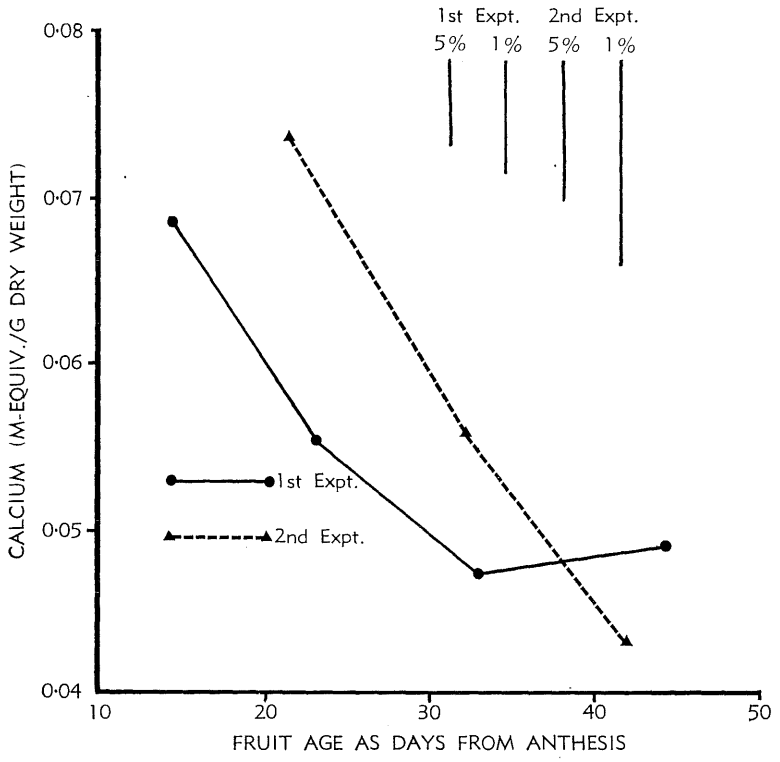

Fig. 5.—Regression lines for calcium content of tomato fruits as milliequivalents per gram dry weight as a function of age.

Distribution of calcium in fruits.—Applications of 2 μc ^{45}Ca as nine 0·005-ml droplets were made within an area 2 cm square to any one of the following three positions on the fruit surface—(a) the stalk and an area around its point of attachment; (b) half-way down the side of the fruit; and (c) the blossom-end. After 2 or 4½ days, slices were taken and freeze-dried before radioautographs were made, using exposures of 1 and 2 days. The sections of the fruit which had caused heavy blackening on the film were then removed with a scalpel and the remainder exposed to a new film for 4 days. The latter exposure defined areas where isotope concentrations were low. If the high-intensity isotope areas were left in the 4-day exposure, serious artifacts were caused by radiation scatter. Figures 6-9 are examples of the distribution patterns obtained with this technique.

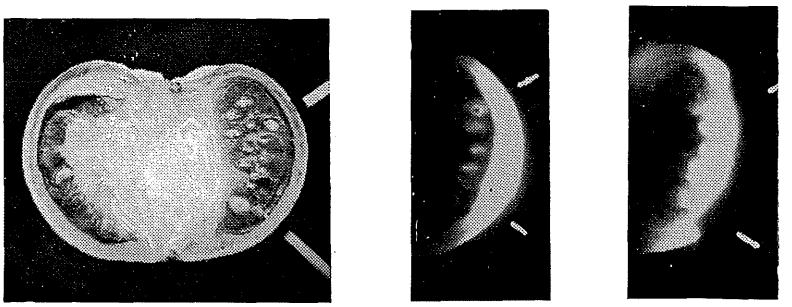

Fig. 6.—Fruit slice and radioautographs showing distribution of ^{45}Ca 2 days after application to side of fruit 4.0 cm in diameter and 21 days from anthesis. (a) Freeze-dried fruit slice. Isotope application was made between white marks. (b) Radioautograph produced by a 2-day exposure, showing localization of most of the absorbed calcium in the pericarp beneath the point of application. Some ^{45}Ca has also been accumulated by the seeds. (c) Radioautograph produced by removing the pericarp beneath the point of application and exposing the remainder of the slice for 4 days.

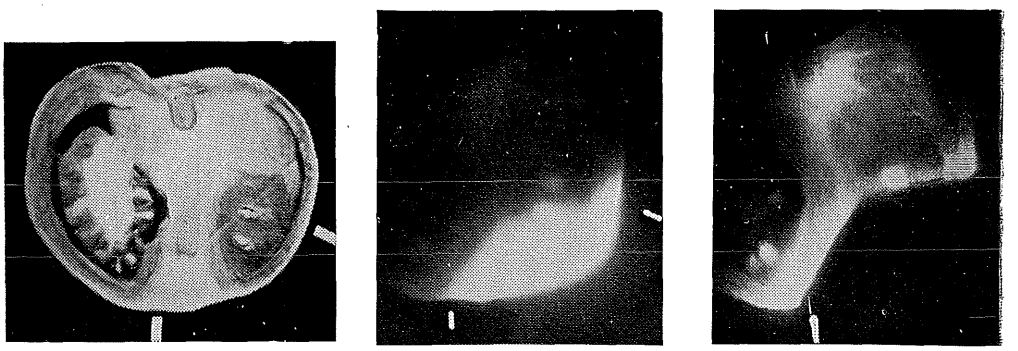

Fig. 7.—Fruit slice and radioautographs showing distribution of ^{45}Ca 4½ days after its application to the blossom-end region of a fruit 4.2 cm in diameter and 22 days from anthesis. (a) Freeze dried fruit slice. Isotope application was made between white marks. (b) Radioautograph produced by a 2-day exposure. Most of the absorbed calcium was located in the pericarp beneath the point of application, with lesser amounts being localized in the seeds and placental tissues. (c) Radioautograph produced by removing areas showing heavy isotope concentration in (b) and exposing remainder of fruit for 4 days. Movement of isotope away from the point of application has occurred in the pericarp and placental tissues. Seeds and vascular elements showed greater isotope concentration than surrounding tissues. Isotope was not detected in the fruit stalk which was radioautographed separately.

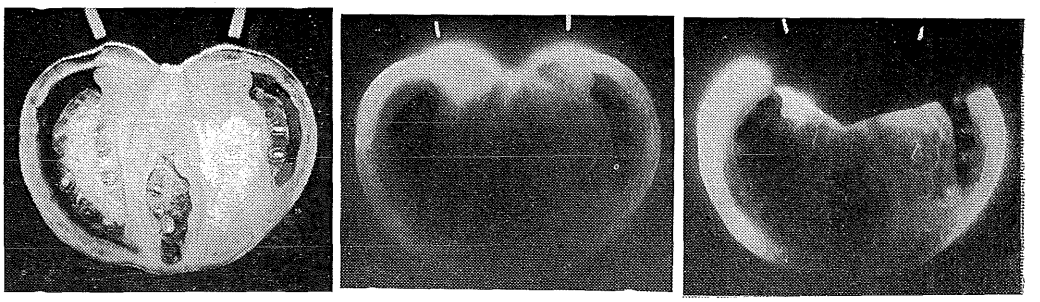

Fig. 8.—Fruit slice and radioautographs showing distribution of ^{45}Ca 4½ days after application to the stalk and surrounding area of a fruit 4.2 cm in diameter and 21 days

from anthesis. (a) Freeze-dried fruit slice. Isotope application was made to the stalk and surrounding area of fruit between white marks. (b) Radioautograph produced by a 2-day exposure showing localization of isotope in the pericarp and to a lesser extent in the placental tissues. Isotope applied to and around the fruit stalk showed greater mobility within the fruit than that applied to the sides or blossom-end. (c) Radioautograph produced by removing section of fruit around the stalk end and exposing the remainder of the fruit for 4 days. Most of the calcium which has moved away from the area beneath the point of application is located in the pericarp.

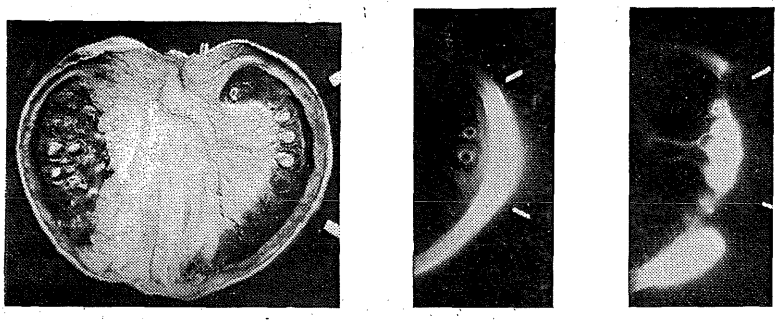

Fig. 9.—Fruit slice and radioautographs showing distribution of ^{45}Ca 2 days after application to the sides of a fruit 4.7 cm in diameter and 22 days from anthesis. Radioautographs clearly show movement of isotope along vascular elements from the seeds towards the stalk. Isotope diffused from the pericarp into the matrix and was then accumulated by the seeds. The outer section of the matrix and the inner wall of the pericarp were in contact in the original fruit but separated during freeze-drying. More isotope has moved along the pericarp towards the blossom-end than has moved in the direction of the stalk. This phenomenon was generally apparent but is not in evidence in Figure 6.

At 4½ days after treatment, most of the absorbed calcium was located in the pericarp around the area of application, with smaller amounts in the seeds, the pericarp further away from the treated area and the placental tissues. Radioautography and direct counting failed to detect isotopic calcium in the fruit stalks or in parts of the plant other than the treated fruits. In fruits examined 2 days after treatment, distribution patterns were similar, but a slightly larger proportion of isotope was found around the point of application.

Seeds showed a greater accumulation of isotopic calcium than the surrounding matrix (Figures 6, 7, 9). Isotope moved from the pericarp into the matrix and then accumulated in the seeds. The pericarp and the matrix separated during freeze-drying and this is apparent in the illustrations. Some movement of isotope along the vascular tissue in the direction of the stalk is seen in Figure 9.

To establish that no movement of isotope occurred during the freeze-drying process, two adjacent slices were cut from a treated fruit and placed with the common surface uppermost. From one slice was cut the section where isotope concentrations were expected to be high. The two samples were then freeze-dried under identical conditions and radioautographs made. Isotope distribution

external to the heavy areas was similar irrespective of the isotope concentrations when freeze-dried. A number of replicates gave similar results. It was therefore concluded that isotope distribution artifacts had not been produced by freeze-drying the samples. Pallas and Crafts (1957) and Levi (1962) have shown that isotope distribution artifacts can be caused by heat-drying plant material.

Significance of absorption by fruits.—From the results obtained, estimates were made of the effect of skin-absorbed calcium on tissues which are susceptible to external blossom-end rot.

From a series of radioautographs for each fruit slice and from direct counts, it was estimated that 90% of the absorbed calcium remained in the pericarp near the point of application to the fruit. The quantity of calcium applied to the lower third of the fruit by a single 0·04M calcium chloride solution sprayed to the point of run-off was calculated from the retention data (Table 2) and the fraction of this which could be expected to be absorbed by the fruit within 48 hr (Figure 3); 90% of the absorbed fraction was then expressed as a percentage of the natural calcium content of the pericarp at the blossom-end (Figure 10). The graph also shows the percentage increase in calcium content on a whole-fruit basis.

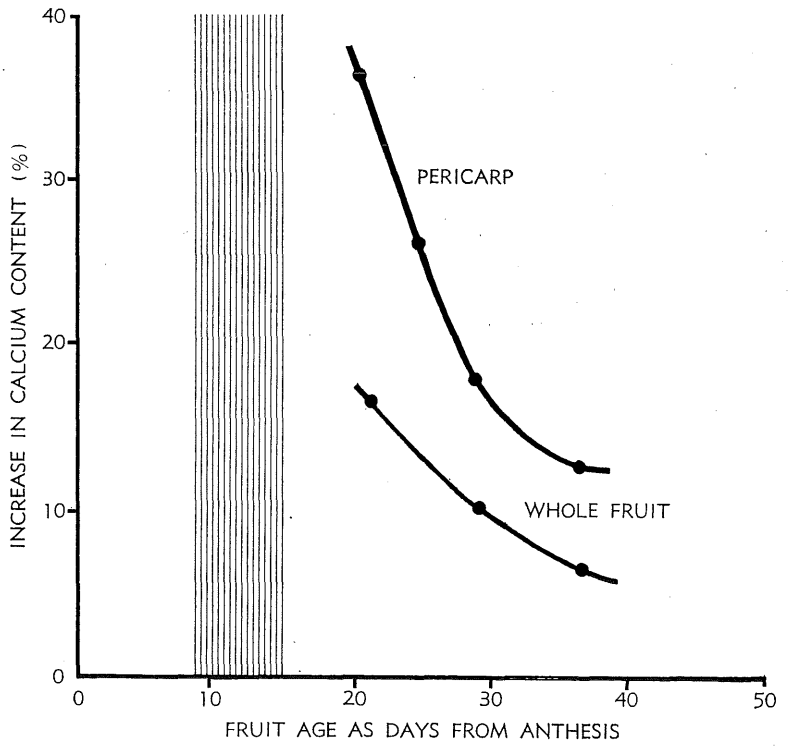

Fig. 10.—Estimated increase in calcium content for whole tomato fruit and lower third of pericarp within 48 hr of the application of a 0.04M calcium chloride solution sprayed onto the fruit to point of run-off.

Incipient stages of blossom-end rot.—Tomato flowers of the variety Grosse Lisse were tagged at anthesis and the developing fruits observed daily for the development of external symptoms of blossom-end rot. The initial stages of the disorder were found in fruits only during the period from 9 to 15 days after anthesis. Fruits older than 15 days failed to develop external blossom-end rot even when conditions were favourable to its formation.

IV. DISCUSSION

The experiments show that the upper leaf surface of the tomato is capable of rapidly absorbing calcium applied in a foliar spray (Figure 2). Solutions containing a fluorescent dye readily penetrate the veins and interveinal areas of the lower leaf surface, but only slight veinal and no interveinal penetration could be detected on the upper surface. Dybing and Currier (1959) concluded that the initial entry of fluorochromes into leaves is similar to that of radioactive tracers, and the results therefore suggest that increased calcium absorption rates could be expected for the lower surface than those presented for the upper surface. Foy (1964) stated that the lower epidermis is usually more easily penetrated by chemicals than the upper epidermis.

The rate of penetration of non-surfactant solutions into the tomato lower leaf surface appeared to be similar whether the stomata were open or closed (Figure 1). Solutions containing a surfactant, on the other hand, penetrated the leaf much faster when the stomata were open. This suggests that calcium intake from foliar sprays might be increased by the inclusion of a surfactant at a suitable concentration.

Surfactants increased the rate of penetration of the dye solution even when the stomata were closed. Microscopic observations suggested that this was due to cuticular penetration, as the dye appeared in the anticlinal walls of the epidermis and in the epidermal hairs. It would therefore appear that surfactants increased the rate of penetration of the dye solution through both the cuticle and the stomata.

The inclusion of a surfactant in the spray solution resulted in a threefold to fourfold decrease in the volume of spray retained on tomato leaf and fruit surfaces at run-off, but allowed only a 25% increase in the concentration of the calcium chloride solution that could be applied without damage. This means that the maximum amount of calcium chloride which could be safely applied to tomato leaf and fruit surfaces was considerably less when a surfactant was included in the spray.

In these experiments the maximum spray loads for the upper surface of the first fully expanded leaf were 32·5 and 8·3 μ g Ca/sq cm for the nil and plus surfactant treatments respectively. From the data presented in Figure 2, the upper surface would absorb 8·3 μ g Ca/sq cm from the 32·5 μ g Ca/ sq cm applied by a non-surfactant spray in 12 hr. Therefore, even though surfactants initially increase the rate of penetration of calcium sprays into tomato leaves,

the effect is only temporary and does not extend over more than 12 hr from spray application. This probably applies also to tomato lower leaf surfaces. It is concluded that surfactants reduce the absorption of calcium by tomato leaves from foliar sprays. Surfactant-free sprays were therefore applied in the translocation studies.

The latent period of 4–6 hr distinguished by Barinov and Ratner (1959) for the absorption of calcium by tomato leaves was not observed in these investigations; the first measurement of uptake by the upper leaf surface made 5½ hr after application showed a 17% absorption of applied calcium (Figure 2).

Spraying repeatedly with calcium solutions in an attempt to saturate the leaves, as suggested by Millikan and Hanger (1965*a*), did not induce translocation of calcium away from the treated leaves. It is not practicable to apply greater concentrations or more frequent applications of calcium chloride than those used without damaging the leaves. The possibility exists that significant translocation of calcium might have been induced had the original calcium levels in the leaves been higher than 1·29 m-equiv./g. Analysis of Grosse Lisse tomato plants grown in the field on a red clay loam showed that calcium values higher than 1·29 m-equiv./g. can be expected only in the old leaves. Leaf samples from plants growing on sandy soils where blossom-end rot is most troublesome generally showed leaf calcium levels very much less than 1·29 m-equiv./g. Therefore where reductions in blossom-end rot have been achieved with calcium sprays, direct movement of this element from leaves to the fruit is an unlikely explanation.

Millikan and Hanger (1965*b*) studied the movement of ^{45}Ca and ^{65}Zn away from clover leaves through collapsed petioles and concluded that the elements moved in the xylem. Clor, Crafts, and Yamaguchi (1963) also noticed xylem movement of various substances away from leaves which had been placed in a saturated atmosphere. They concluded that such a reversal of the transpiration stream is unlikely to occur under field conditions. The conclusions of Dybing and Currier (1959), Wittwer and Teubner (1959) and Vaadia and Waisel (1963) support this view. The injection technique used by Millikan and Hanger (1965*a*, 1965*b*) might have resulted in a reversal of the transpiration stream and given abnormal distribution patterns.

Absorption of foliar-applied calcium by tomato fruits was inversely related to age. Fruits aged 5–8 days from anthesis absorbed more than 90% of the applied calcium within 48 hr. Data from absorption studies on these fruits were not used for the analyses since tomatoes of this age are easily damaged when the solutions are applied. Factors which may be important in determining the faster absorption rates of the young fruits include a thinner cuticle and a higher respiration rate.

The effect of a surfactant in the foliar spray on the absorption rate of calcium by fruits is not clear. Although 0·06M calcium chloride solutions containing a surfactant did not damage the fruits, the maximum safe concentration which

could be applied is 0·05M, since the higher level may damage the leaves. Similar calculations to those used for leaves indicate that, for a fruit aged 20 days from anthesis, the maximum calcium chloride spray loads which could be safely applied are 32·7 and 15·6 μg Ca/sq cm for the nil and plus surfactant treatments respectively. From the results presented in Figure 3, the fruit could be expected to absorb approximately 8·2 μg Ca/sq cm from the applied 32·7 within 48 hr. Figure 3 suggests that for a fruit in the blossom-end rot susceptible stage, namely 9–15 days from anthesis, calcium absorption rates from the non-surfactant spray would be higher. To increase absorption of calcium by 9-day to 15-day-old fruits over the 48-hr period, surfactants would probably need to more than treble the absorption rate of the non-surfactant spray. This possibility seems unlikely. Sargent and Blackman (1962), who studied the penetration of 2,4-D into leaf discs of *Phaseolus,* using a technique in which there was no appreciable change in the composition of the external solution during the treatment period, reported a twofold increase in penetration rates of 2, 4-D from surfactants.

Radioautographs revealed that most of the skin-absorbed calcium remained in the pericarp near the point of application and none appeared to move away from the treated fruits to other parts of the plant. Martin and Lewis (1961) found that ^{45}Ca injected into the carpel cavity or painted on the outside of apple fruits appeared in both spur and branch leaves after water stress. Plants used in the present investigations did not suffer serious moisture stress during the treatment period, the maximum temperature experienced being 77°F, this being accompanied by 55% relative humidity. One indication of movement of calcium back along the vascular strands is seen in Figure 9.

Figure 10 indicates that a single spray of 0·04M calcium chloride applied to wet the fruit to the point of run-off could increase the calcium content of the pericarp at the blossom-end of fruits in the rot-susceptible stage by more than 30% within 48 hr. The increase in the calcium content of fruits by sprays applied directly to them is greatest when they are in the early stages of growth, even though their calcium content expressed as milliequivalents per gram is high at this stage. The chief factors favouring the greater calcium increase in young fruit are a higher absorption rate and a greater surface-to-volume ratio.

Since Grosse Lisse tomato fruits are susceptible to the development of blossom-end rot only during the period 9–15 days after anthesis, foliar-feeding with calcium to prevent the disorder should aim at supplying calcium during this critical period. Spurr (1959) suggested that the actual deficiency of calcium probably occurs in the fruit tissues at least 1–2 days before symptoms become apparent. Supplementary calcium sprays might therefore be necessary in Grosse Lisse during the period 7–14 days after anthesis.

Under field conditions, the efficiency of calcium foliar sprays would probably be somewhat less than that estimated from the experimental data. Other spray residues on the fruit may reduce the volume of spray retained on the fruits and the rate of calcium absorption. The accessibility of the fruits to spray materials

would also be influenced by the method of trellising and the amount of leaf cover. To be effective, the sprays would need to wet the fruits at the blossom-end. When sprayed past run-off, the solution tends to run down the sides to the blossom-end of the fruit, which may be wetted even though not directly accessible to sprays.

Geraldson (1957) has pointed out that numerous soil conditions affect the incidence of blossom-end rot in tomatoes and that calcium sprays are intended only as a supplementary treatment when attention to these factors has failed to give desirable control. The observations of Westerhout (1962) suggest that this is most likely following conditions of high evapotranspiration.

These results suggest that direct absorption of calcium through the skin of tomato fruits may be responsible for the reductions in blossom-end rot achieved with calcium foliar sprays by Evans and Troxler (1953), Geraldson (1957) and Piglionica (1961). The alternative possibility of direct translocation of calcium from the leaves to the fruits is not supported by these investigations.

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