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Halvard Baugerød

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ROOTS VERSUS FRUITS IN THE CUCUMBER

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RØTTER MOT FRUKTER I VEKSTHUSAGURK

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NORGES LANDBRUKSHØGSKOLE
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Innholdsfortegnelse

FORORD

Denne avhandlingen omfatter studier angående rotdød i veksthusagurk. Studiene ble gjennomført ved Institutt for Grønnsakdyrking fra 1982 til 1986.
Jeg vil takke alle ansatte ved instituttet for deres kollegialitet og hjelpsomhet i denne perioden. Spesielt vil jeg takke Karin Svinnset som har hatt det daglige ansvar for de fleste forsøkene og har gjort dette på en fremragende måte. Min veileder, førsteamanuensis Halvard Baugerød vil jeg takke for fine diskusjoner og god veiledning både med forsøkene og skrivingen. Marit Huse og Elisabeth Olsen takkes for omforming av et uleselig manuskript til denne avhandlingen.

Ås, januar 1987

II A literature review concerning root death in cucumber and other crops.

Abstract

In the litterature concerning physiological root death,competition for assimilates between fruits and roots has often been proposed as the cause of root death. In this review an analysis of this problem was attempted by consideration of assimilate production, transport and distribution in normal plants and in plants in which the balance between source and sinks has been changed, with special reference to the cucumber. Fruit production in the cucumber is cyclic, in periods of little fruit growth root growth is vigorous and v.v.. The distribution of assimilates in the vegetative plant depends on light and temperature, it may affect root morphology as well. In the generative plant long term distribution seemed to be adequate, but short term studies have revealed a possible shortage for the roots.

Reduction of the fruit load has not prevented root death, nor has reducing the root mass aggravated it. Reduction of the leaf area increased photosynthetic efficiency in the remaining leaves, but did not affect root death. It seemed that competition for assimilates might be a problem during some phases of fruit growth, but it would not be the cause of root death. Further research, directly on root death, is needed. Plant hormones are also suggested to be playing a part.

Introduction

Production of early greenhouse cucumbers (*Cucumis sativus* L.) is often accompanied by problems with the roots. The term "root death" has been coined for this, though it is not accurate. The roots become brown, later the cortex decays and roots may become slimy. However, when root growth is restarted, new roots are formed which are laterals from the "dead" roots. The period between root death and formation of new roots may vary and is also considered a characteristic of root death. Plants may wilt on sunny days when they are affected with root death. Root death occurs in all seasons and all growing media, but is more severe in spring.

The phenomenon has been known for a long time, but only recently has one tried to gain more insight into the problem. Typical for root death of cucumber and other crops is its timing. Root death symptoms always occurs a short time (dependent on the crop) after fruit sets, in the case of cucumber 12-14 days. Therefore, it was suggested that root death is caused by competition for assimilates between roots and fruits.

In this paper first a review is given of research on fruit production in cucumber in which indications of root death are pointed out. Secondly assimilate production and distribution is reviewed for cucumber and some other crops. Thirdly experiments, in which assimilate distribution and/or transport and competition between roots and fruits is changed, are discussed in connection with root death of cucumber and other crops.

Root death and fruit production

Root death as such is only mentioned in relatively recent papers. However, in older reports one may find indications of root death, and also root growth was studied in some of these. Root growth of the cucumber follows a cyclic pattern (figure 1). At the onset of fruit growth root growth decreases and eventually stops. The size of the root mass reaches a minimum when the fruit load is maximal. This prevents the setting of new fruits which in turn makes root growth possible. When the roots have regained a certain size fruit set increases which inhibits root growth and so on.The first cycle shows the most severe root death. The reason for this is probably that the plants have a small leaf area and are growing under bad light conditions as in practical growing in spring (Van der Post, 1968). Hence fruit production also follows a cyclic pattern, which is not desirable from the growers point of view.

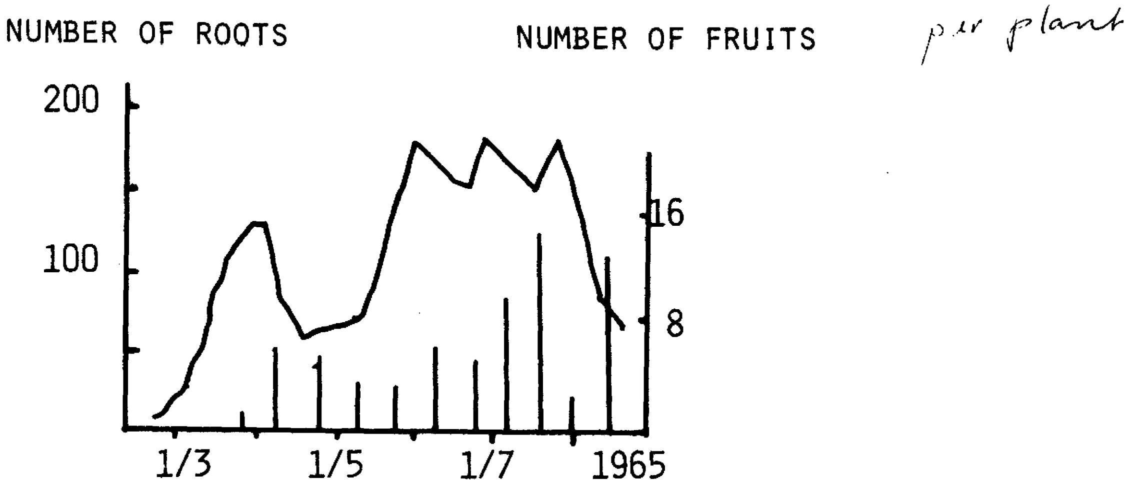

Figure 1. Number of healthy roots and yield of fruits of cucumber cultivated in concrete containers (Van der Post, 1968).

Already in 1934 McCollum had noticed that fruit growth inhibited vegetative growth. He used a monoecious, non-parthenocarpic cultivar and observed that vegetative growth was inhibited until seed development was completed. Also parthenocarpic fruits inhibited vegetative growth to some extent, but complete inhibition was only obtained with seeded fruits. McCollum (loc. cit.) assumed there was a competition for assimilates between vegetative and generative parts. He expected, but did not find accumulation of assimilates in any part of the plant before the start of fruit growth.

Carlsson (1973b) noticed that yield was reduced by seeded fruits in a parthenocarpic cultivar. The earlier seeded fruits developed the stronger was the reduction in yield.

In monoecious cultivars grown for parthenocarpic fruits cyclic fruit production was observed by Von Hösslin and Sieber (1958). When big fruits were harvested the number of fruits was lower than with small fruits. Besides, fruit quality decreased and abortion increased with bigger fruits. The plant was more vigorous, with more side-shoots when small fruits were harvested than when fruits were left on the plant.

In another experiment Carlsson (1973a) compared production in number of fruit and kg when fruits were harvested at specific weights. The number of fruits decreased with an increased fruit weight. The maximum kg yield was reached at different fruit weights for different cultivars.

De Stigter (1969) used plants in which there was just one leaf to each fruit. He observed competition between fruits and roots. The roots that "died" first took the longest time to recover. He assumed that these were roots connected to the same vascular bundles as the first fruit. There was also competition between fruits. The first fruit inhibited growth of the younger fruits, when it was removed the second fruit became dominant. Fruits might be inhibited 3-4 times in their development.

Also in gynoecious cultivars the cyclic fruit production pattern has been observed (Liebig and Krug, 1976; De Lint and Heij, 1982). Root death has become a problem in gynoecious, parthenocarpic cultivars also, probably because vegetative growth is very much restricted in modern growing techniques, as compared with McCollums experiments.

In all cases a high early production was combined with a low total production. This could have been caused by a more severe root death in plants with a bigger fruit load, especially in early spring. In seeded fruits seed growth is also an important sink, the competition with the roots might be even more severe. When the root mass is reduced fruit set is very low, and a lot of ovaries will abort, as was also observed. Besides bigger fruits will compete more between themselves.

The same cyclic fruit production was also observed for tomato (Leonard and Head, 1958), sweet pepper (Kato and Tanaka, 1971) and melon. Van der Post (1968) showed that in all these crops root growth is opposed to fruit growth.

Assimilate production and distribution

Vegetative plants.

In a vegetative plant (h.l. before flowering) mature leaves will be sources of assimilates, the apex, young leaves and roots will be sinks. Under low light conditions the net assimilation rate (NAR) of cucumber was highest at 18°C, compared to 12 and 24°C air temperature. Then also root growth was maximal (Kleinendorst and Veen, 1983). Ikeda (1978b) showed that the highest rate of photosynthesis occurred between 10-20°C.

The transition from sink to source in leaves of cucumber depended on light and temperature conditions (Pharr and Sox, 1984). In tomato the first leaf did not become a source until 30% of its final size was reached (Ho et al., 1984). The authors compared this result to other studies on tomatoes, cucumbers and other crops and found that usually the leaf was 30-50% of its final size before it became a source.

In the cucumber equal amounts of assimilates were transported during day and night (Kanahama and Hori, 1980). In the tomato Ho et al. (1984) found more export during the day than during the night (80 vs. 20%).

In cucumbers transport was reduced at 5°C compared to higher temperatures and also distribution was affected by temperature (Kanahama and Hori, 1980). A low air temperature would decrease the shoot/root ratio (S/R) and this was also observed by Murakami and Inayama (1974) who compared 14 and 20°C night temperature. Challa and Brouwer (1978) observed that this was because of a reduction of root respiration, the dry matter content was not changed. The same was observed in other crops, e.g. tomato (Hori and Shishido, 1978).

In addition, Moorby and Graves (1980) noticed that root morphology of tomatoes changed with the temperature of the roots. At 15°C the roots became thick and brown, at slightly higher temperatures a mat of coarse roots was observed. At 23°C they observed thin, white, healthy roots with a lot of laterals. At 30°C root morphology was the same as at 15°C.

Root growth was closely related to NAR, because the roots are completely dependent on assimilate import and have little reserves. An important question with regard to root death is whether S/R, root surface area (morphology), root dry weight or root activity is the most important character.

Generative plants

Photosynthesis of cucumbers increased when fruit growth started, 80% of the exported assimilates were transported to the fruit. The absolute amount available to the vegetative parts remained the same (Barrett and Amling, 1978). On the other hand, it was observed that 95% was exported to the fruit by the leaves closest to it. The demand of the fruit was highest after 4-6 days (about 0.5 g dry weight) of fruit growth. Source capacity seemed to be limiting rather than sink strength of the fruits (Murakami et al.,1982).

The relative sink strength of the roots was greatest at 12^oC air temperature, when the relative sink strength of the fruit was minimal. At both higher and lower temperatures root sink strength decreased and fruit sink strength increased. Transport of assimilates to the roots occurred mainly at night (Kanahama and Hori, 1980).

In contrast to the vegetative phase there was no accumulation of starch in the leaves of generative plants. Fruit growth depleted the leaves during the night. The leaves avoided competition partially by growing as much during the day as during the night. The maximum growth rate of the fruit was calculated to be 3.3 g assimilate/day. This amount could be supplied by 14 dm^2 leaf area. In addition, maintenance and growth of other plant parts must be provided for (Pharr et al.,1985).

Schapendonk and Challa (1980) found under lower light intensities than Pharr et al. (1985) a maximum growth rate of 3.4 g CO_2/day for a fruit weighing 6 g dry matter. Maximum growth rate was reached after 12-14 days. The difference with the Japanese results might be caused by the use of different final fruit weights (Ito, pers. comm. 1985). Schapendonk and Challa calculated the leaf area required for growth per fruit including plant growth to be 20 dm^2. The assimilation capacity of the fruit itself seemed to be big enough to supply for its maintenance respiration.

In the tomato distribution of assimilates from the first 10 leaves was studied by Russell and Morris (1983). All leaves exported assimilates to all plant parts, the oldest leaves (1-4) mainly acropetally, the younger leaves (5-9) mainly basipetally. The truss, formed after the ninth leaf, was placed between the orthostichies of leaves 1 and 6 and 3 and 8. It received its assimilates mainly from these leaves. The maximum growth rate of tomato fruits was reached 25 days after pollination (Ho, 1984). Hurd et al. (1979) observed that the S/R of the vegetative parts remained constant throughout the season, with the exception of a period when the fruit load was maximal. Although the overall distribution of assimilates to the fruits was about 80% of the total export, it was 90% at the time of maximal fruit load.

The fruit load of both cucumber and tomato is maximal at the time of the first occurrence of root death. Then the plant is relatively small, and several fruits are growing. It seemed that source capacity was limiting growth, especially as root activity must be higher at this time to meet the demands of the growing fruits and shoot. The same absolute amount of assimilates to the vegetative parts might be too little at this time. If the fruit for even a short time receives more than 80% of assimilates, which is the mean for the whole season, competition is unavoidable.

So far only the ordinary development of the plants has been discussed. In order to study root death's connection with fruit production measure had to be taken changing root mass, leaf area and/or fruit load. These experiments will be discussed hereafter. Very little research has been done, so also studies not involving the roots will be discussed. Most research has been done with tomatoes.

Changes in fruit load.

Liebig (1978) compared cucumber plants with and without fruits and noticed that the leaf area, especially of gynoecious cultivars, was reduced in plants with fruits, Photosynthetic efficiency was increased but probably not enough to avoid competition.

Also the root mass became bigger in plants without fruits than in plants with fruits. Root death was not prevented, although plants without fruits had less severe root death than plants with fruits (Van der Vlugt, 1986).

In the tomato the effects of truss removal and truss thinning have been studied with regard to photosynthesis, translocation and distribution of assimilates. In a long term experiment Hurd et al. (1979) observed that root growth was reduced before flowering and ceased completely about 1 month after flowering. When the fruit load was reduced to 3 fruits per truss reduction and cessation of root growth were also observed, but the final root mass was bigger than in plants with a full fruit load. They assumed that there was a functional balance between vegetative and generative growth independent of fruit load. They suggested that the vegetative mass at the beginning of fruit production determined the occurrence and degree of root death.

Starck et al. (1979) studied the photosynthesis every other week, starting at flowering, in tomato plants with and without fruits. In some cases fruits were kept in the dark to prevent their photosynthesis. The total dry matter production (roots not included), was the same for all treatments, fruits reduced the growth of the vegetative parts. Photosynthesis and dark respiration were the same in plants with and without fruits after 2 weeks. After 4 weeks photosynthesis was lower in plants without fruits than in the other treatments. At the end of the experiment photosynthesis was also lower in ? plants with fruit in the dark, than in plants with fruits. Their conclusion was that photosynthesis was not directly related to sink demand.

When the first truss of tomato plants was removed NAR decreased (Tanaka and Fujita, 1974).Translocation from the lower leaves was reduced, but their assimilates were redistributed to the other trusses. The total dry matter accumulation was the same in plants with and without the first truss. They observed that assimilate transport to the roots was adequate in high light conditions, but decreased in low light conditions.

Quast (1977) also found an unchanged dry matter production in tomato plants with and without fruits. Without fruits more carbohydrate reserves were found in all plant parts. The dry matter content of the roots was highest in plants without fruits.

Ho et al. (1983) carried out experiments with plants in which the source sink system was reduced to one truss and one leaf. Assimilate transport to the roots was stopped. In a low light intensity photosynthesis was not changed because of removal of the truss, in contrast to high light intensity. More carbohydrates were accumulated in leaf and stem after truss removal, irrespective of light conditions.

Hall (1977) shaded or removed the first fruit on sweet pepper plants. Without fruit the root system continued to grow after it had stopped in plants with fruit. Eventually a reduction in root mass was also observed in plants without fruit. The dry matter content of the roots decreased after flowering in both treatments, but more abrupt and severe in plants with fruit. The rate of photosynthesis was influenced by the source-sink balance. Photosynthesis was reduced by 30% in high light conditions and less in low light conditions. Compared to plants with fruit, more carbohydrates were accumulated in plants without fruit in leaf and stem after fruit removal (Hall and Milthorpe,1978).

In bean plants the pods were the strongest sinks, the amount of assimilates available to the roots decreased. The nearest leaf was the main assimilate supplier to the pods. When the pods were removed this leaf redistributed its assimilates to all plant parts (Olufajo et al., 1982).

Total dry matter content of the plants was the same in plants with and without fruits in all crops investigated. Reduction in vegetative growth was observed and must be due to competition between fruits and vegetative parts.

In low light conditions also photosynthesis remained unaffected, showing that dry matter production was below maximum. The roots would be more affected than the shoot if, as in vegetative plants, transport to the roots was reduced under low light intensities.

Changes in leaf area

Defoliation in cucumbers was often carried out in order to reduce vegetative growth. In monoecious cultivars this had the additional advantage of increasing the number of female flowers, and thereby probably increasing production (Liebig, 1978). He compared a monoecious (cv M) and a gynoecious (cv G) cultivar in several deleafing treatments. Cv M gave a better yield with deleafing compared to not deleafing. Cv G showed a tendency to decreasing yield with more severe defoliation. The reduction of the leaf area was not completely compensated by increased photosynthetic efficiency.

Van Uffelen and Bulthuis (1984) compared plants with one and two shoots. The 2-shooted plants gave a low early yield, but the total yield was increased when both shoots came from the lowest nodes.

Hurd and Mountifield (1980) compared a compact and a vigorous tomato cultivar. Both were grown with and without an extra side-shoot. The S/R was bigger in the vigorous cultivar and was not changed by the extra shoot. The compact cultivar gave a very high early yield and relatively low total yield, the side-shoot did not influence the number of fruit per truss. The leaf area decreased after flowering. This cultivar had more severe root death than the vigorous cultivar, this was not reduced by the extra side-shoot. In the vigorous cultivar early yield was low, but total yield was high. The side-shoot reduced the number of fruit per truss. The leaf area remained the same throughout the season. They suggested one should use more vigorous cultivars in hydroponics and not try to manipulate the vegetative/generative ratio.

The leaf area was decreased by more vigorous defoliation than normal in a tomato crop, it was increased by allowing one leaf of each side-shoot to develop. A large leaf area decreased early yield but total yield was similar to that of a normally defoliated crop. Rigorous defoliation did not influence early yield, but reduced total yield. (Lamm, 1956).

Tanaka and Fujita (1974) also removed leaves in their experiments, either the oldest, below the first truss, or the youngest, above the first truss. When all leaves were removed transport of assimilates to the roots was stopped. Removal of the oldest leaves had little effect on the trusses. Removal of the youngest leaves decreased truss weight, especially of truss numbers 2, 3 and 4. When 30% of the area of each leaf was removed this had no effect on dry matter in trusses or stem, but the dry matter in the leaves decreased.

In defoliated sweet pepper plants less carbohydrates were found in leaf lamina and stem than in normal plants. The effect was stronger when the rate of photosynthesis was higher (Hall and Milthorpe, 1978).

Again the light conditions proved to be very important. The production of assimilate must be maximal in order to obtain good and regular production.

Increasing the leaf area with an extra shoot disturbed the balance between vegetative and generative growth and resulted in a low early yield. However, the total yield was equal or higher than in the control plants of all crops studied, i.e. the roots have suffered less.

Changes in root mass

Carlsson (1963) showed that cultivars with a larger root mass gave higher yields than cultivars with a small root mass. He managed to increase yield by grafting a little productive scion on a vigorous root system. It seemed that a large root mass was needed to compete with the fruits.

In our grafting experiments we did not find differences in yield (Van der Vlugt, 1986, yield not published). The root masses were not significantly different. Grafting on *Cucurbita ficifolia* prevented root death.

Tachibana (1982) studied the cucumber/*Cucurbita* graft at different temperatures. *Cucurbita* itself or as a rootstock had a lower temperature optimum than cucumber. It was assumed that *Cucurbita* roots were a better sink than cucumber roots because their respiration was higher at lower temperatures.

De Stigter (1971) compared cucumber and melon on their own roots or grafted on *Cucurbita ficifolia*. In intact plants the starch content of the lower stem decreased in the order *Cucurbita* - cucumber - melon. The graft with melon on *Cucurbita* showed more starch above the graft than the graft with cucumber, but less in the rootstock. The starch content of the rootstock in the graft cucumber/*Cucurbita* was less than in *Cucurbita*. He assumed that the *Cucurbita* roots were a stronger sink than cucumber or melon roots.

Scanlan and Morgan (1982) increased the root mass of tomatoes by increasing the nutrient supply. They increased vegetative growth relative to generative growth. The root death was not observed.

One would expect more root death in root pruning experiments. Our experiments showed that the plants had recovered from root pruning at the time of root death. It was concluded that root age was not important in connection with root death (Van der Vlugt, 1985).

Kobza (1977) also observed increased root growth after root pruning of cucumber. After 20-30 days the original shoot/root ratio was restored and root growth rate reduced to maintain this ratio.

In vegetative bean plants transport of assimilates was studied in plants with intact roots or with 1/2 root mass. Acropetal transport rate was reduced in plants with 1/2 root mass. Basipetal transport rate was the same for both plants. The total transport was reduced after root pruning, but not as much as the root mass. It was suggested that the roots supply hormones to the shoot. They sent less hormones from a pruned root system which reduced shoot growth and gave relatively more transport to the roots (Ghobrial, 1983).

It seemed that a larger root mass was a better competitor. Cucurbita roots might be good competitors because they accumulate more assimilates for some other reason.

In our root pruning experiment the recovering period before root death was expected, was almost as long as the one observed by Kobza (1977). Root death of some roots might possibly be prevented if root pruning was carried out later.

Discussion

The litterature concerning root death is very limited. One might draw conclusions from observed changes in as-similate production, transport and distribution, but the connection with root death remains to be proved.

In commercial cucumber growing yield is somewhat reduced by root death but equally important is the reduction in quality of the fruits. De Stigter (1969) showed that the third and fourth fruit need a longer time to develop.

Root death is more of a problem in the cucumber than in tomato, because of the stronger dominance of the above-ground parts. Therefore research on root death should be done with the cucumber.

Commercial cucumber growers start the growing season in early winter, when the light conditions are very bad. Under low light conditions the plants are not able to increase photosynthesis in order to meet the increased demand for assimilates. The roots are in a special situation because they have to import all assimilates and have very few reserves. The transport to the roots occurs mainly at night , when also the fruits demand a lot of assimilates. In addition, Tanaka and Fujita (1974) showed that transport to the roots is low under bad light conditions. All in all this explains why root death occurs and is most severe in spring.

It is obvious then that a high early production inhibits root growth severely and the suggestion by Hurd et al. (1979) that one should try to get a big vegetative plant before fruit production seems logical.

So far, increased root mass has not given any results. For uptake of water and nutrients the root surface area is the most important factor. It should be investigated whether the balance between root surface and root dry weight is different before and after root death.

The distribution and transport of assimilates is also affected by plant hormones and the onset of fruit growth might alter the hormonal balance in the plants (Lenton, 1984). In general, plants change their hormonal balance when changing from vegetative to generative growth. It seems difficult for the plants to have both flowers and fruits at the same time, possibly also because of different hormonal requirements.

Conclusion

Root death may be caused by competition for assimilates between roots and fruits. In commercial cucumber growing this is aggravated by the light conditions in early spring. Competition does not seem to be the only cause of root death because it is not prevented by keeping the plants vegetative.

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ROOT DEATH IN CUCUMBER UNDER DIFFERENT COMPETITIVE CONDITIONS OF THE ROOTS

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Abstract

Root death in cucumbers at the onset of harvesting may be caused by competition for assimilates between fruits and roots. The experiments were carried out in NFT.
Root death was prevented in most cases by replacing the root system with that of *Cucurbita ficifolia*. Grafting on other cucumber cultivars did not prevent root death in 'Farbio'. Next, the size of the root mat was 1/2 - 1 or 2 x that of the control. Roots were pruned either at planting or when the plants were flowering. The size of the root mat at the time of root death was not significantly different for the treatments. However, weakened plants took longer time to recover from root death.

Topping at flowering (-T) and deflowering (-F) treatments were combined (control = +T+F). Plants with fruits took longer time to recover from root death than plants without fruits. The root mat was significantly larger in plants without fruits. In none of the experiments root death was prevented completely. Therefore, root death is not merely caused by competition for assimilates.

Introduction

Physiological root death of cucumbers occurs about 2-3 weeks after flowering, around the time the first fruits are harvested. Anatomical studies have shown that the cortex of the roots decays (Daughtrey and Schippers, 1978). However, the seemingly dead roots may produce new lateral roots after some time. As physiological causes of root death have been suggested competition for assimilates and changes in the hormonal balance in

connection with the transition to the generative phase (Hurd & Mountifield, 1978; Tucker, 1978, 1981). The purpose of our experiments was to establish whether root death is caused by competition for assimilates or not.
The object was pursued by changing the root mass, by changing the fruit load and by changing the assimilating area.

Carlsson (1963) showed that varieties with a larger root mass gave better yield and also grafting onto larger root masses gave better yield. Larger root mats might be better competitors for fruits. Differences between cultivars regarding root death have been observed (Daughtrey & Schippers, 1978). The root competiveness might be increased by grafting on an extra or a larger rootstock, or be reduced by pruning.

The total photosynthetic activity of the plants increased when fruits were developing (Barrett and Amling, 1978), but the fruits monopolised the assimilates. Hall (1977) showed that the size of the root mat of deflorated plants increased after commencement of flowering until a maximum was reached and then decreased again. Fruited plants did not reach the maximum.

Materials and methods

For all experiments the variety 'Farbio' was used. Seeds were sown either in rockwool or in peat. Artificial light to 18-hours day was given until March 15 both during propagation and after planting. Plants were transferred to NFT-gullies 3 weeks after sowing. The gullies were 4.5 m long, with 10 plants/gully, plant density 1.4 plants/m^2. There were 2 replications of each treatment in each planting. The EC was measured daily and adjusted to 2.0-2.5 mS. The pH was measured every other workday and if necessary adjusted with KOH or HNO_3 to pH 5.5-6.5.
<u>Grafting</u>. As rootstocks were used <u>Cucurbita ficifolia</u> and the cucumber varieties 'Farbio' and 'Marketmore 76'.
<u>Cucurbita</u> seeds were sown a few days earlier than the 'Farbio' graft, the other rootstocks were sown simultaneously with the grafts. Grafts were made by the approach graft method

when the seedlings were about 9 days old. Then they were grown under high humidity for 10 days until the grafts were cut from their roots. They were gradually acclimatized to lower humidity again before they were planted. The grafting experiments were planted in 1982: March and May, in 1983: March, June and August and in 1984: February.

Root pruning. Root pruning was carried out at two different times. At planting (vegetative) the roots were halved by taking away 1/2 of the medium. At flowering (generative) the root mat was halved by cutting away 1/2 of the root mat in the gully, leaving the pot intact. It was assumed that some of the roots that had been cut were connected with roots in the other half of the mat and that therefore the root mat was effectively halved. The root mat was doubled by grafting two 'Farbio' onto each other and leaving both root systems and only one shoot. The experiments were planted in January and April 1985.

Detopping and deflowering. Fruits were prevented from developing by picking the flowers as soon as they opened. This operation was continued until the plants reached the wire. Some of the plants were topped as soon as the first flowers opened. Experiments were planted out in 1984, in August, and in 1985, in January.

Root death symptoms were subjectively put in 3 categories, browning: the roots are no longer white, but no actual root death is seen, root death: roots become darker brown and sometimes slimy, formation of new roots: after a while new roots are formed, the period between root death and formation of new roots - (n-r) - may vary and is also considered as a characteristic of root death.

Results

Grafting.

Table 1. Root death symptoms of 'Farbio' when grafted on different root stocks. Relative order in which symptoms were observed, 1 = earliest, 4 = latest, - = not observed.

Rootstock	Browning	Root death	Formation of new roots	N-R
None	-	2	1	1
Cucurbita	1	-	-	-
'Marketmore 76'	2	3	3	1
'Farbio'	3	1	2	3 ^^

Because growth rates were different in different seasons only the order in which the treatments showed root death is given in Table 1. Grafting on Cucurbita prevented root death in 1982, although in later experiments root death sometimes was found, but always less severe than in the control. The graft 'Farbio' on 'Farbio' was a control for the effect of grafting in itself. It seemed that grafting weakened the plants, although this may have been caused by our inexperience. The graft on 'Marketmore' did nor prevent root death. It was observed that 'Marketmore' itself grows slower than 'Farbio'. It seemed that the order of susceptibility to root death was Cucurbita < 'Marketmore'<none<'Farbio'. The roots of Cucurbita were coarser than those of 'Farbio', the total root mass varied and was not always bigger than that of 'Farbio'.

Root pruning.

Root death symptoms occurred at the same time in both experiments, therefore the results were combined in Table 2.

Table 2. Root death symptoms of 'Farbio' plants, with differently sized root mats, in days after planting.

Treatment	Browning	Root death	Formation of new roots	N-R (days)
Control	24.2	34.5	39.0	4.5
Pruned veg.	25.8	32.5	40.0	7.5
Pruned gen.	24.8	32.7	40.0	7.3
Grafted	23.8	32.2	38.8	6.5

The differences between treatments were not significant in the analysis of variance. A regression analysis was also carried out with pruned roots counting as 1/2, the control = 1 and the graft = 2. No significant effect was found. The size of the root mat was estimated in an arbitrary scale from 1-5, 5 is the biggest. The actual size of the root mat at the time of root death was not significantly different for the treatments.

Detopping and deflowering.

The detopping and deflowering experiment showed different results in both replications with regard to the effect of topping (Table 3).

Table 3. Root death symptoms in days after planting in various detopping (-T) and deflowering (-F) treatments (control = +T+F) of 'Farbio'
A: 1984 B: 1985

Treatment	Browning		Root death		Formation of new roots		N-R (days)	
	A	B	A	B	A	B	A	B
+T+F	22	40.5	28	50.0	30	64.0	2	14.0
+T-F	26	36.0	28	53.5	28	59.0	0	5.5
-T+F	24	34.5	28	56.0	44	57.0	16	1.0
-T-F	21	31.0	26	52.5	29	55.5	3	3.0

This might have been caused by the different growing seasons. Plants with fruits developed new roots after a longer interval than plants without fruits on both replications. The root mat of plants without fruits was significantly larger ($P<0.05$) than of plants with fruits at the time of root death.

Discussion

Grafting on Cucurbita ficifolia was the only way of preventing root death in these experiments. Even those plants might show some symptoms sometimes.
The roots recovered from pruning before root death. The plants would try to maintain the shoot/root ratio and the flow of assimilates to the roots is increased. Kobza (1977) observed that the cucumber recovered in 20-30 days. The new roots seemed to lose their competiveness after this. The root systems in the pruning treatments would probably be more branched and also younger (generative) than in the control. Root age appeared not to be important with regard to root death, neither did branching.
An extra root system did not influence shoot growth and did not provide a buffer against root death. The suggestion presented itself that root death is caused by an impulse from the shoot to which the roots are more or less susceptible. Other root systems might be less susceptible, thus a positive effect of

grafting onto root systems of other varieties could be expected (Carlsson, 1963; this experiment) and differences between cultivars might be explained (Daughtrey and Schippers, 1978).

The impulse did not seem to be mere competition for assimilates, because also plants without fruits got root death. Competition for assimilates may have influenced the interval for recovery of the roots.

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I. The effect of the nitrogen concentration in the recirculating nutrient solution on root death in cucumber.

Dept. vegetable Crops. Agric. Univ. Norway, As, Norway
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Summary

The nitrogen concentration of the nutrient solution was reduced for a short period, in order to get a bigger root mass and less root death than normal. Root death was reduced but not prevented by manipulating the nitrogen concentration. There seemed to be a connection between root death and the time of the first harvest.

Introduction

Physiological root death, occurring a few weeks after flowering in cucumber, may be caused by competition between fruits and roots. Therefore, an improved root system would be a better competitor and hence less susceptible to root death.

High nitrogen concentrations in the nutrient solution increased vegetative growth of tomatoes compared to generative growth, but mainly shoot growth was improved[2]. A low nitrogen concentration, giving a low shoot/root ratio, would then be an advantage with regard to root growth, but would also increase fruit load.

More root death was observed in tomatoes grown in a low nitrogen concentration continuously, than in the high nitrogen concentration even though the root system was relatively larger[3]. Early yield and quality of tomatoes were reduced both by increased EC and increased nitrogen concentration; total yield was reduced only with increased nitrogen concentration[4]. In contrast, the total yield of cucumbers was improved by a high nitrogen concentration[1].

It was decided to give a low nitrogen concentration only during a short period in the vegetative growth phase of the plants, in order to obtain a bigger root mass and prevent root death, and then return to a normal concentration.

Materials and methods

Seedlings of the cv. 'Farbio' were raised in 9 cm plastic pots filled with peat. After 3 weeks of propagation they were planted in NFT gullies, on 2 Jan. and 29 Feb. 1984 respectively. Until 15 March additional artificial light was given 18 hours a day.

The nitrogen concentration of the nutrient solution was varied in the following way: the control treatment (++) received a complete nutrient solution in the two first weeks after planting. Two treatments got the nitrogen concentration reduced during the first (-+) or second (+-) week after planting. The fourth treatment (--) received a low nitrogen concentration during both weeks. Afterwards all treatments got the complete nutrient solution which was made up by $Ca(NO_3)_2$ (195 ppm Ca, 137 ppm N.) and a commercial fertilizer supplying the other nutrients (73 ppm N, 41 ppm P, 206 ppm K, 34 ppm Mg, 2,2 ppm Fe,0,97 ppm Mn, 0,25 ppm B). 2 ~ 7.

In the first experiment a low nitrogen concentration was obtained by replacing $Ca(NO_3)_2$ with 131 ppm K and 47 ppm N as KNO_3. In the second experiment no KNO_3 was added. In this way calcium and nitrogen effects became confounded.

Results

There were no visible differences between treatments in the size of the root mat. Root death came later in the first than in the second experiment, but not at a later stage in the development of the plants. In both experiments nitrogen had an effect on the time of root death and especially the period between root death and formation of new roots. The timing seemed to have opposite effects on different symptoms.

Table 1. Effects of varying the nitrogen concentration on root death symptoms (in days after planting) in cucumber. First experiment means for 2 replicates.

Nitrogen treatment					
Week 1	Week 2	Browning	Root death (R)[1]	Formation of new roots (N)	N-R (days)[2]
+	+	29	44.0	51	7.0
+	-	30	38.0	49	11.0
-	+	30	40.5	49	8.5
-	-	29	43.0	50	7.0

1) The interaction between nitrogen level and time was significant at the 10%-level.

2) The effect of the nitrogen concentration in the first week was significant at the 10%-level, the effect of the second week was significant at the 2.5%-level.

In the first experiment root death came earlier when the nitrogen concentration was low in the first week, but also recovery came sooner. In the second week nitrogen had the same effect on root death but the plants took longer time to recover. Harvesting started on day 44 for all treatments, i.e., root death occured at the same time or earlier than the first harvest.

Table 2. Effects of varying the nitrogen concentration on root death symptoms (in days afterplanting) in cucumber. Second experiment.

Nitrogen treatment					
Week 1	Week 2	Browning	Root Death (R)[1]	Formation of new roots (N)[2]	N-R (days)[3]
+	+	24.0	30.0	41	11.0
+	-	24.0	33.5	37	3.5
-	+	25.5	29.0	43	14.0
-	-	26.5	35.0	43	8.0

1) The effect of the nitrogen concentration in the second week was significant at the 5%-level.

2) The effect of the nitrogen concentration in the first week was significant at the 2.5%-level.

3) The effect of the nitrogen concentration in the first week was significant at the 10%-level.
The effect of the nitrogen concentration in the second week was significant at the 1%-level.

The results from the second experiment were different, also the formation of new roots was significantly delayed by a low nitrogen concentration in the first week. Harvesting started on day 34 for the control and on day 31 for the other treatments. When the nitrogen concentration was high in the second week root death came before harvesting and the time for recovery is the largest.

Discussion

The nitrogen concentration seemed to have an effect on root death, however, root death could not be prevented by manipulating the nitrogen concentration.

The differences between the experiments may be due to the occurence of root death relative to harvesting.

It seemed to be an advantage if root death were to occur after the first fruits have been harvested. Then the fruit load would be less at the time of root death. Also, a late root death would mean a bigger plant with a larger assimilating area and possibly less starvation of the roots than an early root death.

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III. The effects of plant density, an extra side-shoot and reduced fruit set on root death in the cucumber.

Dept Vegetable crops
Agric. University of Norway
Report no: 146

Abstract

An attempt was made to prevent physiological root death by lowering the plant density, then the plants would shade less for each other, and more assimilates would be available to the roots. An alternative approach was the growing of an extra side-shoot which would also increase the assimilate supply to the roots. In the experiment both treatments were combined. The size of the root mat was dependent on treatment. Root death occurred after the first fruits had been harvested. The period for recovery after root death was the longest in the highest plant density.

In another experiment the number of leaves per fruit was varied, i.e. flowers were pinched from specified nodes in order to increase the assimilate supply to the roots. Root death seemed to occur earlier in the relatively more vegetative plants than in the more heavily loaded plants. More vegetative plants also needed longer time to recover than heavily loaded plants.

The effect of vigorous vegetative growth on root exudation and its relation to root death is discussed.

Introduction

According to one hypothesis physiological root death of cucumber (<u>Cucumis sativus</u>) is caused by competition for assimilates between roots and fruits (Van der Vlugt (II)). Thus, variation of the plant density may influence root death by changing the assimilate supply.

A correlation has been found between plant density and spatial arrangement and fruit weight and quality. (Bakker and Van de Vooren, 1984).

Carlsson (1973) observed that gynoecious cultivars could be grown at greater density than monoecious ones. With increasing plant density the plants will shade each other more. Liebig (1983) investigated the relation of leaf area index (LAI) with plant density and found that until LAI=1 plants are not interacting with each other. With LAI=2 plants started the generative growth phase. The maximum LAI reached by cucumbers in a greenhouse was LAI=3, independent of plant density.

With a high plant density the mutual shading will be large, very few leaves per plant will be able to perform at maximum photosynthetic rate. Especially in winter the light conditions near the ground are so poor that they may lead to leaf-fall (Nederhoff, 1984). With regard to root death maximal photosynthesis was considered necessary. A lower plant density would improve the situation for the individual plant. However, a lower plant density would lead to decreased production. Therefore it was decided also to grow some plants with extra side-shoots in order to raise productivity. At the same time, the extra leaf area from the side-shoot may improve the assimilate supply to the roots and thereby prevent root death .

Hurd and Mountifield (1978) compared a vigorous and a compact tomato cultivar, with and without side-shoot. They did not obtain beneficial results with a side-shoot, that might be because they did not change plant density.

In Norway cucumber fruit production is started in the 4th -6th node and plants will be affected with root death. A cucumber fruit needs the assimilate production of 5 leaves at maximum photosynthesis (Challa and Schapendonk, 1984), besides, the plants themselves have to grow. It was assumed that production was being started too early. Complete removal of fruits did not prevent root death (Van der Vlugt, 1986). The effect of reducing the fruit load was investigated.

Materials and methods.

For all experiments seedlings were raised in 7.5 cm rockwool cubes and set out in NFT gullies 3 weeks after sowing. Gullies were 20 cm wide and 1 m apart. The nutrient solution was recirculated continously. The E.C. was measured daily and adjusted to 2.0 - 2.5 mS. The pH was measured every other work day and if necessary adjusted with KOH or HNO_3 to pH 5.5 - 6.5.

In a preliminary experiment the gynoecious cucumber cultivars Farbio, Farbiola, Saskia and Corona were compared with regard to vigour and root death. No significant differences were found. In the present experiments the cultivar Farbio was used.

Plant density experiments.

The number of plants per 4.5 m gully was 2,4,8 or 10. When there were only 2 plants per gully 2 side-shoots were taken out of each plant, giving a shoot density of $0.86/m^2$. With 4 plants/gully one side-shoot was taken out, giving a shoot density of 1.1 $shoot/m^2$. In the other treatments plant density was 1.1 and 1.4 $plants/m^2$ respectively. The shoots were taken out as soon as possible (from the lowest nodes). Both main stems and shoots were trained according to the umbrella system. There were 2 replicates of each treatment in each experiment, planted on 9 April and 29 July 1985.

Fruit load experiment.

The plant density was 1.4 $plants/m^2$, planted on 3 and 10 June 1985 respectively. In the control treatment (1) all the fruits which developed spontaneously were left on the plant (1 leaf/fruit).

In the other treatments flowers were removed at anthesis, leaving every 3rd, 5th or 7th fruit. In this way each fruit had a constant number of leaves. After harvesting leaves were removed, leaving the required number of leaves for the next fruit.

Root size was measured on a scale from 1 to 5, 5 was an exceptionally big root mass. Root death symptoms - browning, root death and formation of new roots - were recorded in days after planting.

Results

Plant density

Harvesting started at day 27 and 25 for the April and July plantings respectively. Early yield included mainly fruits from the main stems, very little from the side-shoots. Regression analysis of the results based on the number of plants gave a better explanation than regression analysis based on number of shoots. Early yield (24 days) increased with increased density in the first experiment (Table 1). In the second experiment the greatest yield after 40 days was obtained with 8 plants/m^2.

Table 1. Early yield of plants grown at different plant densities, means of two gullies. A:planted in April, yield from day 27 to 51. B: planted in July, yield from day 25 to 65.

Plant density/ shoots per plant	Number of 1^{st} class fruit		Total number of fruits		kg/m^2	
	A***	B**	A***	B**	A***	B*
2/3	33.5	40.5	58.0	80.0	3.436	4.055
4/2	60.5	60.0	95.0	108.0	5.430	5.475
8/1	81.5	79.5	130.5	145.5	7.188	7.570
10/1	95.0	62.5	172.0	118.5	9.464	5.655

*=$P<0.05$ **=$P<0.025$ ***=$P<0.01$

The size of the root mats was assessed several times during the experiments. An analysis of variance was carried out for all treatments and days of observation. In the first experiment the effects of time and plant density were both significant ($P<0.05$). In the second experiment only the effect of time was significant (Table 2). At all densities maximum root size was reached on the day of the first harvest. Afterwards root size would decrease a little and fluctuate.

Table 2. Mean size of the root mat during the whole experiment by an arbitrary scale. A: planted in April, B: planted in July.

Plant density/ shoots per plant	A	B
2/3	3.2	3.2
4/2	3.6	3.5
8/1	3.8	3.6
10/1	3.9	3.4

Table 3. Root death symptoms (in days after planting) in plants grown at different plant densities. Means of two gullies. A: planted in April, B: planted in July.

Plant density/ shoots per plant	Browning		Root death R		Formation of new roots N		N-R (days)	
	A***	B*	A	B	A□	B	A□	B
2/3	21.0	22.0	40.5	33.5	46.5	37.0	6.0	3.5
4/2	22.0	22.0	41.0	30.0	48.0	59.0	7.0	29.0
8/1	32.5	23.0	42.0	28.0	47.5	34.5	5.5	6.5
10/1	32.5	23.0	40.5	30.0	51.0	46.5	11.5	16.5

□=P<0.10 *=P<0.05 **=P<0.025 ***=P<0.01

Browning of the roots was delayed in both experiments with increased plant density (Table 3). The trend seemed to be the same in both experiments with delayed formation of new roots at greater plant density. The treatment 4/2 in the second experiment seemed to have behaved anomalously.

Fruit load.

Regression analysis was carried out with the number of leaves per fruit as independent variable. Harvesting started on day 23 and lasted 16 days in experiment A, and on day 24, lasting 20 days in experiment B (Table 4). In both experiments a significant increase in yield was found with the heavier fruit load.

[illegible] ?

Table 4. Yield of plants with different numbers of leaves per fruit. Means of two gullies with 10 plants each. A: planted 3. June, yield from day 24 to 44. B: planted 10. June, yield from day 23 to 39.

Leaves/ fruit	Number of 1^{st} class fruits		Total number of fruits		kg/m^2	
	A***	B***	A***	B***	A***	B***
1	47.0	48.5	79.0	91.0	4.798	4.644
3	36.5	37.0	53.0	58.5	3.880	3.804
5	23.5	31.0	35.0	42.5	2.248	2.881
7	20.5	20.5	30.0	34.0	1.947	2.157

*=P<0.05 **=P<0.025 ***=P<0.01

Table 5. Root death symptoms (in days after planting) in plants with different numbers of leaves per fruit. Means of two gullies. A: planted 3. June, B: planted 10. June.

Leaves/ fruit	Browning		Root death R		Formation of new roots N		N-R (days)	
	A	B	A	B	A	B	A	B
1	27.5	23.0	37.0	28.0	40.5	40.5	3.5	12.5
3	34.5	26.5	37.0	30.0	40.5	37.0	3.5	7.0 ?
5	23.0	24.0	35.0	28.0	40.5	43.0	5.5	15.0
7	23.0	24.0	35.0	26.5	40.5	35.0	5.5	8.5

Only in the first experiment significant differences in recovery period (N-R) were found, the treatments with less fruit actually requiring a longer recovery period (Table 5). The tendency seemed to be the same in both experiments: earlier and more severe root death with less fruit load.

Discussion.

Although the size of the roots in the treatments with the lowest plant densities may have been underestimated, they showed a strong correlation between root size and yield as was already observed by Carlsson (1963). The differences in root death symptoms between the April and July plantings may be caused by the different growing seasons as also the yields indicate.
The side-shoots did not produce fruit in the t~~o~~pical period for y root death. They may have served as assimilate supplies to the roots after their leaves were fully developed.

Root size and root death correlated better with plant density than with shoot density, indicating that the number of shoots is not important provided photosynthesis conditions are satisfactory.

The number of leaves per fruit was increased by the side-shoots, which had a beneficial effect on recovery after root death, in contrast to the fruit load experiment.

In the fruit load experiment plants with a high number of leaves per fruit showed more severe root death than plants with a low number of leaves per fruit. However, these plants were all grown at a high plant density.

In a closed system like NFT root exudates will remain in the root zone. It has been suggested that the plants produce some substances which are toxic to themselves at high concentration (Van der Vlugt, 1986). With more plants per gully a build-up of toxic substances will be more rapid than with fewer plants per gully.

Pegg (1986) showed that more vigorous tomato plants had a more active root system and also exudated more than less vigorous plants. This would be in agreement with the results presented here. Either fewer plants or more heavily loaded plants produce less exudates than vigorous plants at high densities.

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IV Root growth of cucumber in wide NFT gullies

Abstract

Growth of cucumber roots was studied in wide NFT gullies. Root growth rate was measured in cm per day and in number of lateral roots per day. Also the average length of the part of the root without laterals was calculated. The periods before and after root death were compared.

Root growth was significantly reduced after root death, but a significant linear correlation was found between growth rate before and after root death. This indicated that a fast growing root mat may suffer less from root death than a slowly growing mat. Also significant differences between seasons were found.

Anatomical studies showed that the cortex was disintegrated when root death occurred. Thereby root surface area was reduced to 30-40%. No early indications of root death could be seen. Roots were still very young, physiologically, when they were affected with root death.

Introduction

The degree of physiological root death may vary with the season, between plants in the same greenhouse and even between roots of the same plant. However, once some roots with root death were observed the other roots would follow (Hurd and Price, 1977; Van der Vlugt, 1986, part I and III).

Daughtrey and Schippers (1980) contended that the cortex decayed when root death occurred. Hayward (1951) mentioned that the cortex may persist for some time after secondary root growth has been initiated. Still, it would mean that roots are very young when they become affected with root death.

Therefore, it was considered necessary to study growth and anatomy of individual roots of the cucumber (*Cucumis sativus*) in connection with root death and if possible to find early indications of root death.

The roots of the Cucurbitaceae can grow very fast,up to 2 1/2 inch (= 6.4 cm) per day in *Cucurbita* (Whitaker and Davis, 1962). The development of the vasculary system of the roots is much slower than the growth rate. Laterals can be initiated very early (Hayward,1951).

Materials and methods

Root growth measurements

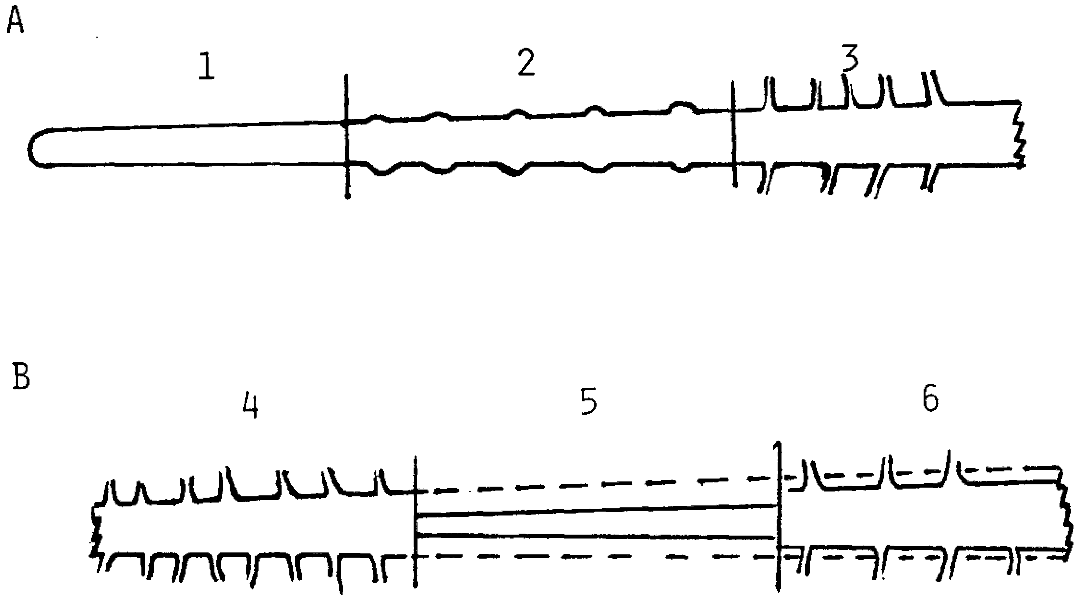
An adaptation was made of the wide trays used by De Stigter (1969a). Instead of an individual system for each plant we put 3 plants in a gully which was 4.5 m long and 0.6 m wide. Four such gullies were supplied with the same nutrient solution which was recirculating continuously. The nutrient solution was maintained at EC 2.0-2.5 mS and pH 5.5-6.5.

The best material for covering the gullies was found to be white polystyrene foam plates, painted black on the lower side. They were easy to move and the temperature in the gully did not become too high.

The gullies were lined with black plastic, no other support for the roots was supplied. Different kinds of netting and non-woven polymer fibre tissue (Agryl) were not satisfactory as lining because of toxic substances and problems with the roots growing through the holes.

Cucumber seeds of the cultivar Farbio were sown in small rockwool blocks (2.5x2.5x4.0 cm) and set out in the gullies 2 weeks after sowing. Natural light was supplemented with 5000 lux of fluorescent light in the period from October 1 to April 1 to 18 hours day. At planting about 6 roots were growing out of the block. Four of them were chosen at random for growth studies.

A wooden label was laid alongside the root, with a mark indicating the position of the root tip. The increase in length and number of laterals was measured 2 or 3 times per week. Also the portion of the root behind the root tip without laterals was measured. (Part 1,2 Figure 1 A).



1. ROOT TIP, NO LATERAL ROOTS
2. LATERAL ROOTS VISIBLE AS KNOTS
3. COMPLETE LATERAL ROOT DEVELOPMENT
4. ZONE JUST DISTAL TO ROOT DEATH ZONE
5. ROOT DEATH ZONE
6. ZONE JUST PROXIMAL TO ROOT DEATH ZONE

Figure 1. A. Parts of the cucumber root used for microscopy before root death.
B. Parts of the root with root death used for microscopy.

The results were divided in the periods from planting to root death and from root death to the end of the experiment. Total length and total number of laterals were divided by the number of days in each period. In each period the average portion of root without laterals was calculated.

When the system was functioning satisfactorily 5 experiments were carried out (Table 1). The first experiment supplied material for microscopy. Experiment 2 was a repetition of an experiment carried out earlier in ordinary NFT-gullies (Van der Vlugt, 1986). In experiments 3 and 4 prevention of root death was attempted by adding auxin. Also the effect on the whole root system was sought when only one root was treated (cf De Stigter 1969a). In the last experiment the effect of earliness was studied, delayed fruit set would give a bigger plant which could be less susceptible to root death.

Root anatomy

Roots excised for anatomical studies were divided in three parts (Fig.1 A). Part 1 was the root apex, part 2 was taken where there were no laterals, only small knots on the roots. Part 3 was the most distal part in which the laterals were fully developed. Roots were embedded in paraffin and cut into 15μm slices with the microtome. The preparations were stained in safranin, picric acid and malachite green. Diameter of root and stele were measured under a light microscope. The percentage circumference was calculated by division of stele diameter with root diameter.

Table 1. Important data in connection with the different experiments.

Planting date	Flowering date	Root death	End of experiment	Treatment
October 26 1984 (1)	November 11	November 21	December 17	None, material for microscopy
February 18 1985 (2)	March 1	March 13	March 22	Root mass halved at planting or at flowering
May 29 1985 (3)	June 7	June 19	July 10	One root of each plant treated with 5 ppm IBA on June 19
July 17 1985 (4)	July 28	August 5	August 21	One root of each plant was treated with 5 ppm IBA on August 5
October 8 1985 (5)	October 24	November 11	December 5	First fruit set in node 3, 4, 5, 6, 7 or 8

Results

Root measurements

The data from all experiments were analysed together with regard to correlation between characters and difference in growth rate before and after root death. The data were analysed by experiment for differences between treatments. The correlations between the studied characters were significant and positive:

Portion without laterals (cm) = 2.4 + 0.96*length (cm/day)
number of laterals/day = 2.4 + 1.82*increase in length (cm/day)
portion without laterals (cm) = 1.8+0.39*number of laterals/day

This explained about 40-60% of the variation. Fast growing roots grew more laterals per day but had also a larger portion without laterals than slow growing roots.

Table 2. Increase per day of different root characters and average portion without laterals before and after root death. Mean of all experiments.

Character	Increase before root death	Increase after root death
Length (cm/day)	2.2	0.8
Laterals (nr/day)	7.2	3.0
Portion without laterals average (cm)	4.5	3.2

For each character the growth after root death was significantly decreased (Table 2). Then it became interesting to know whether there was some correlation between growth before and after root death. Figures 2, 3 and 4 show the correlation between the increase for length, and number of laterals before and after root death by experiment and the correlation for portion without laterals before and after root death.

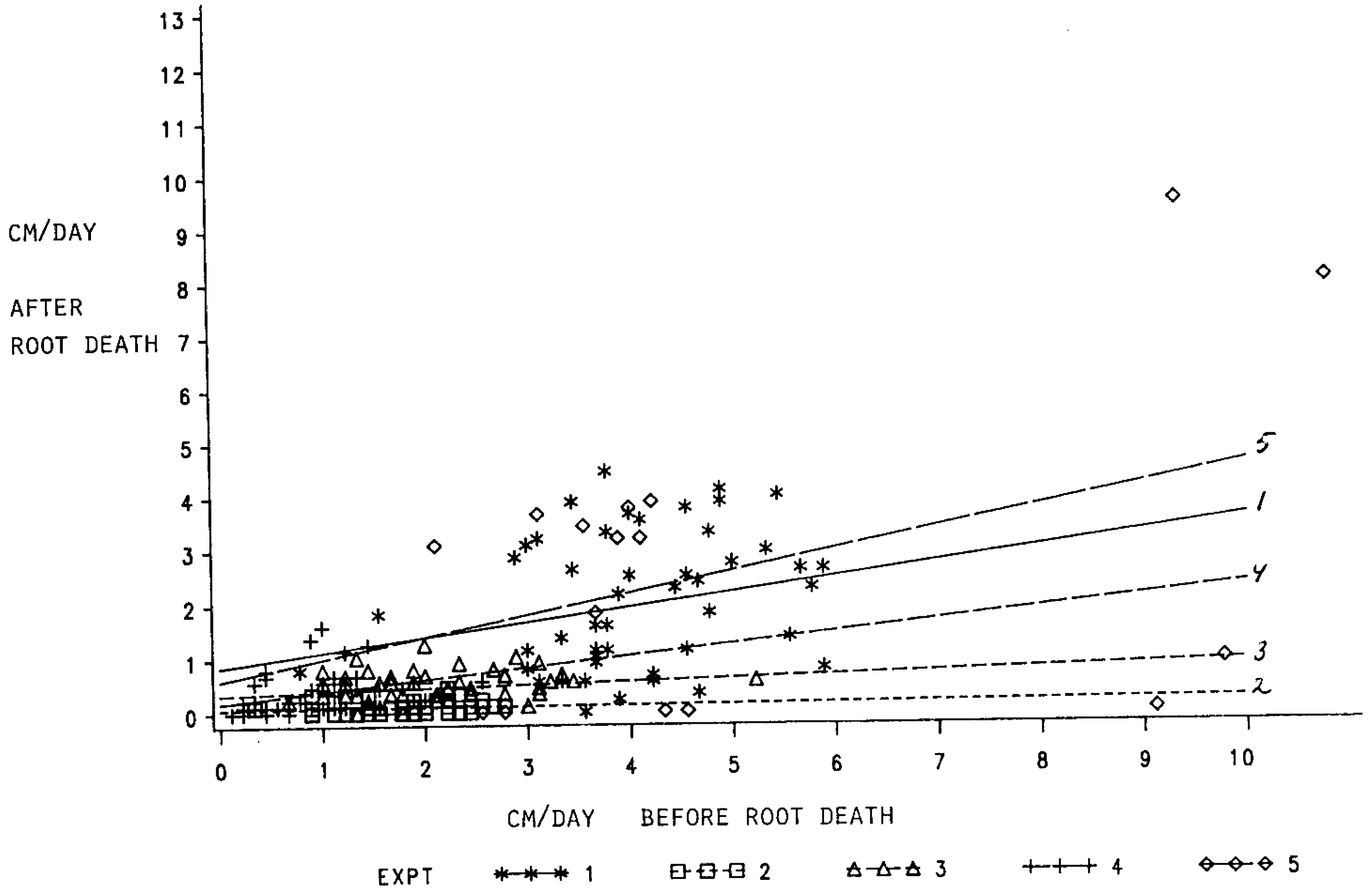


Figure 2. Linear correlation between growth in cm per day of cucumber roots before and after root death Data plotted separately for the experiments.

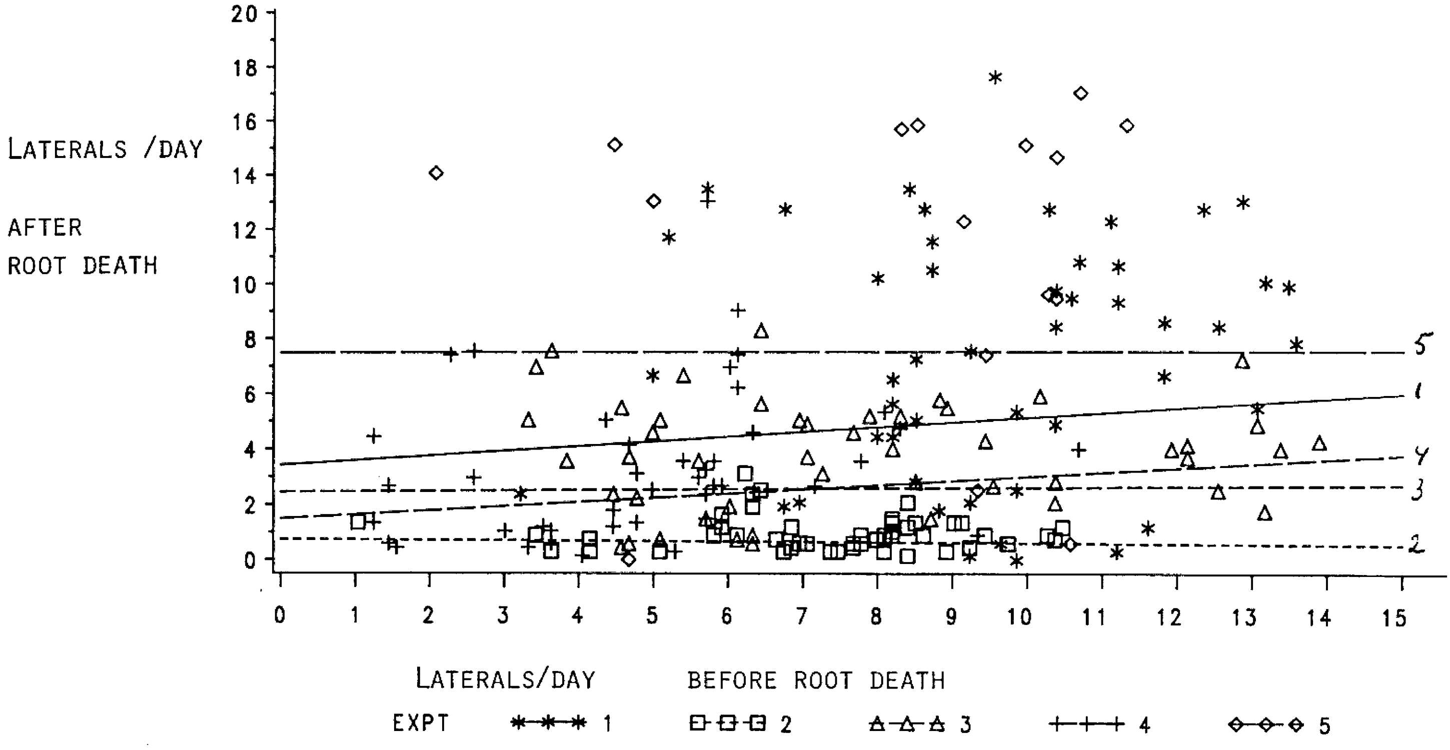


Figure 3. Linear correlation between growth of cucumber roots in number of laterals per day before and after root death. Data plotted separately for the experiments.

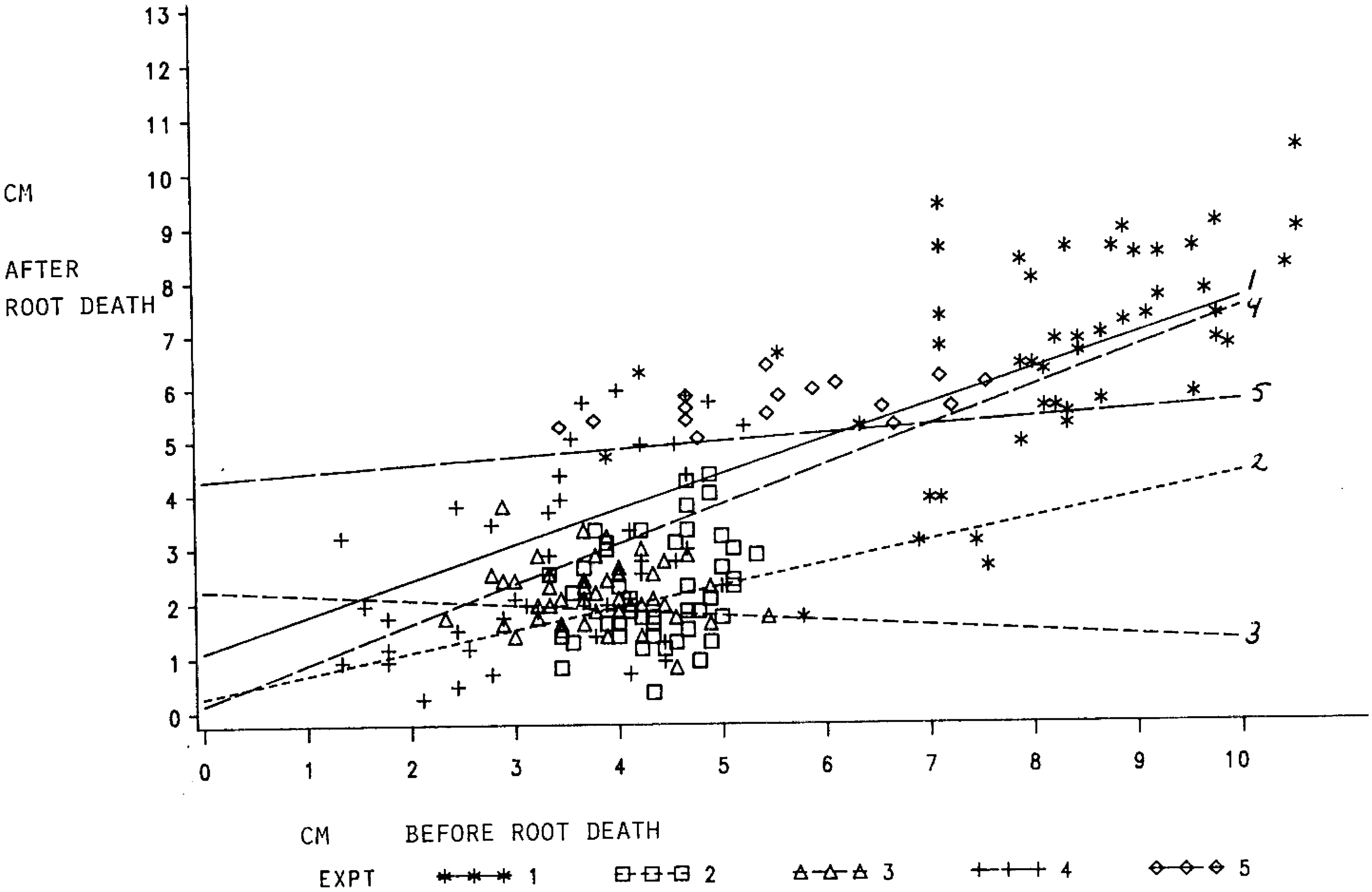


Figure 4. Linear correlation between ~~growth~~ length of cucumber roots ~~in number of~~ without laterals ~~per day~~ before and after root death. Data plotted separately for the experiments.

A positive correlation was found, fast growing roots were less inhibited after root death than slow growing roots. This explained about 50% of the variation. It seemed that the results from the same seasons were grouped together. Linear models of the following type were tested:

Character after rootdeath =character before root death + season

This increased the explanation of variation considerably and gave very significant results for all characters. Especially the results from the autumn were significantly different from the other seasons.

When all the data were analysed significant differences between treatments were found which coincided with differences between experiments. Within experiments differences between treatments were not significant.

This showed that even though not all roots were simultaneously affected to the same degree the growth of all roots was reduced. Root growth might stop completely for some days and then be resumed. In the period with little root growth laterals might be developed to within 1 mm from the root apex. Sometimes one of these laterals would take over from the main root.

Root anatomy

The root measurements showed that the parts of the roots which were examined were not more than a few days old. Root preparations were made from a plant when it was 28-63 days old.

Figure 5 shows a typical root in region 3. In some cases the metaxylem was fully developed with the characteristic central trachea. The cortex would consist of about 7 layers of cells outside the endodermis. The epidermis might still be intact. Very few root hairs were formed in NFT.

The development of lateral roots in region 2 could readily be observed under the microscope. Sometimes it would seem that part of the cortex was being dissolved (Figure 6), but some days later this could not be observed in another root.

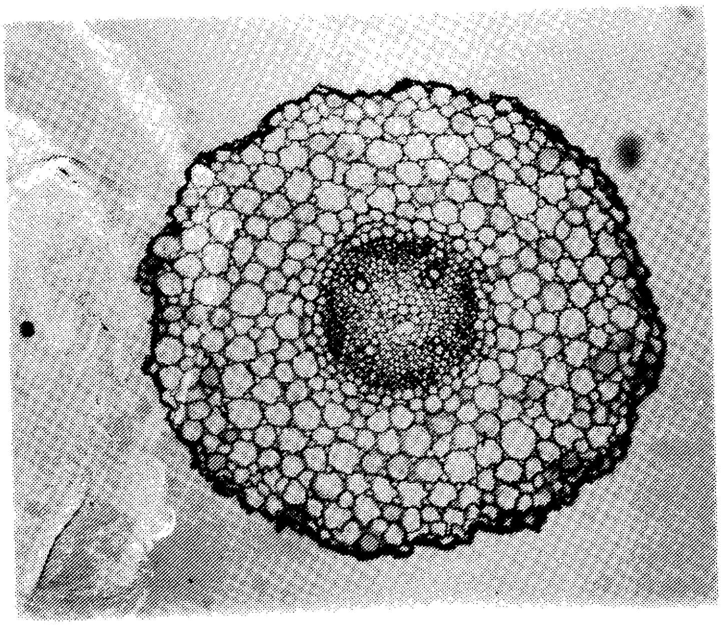


Figure 5. Part 3 of a cucumber root on day 63. Metaxylem is under development, the cortex consists of 7 layers of cells outside the endodermis.

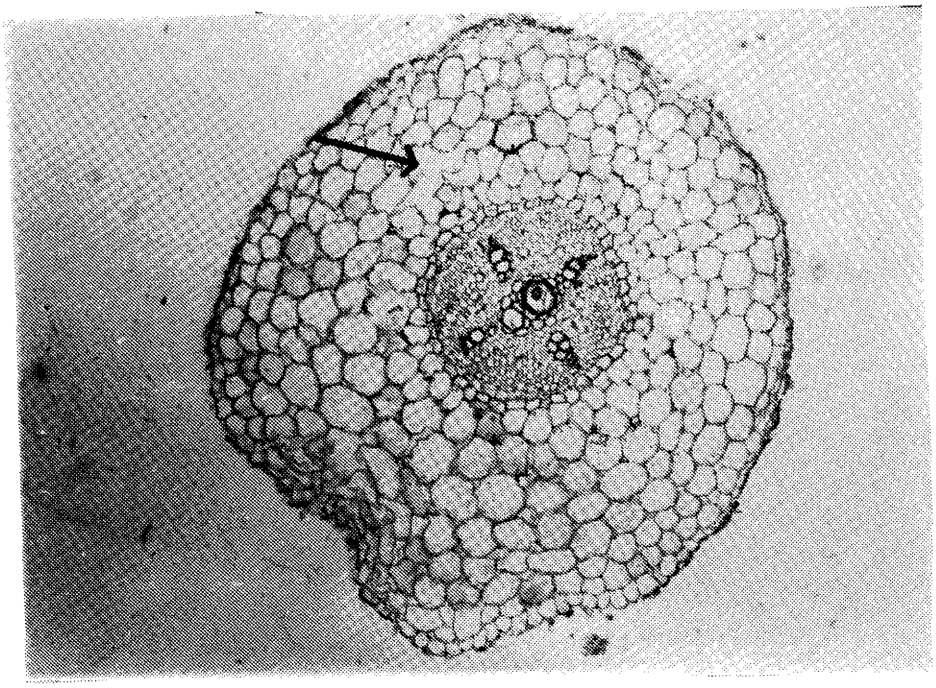


Figure 6. Part 2 of a cucumber root on day 41. Some cells in the cortex seem to be dissolved (arrow).

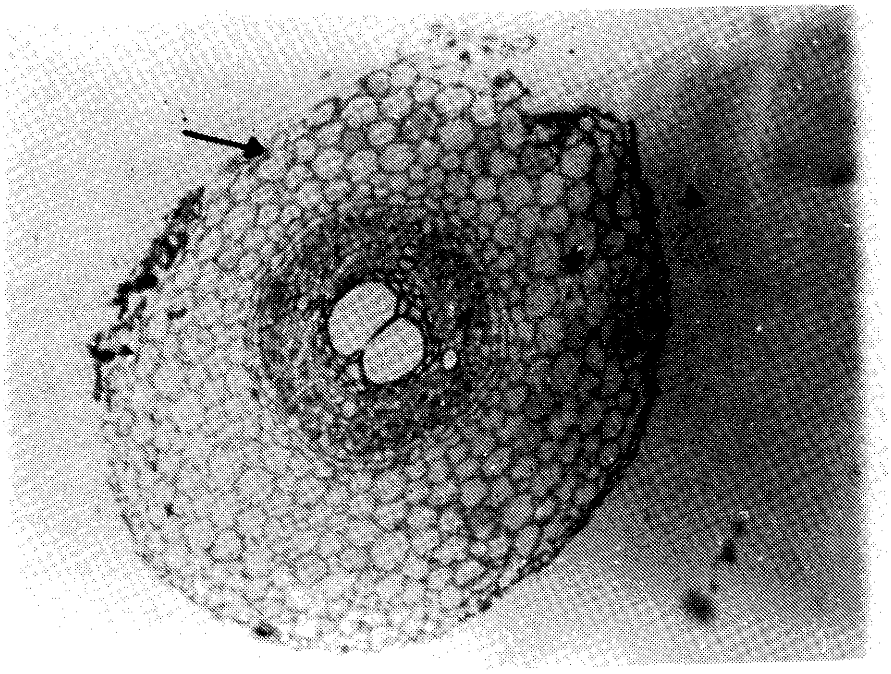


Figure 7. Radial section of a cucumber root from the zone just distal to the root death? zone on day 63. The outer layers of the cortex are getting disrupted (arrow).

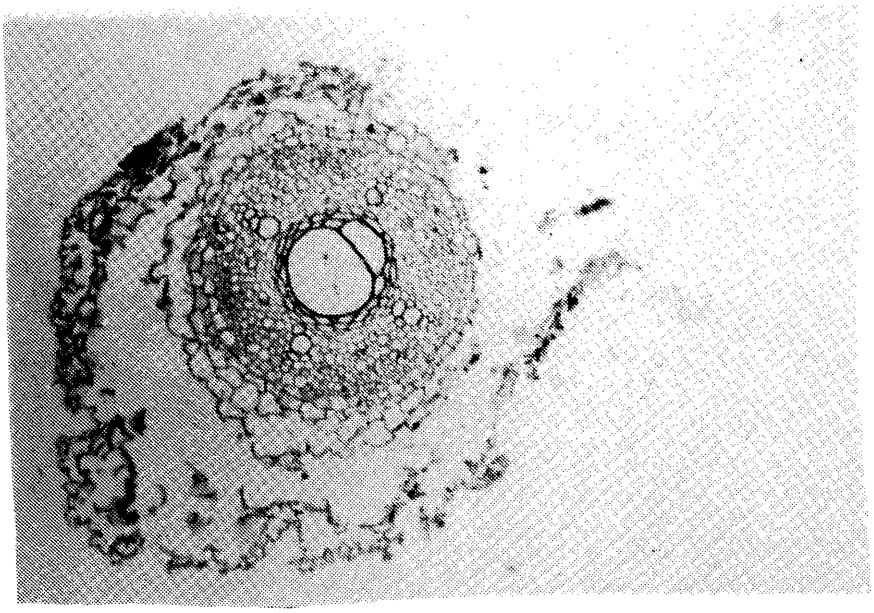


Figure 8. Radial section of a cucumber root in the root death zone on day 63. The cortex is almost completely dissolved, the endodermis cells have collapsed.

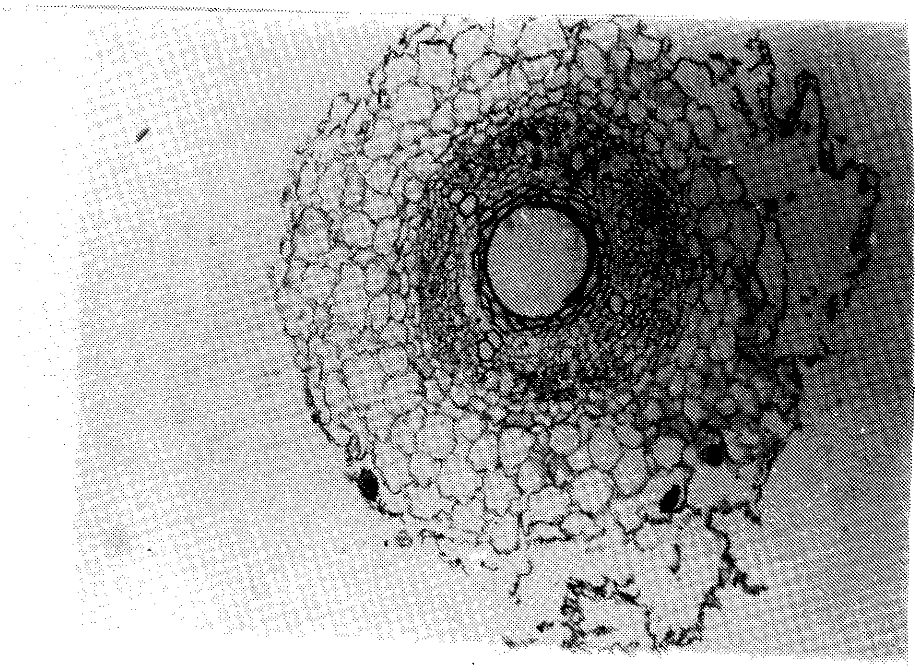


Figure 9. Radial section of a cucumber root in a zone proximal to the root death zone on day 63. Some layers of cortex still remain.

On day 63 root death was visible in part of the root (Figure 1 B). In region 1,2 and 3 no differences from earlier observations were observed. In region 4, just below the root death zone, the cortex seemed to be destroyed from the outside (Figure 7). Within the root death zone the cortex was almost completely dissolved (Figure 8), but in an older region of the root at least some layers of cortex remained (Figure 9.) In these roots no secondary root growth was observed. The part of the root which was affected with root death was not more than 10 days old, being about 20 cm from the tip. The destruction of the cortex reduced the root surface area which in turn reduced water and nutrient uptake. The reduction could be to 30-40% of the original root surface (Table 3).

Table 3. The circumference of the stele of cucumber roots are percentage of the circumference of the whole root in different experiments.

Experiment	Stele % of root	Remarks
1	34.4	Regions 1 and 2 had a larger percentage than region 3 of the root.
2	24.5	Region 1 had a larger percentage than the other regions.
4	40.8	The cortex was disintegrated from 3 days after IBA application. About 4 layers of cells remained.
5	37.5	The oldest region, about 30 cm from the tip, had secondary root growth, the stele increased in size relative to the whole root. The younger regions had in average 31.8% stele.

Discussion

The statistical analysis showed there was a general reduction in root growth rate when some of the roots got root death. Part of the variation could be explained by the growth rate before root death, which proved that a healthy and vigorous root system is preferable. Reduced growth rate and loss of material explained the decrease in root mass observed by many workers (De Stigter,1969b; Van der Post, 1968; Hall, 1977). Wilting which is sometimes observed in connection with root death, can be caused by the reduction in root surface area.

The roots were still in the primary stage of development when root death occurred, and they were also very young. Presumably destruction of the cortex was very rapid~~ly.~~ The root measurements showed why renewing the root mass by root pruning had no effect on root death (Van der Vlugt, 1986).

The general reduction in root growth rate might be explained by root exudates poisoning the roots. Even though not all roots are destroyed immediately all will suffer from a high concentration of exudates. Exudates would not seem to be the only cause of root death, since hormone treatment with full fruit load, did not prevent root death. (Exp. 3 and 4). On the other hand reduction in fruit load did not prevent root death either, (Exp. 5, Van der Vlugt 1986).

Acknowledgements

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V. The effect of plant growth substances on root death

Abstract.

Root exudates have been suggested to influence physiological root death. In a closed system like NFT accumulation of exudates to toxic amounts may occur. Among root exudates plant growth substances have been found. Some of these were investigated in the present experiments because of their large influence in small amounts.

The effects of concentration, duration and time of application on root death in the cucumber were investigated for IBA, TIBA and silver ions. Auxin increased root death irrespective of concentration. Time of application had a certain effect. TIBA did not counteract the effect of auxin.

After auxin treatment the roots became coiled as after ethylene treatment. Auxin effects are often mediated through ethylene. Silver ions, inhibiting ethylene action, did not prevent root death. It is concluded that plant growth substances may have a part in root death.

Introduction

Indications have been found of root exudate involvement in physiological root death (Van der Vlugt, in prep.). Exudates may accumulate in the nutrient solution because of NFT being a closed system. These exudates could become poisonous to the roots above a certain concentration.

Vancura and Hanzlikova (1972) studied the exudates from cucumber seeds and seedlings. They found that exudates may be peptides, amino acids, organic acids and carbohydrates. They also observed that the composition of the exudate was different for seed and seedlings.

The timing of root death could be explained either by the total amount of exudates or by the occurrence of special substances in the exudate at a certain time and in a certain concentration.

In the tomato it was seen that also plant hormones occur in the root exudate (Cooper, 1979). A small change in the level of plant growth substances could have a large effect like root death.

In this study the effects of auxin and other substances involved in auxin transport and action on root death were investigated.

Exogenous auxins inhibited root growth, except at very low concentrations (Nissen 1985) and stimulated lateral root initiation. The pH (± 6.0) of the nutrient solution would render auxin metabolically active (Rao et al., 1976). The effect on root elongation may be caused by auxin stimulated ethylene production (Nissen, 1985). Endogenous auxin may have the same effect. Auxin from the shoot is transported to the roots. In the roots most of the auxin was found in the stele (Batra et al., 1975). When transport was inhibited, they observed that auxin was taken up by the cells and growth was inhibited. Both ethylene and TIBA affected auxin transport in roots. TIBA inhibited auxin efflux from the cell (Depta et al., 1983). Lira and Freytag (1971) observed that TIBA and ethylene counteracted each other.

Materials and Methods

The glasshouse cucumber cv Farbio was used in all experiments. In one experiment also cv. Corona was used (Table 1). Seeds were sown in rockwool blocks (7.5 x 7.5 x 7.5 cm) and propagated for 3 weeks. Then the plants were placed individually in 10 l containers. The containers were completely filled with nutrient solution (EC 2.0 - 2.5, pH 5.5 - 6.5). Air was bubbled through the solution continuously. Containers were refilled with nutrient solution every day. EC was measured every day. pH every other work-day. Plants were trained according to the umbrella system. In the period from October 1 to April 1 additional light was given to 18 hours day. In some experiments 10 plants were grown in a 4.5 m long gully, supplied by a 50 l catchment tank.

The potassium salt of indolebutyric acid (IBA) was dissolved in water, if necessary with a few drops of KOH, in a concentrated solution. Aliquots were syringed into the nutrient solution to the desired concentration. The same procedure was used with silver nitrate. 2,3,5-triiodobenzoic acid (TIBA) was mixed with lanolin in the desired proportion (w/w) and smeared around the hypocotyl, 20 mg of the mixture was used per plant. Data for the experiments are given in Table 1.

Table 1. Important cultural data from the experiments.

Experimental period	Growing medium	Treatment	Plant growth data
<u>1982</u> 22. Feb.- 7. April (1)	Containers	IBA 0, 1, 2, 5, 10 ppm added day 11	flowering day 11 first harvest day 30
13. April- 20. May (2)	Containers	IBA 1 ppm added day 20 or 27 or 35	flowering day 17 first harvest day 35
21. June- 11. Aug. (3)	Containers	IBA 1 ppm added day 18 or 25 change/no change of solution after 1 week	flowering day 9 first harvest day 21

Table 1 seq.

1983			
17. Jan.-11. March (4)	Containers	IBA 0, 1, 10, 20, 40 ppm added day 28	flowering day 16 first harvest day 35
16. May-28. June (5)	Containers	IBA 0, 10, 20, 40 ppm 1 week added day 28 'Farbio', 'Corona'	flowering day 17 first harvest day 32
1984			
2. July-10. Aug. (6)	Containers	TIBA 0.5 or 1% applied day 21 or 28	flowering day 14 first harvest day 23
13. Aug.-25. Sept. (7)	Containers	TIBA 1 or 2% applied day 16 or 23	flowering day 14 first harvest day 24
24. April-18. June (8)	Gullies	$AgNO_3$ 1 or 10 ppm for 24 hours added day 27 or 34	flowering day 15 first harvest day 29
2. May-25. June (9)	Containers	$AgNO_3$ 0.1 or 1 ppm on day 16 or 22 for 6 or 24 hours	flowering day 14 first harvest day 26
13. Aug.-10. Oct. (10)	Gullies	$AgNO_3$ 1 ppm added every 4th day from day 16	flowering day 13 first harvest day 22

Results

Three days after addition of IBA lateral root development was observed. In table 2 the effects of different auxin concentrations are shown. Auxin treatment prolonged the recovery period (Table 2 A, C). Root death often occurred before harvesting of the first fruit (Table 2 B). There seemed to be no real differences between concentrations. No significant differences were found between cultivars, therefore the results were pooled (Table 2C). With the highest concentrations (20 and 40 ppm)

Table 2. Effect of different concentration of IBA in the nutrient solution on root death symptoms in days after planting of the cucumber. A. The effect of IBA connections of 0-10 ppm. Experiment 1 carried out with 8 containers per treatment, February-April 1982.

IBA concentration (ppm)	Root death (R)	Formation of new roots (N)	Recovery period N-R (days)
0	26.2	35.9	9.7
1	21.9	35.4	13.5
2	22.0	33.4	11.4
5	21.9	33.1	11.2
10	21.0	31.6	10.6

B. The effect of IBA concentration of 0-40 ppm Experiment 4 carried out with 8 containers per treatment, January-March 1983.

IBA concentration (ppm)	Browning	Root death R	Formation of new roots N	Recovery period N-R (days)
0	30.0	34.0	39.9	5.9
1	31.8	35.6	38.4	2.8
10	30.0	33.2	37.6	4.4
20	30.0	33.9	37.8	3.9
40	31.0	34.4	38.1	3.7

C. The effect of IBA concentration 0-40 ppm. Experiment 5 carried out with 10 containers per treatment, May-June 1983. Average for both cultivars.

IBA concentration (ppm)	Browning	Root death R	Formation of new roots N	Recovery period N-R (days)
0	30.4	33.4	35.6	2.2
10	30.9	34.2	37.1	2.9
20	30.9	34.7	39.9	5.2
40	30.6	35.0	41.5	6.5

side-effects were noted. The lower part of the stem, especially the hypocotyl, burst. The lateral roots initiated by the auxin treatment developed laterals themselves very soon so that 2 or 3 roots seemed to come out of the root at the same place.

In the auxin treatments the root tips often became coiled. This was also observed sometimes in untreated plants (Figure 1).

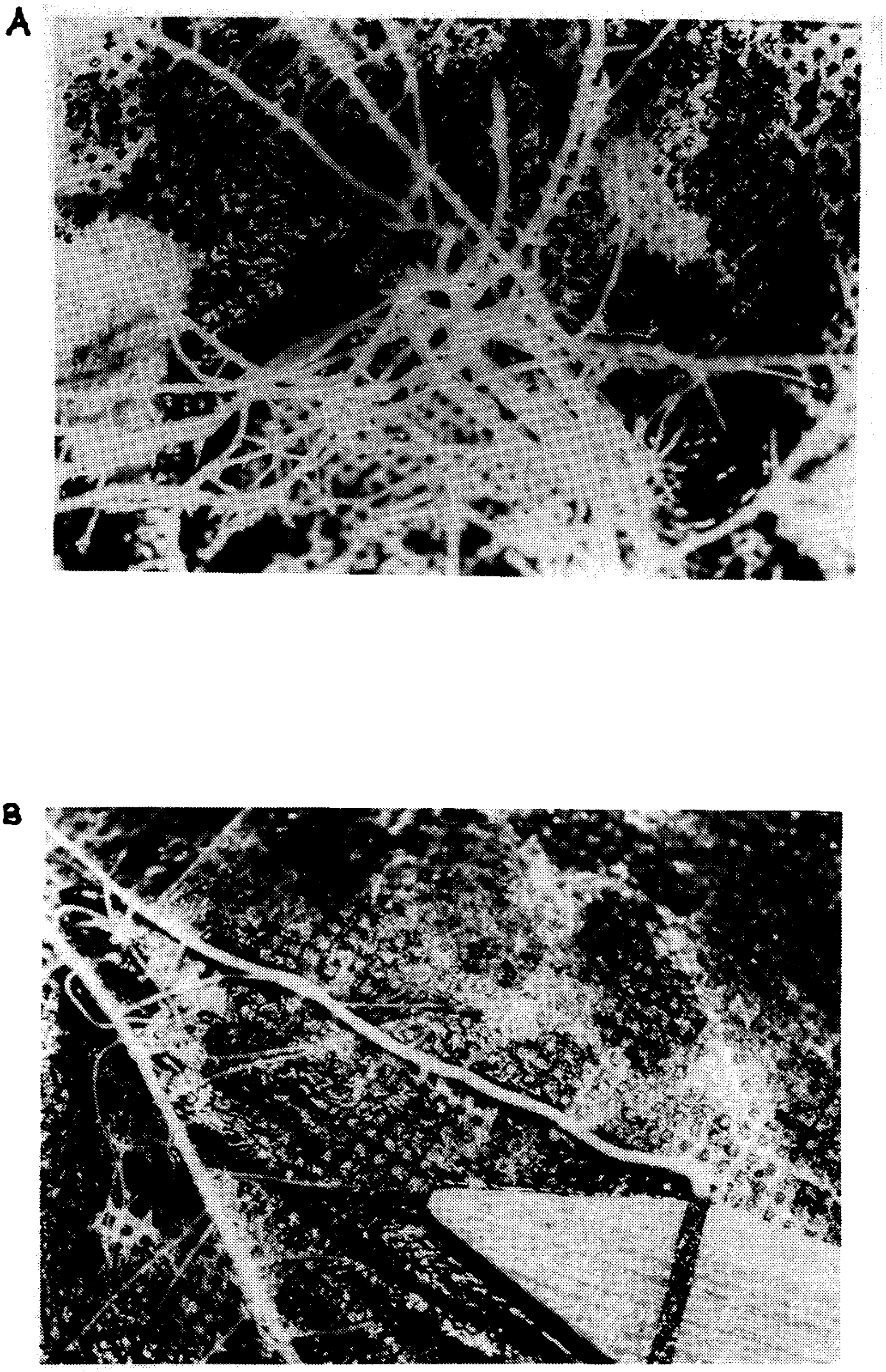

Fig. 1 A. Part of a cucumber root mat with swollen and curved root tips, occurring naturally.

B. Coiled root tip of cucumber, occurring naturally in NFT.

The time of auxin addition seemed to be important, therefore this was studied in some other experiments (table 3). It seemed that root death was more severe with the later addition of auxin. However, the treatment was given so near the time of natural root death that no significant differences were observed.

Table 3. Effect of 1 ppm IBA added to the nutrient solution at different times on root death of the cucumber.
Root death symptoms in days after planting. A. Average of 10 containers per treatment. Experiment 2, carried out in April-May 1982.

Day of IBA addition	Browning	Root death R	Formation of new roots N	Recovery period N-R (days)
not added	28.3	29.8	42.7	12.9
20	28.6	32.0	40.1	8.1
27	29.4	33.0	40.0	7.0
35	29.6	33.0	41.8	8.8

B. IBA was added on day 18 or day 25 and the nutrient solution changed (c) or not changed (nc) after one week. Average of 10 containers per treatment. Experiment 3, carried out in June-August 1982.

IBA addition/ change of solution	Browning	Root death R	Formation of new roots N	Recovery period N-R (days)
not added c	24.6	29.0	32.6	3.6
18 nc	23.8	28.8	30.1	1.3
18 c	23.4	27.2	31.5	4.3
25 nc	24.4	27.9	32.0	4.1
25 c	25.8	29.5	34.4	4.9

Table 4. Root death symptoms in days after planting, for cucumber plants treated with different 2,3,5-triiodobenzoic acid (TIBA) concentrations at different times. Experiments carried out July-September 1984.

Experiment/ Day of application	Concentration % TIBA	Browning	Root death R	Formation of new roots N	Recovery period N-R (days)
6/	0 (control)	28.4	34.8	37.4	2.6
7/		19.2	26.4	29.8	3.4
7/16	1.0	17.6	25.4	31.0	5.6
	2.0	16.5	27.2	30.4	3.2
6/21	0.5	28.2	37.2	38.9	1.7
	1.0	27.2	34.4	39.2	4.8
7/23	1.0	20.6	27.1	31.6	4.5
	2.0	18.5	28.1	31.8	3.7
6/28	0.5	26.1	35.1	38.5	3.4
	1.0	29.0	33.2	37.1	3.9

If endogenous auxin is involved in root death in the same way as exogenous auxin, the stress might be relieved with TIBA treatment. Different concentrations of TIBA were tried and applied at different times (Table 4). A negative correlation was found between concentration and root death symptoms. A positive correlation was found for the time of application. Root death always occurred, in spite of TIBA treatment.

Table 5. Root death symptoms in days after planting. Plants were treated with 1 ppm $AgNO_3$ in the nutrient solution at different times. The treatment 16/30 got 2 $AgNO_3$ applications on day 16 and 30. Data from all experiments, 8-10, control from exp. 10.

	Day of $AgNO_3$ addition to the nutrient solution										
	16	16/30	20	22	24	27	28	32	34	36	Control
Browning	17 19	17	17	23	22	23	28	20	26.5	24	20
Root death R	27 41	27	27	38.7	29	32.5	27	24	34	27	27
Formation of new roots N	31 42	31	34	39	38	42.5	34	29	35	34	31
Recovery period N-R (days)	4 1	4	7	0.3	9	10	7	5	1	7	4

Ethylene could also influence auxin transport. Silver ions inhibit ethylene action. The results of the treatment with silver ions are given in Table 5. The $AgNO_3$ concentration of 10 ppm in the first experiment was too high. The plants wilted. No significant differences between concentrations or duration of treatment were found in the other experiments. The time of addition seemed to have had some effect, especially when treatments were considered in groups which could have been influenced by the silver ions relative to root death of the control. In the earliest addition silver ions did not aggravate root death.

Discussion

Coiled roots were observed both after auxin treatment and in connection with naturally occurring root death in NFT. Woods et al. (1984) observed coiling of tomato roots after ethylene treatment. Geneve and Heuser (1983) studied the interaction between auxin (IAA and IBA) and ethephon. They found that the roots were coiled because ethylene removed polarity.

In connection with root death it was observed that growth decreased and also the number of laterals decreased (Van der Vlugt in prep.). Ethylene also inhibited growth and decreased the number of laterals (Jackson, 1983).

The similarity between root death and ethylene effects seemed obvious. It would be more difficult to find out how the required level of ethylene was accumulated.

The roots might become more sensitive to growth substances in the nutrient solution after flowering. Frimanslund (unpublished, 1980) grew cucumber seedlings in nutrient solution from plants with dead roots. The seedlings remained healthy. Daughtrey and Schippers (1980) got varying results with the use of old nutrient solution for tomatoes. A certain predisposition seemed to be necessary.

The trigger might be auxin-induced ethylene production or ethylene accumulation in the nutrient solution. Increased transport of auxin would have to occur just prior to root death. The solubility of ethylene is quite high, large concentrations may occur in the nutrient solution (Jackson, 1980).

Ethylene is also involved in the formation of aerenchyma. Aerenchyma formation has been observed even in well aerated hydroponics (Drew et al., 1981). The effect of aerenchyma formation is twofold. Large air spaces in the roots make an adequate O_2-supply to the roots possible and the demand for oxygen is reduced because there are fewer cells.

In root death the number of cells is also reduced although it seemed that destruction of the root bark started from the outside (Van der Vlugt, in prep.). Possibly not lack of oxygen but lack of substrate for respiration leads to root bark destruction by ethylene in the case of root death.

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VI Plant growth and chemical analysis

Abstract

Physiological root death of cucumber was studied in plants grown individually in containers. During 2 months growth, water and nutrient uptake, nutrient distribution and assimilate production and distribution were observed. The shoot/root ratio (fresh weight) increased until harvesting, the generative/vegetative ratio increased from flowering through the whole period. The rate of fruit production and the leaf area observed indicated that assimilate production was barely enough for fruit production, other plant parts would starve.

The uptake and transport of nutrients was shown to be reduced after harvesting started. Reduction in uptake may have been caused by reduction in root surface area after root death. With the onset of fruit production it was seen that the content of nonstructural carbohydrates in other plant parts decreased. It seemed that root death in this experiment was caused by the sink strength of the fruit with regard to both assimilates and mineral nutrients.

Introduction

Physiological root death of the cucumber (Cucumis sativus L.) may be caused by competition between roots and fruits. The dominance of the fruit would affect the whole plant. Van der Post (1968) showed that shoot growth stopped and the root mass was diminished after fruit growth was initiated. Therefore the top/root ratio increased tremendously. The decrease in root mass was associated with root death (Van der Vlugt, part 4), the order of events is not known, however.

Also the uptake and transport of nutrients may be affected by fruit growth and root death. Iron deficiency symptoms have often been observed in plants with root death. Deficiencies of other elements not relocated within the plants may also be expected. Khudheir and Newton (1980) studied nutrient uptake in tomatoes in connection with root death. They found that uptake of all elements decreased in plants affected with root death and that uptake of boron and manganese decreased earlier than that of the other elements.

Synthesis

Assimilation and distribution of stachyose and other sugars in the cucumber plant have not been studied in connection with root death.

The purpose of this experiment was to study growth, mineral nutrition and assimilate production and transport in the cucumber in relation to root death. The elements investigated were N,P,K as major nutrients, Fe and Ca as elements not easily redistributed in the plant and B and Mn as possible indicators of root death. Of the carbohydrates the primary product (hexoses, sucrose), the transport unit (stachyose) and the storage unit (starch) were studied.

Materials and methods

Seeds of the cucumber cultivar Farbio were sown in rockwool blocks (7.5x7.5x7.5 cm) in September 1985. On October 14 (= day 24), the plants were placed in 10 l containers. The rockwool block was fitted in the lid, sticking out 1 cm.

During propagation and after planting the plants received additional artificial light, 180 W/m^2 installed of SON and HPI lamps, for 18 hours/day. The plants were trained upward to the wire. After they reached the wire the top grew downwards. All sideshoots were pinched, all fruits were allowed to develop.

The containers were filled with nutrient solution. Air was bubbled through the solution continuously. The solution was supplied from a 250 l tank. Whenever the tank was refilled a sample was taken for chemical analysis. The standard solution contained in ppm: 200 nitrate-N, 30 P, 420 K, 200 Ca, 1.5 Fe (chelated), 1.0 Mn, 0.5 B and adequate amounts of the other elements. The solution in the tank showed small deviations from the standard solution. The containers were refilled once every day, the volume supplied was measured for each plant separately.

Ca, Fe and Mn in the nutrient solution were determined with a flame atomic absorption spectrophotometer. Potassium was determined with a flame photometer. The molybdo-vanadate complex with phosphorus was determined spectrophotometrically. Boron was determined spectrophotometrically with carminic acid (Rosenfeld and Selmer-Olsen, 1979). Nitrate-N was determined colorimetrically with a Technicon Auto-analyzer after reduction of nitrate with a Cd-reductor and addition of sulphanilamide and N-1-naphtylethylenediamine (Henriksen and Selmer-Olsen, 1970).

At planting each plant was given a number. The numbers were randomised throughout the greenhouse. Twice weekly (day 24, 27, 31, 34 etc.) 3 plants were taken for measurements and chemical analysis in numerical order. Leaves, which were not dried out and longer than 5 cm, were measured. Leaf area was calculated as length x width x 0.72 according to Graf-Marin (Liebig, 1978, p.17-18).

Fresh weight was determined for all plants: roots (without the rockwool block), stem segment including leaves nrs 4 and 5, top (6 uppermost unfolded leaves + stem and apex), fruit and complete shoot. Whenever sideshoots were pinched, old leaves removed or fruits picked before the whole plant was taken, these parts were also weighed. The weight was later added to the total.

For organic chemical analysis plant parts from 2 plants were thoroughly mixed and extracted with 86% ethanol. The residue after filtration was used for starch determination after a modified method of Pharr and Sox (1984). The filtrate was used for total sugar and stachyose determination. Total sugar was measured as glucose after a modification of the method of Hagedorn and Jensen. For stachyose determination the filtrate was concentrated and analysed by paper chromatography. Whatman nr 4 filterpaper was used, perpendicular to fibre direction, descending eluation with n-butanol:acetic acid: water=200: 50: 250 upper phase. Stachyose was hydrolysed by a method developed by Mrs. G. Remedios (not published) and the hexoses were developed with silvernitrate.

The third plant was used for inorganic chemical analysis. Nitrate-N was extracted by boiling the fresh material in 0.01 M $CuSO_4$ solution, a quantitative determination was made with an ion-selective electrode (Øien and Selmer-Olsen, 1969). The other elements were determined in a hydrochloric acid solution (5%) of the ash. Ca, Fe and Mn were determined with flame atomic absorption spectroscopy. P was determined colorimetrically as the molybdo-vanadate complex (Boltz et al., 1977). Potassium was determined in a flame photometer. Boron was determined with a spectrophotometer as a complex with carminic acid in concentrated H_2SO_4 (Oelschlager, 1956).

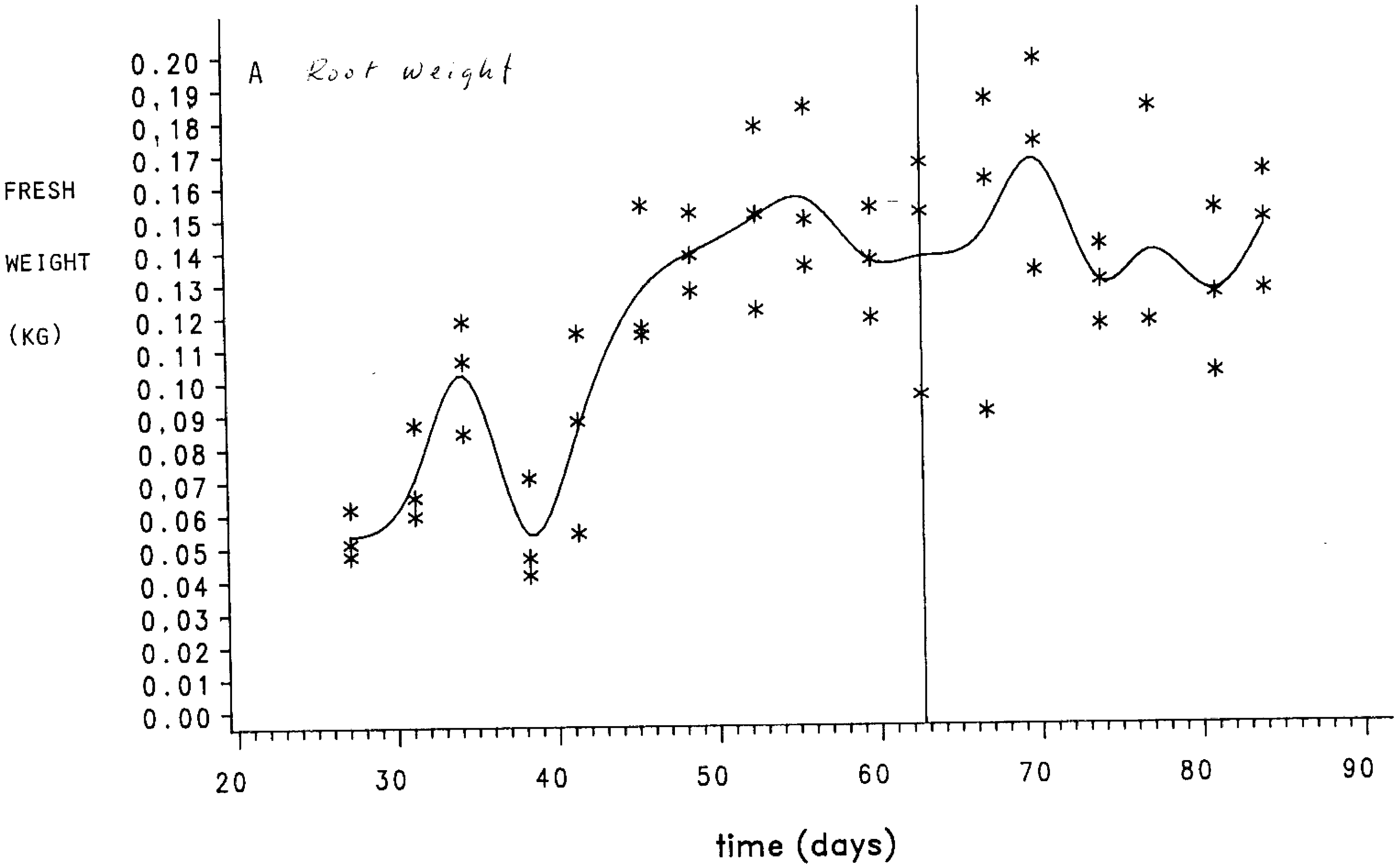
Total weight and total leaf area per plant were calculated for all days of observation. Curves were fitted using a spline routine that minimized a linear combination of the sum of squares of the residuals of fit and the integral of the square of the second derivative (Reinsch, 1967).

Results and discussion

The plants developed very well, however, from the end of November (day 66) excessive ageing of the plants occurred. Flowering occurred on day 38, the first fruits were harvested on day 55 and root death occurred on day 62.

In another experiment (not published) the average volume of the roots was observed to be about 0.2 l. This did not affect the calculation of the uptake of nutrients seriously until the end of the experiment when a more dilute topping up solution was used.

Root weight was more or less constant after a short while (Figure 1a), but shoot weight continued to increase (Figure 1b). The shoot/root ratio increased. Leaves 4+5 were followed throughout their development,their weight showed a small decline in the end as is usual (Ho et al., 1984). Also the top of the plant decreased in weight after harvesting had started. Pharr and Sox (1984) noticed that all plant parts above the fruit decreased in weight.


A Root weight
FRESH
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(KG)
0.20
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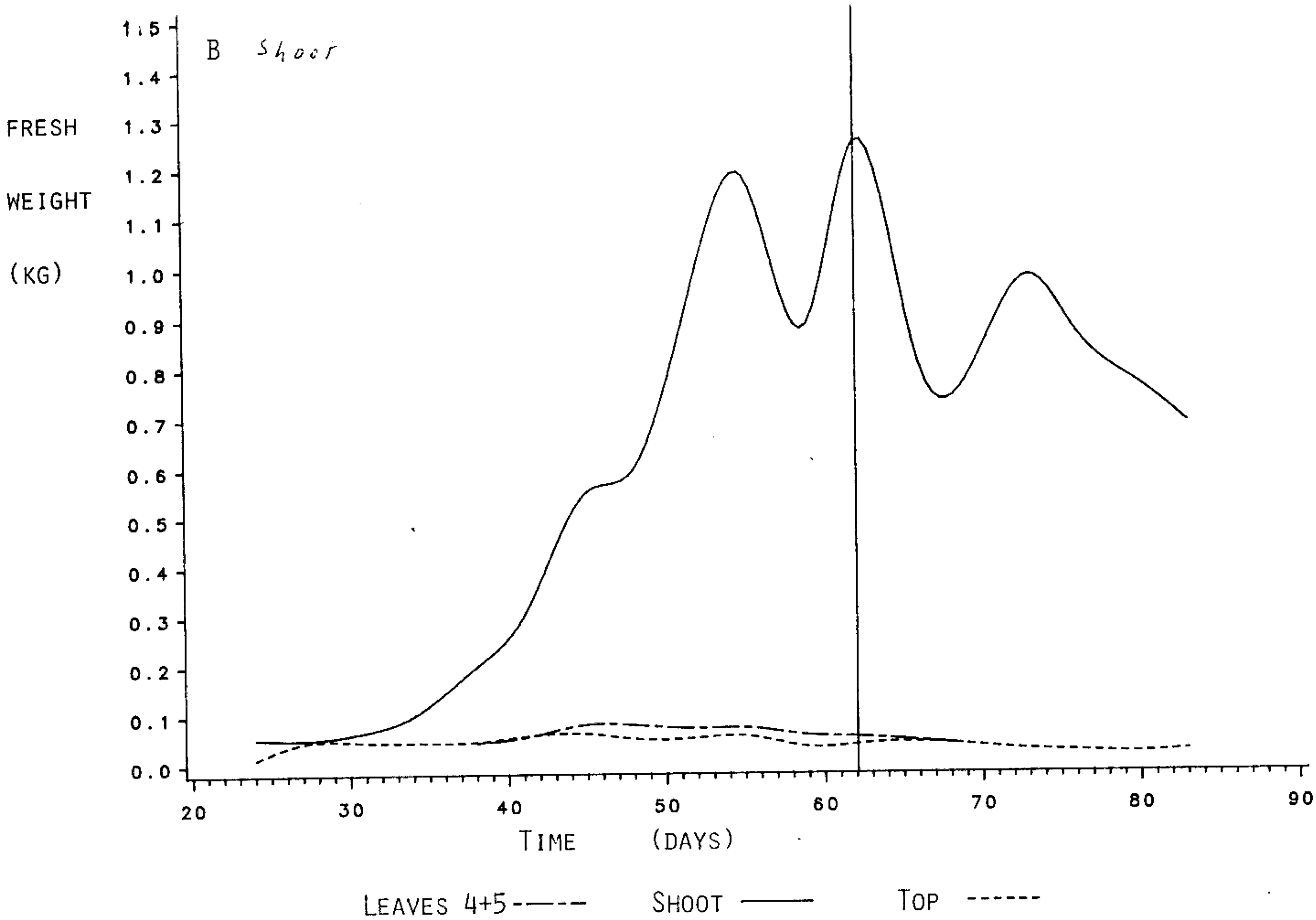
B Shoot
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TIME (DAYS)
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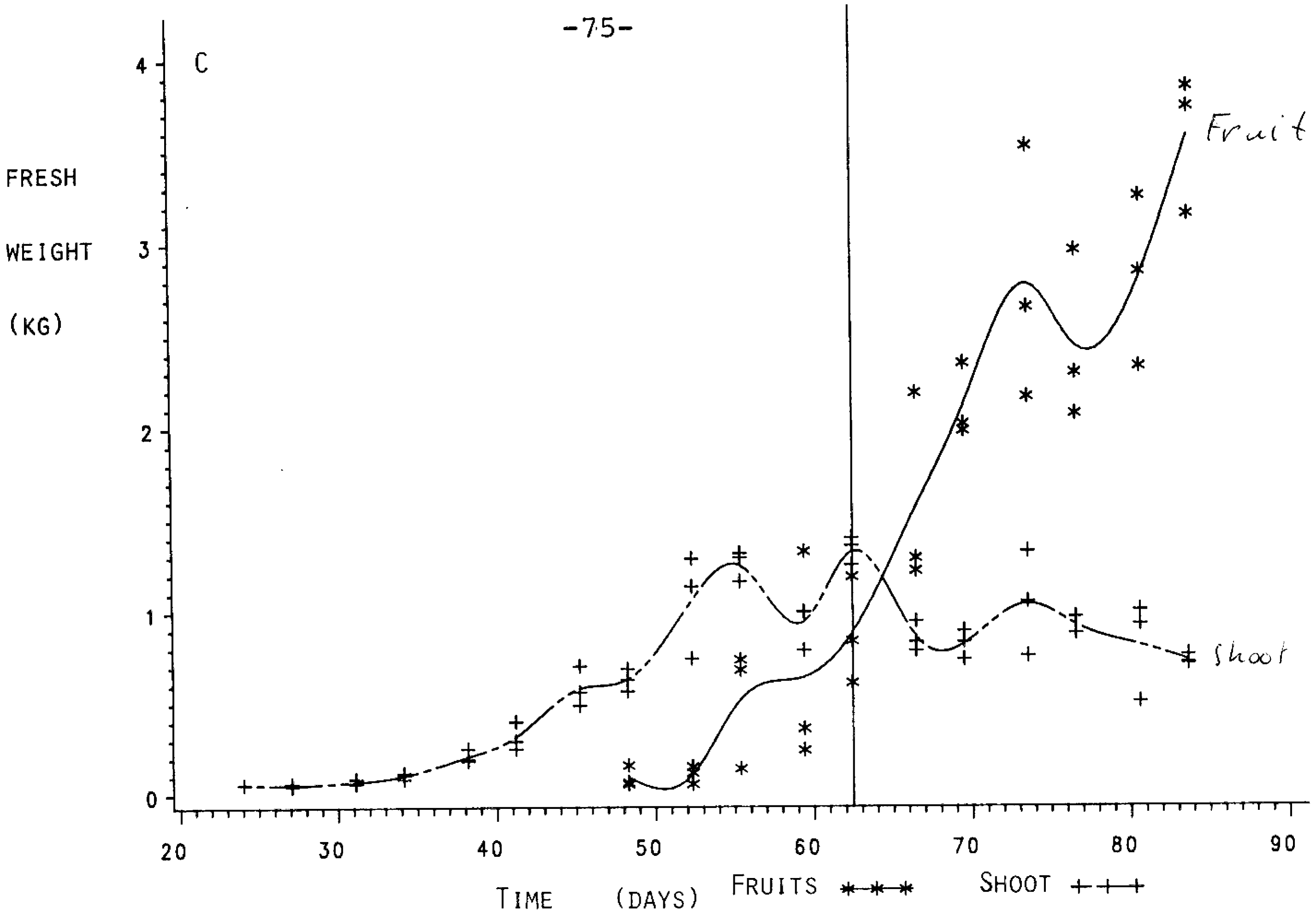


Figure 1 Development of fresh weight (kg) in different plant parts of the cucumber. Root death occurred on day 62. A. Root weight per plant. B. Weight distribution in the shoot per plant. C. Weight of the whole shoot and all fruits per plant.

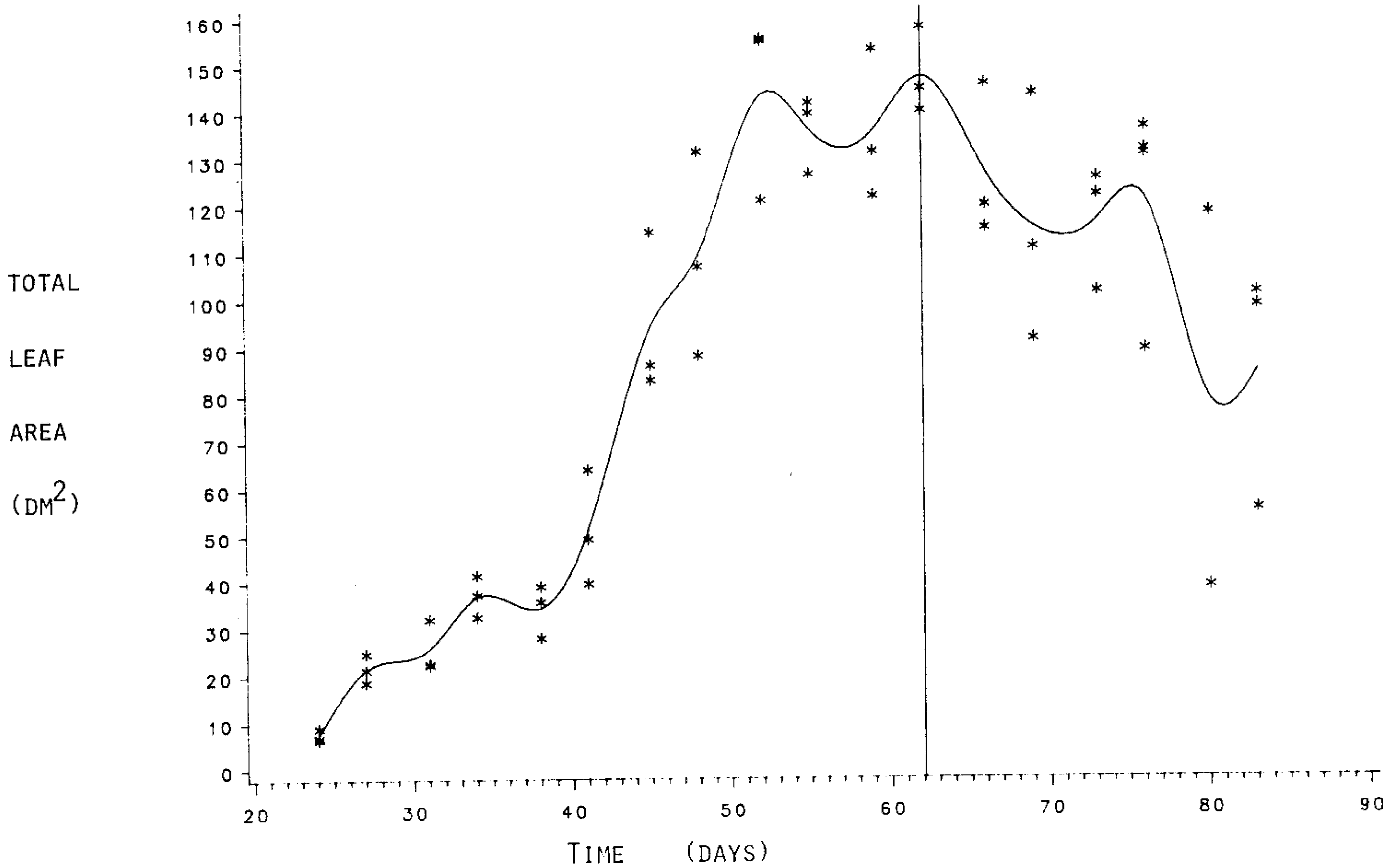


Figure 2 Total leaf area(dm^2) per plant. Cucumber leaves were longer than 5 cm and not dried out. Root death occurred on day 62.

The weight of the total fruit mass increased almost linearly with 96 g fresh weight per day (Figure 1c). Fruits were harvested when they weighed 300-400 g. Between two successive harvests the fruit mass increased with 300-400 g. Several fruit were developing at the same time, which meant that the plant carried a load of at least 500 g fruit from day 55 onward.

On average the dry matter content of the fruits in this experiment was 3.6%. The increase in dry matter was 3.5 g CH_2O produced assimilated per day, which agreed with the results of Pharr et al. (1985). Total leaf area reached a maximum of about 150 dm^2 on day 52 (Figure 2). Afterwards the total leaf area decreased because of excessive ageing. For the production of 3.5 g CH_2O 5 g CO_2 is needed. The average leaf used 170-210 mg CO_2/dm^2/day in the experiment of Schapendonk and Challa (1980) who used 14 hours photoperiod. The average leaf area per leaf was 5.5 dm^2 in this experiment. For 3.5 g CH_2O one would need 5-6 leaves which have a total area of 27.5-33 dm^2. The total leaf area, 150 dm^2, could support 4.7 fruits which is the observed number which can develop at one time (De Lint and Heij, 1982). The results indicated that the leaf area was barely (hardly) sufficient for maintenance and growth of other plant parts than the fruits.

The average water uptake varied considerably (Figure 3). Until root death variation in water consumption agreed with variation in radiation (Anon., 1986). After root death the correlation was less clear.

The EC in the containers increased gradually, therefore, at the end of the experiment, a more dilute topping up solution was used. Because of the calculation method uptake of nutrients agreed with water uptake, only at the end of the experiment nutrient uptake decreased. The EC was not taken into account in calculating nutrient uptake, this may have led to overestimating the actual amount taken up. Still, our results agreed more or less with the litterature. E.g., the average water consumption in this experiment was 0.9 l per plant per day. This estimate was low because there were more plants in the beginning of the experiment. Maximum 467 mg nitrate-N and 651 mg K were taken up according to the calculation with 2.4 l water. Adams (1980) found in his plants an average uptake of 1.14 l water with 250 mg nitrate-N and 380 mg K per day. In the tomato even higher rates have been found (Adams and Massey, 1984).

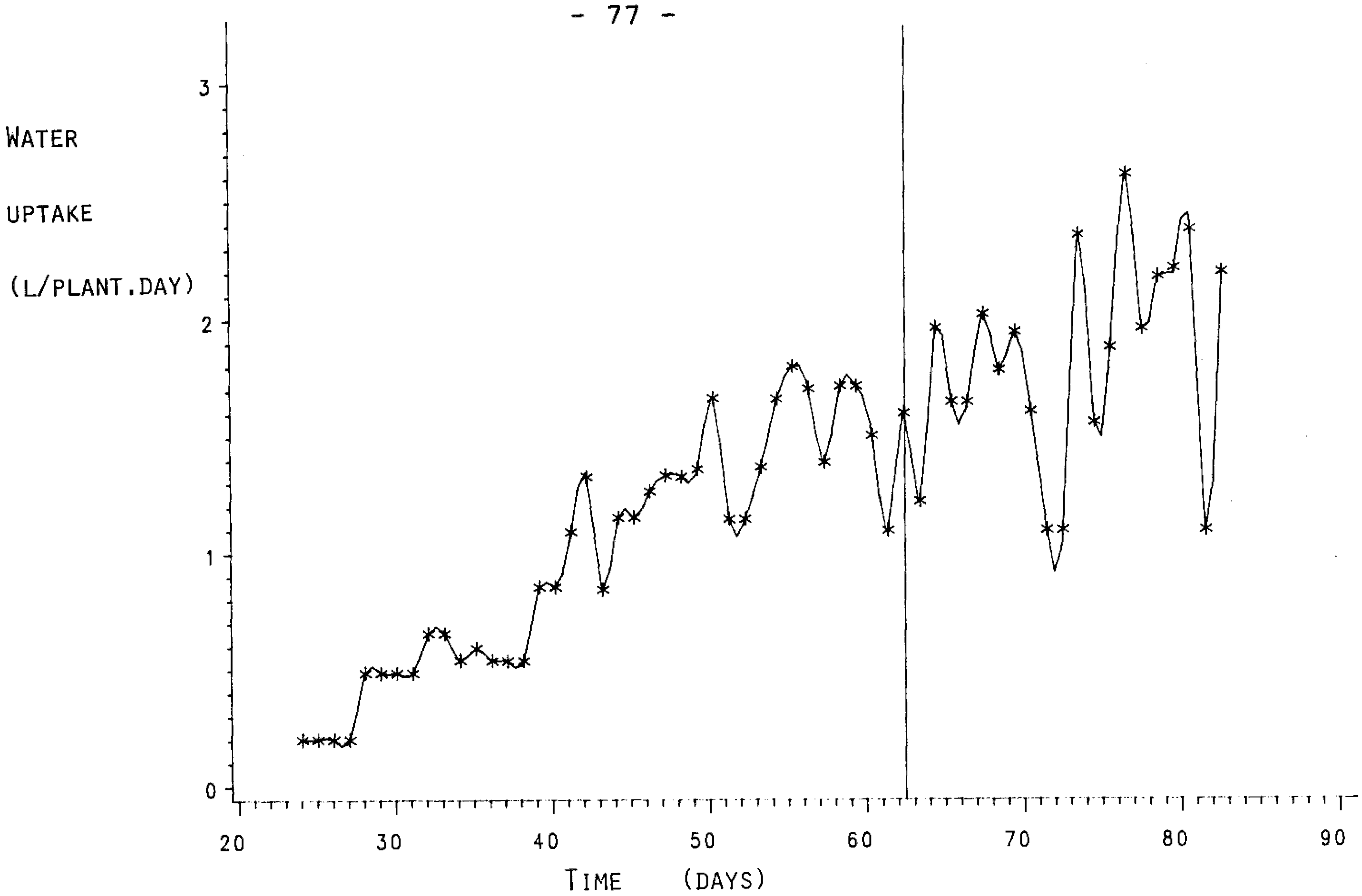
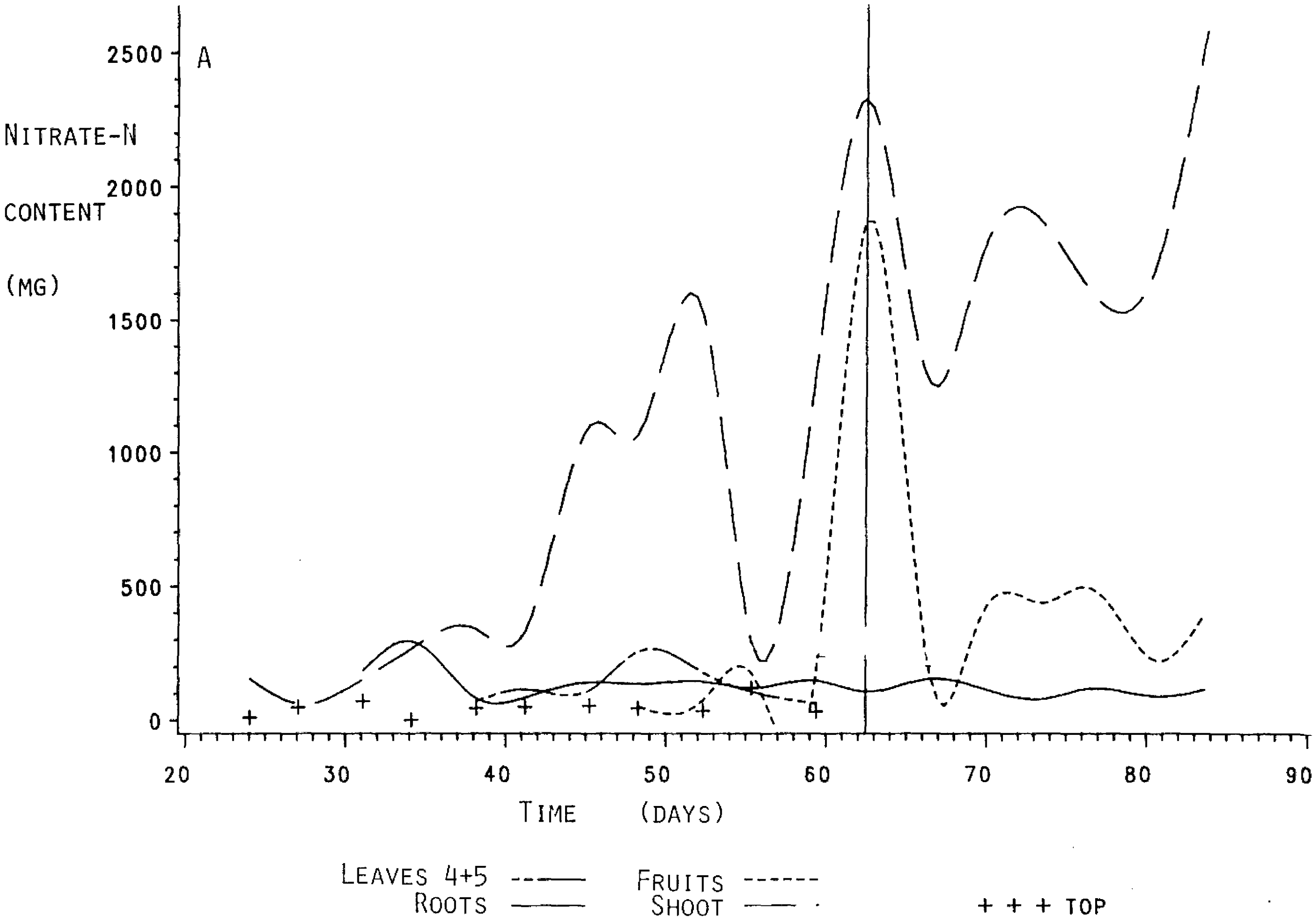
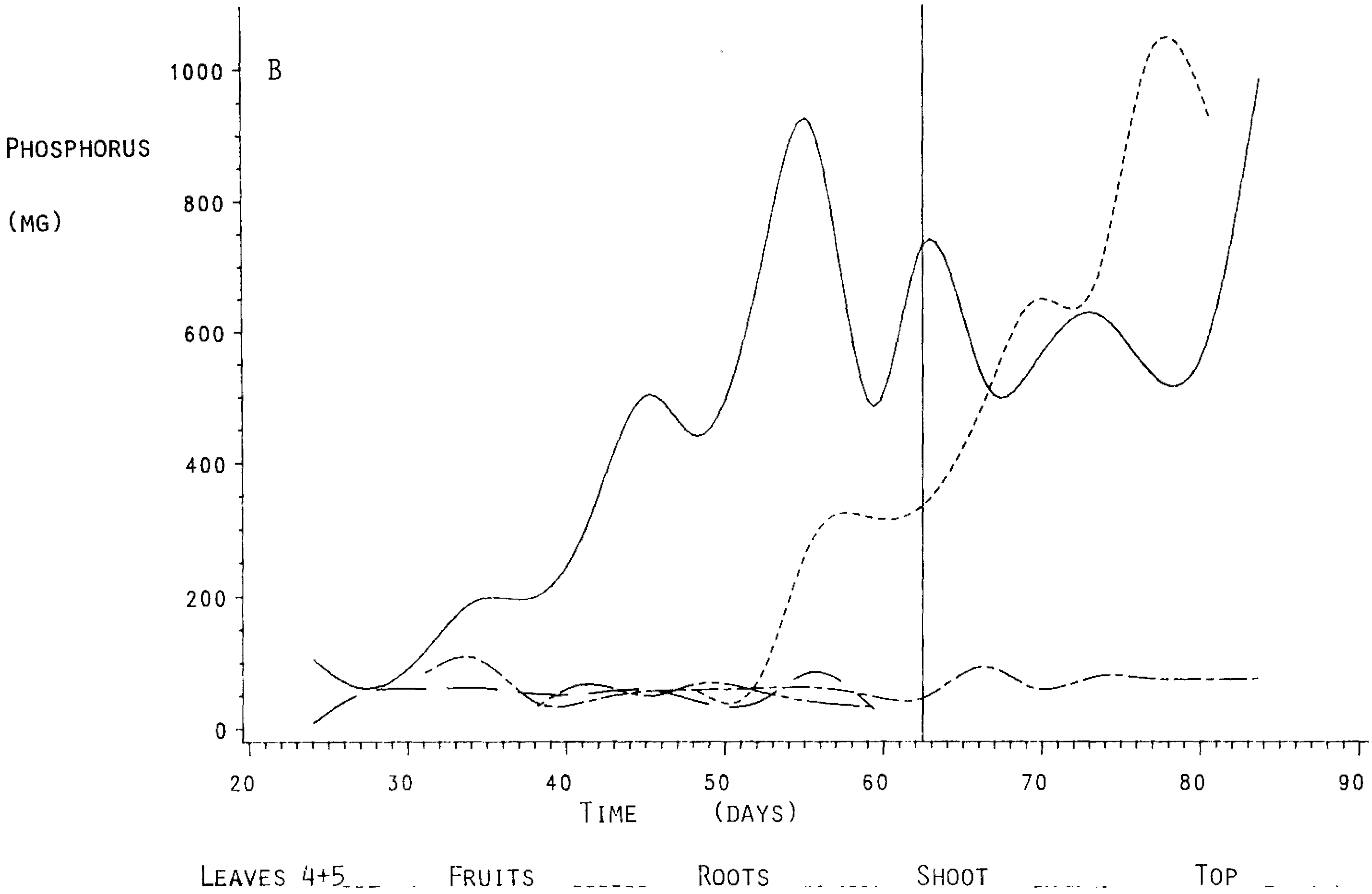


Figure 3 Average water uptake (l/plant.day) of the cucumber. Root death occurred on day 62.

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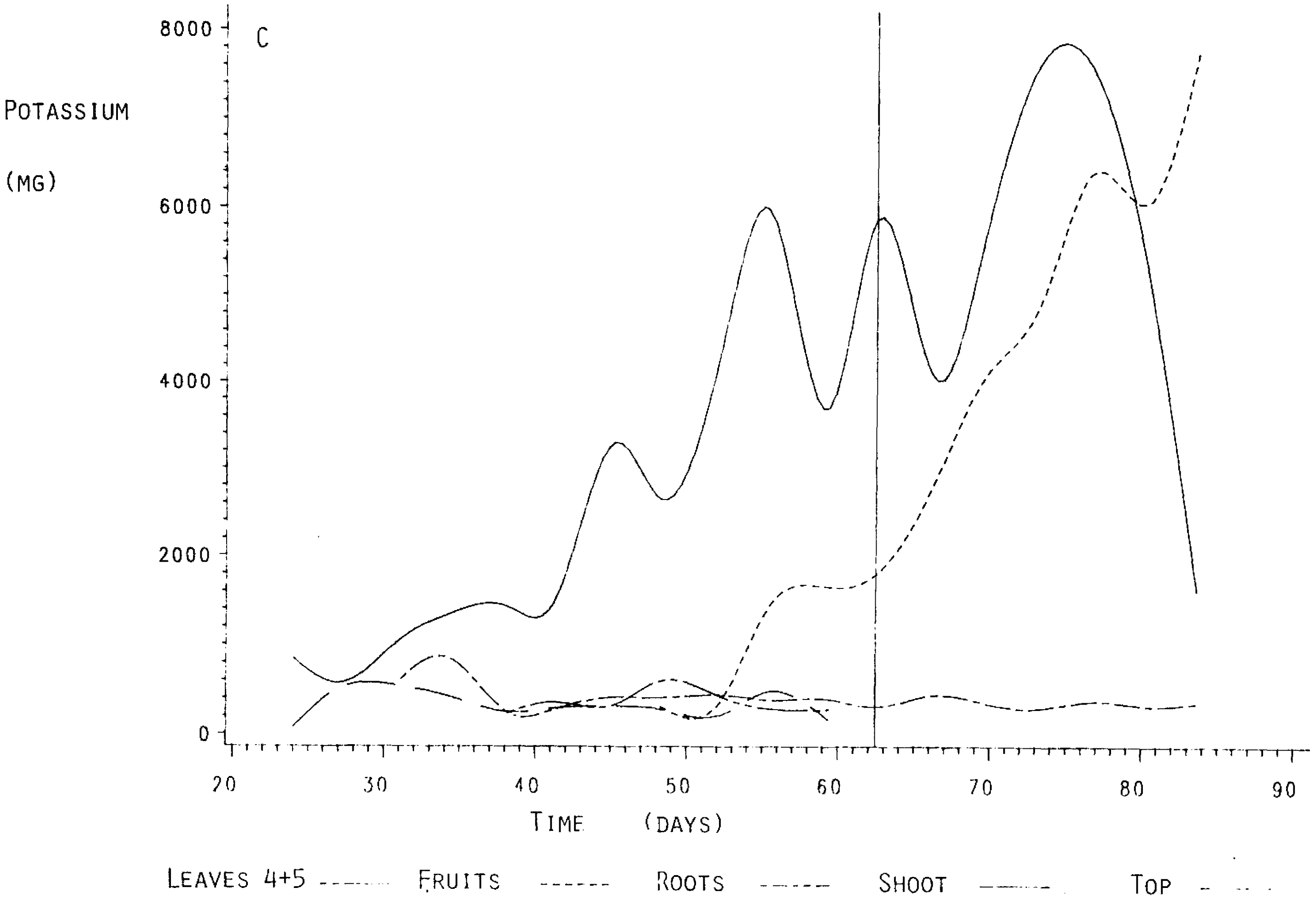
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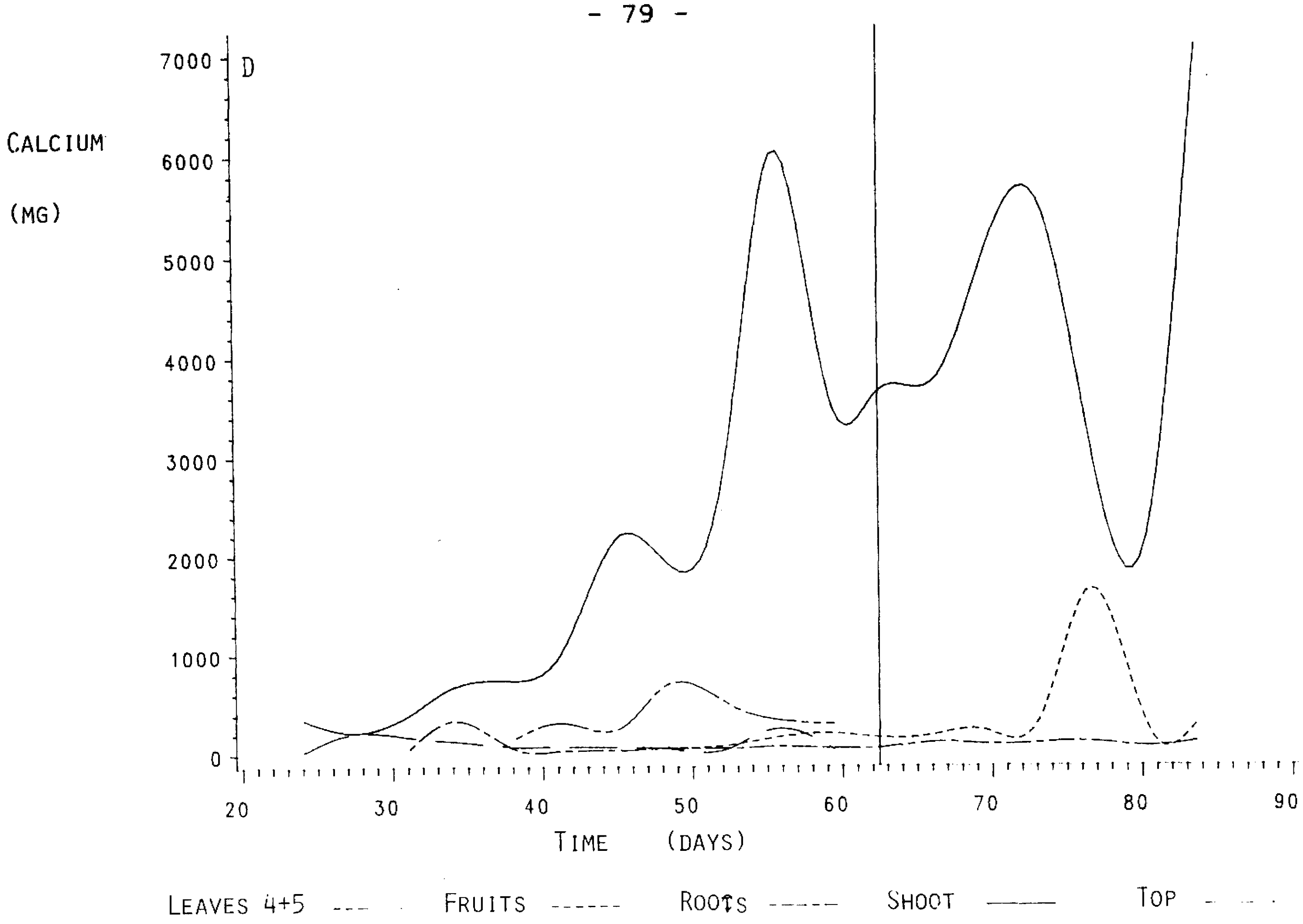
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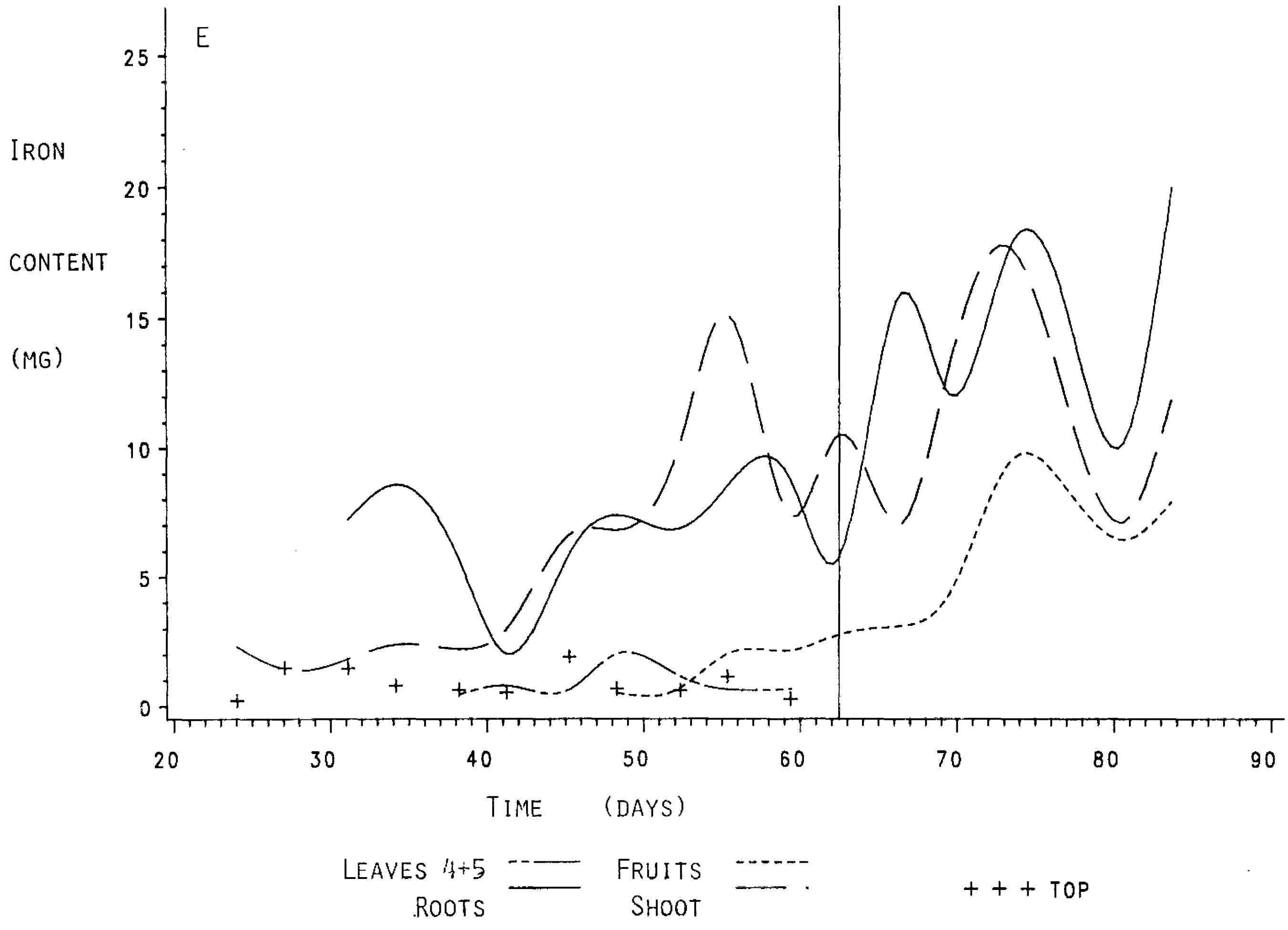
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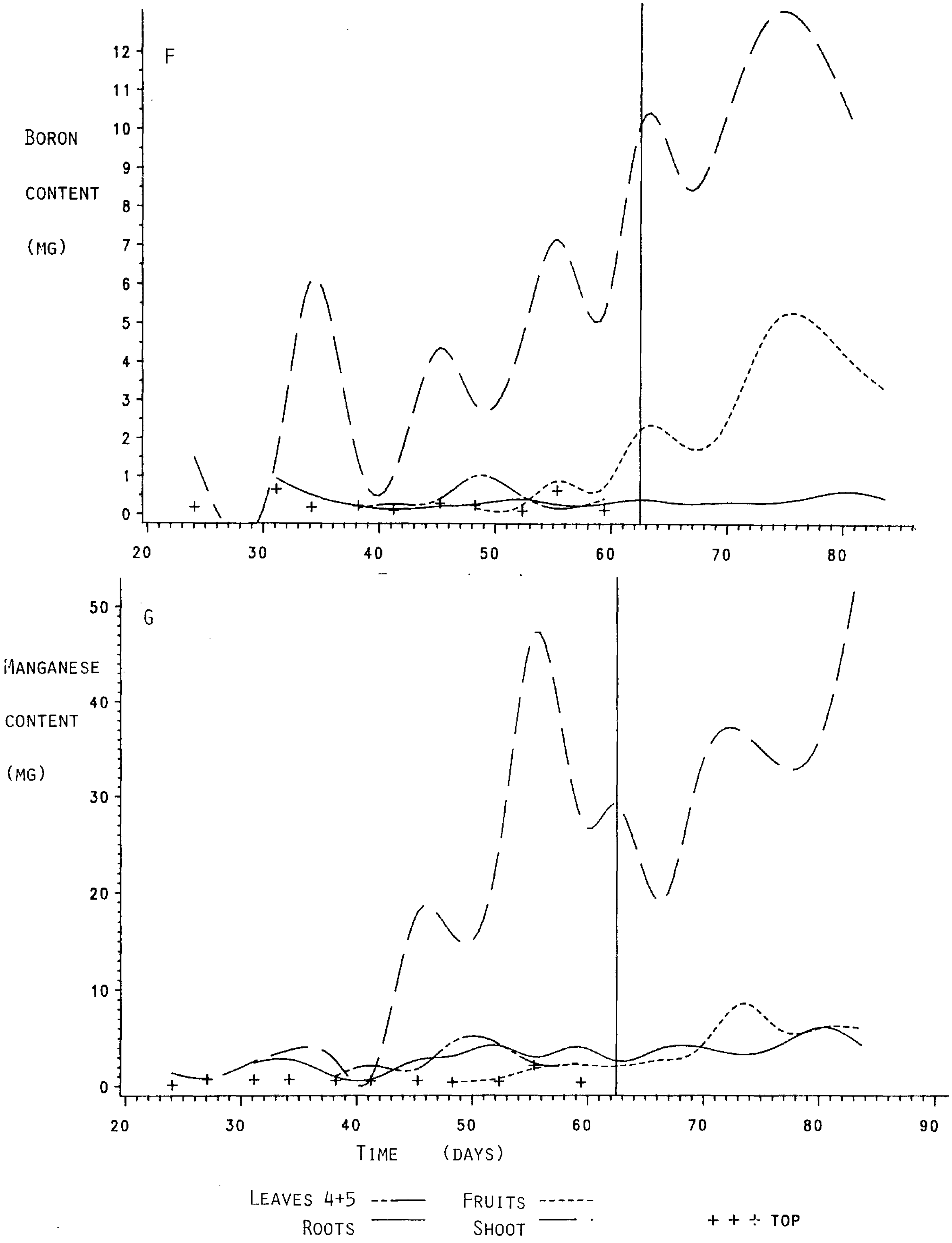


Figure 4 Actual content (mg) of different minerals in different parts of cucumber plants 24-83 days old. Root death occurred on day 62.
A. Nitrate-N content B. Phosphorus content C. Potassium content D. Calcium content E. Iron content F. Boron content G. Manganese content.

The distribution of the nutrients in different plant parts is shown in figure 4. The nitrate content in the roots was not affected by root death. The nitrate content of leaves 4+5 showed a peak on day 48. Nitrate is reduced in the leaves (Matsumoto and Tamura, 1981). Both fruit and shoot contained much nitrate on the day of root death. The total content of nitrate-N remained constant after root death, though differently distributed between shoot and fruit. The shoot may have lacked energy to reduce nitrate.

The amount of phosphorus in the roots increased gradually after a minimum on day 41. The amount of P in the fruit increased while it decreased in the shoot. The fruit seemed to get P at the expense of the shoot. Transport from the roots seemed to be failing.

The leaves and to a lesser degree the tops contained most of the potassium in the shoot. This was especially noteable when the plants were young. The potassium content in the roots remained constant while it decreased in the shoot after root death. The uptake by the fruit continued, seemingly at the expense of the shoot.

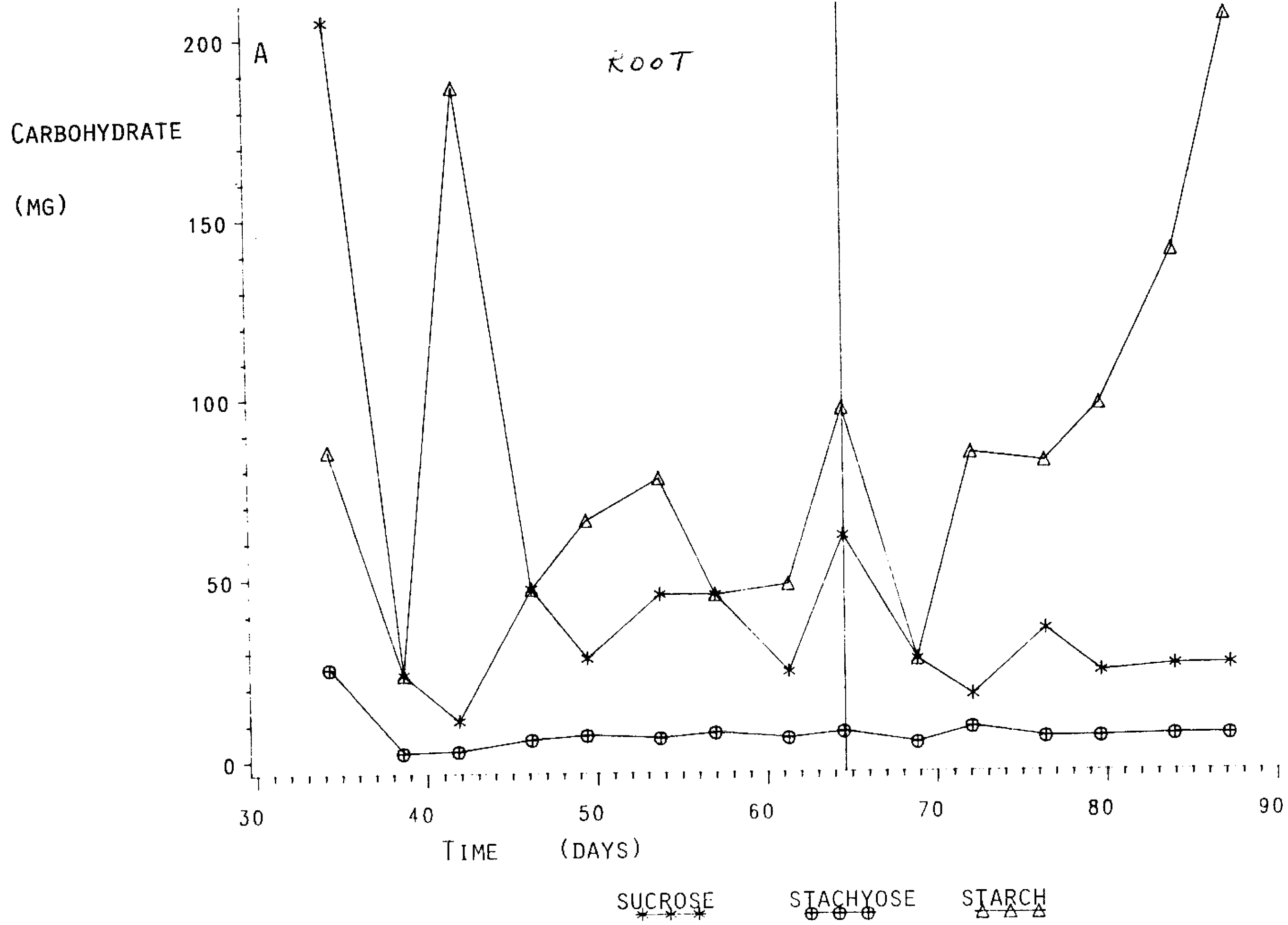
The fruit contained very little calcium. A low calcium content was found in the shoot around root death. Calcium uptake and transport seemed to be little affected by root death. Root death occurred at some distance from the root tip. Calcium is taken up by the distal 20 cm of the <u>Cucurbita</u> root (Clarkson 1981), therefore uptake might not have been so much affected.

The iron content of the root was high and increased even faster after root death. The increase in shoot and fruit was less. Transport of iron may have failed because of precipitation of iron phosphate in the roots, as observed by Wanasuria and Kuhn (1977).

The boron content of shoot and fruit increased steadily, although the boron content per fruit decreased. The manganese content increased in the root. It reached a maximum in the shoot on day 55. Thereafter the fruit may have obtained manganese through relocation rather than transport from the roots.

Ward (1967) analysed leaf blades, petioles, stem, roots and fruits separately for N, P , K, Ca. Only leaves 4+5 and roots were compared with his results. In this experiment we found a higher content for all elements and plant parts, except $\overset{NO_3^-}{N}$ in the leaves and Ca in the roots which agreed with Ward's results. On the other hand the content of minerals never reached toxic levels as given for boron by Bergmann et al. (1965) and manganese by Osawa and Ikeda (1974) and Geissler et al. (1976).

Summing up, it seemed that mineral uptake and transport were both affected by root death, but differently for the different elements. Reduced uptake might be explained by the reduction in root surface area. Van der Vlugt (part 4) showed that the stele diameter is only one third of the root diameter. In root death the cortex until the endodermis is destroyed (ibidem), the mere reduction in surface area could explain a reduction in uptake with two thirds. Not the whole root system is affected simultaneously, but debris from the cortex may make diffusion more difficult. A reduction in uptake with 0-60% could be expected. Transport of nutrients may have been diminished because of lack of assmilates in the roots, which is supposed to be the case in root death.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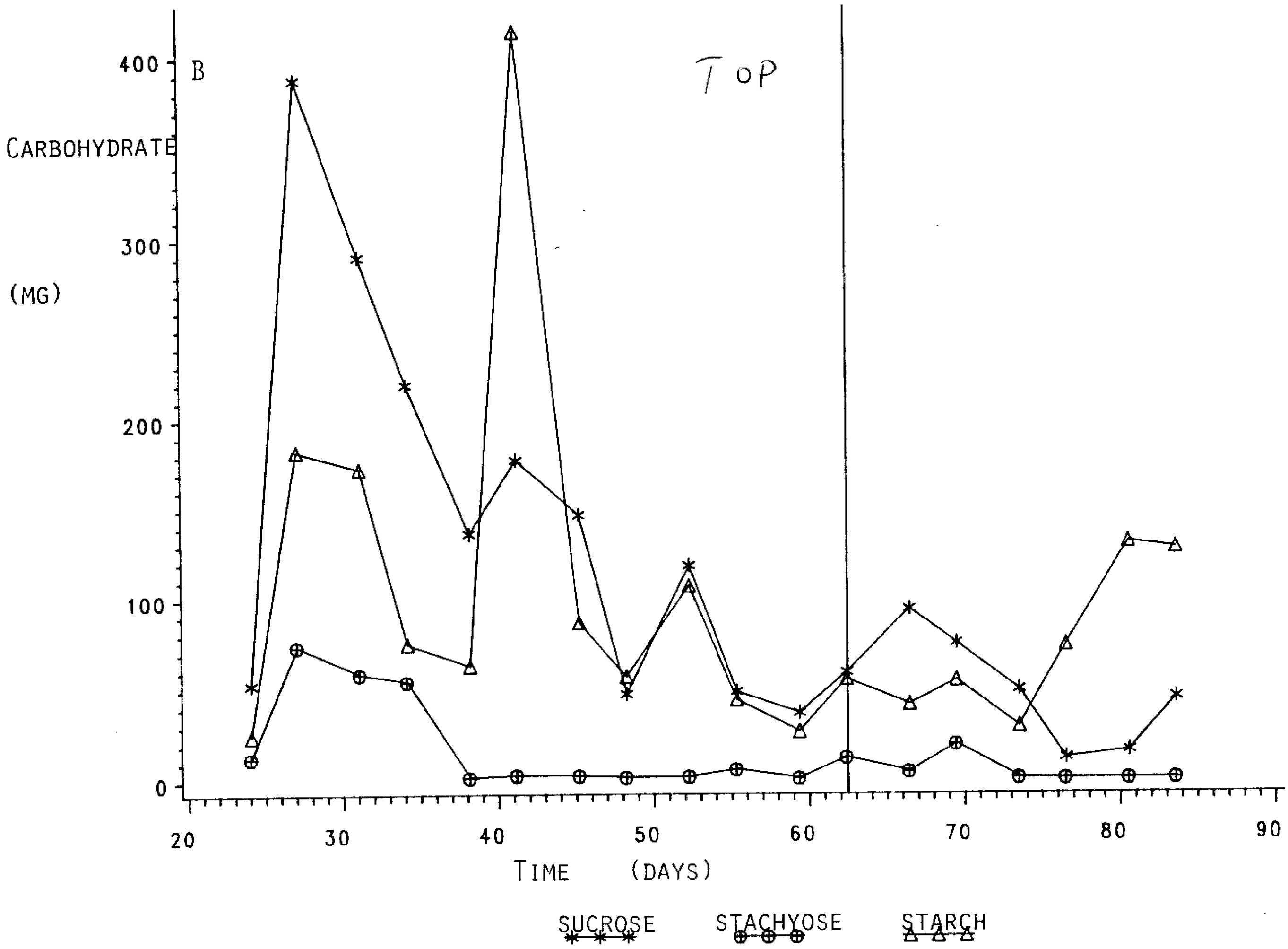
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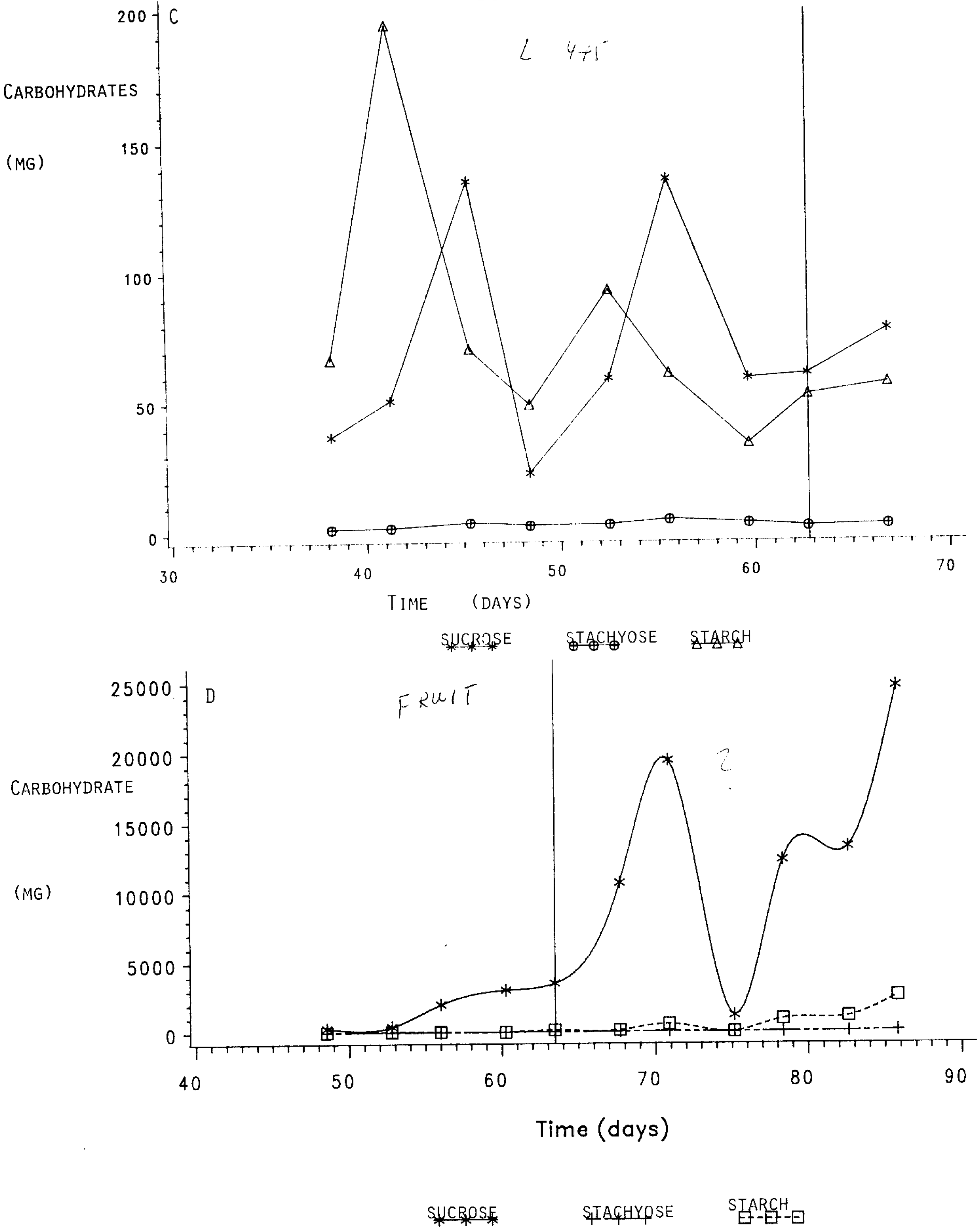

Figure 5 Content (mg) of different carbohydrates in different plant parts of the cucumber in relation to root death (day 62). A. Carbohydrates in the root B. Carbohydrates in the top C. Carbohydrates in leaves 4+5 D. Carbohydrates in the fruit.

Figure 5 shows the content of sucrose, stachyose and starch 3 hours after the lights were switched on. Stachyose was used immediately in the roots. The total content of nonstructural carbohydrate was low from day 45-73, after that especially the level of starch increased. With age the starch content of leaves 4+5 decreased while the sucrose content varied. The stachyose level was low all the time.

In the top the content of all carbohydrates analysed decreased after flowering. Possibly the starch level increased again after day 73, this would be in contrast to the decrease in weight observed. The fruit contained mainly sucrose. The sucrose content of individual fruits decreased towards the end of the experiment.

The results indicated that the fruit is the strongest sink for assimilates also. It can monopolise up to 95% of the assimilates from the nearest leaves (Murakami et al., 1982), or 80% of the total production of the plant (Barrett and Amling, 1978).

Conclusion

It seemed that competition for assimilates was the main factor triggering root death in this experiment. Assimilate production was barely sufficient for fruit growth. Because of starvation root bark cells died, which diminished the area through which mineral uptake could take place. Also the dead cells may have hindered diffusion to the living part of the root. Transport of minerals was also reduced because of lack of energy.

Deficiencies could develop in the shoot, since the fruit also was an effective sink for minerals. The plants reacted to the deficiencies by increasing root growth, an accumulation of starch was seen at the end of the experiment.

The whole process started after flowering but reached its climax when the first fruit were harvested. Then fruit production rate had come into the linear phase of the sigmoidal growth curve.

Acknowledgements

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VII The verdict: fruits are accessory to root death. Exudates are the cause?

Abstract

In earlier reports fruits were shown to be competing with the other plant parts for assimilates. However, incomplete or complete removal of the fruits could not prevent root death. Therefore competition for assimilates is not considered to be the primary cause of root death.

Root exudates also became suspects because of the experiments. The li-terature on root exudates showed that they may be toxic to the plants themselves or to other plant species. The amount and the composition of the exudate varies with growth and development of the plants. The root exudates from the cucumber may be autotoxic, the amount of exudate increased after flowering.

The conclusion is that exudates probably are the cause of root death in most cases. A heavy load of fruits or bad growing conditions may cause root death by competition for assimilates in addition to exudation. Therefore in winter and spring crops of cucumber root death is more severe than in a summer crop.

Key words: cucumber Cucumis sativus root exudates.

Introduction

In this series two factors have been mentioned as causes of physiological root death of the cucumber (Cucumis sativus L.): 1. competition for assimilates between roots and fruits, 2. root exudation.

From the time of constant fruit production rate the growth rate of the fruits was such that competition occurred. This occurred after harvesting of the first fruit. Then root death caused by competition can be expected (Van der Vlugt, part VI). On other occasions root death occurred before harvesting or even in vegetatively growing crops, then exudation was assumed to be the cause of root death (Van der Vlugt, part I and III, Van der Vlugt, 1986).

My experiments were directed towards the effects of fruit growth. In this paper they were re-examined with regard to root exudates. Litterature on exudates was reviewed to find a possible role of exudates in root death.

Indications of the role of exudates in root death.

The results from our experiments confirmed the impression that root death is less severe in summer than in winter. Light conditions are better in summer, so competition is not expected to be as important as in winter. Another factor must be involved in root death, presumably root exudates.

In the high nitrogen treatment (Van der Vlugt, part I) relatively fewer fruits were expected than in the low nitrogen treatments, the assimilate supply to the roots could be larger, therefore the roots also exuded more. Root death occurred before harvesting in this treatment. Pegg (1986) showed that tomato roots exuded more when the assimilate supply was larger.

The same effect was shown in different ways in the cucumber experiments with different fruit load and different plant density (Van der Vlugt, 1986,Van der Vlugt, part III). Root death occurred in all treatments, more plants and fewer fruits gave a higher concentration of exudates. It must be assumed that Cucurbita roots are less susceptible to exudates or are exuding less than cucumber roots.

In the experiments in wide gullies or in containers a large volume of nutrient solution was available to the plants (Van der Vlugt, part IV, V and VI). Then it would take longer time to reach toxic concentrations of exudates than in commercial installations. In this case the fruits would be more important. It was found that vigorous root growth was an advantage in these experiments. A vigorously growing root system may be supposed to be a good competitor, if the exudate concentration is kept low.

Other effects of root exudates

Root exudates have been investigated in connection with weed growth and crop rotation. Auto-intoxication has been directly shown for the asparagus (Young, 1984). New plants have difficulties in establishing in an asparagus field. Indirectly it has been shown for wheatgrass. Bokhari and Singh (1974) obtained more plant material from plants which had been cut than from control plants. In the cut plants they assumed less material to be exuded from the roots, and therefore no inhibition of root growth when needed for regrowth of the aerial part of the plant. In *Cucumis* spp. and sweet pepper plants being kept vegetative, root growth stopped after a while and root death symptoms could be seen (Van der Post, 1968; Hall, 1977). One may assume that root exudates caused this root death.

Root exudate: quantity and composition

Many seemingly contrasting results have been obtained in experiments with root exudates. The composition of the root exudate varied with the plant growth stage (Vancura and Hanzlikova, 1972; Caussanel and Kunesch, 1979). The effect of root exudation on other plant species depended on the combination of species and plant growth stage of the exudate donor (Pope et al., 1985). A larger amount of exudates gave more inhibition (Caussanel and Kunesch, 1979).

In several experiments it has been tried to remove exudates and their effect. Abdel Rahman and Newton (1984) used activated carbon successfully to prevent root death in the tomato. In our experience with cucumber this was not successful. In another experiment with lettuce and other crops Stevens and Tang (1985) found that the hydrophilic substances in the exudate from *Bidens pilosa* were most toxic.

Caussanel and Kunesch (1979) studied the composition of the exudate of the common lambsquarters (Chenopodium album) and its effect on growth of maize seedlings. They observed that oxalic acid as in many other C_3-plants, was the active component and that the amount of oxalic acid increased considerably after flowering of the weed.

The nutrient solutions from the growth analysis experiment (Van der Vlugt, VI) were stored at 5°C in the dark for 1 year and used for exudate analysis. The exudates had accumulated from day 24. Seeds of cucumber and maize were germinated in Petri dishes with 2 x 2 ml distilled water at room temperature. Respectively 4 and 5 days after sowing the primary roots were measured and the seedlings transferred to 2 x 2 ml of the different nutrient solutions, 8 cucumber and 10 maize seedlings per dish. After 3 resp. 5 days the roots were measured again and the increase calculated relative to the original length since the original length varied both within and between Petri dishes (Table 1). The nutrient solutions were titrated, oxalic acid was used as a standard. The results showed an increase in titratable acids until root death. Growth of the seedlings seemed to be stimulated at first, but then decreased at higher acid concentrations. It seemed that acids in the cucumber root exudate had a growth inhibiting effect at high concentration. The inhibition was less severe than with 5 meq/l of oxalic acid, which inhibited growth of both species completely.

Table 1. Amount of titratable acids in the nutrient solutions taken from cucumber plants 27-83 days old. The plants flowered on day 38, the first fruits were harvested on day 55, root death occurred on day 62. Length of cucumber primary root after 3 days in the different nutrient solutions relative to their original length. Length of maize primary root after 5 days in the different nutrient solutions relative to their original length.

Day	Titratable acids (meq/l)	Cucumber roots	Maize roots
27	1.6	0.9	4.3
31	1.8	1.1	8.9
34	2.5	3.5	7.9
30	2.2	1.9	6.6
41	3.2	1.6	9.7
45	2.1	1.4	8.5
48	3.1	1.1	5.4
52	4.4	1.3	6.6
59	4.9	1.5	5.1
62	5.0	1.2	6.1
66	4.9	1.0	7.3
69	6.3	0.8	2.5
73	2.9	1.1	5.4
76	3.1	0.9	6.2
80	1.0	1.2	10.9
83	1.2	1.4	-

Exudation in NFT

The nutrient solution in NFT (nutrient film technique) is different from that in soil in that the concentration of nutrients is much higher in NFT. Root exudation in itself may be less in NFT because there are no abrasive soil particles to cause wounds and thereby more exudation (Hale and Moore, 1979). The NFT gullies form a closed system in which exudates may accumulate. Low concentrations of exudates may have a stimulating effect (Caussanel and Kunesch, 1979), but the concentration will increase to toxic levels. A larger volume of nutrient solution per plant will delay the attainment of toxicity.

The role of micro-organisms in exudation is little understood. In NFT probably a new situation exists, with few naturally occurring organisms in the beginning and after a while a microflora which may or may not be different from that in soil. The micro-organisms may use plant exudates and stimulate or inhibit exudation from the plants. Different organisms have different effects and differences between soil and NFT may occur. These have been investigated very little so far (Hale and Moore, 1979; Pegg, 1986).

Conclusion

Root death is caused by either competition for assimilates or root exudation. The latter is considered to be the most important. The former is only of importance under disadvantageous growing conditions. Both factors occur in a natural situation, their additive strength determines the severity of root death. If it is possible to manipulate exudation or build-up of exudates in NFT vegetable production in NFT would have great possibilities.

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