

CALCIUM CONTENT OF FRUITS AND STORAGE TISSUES IN RELATION TO THE MODE OF WATER SUPPLY

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ABSTRACT

Experiments were performed to elucidate the process of uneven distribution of Ca between different parts of the plant. The Ca-contents of fruits and storage tissues are usually extremely low, and as a result local disorders may occur.

The primary distribution of ^{45}Ca was found to be closely linked to the distribution of water along the xylem vessels. During the period of fast growth no or hardly any water and ^{45}Ca entered tomato fruits, apples, potatoes or seeds of the broad bean.

This phenomenon is explained by accepting the existence of a mass flow transport in the phloem. This mass flow can supply the necessary water along with most other nutrients, but does not carry any worthwhile amount of Ca.

In a further series of experiments it is demonstrated that conditions conducive to predominance of the sieve tube transport result in a lowered Ca-content of tomato fruits and increased blossom-end rot. Conditions favouring an auxiliary supply of water via the woodvessels reduce the disease incidence and the K/Ca ratio of the fruits.

1. INTRODUCTION

In plants certain physiological disorders can occur which are correlated with local insufficiency of a special element. In tomatoes the incidence of blossom-end rot increases as the calcium content of fruit diminishes and the K/Ca ratio rises (EVANS and TROXLER, 1953; GERALDSON, 1957; LYON *et al.*, 1942; MAYNARD *et al.*, 1957). Bitter pit of apples also shows a relationship to a low calcium content of the fruit (ASKEW *et al.*, 1959, 1960; BAXTER, 1962; BOUHIER DE L'ECLUSE, 1962; KIDSON *et al.*, 1963; MARTIN *et al.*, 1964; VAN SCHREVEN *et al.*, 1962, 1964). In peas the occurrence of marsh spot is related to a manganese deficiency, which can hardly be cured by spraying the leaves only with this element (HENKENS and JONGMAN, 1965). Internal tipburn of cabbage is also correlated with a local low Ca-content (MAYNARD *et al.*, 1965).

One of the most striking characteristics of a number of these disorders is that the calcium content of the organs, which may be affected, is always very low in comparison to that in the sprout. If the general supply status of the plant diminishes the content in these tissues becomes so very low as to result in a mineral unbalance.

Data on blossom-end rot published by GERALDSON (1957) show that the tomato fruit contains only as much as 0.10-0.24 % Ca, while the leaves have a level of 0.84-4.14 % on dry weight. Data given by WARD (1964) confirm this very uneven distribution of calcium. According to Garman (BOUHIER DE L'ECLUSE, 1963) the calcium content of apples is only 1/20-1/80 part of that in the leaves. This low

calcium content of the fruit is the result of a very slow influx of this element into the growing apple, especially in comparison to the much better supply with assimilates, N, P and K (ASKEW *et al.*, 1959, 1960). Potatoes also show a low calcium content compared with the sprout (HAGEMANN, 1964) and extremes can be linked with a poor keeping quality of seed potatoes in storage. Distribution of radioactive strontium, which behaves similar to calcium, in the potato shows the same pattern (MECKLENBURG and TUKEY, 1963). Investigations by LÄUCHLI (1962) on the distribution of strontium administered to pea plants also demonstrate that the relative content of the seeds is only 1/25 of that of the leaves and stems and 1/12 of that of the carpels.

The above mentioned facts demonstrate that calcium is not evenly distributed over the plant. This might be related to a restricted supply, a conclusion which was already drawn by MASON and MASKELL (1934) in regard to cotton seed. Thus the possibilities of transport will have to be considered.

Transport of calcium from cell to cell in the symplasm is noticeably slow (ARISZ) and as usually larger distances are involved, this pathway can be left out of consideration. Two modes of long distance transport exist in the plant: either along with water in the woodvessels or by means of movement in the sieve-tubes.

The primary means of distribution of root-absorbed calcium will be in the transpiration current or otherwise induced water transport in the xylem. The calcium carried along this way undergoes continuous loss, exchange or gain (BELL, 1963; BIDDULPH *et al.*, 1961) with the surrounding tissues. So, although calcium transport entirely depends on water movement in these vessels the amount transported does not have to be highly correlated to the amount of water arriving at a certain destination.

For several ions the phloem forms a second pathway of transport. Most evidence related to calcium points to the fact, that this ion is more or less immobile in the sieve tubes (BIDDULPH *et al.*, 1958; CRAFTS, 1961; MASON and MASKELL, 1934; NORTON and WITWER, 1963; ZIEGLER, 1962). In the few cases where redistribution of calcium has been demonstrated it often does not seem necessary to suppose that a phloem transport is involved (BUKOVAC *et al.*, 1956; FERRELL and JOHNSON, 1956; VLASYUK and GRODZINSKII, 1960, 1965). If calcium can escape into the apoplast (mainly the cell walls and the xylem), transport along with water following hydrostatic gradients is a possibility (CRAFTS, 1956). The very slight transport of calcium in the sieve tubes is easily understood when their very low calcium content is taken into account. Analysis of exuding phloem-sap by TAMMES and VAN DIE (1964) show a calcium content of 0.014 mg/ml and a K/Ca ratio of 120.

In regard to the fact that calcium supply is linked to water supply over the xylem it seemed necessary to investigate the water movement to the affected organs. Former research on peanuts (WIERSUM, 1951) had already lead to an explanation of the missing calcium supply of the pods of *Arachis*.

2. EXPERIMENTS ON WATER AND CALCIUM TRANSPORT IN THE XYLEM

2.1. *Experiments with tomatoes*

Tomato-plants (var. Moneymaker) were grown till they carried 3-4 trusses. At this stage the lowest truss would already carry some nearly full grown fruits. The plants were taken out of the pots and the roots washed free of soil. They were then transferred to a half strength nutrient solution.

For the experiments a glass vessel was filled with 600 ml of this dilute nutrient solution to which about $10 \mu\text{C } ^{45}\text{Ca}$ had been added. Some dye in the form of Light Green was added to obtain a blueish solution. The plants were then put into this solution after having cut away most of the roots. This was done to allow free entrance of the dye into the xylem, which was to be used as a visual tracer for water-transport.

The experiments lasted 3-4 days and during that time the plants were in the laboratory under additional artificial lighting. At the end of the experiment different parts of the plants were inspected for presence of blue colouration. Fruits were cut lengthwise into slices 2-3 mm thick near the centre. The parts to be investigated further were cut off the plant and then dried at 105°C . Sometimes a provisional radioactivity measurement was performed on the fresh material.

Distribution of ^{45}Ca was investigated by means of autoradiography. The exposures on the Kodak No Screen Medical X-ray film usually lasted about 14 days. Longer exposures did not show activity in parts not already showing up in the ordinary exposure time.

The distribution of Light Green in the plants was usually as follows. All leaves showed a blue colour along the veins and sometimes even in the parenchymatous tissues. The intensity was variable over the different leaves. Often the younger leaves at the top showed the best colouration. The blue colour could also be detected in the stems of the trusses and even in the pedicels and calyx of the fruits. Inspection of the fruits, however, showed an abrupt ending of the colouration at the point where the pedicel is attached. Only in 1 or 2 cases could some slight trace of blue be detected in one of the many larger veins in the fruit wall.

The pattern of distribution of ^{45}Ca correlates with the occurrence of Light Green. Leaves, stems, young flowers, pedicels and calyx could all contain this ion. As far as the fruits are concerned blackening of the film was only found at the extreme base of young, small fruits, while never any ^{45}Ca could be recorded in medium or larger sized fruits. In Plate I the result of an experiment is depicted.

In one experiment water consumption by the plant and growth of the fruits was measured. The plant with 15 expanded leaves absorbed about 240 ml solution. A single leaflet may thus average a waterloss of a bit more than 2 ml. The increase in size of some half grown tomatoes was even slightly more. But none the less they do not receive any colouring substance or ^{45}Ca .

2.2. Experiment with apple

A few twigs, carrying young fruits, were cut from an old Jonathan tree. In the laboratory a fresh cut was made and the twigs placed on the same dilute nutrient solution with Light Green and ^{45}Ca added. Within a few hours the first traces of colour could be detected in the leaves.

After 2 days the twigs were removed and inspected. The results are given in Table 1 and Plate II.

TABLE 1
Distribution of Light Green and ^{45}Ca in apple twigs

twig	colour	^{45}Ca
I leaves	strong colour	high content over whole lamina same pattern of distribution
2 cm fruit	some near base	
3 cm fruit	base and veins along cavity	
II leaves	well coloured	high content some Ca in base and decreasing towards tip Ca in stem and main central veins
1½ cm fruit	some colour	
1½ cm fruit	some colour	
4 cm fruit	colour in base, along cavity and tip	

Again we find that the leaves obtain a large amount of Light Green and ^{45}Ca , while the amount entering the fruits is small in comparison.

2.3. Experiments with potatoes

The plants used in the experiment were grown in the glasshouse in plastic pails, the bottom of which had been replaced by a wire screen. The lower part of the pail was filled with garden soil and on top of a layer of nylon gauze sand was filled in. The pails were placed on top of vessels containing a dilute nutrient solution. In this setup part of the root system would grow from the soil into the solution. Growth of stolons and young tubers was restricted to the top layer of sand.

For the experiments the protruding root system was partly cut off and the plants in the pails were placed on top of a vessel containing a dilute nutrient solution + Light Green and $10 \mu\text{C}^{45}\text{Ca}$ per 600 ml. Usually part of the stems were cut off to remove excess foliage. A comparison was always made between plants with the stolons and young tubers buried in the sand and plants where the sand had been removed to expose these organs to the air.

The period of uptake varied from 2–5 days.

Inspection of the plants at the end of the experiment usually showed a light colouring of the leaves, mainly in the veins, and blue coloured xylem in the stems. As far as the stolons and young tubers are concerned there was generally a clear blue colour visible in the stolons exposed to the air. Cuts through the tubers exposed the blue colours in the vessels and sometimes the eyes were coloured. If the stolons and the tubers had remained buried in the sand an exceptional blue colouration would be noticeable if the sand had been very dry. In well moistened sand these parts remained white.

The results of the radioautographs demonstrated a corresponding distribution of ^{45}Ca . Colouring of the leaves and their filmprints showed a good correlation. Stolons exposed to the air gave the strongest blackening on the films. Exposed tubers were found to contain ^{45}Ca in reasonable amounts, mainly at the base and in the tissues between the circle of veins and the surface. Buried stolons and young tubers were generally devoid of any ^{45}Ca .

We may conclude that under normal circumstances the water taken in by the roots is nearly all transported to the aboveground parts of the plant, carrying along the ^{45}Ca and the dissolved Light Green. Only if the transpiration of the stolons and young tubers is raised by exposure to air does a worthwhile amount of the absorbed solution enter these organs. An example of the results is depicted in Plate III.

2.4. *Experiment with broad bean*

Medium sized plants grown in pots were taken into the laboratory and their roots washed free of soil. All smaller roots were cut off and the plants were placed with their root stumps immersed in a dilute nutrient solution + Light Green and ^{45}Ca .

At the end of a 2-4 days absorption period the plants were inspected, samples removed and dried before being autoradiographed.

Inspection showed that the blue colour could be clearly seen in all plant parts: stems, leaves, flowers, young fruits and even in full grown fruits, mainly in base and tip. These large pods were carefully cut lengthwise through the main veins for further examination. The blue colouring could be traced all along the cut xylemvessels of the main carpel veins. There was, however, an abrupt ending of the colouration at the point where xylem vessels branched off to the seeds. Nowhere in the connecting strands or in the seeds, either small or large, could any colour be detected.

The results of the autoradiographs as given in Plate IV show exactly the same distribution for ^{45}Ca . This ion can be found in all parts of the plant and is even present in the pods to a fair amount. None, however, was ever traced in the sliced seeds.

For this plant we may conclude that the flow of water over the xylem to the seeds, by which means the main supply of Ca must occur, is restricted. All other parts are well supplied.

2.5. *Discussion*

All previously described experiments demonstrate the fact that certain plant parts, which are known to be relatively low in Ca-content, show a restricted or wholly lacking flow of water through the xylem to these organs. DE KOCK (1964) also suggests the uneven calcium distribution as being linked to a large water supply for transpiration or a large supply of assimilates. This restricted xylem water influx does not necessarily hold for their whole period of growth. The water supply by means of the woodvessels seems to be most

severely restricted when the affected parts are in a stage of fast growth. When these parts, such as tomato fruits are still very small there still seems to be an influx of water and of ^{45}Ca . Corresponding behaviour has been noticed for buds of pear trees (GOUNY and HUGUET, 1964).

The pattern of distribution of ^{45}Ca more or less corresponds to the flow of water in the wood-vessels as indicated by the colouring. The main point is, that lack of calcium supply is always linked to an inhibited flow of water in the xylem to these parts. If the flow is only restricted – as is the case in young apples – the influx of Ca decreases accordingly.

Confronted with the fact that all plant parts investigated are organs, which show a large increase in size and thus surely will need a large supply of water this discrepancy needs explaining.

For an explanation reference can be made to a conception at which MÜNCH (1932) arrived in his work on transport in the phloem. The hypothesis of transport in the phloem occurring by means of mass flow (CRAFTS, 1961; ZIEGLER, 1963) implies that a large amount of water in which the assimilates are dissolved moves towards the sinks where the substances are laid down (CRAFTS and CURRIER, 1963). If the total consumption of water in these parts – growth plus transpiration – is not too high the amount of water arriving by means of the phloem could even be in excess of the needs. Excess water is then supposed to flow back in the xylem (MÜNCH, 1932). Recently, results obtained by ZIEGLER (1963) give evidence supporting this interpretation.

3. EXPERIMENTS TO INFLUENCE CALCIUM TRANSPORT BY MEANS OF RETARDED OR ENHANCED WATER TRANSPORT IN THE XYLEM

Taking the explanation given above for granted the possibility of shifting the balance between waterconsumption and supply of water over the phloem was investigated. The idea was that restricted transpiration of the fruits or faster growth of these parts should lead to a dominance of water supply over the sieve tubes. Contrary, retarded growth of the fruits should lead to a relative increase of transpiration in the total waterconsumption, which might bring about the necessity of additional water supply over the xylem. This additional influx of water should result in a better calcium supply.

3.1. *Experiments with tomatoes*

An experiment based on the considerations given above was performed in which it was attempted to modify the incidence of blossom-end rot in tomato-fruits by appropriate treatments.

Five sets of tomatoes were grown with intervals of three weeks. Young plants of the variety Renova were planted in buckets filled with a sand-peat mull substrate. Fertilizing was done in a manner to obtain susceptibility to blossom-end rot. The plants were detopped after formation of the sixth truss and each truss was allowed to carry only five fruits.

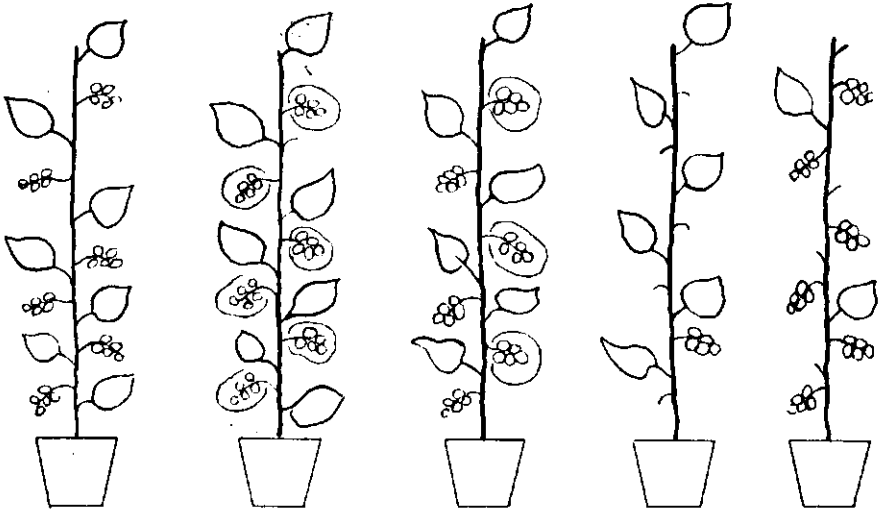


Fig. 1

Schematic drawing of the five treatments imposed on the tomato plants: control, bagged, alternatingly bagged, only 1 truss left, defoliated.

The following treatments were applied (Fig. 1)

- 1 control, normal with 6 trusses of 5 fruits
- 2 restricted transpiration, all 6 trusses enclosed in translucent plastic bags
- 3 alternating, free and enclosed trusses alternating
- 4 enhanced growth, only 1 truss remains on the plant by removing the 5 others
- 5 restricted growth, only 1/3 of the foliage left on the plant carrying 6 trusses

Growth of the fruits was recorded by weekly measurement of the diameters.

The data in Table 2 clearly show that the treatments imposed have indeed influenced the growth rate. Transpiration must have been affected as water condensed in the bags, so the atmosphere around the fruits must have been near to saturation.

The effect of the treatments on the fruits is given in Table 3 and

TABLE 2

Average increase of fruit diameter in mm/day of identical trusses in each of the 5 series

enhanced growth 1 truss	normal control	retarded growth 1/3 leaf
0.98	0.96	0.95
1.26	1.15	1.13
1.54	1.14	1.01
1.12	0.99	0.93
1.09	1.08	1.00

$P = 0.0008$

TABLE 3
Percentage blossom-end rot in relation to growth rate and transpiration

series	bagged	1 truss	control	1/3 leaf
1	20	0	20 / 0 {	0
2	100	100	0	0
3	25 / 80 {	80	0	0
4	60	20	0 / 20 {	0
5	0	0	0	0
average	47.5	40	6.7	0 $P < 0.1$

TABLE 4
K/Ca ratio in fruits of identical trusses in different treatments

series	bagged	1 truss	control	1/3 leaf
1	16.0	12.7	14.8 / 13.3 {	7.7
2	21.9	20.5	15.1 / 15.4 {	11.7
3	15.4 / 15.6 {	14.1	11.2	9.7
average	17.2	15.8	14.0	9.7 $P = 0.017$

in Table 4 the data on chemical constitution are summarized. The results clearly form a confirmation of what was expected. The incidence of blossom-end rot is the highest under conditions of reduced transpiration. Faster growth also gives a high percentage affected fruits, while restricted growth rate results in a low disease incidence. The K/Ca ratio correlates with the percentage diseased fruit. Reduced transpiration does indeed lower the Ca-content, while retarded growth results in the highest Ca-percentage. Enhanced growth rate mainly results in a high K-content, which may be the result of increased influx via the phloem along with the assimilates.

A Ca-content less than 0.08% on dry matter always gives rise to blossom-end rot. If the calcium content rises above 0.12% all fruits are healthy. These data are well in accord with those given by GERALDSON (1957).

The conclusion is that the results lend support to the idea that the tomato fruit obtains its water by means of two different pathways, the most important of which is the phloem. The Ca-supply is related to the amount of additional water drawn towards the fruit by means of the xylem.

This interpretation gives us an understanding of the observations that the incidence of blossom-end rot in horticultural practice is related to an insufficient water supply under conditions of high transpiration (EVANS and TROXLER, 1953; HÅRDH, 1957), low Ca-

and high K-content of the soil (EVANS and TROXLER, 1953) and fast growth as may be induced by a high N-fertilization (HÅRDH, 1957; DE VRIES, 1958).

3.2. *Experiment with apple*

The experiment was performed on an old, rather poor, Jonathan tree. Two treatments were applied. On the south side of the tree many smaller twigs were pruned and the remaining twigs partly defoliated. The purpose was to retard development of the fruits occurring on them. At the opposite side of the tree pruning was also carried out and the remaining very young fruits along with some leaves were enclosed in translucent plastic bags. The remaining fruits on the tree were taken as controls. At ripeness the fruits remained small and were often somewhat misshapen as a result of insect damage.

After harvesting them the fruits were cut into pieces and dried. Later they were ground to a coarse powder, ashed and analysed for Ca and K.

The poor quality of the material and the restricted number of analyses did not give significant differences. A very slight indication was obtained that bagged apples might contain a lower Ca-content, while the K-content remains unaltered. This could mean a corroboration of the results obtained on tomatoes.

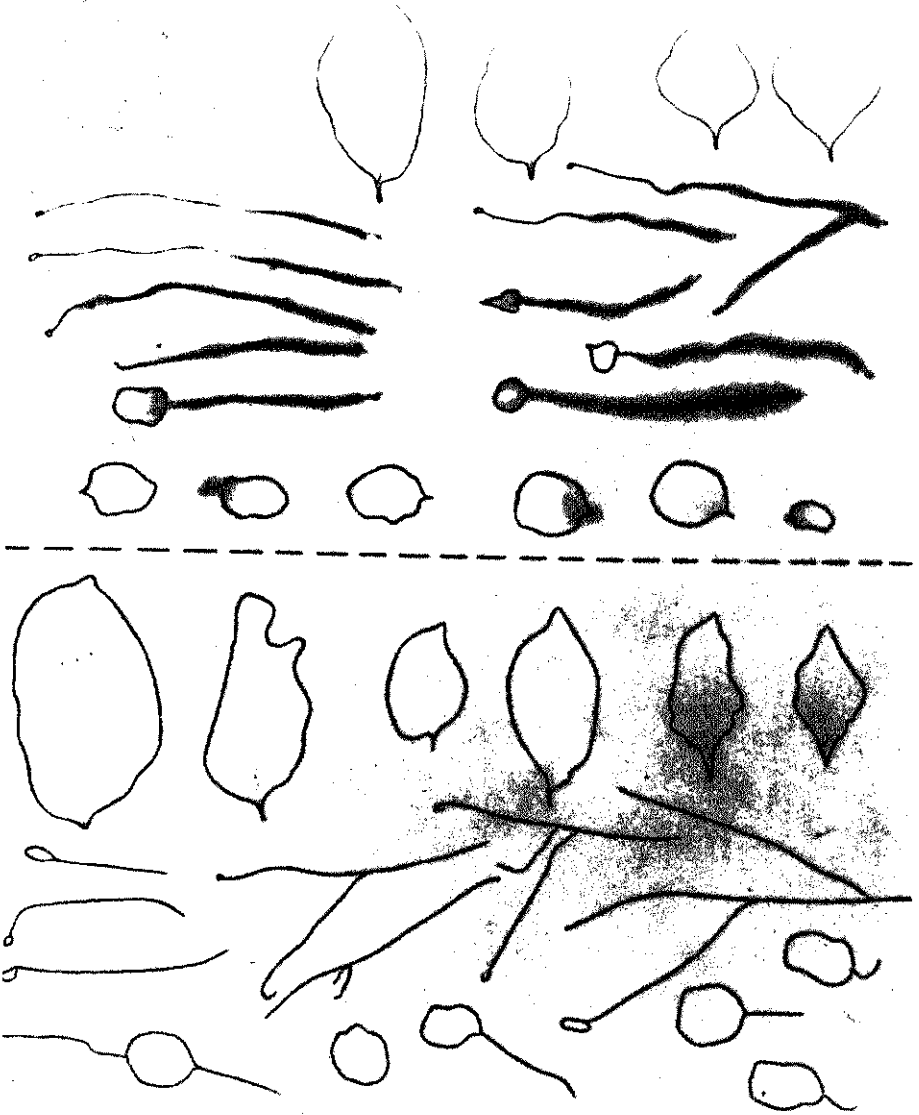
That the imposed treatments can have the expected effects is already to be found in the literature. BOULAY and LEBLOND (1963) notice a higher incidence of bitter pit of fruits grown in bags. BOUHIER DE L'ECLUSE cites Krause that defoliation before plucking diminishes bitter pit (1962).

The validity of the supposition that the growing apple fruit in its stage of fast growth receives little water over the xylem is supported by the fact that the influx of N, P, and K follows the gain in weight and Ca-influx is extremely slow (ASKEW *et al.*, 1959/60, 1960). The same contrast in behaviour regarding influx in the cherry seed for ^{90}Sr and ^{137}Cs has been noticed by EYNARD (1963). In this stage the Ca-content of the apple undergoes a relative dilution.

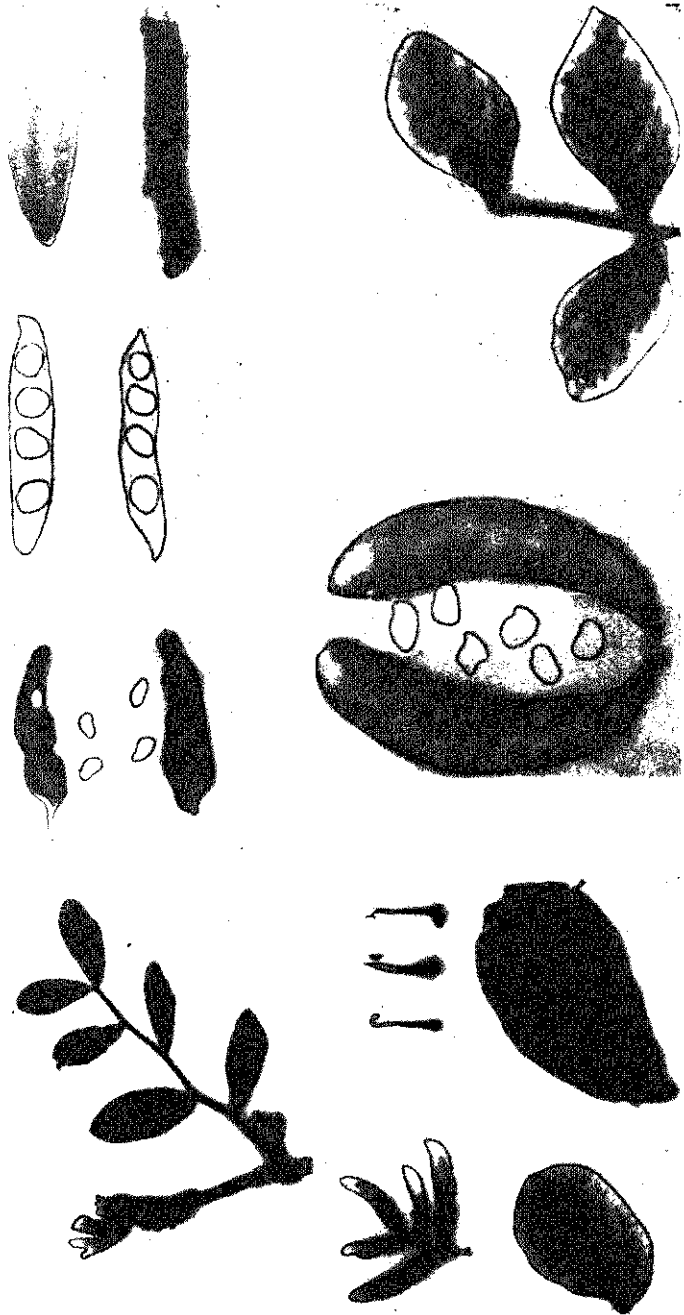
That fruits growing on the sun-exposed side of the tree have better keeping qualities in regard to bitter pit than those on the more shaded side, can possibly be explained by envisaging a higher transpiration. This difference has been noticed in practical experience with certain varieties in South Africa (de Haan).

3.3. *Discussion*

The results of these experiments, which are based on the supposition that there are two modes of water supply to these fruits, support the idea that the balance can be shifted. The Ca-supply is correlated with the amount of water entering by means of the xylem, which during certain periods is very small. So this investigation indirectly demonstrates the validity of the conception that transport in the phloem occurs by means of mass flow.



Autoradiographs of ^{45}Ca distribution in the potato. Upper part: plant with stolons and young tubers exposed to air shows Ca both in leaves, stolons and tubers. Lower part: plant with buried stolons and young tubers only has ^{45}Ca in the leaves.



Distribution of ^{45}Ca in the broad bean. Ca is detectable in all plant parts except the seeds.

This balance between the two modes of water supply varies during development. In our own experiments we found a good supply of water and ^{45}Ca entering flowers and very young fruits by means of the woodvessels. In the stage of expansive growth this supply is more or less eliminated. The situation can again change in full grown fruits. This can be deduced from the data given by ASKEW *et al.* (1959, 1960) on the mineral content of the apple during growth. The young apple starts with a more or less normal Ca-content. Then comes a period of extremely low influx and a strong dilution. Only when the flux of assimilates, N, P, and K comes to an end at ripeness, does the Ca-content rise again. This would mean that with the diminishing supply of organic materials also the water influx over the phloem decreases and that xylem influx bringing in Ca-containing water partly takes over.

A number of experiences in apple growing can now be well understood. Severe thinning of apples, resulting in fast growth and large sized fruits, favours susceptibility to bitter pit and other storage disorders (SHARPLES, 1964). Large size fruits are in general more susceptible to bitter pit (BEYERS, 1962; VAN SCHREVEN *et al.*, 1962). Late plucking usually diminishes the incidence of bitter pit in storage. High water consumption by the leaves and slow supply from the soil enhances the incidence of bitter pit (BEYERS, 1962, n.n. 1964).

4. GENERAL REMARKS

From the results of these experiments the conclusion could be drawn that especially in their period of fast growth the investigated storage organs receive no or hardly any water at all by means of the xylem. Thus the most obvious means of Ca-supply is more or less eliminated.

The increase in volume and dry matter of these parts in the same period requires an influx of both water and assimilates along with mineral substances. The most obvious explanation is that these are supplied simultaneously by means of a mass flow, occurring in the phloem. Taking into account the extremely low Ca-content in the sieve tubes (TAMMES and VAN DIE, 1964; ZIEGLER, 1962) their ineffectiveness in Ca-transport is readily understood.

Although many investigators (BIDDULPH *et al.*, 1958; CRAFTS, 1961; ZIEGLER, 1962) have demonstrated the immobility of calcium in the phloem, there still remain some reports on redistribution of calcium in the plant, where previously absorbed calcium is shifted from one site to another. It seems likely that much of this evidence (BUKOVAC *et al.*, 1956; FERRELL and JOHNSON, 1956; KESSLER and MOSZICKI, 1958; MOSOLOV *et al.*, 1957; PETROV-SPIRIDONOV, 1964; ROBERTSON, 1963; VLASYUK and GRODZINSKII, 1960, 1965) can be explained by release of calcium into the woodvessels and displacement along the xylem following gradients of uneven waterstress (BIDDULPH *et al.*, 1959). A confirmation of this explanation was obtained in one of a few auxilliary experiments. ^{45}Ca applied to an immersed leaf could be

detected in a nearby leaf exposed to a dry atmosphere. The plants were kept on a restricted water supply during the experiment to enhance the opportunity of inducing abnormal water movements.

Only under abnormal conditions, if the tissue is flooded with free calcium, does it seem to enter the phloem and to be transported by this means (ABUTALYBOV and DZHANGIROVA, 1961; MILLIKAN and HANGER, 1965).

SUMMARY

As a number of disorders in fruits and storage tissues is related to an insufficient Ca-content the mode of transport of this element was investigated. This mode of transport should also be able to explain the general very low Ca-content of these parts in comparison to leaf and stem tissues.

In a series of experiments with tomatoes, apples, potatoes and broad beans it could be shown that the distribution of ^{45}Ca follows the same pattern as that of the dye Light Green, which is carried along in the transpiration stream. During the period of fast growth neither dye nor ^{45}Ca enters the fruit, seed or the tuber.

This behaviour could be explained by accepting the occurrence of massflow in the sieve tubes supplying these parts with assimilates, water and other minerals, as the phloem-sap is extremely poor in Ca.

This explanation was further tested in experiments in which it was tried to shift the existing balance between the two modes of water supply. Restricted transpiration of the tomato-fruits, which eliminates accessory entrance of water via the xylem, indeed resulted in a still lower Ca-content and a higher incidence of blossom-end rot. Enclosing apples in plastic bags resulted in the same phenomenon. Reducing the water supply by means of the phloem by restricting growth rate resulted in a higher Ca-content, which is explained by accepting an accessory influx of water via the xylem.

The interpretation as given can explain a number of practical observations on the occurrence of blossom-end rot in tomatoes and bitter pit in apples.

In discussing the results it is pointed out that much evidence on redistribution of Ca may be explained by release into the xylem and translocation along with water in the woodvessels.

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