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Rootsystems as they are influenced by the circumstances under which the crop grows, especially in soilless culture.

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1. Introduction

More and more glasshousecrops are cultivated on soilless systems. The nutrition is given as a nturient solution, while the roots are supported in rockwool and polyurethane foams. Sometimes the cultivation takes place on a waterculture technique like nutrient film technique. The trend in the future is an increasing grade of recirculation of the nutrient solution. One of the reasons for recirculation is that damage to the environment has to be as small as possible. Draining to the subsoil has to be avoided. Soilless systems has further as an advance the possibility of a high degree of regulation. Much knowledge of the backlying processes has however been required to steer the plant in the most efficient way.

Purpose for the grower shall be a maximal yield and quality with a minimum of nutrients and energy. This means a minimal root system in relation to the shoot with a maximal uptake activity. Further a certain resistace of the root system to altered environmental circumstances is required. Important is how the rootsystem has been composed from smaller and thicker - sometimes lignified - roots and the relation with the uptake of different nutrients.

Root-morphology is influenced by a large number of factors. Reviews about this have been given by Van Dorp (1977) and Feldman (1984). The spatial construction of the substrate and the penetration resistance are such factors. Further aeration, roottemperature, availability of water, suction pressure and the nutrient composition in the solution are other factors.

Another influence can be the presence of organic compounds in the root-environment. Especially growth regulators can alter the morphology of the root-system strongly. Humic compounds from the organic matter in a soil can be another influencing factor.

"Can it be useful to add this kind of compounds in soilless culture?" is further a question that can be put. Also is it possible that the plant itself can give exudates in the medium which influence the uptake-process in the rhizosphere. If these compounds accumulate positive and negative influences on plant growth are possible.

In the knowledge about the relationship substrate, nutrient solution, environment, root, uptake are still shortages. The aim of this paper is now to give some information about the factors which influence rootmorphology and the uptake capacity during the cultivation of the crops especially in connection with soilless cultures. A summary of literature data will be given. Further some first results of own research about the influence of the spatial building of the substrate on the roots and on uptake from work at the Glasshouse Crops Research Station will be given.

2. Factors which influence the root system and the uptake capacity

The factors in the environment of the root can exert their influence both by altering the morphology of the root system as well as the absorption rate of the individual roots.

Factors in the root environment are penetration resistance, oxygen content, root temperature, water content, nutrient content in the solution and so on. But also the spatial forms of the substrate in which the roots grow will have an influence. It is however difficult to unrafle the influence of these factors because they are interrelated and difficultly to vary separately. It is still more difficult because also the shoot has an influence on the root function. Further the shoot itself is again influenced by other factors like light intensity.

For a short period it will be possible to express the root function by a formula which is comparable with that given by Protopapas and Bras (1987) as follows:

$$U_i = \sum (\psi^i_{su_j} - \psi^i_{r_j}) \frac{\text{root } Y^i_j + p \times \text{root } O_j^{\,i}}{K_r} \times f^i_T \times f\theta^i_{su} \times f^i_O \times \ldots \qquad \text{Formula I}$$

for the water uptakerate U_i from the substrate in $g.m^{-2}$ substrate on

The symbols in this formula are:

$\sum$ - summation over all compartiments in a m^2 substrate

j - compartiment j in the substrate

ψ^i_{suj} - the effective waterpotential in the substrate on time i in compartiment j

ψ^i_{rj} - the waterpotential in the roots on time i in compartiment j root Y_j^i = weight of young roots in compartiment j on time i

root O_j^i = weight of old roots in compartiment j on time i

p = the proportion of the rootsurface of the old roots, which is still active in uptake

K_r = effective resistance of the roots for wateruptake per unit weight

f_T^i, $f_{\psi su}^i$, f_O^i are the functions for the effect on the function of temperature, waterpotential in the substrate, oxygenpressure at the rootsurface, and so on.

$\psi_{su}^i = \psi + \psi_g + \psi_{osm}$

ψ = matrixpotential, which will be the most important component (among others this is influenced by the properties of the substrate)

ψ_g = gravitational potential

ψ_{osm} = osmotic potential

For the nutrient elements comparable formulas can be put coupled to the wateruptake. Corrections must however be applied for selectivity for the specific nutrient and differences in the functions which gives the dependence with environmental factors.

A number of separate factors in the root environment can be distinguished now which influence in the form. 1 area and activity of the roots.

2.1. Density or penetrationresistence is an important influence, which influences both branching and elongation. For elongation the plant cell has to surmount the wallpressure and the substratepressure ($P+W+\sigma_s \leq$ Posm, in which P = hydrostatic pressure, W = wall pressure, σ_s = the external pressure in the substrate and Posm = osmotical pressure in the root cell).

The root cells in the direction with minimal resistance elongate most strongly.

Roughly speaking penetration of roots is in general inhibited above a counterpressure of about 1 Mpascal, although decrease of elongation has sometimes found already with 50 kPascal (Gerard et al, 1972, Heuvelink, 1984 and Feldman, 1984). The pressure which the roots can exert depends also on the oxygenpressure around the roots.

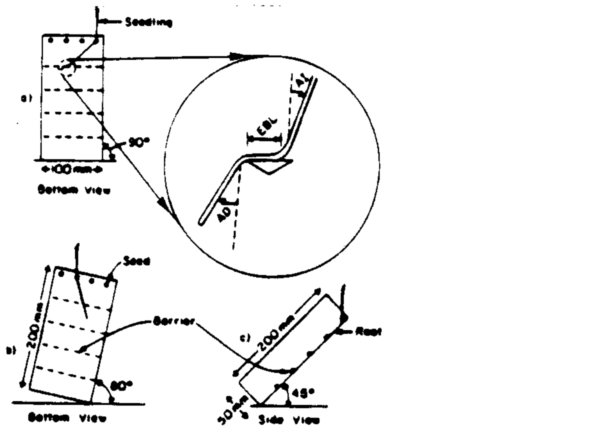

Fig. 1. Rhizotron placement: (a) Bottom view showing seed and barrier placement; the small circular area has been enlarged to show corn (*Zea mays* L.) primary root deflection by a barrier where AI is the angle of incidence, EBL is effective barrier length, and AD is the angle of deflection. (b) Bottom view similar to (a) except rhizotron has been tilted sideways 10°. (c) Side view.

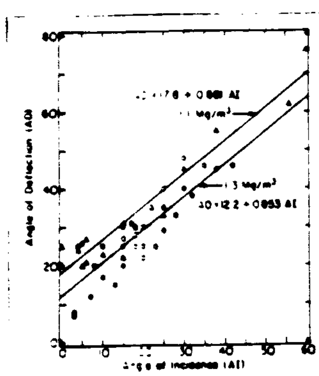

Fig. 4. Linear regression of the angle of deflection (AD) on the angle of incidence (AI) for soil bulk densities of 1.1 Mg m⁻³ (▲) and 1.3 Mg m⁻³ (O).

1A. Type of barrier (plexiglass) used in the experiments with corn.

1B. Relation between the angle of deflection (AD) and the angle of inflection (AI) when roots pase a barrier.

Fig. 1. Effect of a barrier on the root angle. From Bandara and Fritton (1986).

The branching of the roots can however already increase with resistances of 50 kPascal (Feldman, 1984). Early lignification (2.5 mm of the root tip) was recorded in stressed roots which had to overcome a large resistence.

2.2. Passing-by obstacles.

Roots have the ability to be able to by pass obstacles. They can pass through small holes. They can alter their direction and than branch on one side of the root. The most fine sideroots of the first order have diameters of 150 um. Experiments with 5 mm wide, flat physical barriers (Figure 1A) from Bandara et al (1986) gave the result of Figure 1B. The explanation of the behaviour of the roots can be based on transversal concentration differences in the root (of growthregulators?) caused by the barrier. It is more difficult to predict the influence of threads of rockwool or canals in polyurethane.

2.3. The oxygensupply of the rootsystem.

In a system like rockwool this supply is a complex process. There are regions with gaseous air but in other regions there is nutrient solution or the fibre of the material. Via gaseous and liquid phase oxygen has to diffuse to the root. Important factors are:

1. Oxygen concentration in the solution.
2. Diffusion rate of oxygen.
3. Partial oxygen pressure in the soil gas.

In the solution of nutrient film technique concentrations of 5-10 mg oxygen.kg^{-1} in the nutrient solution are normal. In the region less than 0.5 mg.kg^{-1} the concentration is very limiting for uptake (Alwan and Newton, 1984). Wiersum (1980) determined with electrodes the diffusion to the roots. A diffusion of about 200 mg oxygen.m^{-2} root surface.$hour^{-1}$ is mentioned there as limiting. For different crops the needed oxygen supply to the roots will differ. With the oxygen-availability the rootmorphology can be influenced. With a limiting supply of oxygen the roots become shorter and more branched.

2.4. The root temperature.

Both rootgrowth and morphology are influenced by the roottemperature.

Further the uptake is temperature dependent. It is possible to give an optimal temperature in different stages of growth for different plants. Higher root temperatures can give higher "shoot":"root"-rations, because of stimulation of the shoot by a higher uptake (Mc Duff et al, 1987). Heuvelink (1984) describes alterations of morphology with different root temperatures. More white thicker and less branched roots and more root-hairs ar in general formed with low temperature. At low root temperatures many root hairs were described. At higher temperatures the root system is more fibrous and soft. About the influence of root temperature on root morphology more research is desirable. Also absorption of limiting elements like magnesium can be influenced with temperature as Sonneveld (1987) describes. Less magnesium deficiency was found in tomato at a root temperature of 24^{o}C than at 19^{o}C. The influence of root temperature varies with the kind of the element (Kosobrukhov et al, 1988). The influence of the root temperature via suberizing of the cell walls and formation of wood wessels in the roots is still difficult to give.

2.5. Wateravailability.

The influence of watercontent and waterdistribution in substrates like rockwool and polyurethanes is quantitatively still uncompletely known. In any case the influence on structure and uptake capacity of plant roots is large. It is however difficult to unrafle this influence from an indirect influence via other physical factors. Uptake of water by roots is strongly correlated with the waterpotential in the medium and this is again related with the pF-curve of the substrate. The waterpotential around the roots is determined also by the matrixeffect of substrates like rockwool. The other factors that are influenced indirect by the watercontent in the substrate are the oxygen concentration, density, resistance against rootgrowth and so on.
Results described of different experiments give not always the same conclusion about the influence on root morphology. Different other circumstances during the experiment are probably the cause. Heuvelink (1984) describes decreasing growth of the rootsystem when there is water shortage. The explanation would be closing of the stomata and a decrease of assimilate transport to the roots. Gerard mentions shorter rootlength of pea with a lower watercontent in soil. Van Dorp (1977) describes a more

extensive rootsystem with longer roots when the soil water content decreases, shaping more favourable conditions for the plant under worse circumstances. Heuvelink (1984) found under moisty circumstances more hairroots. When the soil is too wet for a period dead root points appear. Heuvelink (1984) gives as an optimal waterpotential traject -0.05 to -0.2 Mpascal. Roots can still grow at -1.5 MPa. Protopas and Bras (1987) found reduction of root function beginning at -0.7 MPa, at -1.5 MPa reduction was 80% and at -2 MPa rootfunction was completely inhibited.
Thus the influence of watercontent in combination with suction pressure is still not clear. The problem is that there are many interactions with other factors.

2.6. Nutrients.

It is difficult to give clear conclusions about the influence of nutrients on root growth, branching and root morphology. A special problem is that there is a strong interaction between the nutrients mutually and also with other factors like light and temperature. The influence on the rootsystem is also often indirect via shoot growth and the distribution of assimilates. It would be ideal as it was possible to give the optimal concentrations for macro- and microelements eliminating the other factors as much as possible. The interactions are the reason that only a few short general remarks about nutrition will be made.
For the rootgrowth a minimum level of a number of elements like nitrogen, phosphorus, calcium, boron and iron appears to be very important (Wiersum, 1980). So calcium has to be about 0.15 mol.part in the nutrient solution (Marschner, 1986). If the concentration becomes low the root-system can adapt to that situation by an increasing size of the root-system. In certain critical periods like that of strong fruit-development deficiency of for instance iron can give root-death.
The concentrations and ratios of nutrients have also a large influence on rootmorphology. Van Dorp (1977) mentions a number of authors who found stimulation of root growth with higher concentration in nutrient solutions. Van Dorp (1977) further describes as a result of one author with a low nitrogen gift much primary root growth and less branching. On the other side results with local application of nitrogen caused more

and longer side-roots on these places. Marschner (1986) found with ammonium-nitrogen and less nitrate more lateral roots which are shorter and thicker. Marschner states also that the root-system with less phosphorus becomes finer with more roothairs in the region of less than 10 uM phosphorus. Sonneveld and Voogt (1985) found in the region of iron deficiency (10 - 20 $umol.l^{-1}$) a finer and more branched root-system compared with sufficient iron. It is possible that the root system compensates in a direction to balance a shortage.
The nutrition have also an influence via the electroconductivity (EC). A higher EC gives shorter, thicker and more branched root-systems than a lower value (Sutton, 1980). De Willigen & Van Noordwijk (1987) found that the roots of tomato in rockwool "choose" a certain EC (about 1.3 - 1.7 $mS.cm^{-1}$) for maximal growth.

2.7. Organic compounds in the root environment.

Organic compounds in the solution in the rhizosphere can influence the weight and the form of the root system. This influence concerns both the mitosis of cells in root tips and the elongation and differentiation of the cells further from the tip. Alterations in the construction of the root system mean that the distribution between finer and larger roots alters and that wood and cork formation takes place. Organic compounds can have a direct influence on the plant cells but also influence via chemical complexation the absorption of ions in the root. The origin of the organic compounds can be different. Thus growth regulators, root exudates, humic compounds from the peat part of soils and artificially added chelates can be distinguished. Also in the group of the growth regulators different types of compound-groups have been described in literature. Thus auxines, kinetines and gibberellines are possibilities. These organic compounds can be used to regulate root-formation in different stages of root-growth. Further humic compounds could possibly useful to be added in water-culture if stimulation is expected. In water culture techniques with complete recirculation accumulation of compounds from the root exudates may become inhibiting for the plantroot.
The role of organic compounds in the transport of inorganic nutrients to the absorbing places on the root will differ for soil, substrate culture and waterculture. In the last case mixing is very intensive which means

that it would expected that the role in transport of nutrients will be smaller.

2.7.1. <u>Humic compounds</u>.

In the soil organic matter is present with a different composition for different soils. This organic matter can be separated by chemical or physical methods in a number of components. The question can be put if addition of products of these separations or comparable synthetic products can be useful for the cultivation in water culture or substrate culture.

The aspects which are important with addition of organic compounds are the influence on the root system (development of small and thick roots, branching, etc.) and the influence on absorption of nutrients by complexation. Burns (1986) describes in a symposium report effects of this type from the work of different research workers. For different crops stimulation of root growth was found in a concentration range of 10 - 300 $mg.l^{-1}$ humic or fulvic acid in nutrient solution. This was for instance the case for tomato.

Stimulation has been found in about the same concentration range of humic compounds for the uptake of nitrogen and micro elemnts (like copper and iron). Certain compounds have a special influence on root initiation, others on root cell elongation. Thus Whittington (1968) mentions stimulation of root initiation by phenolic compound in the humus. Marschner (1986) mentions high molecular fulvic acids as active in root initiation and stimulation of root elongation. High concentrations of lower molecular compounds can cause inhibition, this is also the case for compounds like phenolics and short-chain fatty acids which originate under anaerobic circumstances. Also Schnitzer and Poapst (1967) describe stimulation of root initiation in plants like bean above 500 mg organic $matter.l^{-1}$.

The organic complexes of micro-elements can stimulate their absorption by plant roots. Burns (1986) describes that for copper, cobalt and iron. Scotti, Frappetta and Silva (1983) find with humic acids of molecular weights smaller than 10000 and larger than 100000 some stimulation of uptake of iron and cobalt respectively in shoot and root. Sonneveld (1984) found for cucumber with addition of organic matter increase in

absorption of calcium and magnesium.
The idea exists that the humic acid under conditions where the molecule is not too large can be taken up also (Burns 1986).

Exudates
Plant roots excrete also organic compounds, a part of which can give also complexes with nutrient ions. Most knowledge exist for iron. Marschner et al (1987) mention "phytositerophores", which translocate iron to the root surface. Further exudates of the plant root are organic acids, amino acids, sugars and phenolic compounds. Schönwitz and Ziegler (1982) mention still certain vitamins. A question which still has to be answered is if these compounds can also be inhibiting in high concentrations, which develops with strong recirculation.

2.7.3. Growth regulators.

A number of groups of growth-regulating compounds influences root morphology. They can potentially be applied to alter the root system in a direction, which we want. Initiation of roots can be stimulated according to Whittington (1967) by catechol, the auxines indolylacetic acid and naphtylacetic acid and combinations of catechol and the two auxins. The concentrations of the auxins IAA and NAA, which are used, are 10^{-5} - 10^{-6} Molar. Also Marschner (1986) states that the both initiation of lateral (side) roots and elongation of rootcells can be stimulated by auxins. Cytokinetines on the other hand inhibite lateral root formation and in high concentrations also the elongation of the root cells. White (1984) mentions gibberelic acid GA3 as a stimulator of plant production in concentrations of 15 uMolar. The effect on root morphology of addition of growth-regulators like indolyl-acetic acid and kinetin is strongly dependent of the concentration. The ratio shoot: root can also be influenced by a number of compounds. The ratio can be decreased with the growth inhibitor CCC and Young (1988) mentions that for instance a new growth regulator BAS 110 W is able to increase the ratio.

Growing circumstances of the plant can influence the auxin levels. This has been described for external pressure on the roots by Feldman (1984) and for root temperature by Tachibana (19..).

It seems to be a possibility that with organic compounds the root-system can be steered. More exact information about the possible compound-choice and the concentration will be useful.

2.8. Carbondioxyde in the root environment

The role of carbondioxyde in the root environment is still not clear in relation to root morphology. Van Dorp (1977) speaks of root growth inhibition. Marschner (1986) states that 1-2% CO_2 in the gaseous phase has a stimulating effect, while 5% CO_2 was inhibitory. Whittington (1968) however mentions stimulation of root branching and root development with 5% CO_2 in the root gasphase. Also Bergmann (1958) describes increased root-hair formation with carbondioxyde. To get clear judgements of this question it will be important to do more exact measurements by Yoshida and Eguchi (1988). The pH around the root is probably also important. An indirect effect via the shoot of carbondioxyde applied to the roots can often not be excluded.

3. The (shoot:root)-ratio

A factor which is important for the efficiency of the root uptake and for the total energy-need of the plant is the (shoot:root)-ratio. Here it deals only with the weights of the both parts. In the following section there is talk of the morphology of the roots in relation with efficieny.

There is a number of factors, which influence the (shoot:root)-ratio. A higher (shoot:root) ratio is caused by:
- factors which limit the availability of assimilates as less light (Brouwer, 1981). The shoot has a priority in using available assimilates (Baston-Wilson, 1988);
- plant-factors as beginning fruit-development (Hurd, 1978).

A lower (shoot:root)-ratio is caused by:
- factors which give higher availability of assimilates to the roots. Thus removing of fruits and flowers has this effect (Göhler and Drews, 1986);
- factors which limit the uptake of water and nutrients. A partial com-

pensation for lower water availability can be also a higher uptake rate (Brouwer, 1981). Roots can also compensate the shortage of nutrients and water also by more root development on the best places.
A number of explanations have been given of the regulation of the (shoot:root)-ratio (Bastow-Wilson, 1988), such as:
- the existance of a fixed relation between shoot- and rootweight;
- via the balance between shoot- and rootactivity;
- via the balance between C and N absorption, translocation and assimilation in cell material;
- via the balance of hormones in root and shoots.

Stutzel (1988) assumes a certain balance between "physiological active" tissues and supporting tissues (Stutzel, 1988).
For the future more knowledge especially about the energy which is consolidated in shoots and roots is necessary.

4. The meaning of the root morphology for the uptake of different elements

Going from the tip of the root to more mature zones with increasing suberization in the endodermis walls and increasing woodformation differences in uptake would be expected.
Upp till now it is insufficient clear which root system is optimal in respect of uptake and energy need. Clear is however that suberization and wood-formation are processes which have a large influence on the absorption of some of the nutrients (Ca and P) and less on others (K). Small, thin roots are more important for calcium and phosphorus than for potassium. The quantitative aspects have been known insufficiently. Below some data are given.
Fitter, Nichols and Harvey (1988) give much attention to root system architecture and nutrient absorption. The classification of root systems based on axes and laterals gives too less information on root function. The authors mention the "herring-bone" structure (one time of branching from a head-axes) as most effective in uptake, but inefficient concerning to transport and tissue volume. The herring-bone structure is compared with systems with a higher degree of branching and wood formation. Their conclusion is that the differences between species are large but that the influence of nutrient level on the root morphology is small.

The coupling of morphology of the root system with absorption occurs especially via maturing of the cells. Wood formation takes place 10-20 cm from the root tip as found for Cucurbita pepo (Harrison-Murray and Clarkson, 1973). Slightly preceeding or concomitant with this lignifying of the Casparian bands in the endodermis beginns. Formation of Casparian walls means that the way via cell wall water is blocked. In the Cucurbita species from the experiment about 30 cm from the tips splits appear in the cortex and suberin is formed in the endodermis in lamellar form. As said is it difficult to give the quantitative consequences of this. Important is however that calcium uptake stopps as suberization of the endodermis and the secondary thickening begins (Figure 2) while potassium uptake and -transport is uneffected. Also the absorption of phosphate declines as the root ages, the effect on the translocation of phosphorus is however smaller than for calcium.
Much information about the uptake activity of different parts of the root system was given by Clarkson (1981) as collected from the literature. Plants like barley, wheat, maize, marrow and pea are mentioned. The results do not carry already to clear conclusions for one element but there are general lines. For potassium uptake takes place in all zones inclusive the suberized and that with secondary thickening. There are sometimes maxima at about 2-5 cm from the tips. Also nitrogen is taken up over the whole root (0-40 cm), a maximum was found for peat at about 1 cm from the tip.

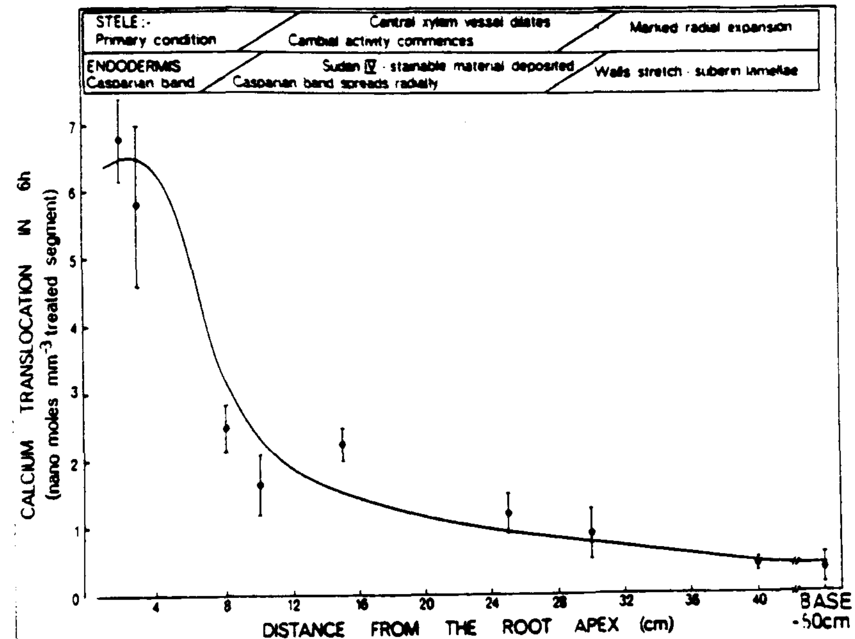

Fig. 2. The variation in calcium translocation along the seminal axis of marrow related to development of the stele and endodermis

Fig. 2. The variation in calcium translocation along the seminal axis of marrow related to development of the stele and endodermis. From Harrison-Murray and Clarkson (1973).

The nitrogen absorption decreases to about 4 cm and stays then constant. Calcium and magnesium are taken up in the unsuberized zones to about 10 cm from the tip. The absorption of phosphorus takes also in the suberized zones but there are higher values near to the top (about 3 cm). Potassium is taken up over the whole root (0-40 cm) but also with maxima near to the tip. Iron is translocated in the region of 1-5 cm from the tip in Fe sufficient plants and 1-8 cm in Fe-dificient plants of maize.

5. Possibilities of steering the root-system

It is possible to steer the root-system in a certain direction with the concentrations of the nutrients. Thus Clarkson found with more phosphate in the soil more branching. However also the uptake rate can be influenced by the concentration like Heinz and Schenk (1987) describe. With low levels of nutrogen they found much increased uptake rates for nitrate uptake.

Probably it is also possible to alter the root systems by giving different resistance for the root growth as described earlier. The large differences between the root-system on nutrient culture and soil do presume that this is possible (Kageyama and Konishi, 1988; Mackay and Barber, 1984 and Heinz and Schenk, 1987).

6. Environmental factors

6.1. Light

It would be profitable if it was possible to give mathematical relations between light intensity and colour on the one side and rootmorphology, rootsurface and absorption of ions to the other side. The influence on rootbranching would be than also important. At the moment it is still not so far. It is however clear that light has an influence on root structure and uptake. Qualitatively the processes are understood a little and it is possible to predict in which direction an alteration in light intensity shall change the root system. In figure 3 and 4 some of the relationships can become clear.

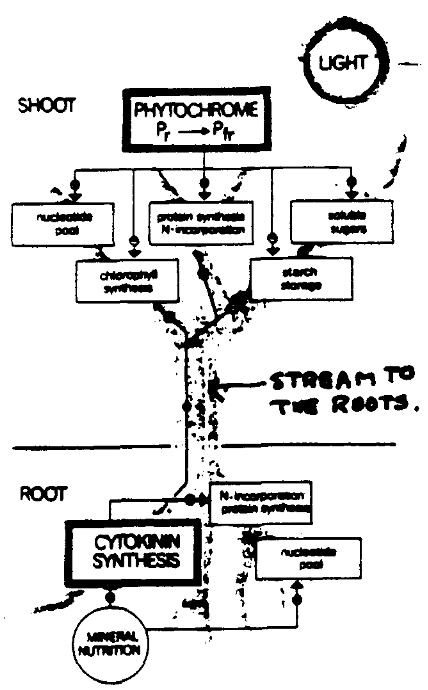

Fig. 3. Model for phenotypic plasticity in higher plants. Mineral nutrition and light are given as stimulating factors (Kuiper, 1984a).

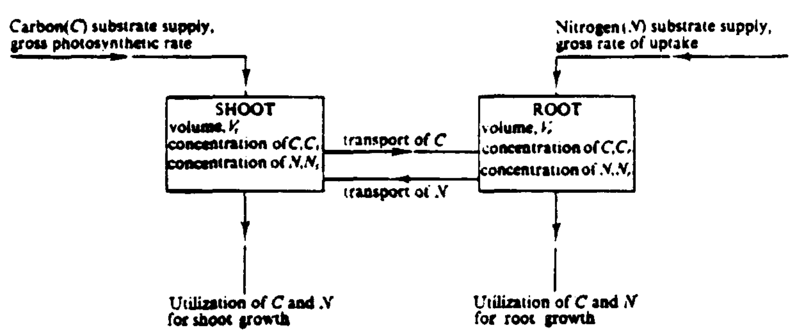

Fig. 4. A carbon-nitrogen limited root-shoot model. From Thornley, 1972.

Thus feedback of transport of assimilates and/or growthregulators can steer the roots (Figure 3). According to Thornley there is a carbon-transport from shoot to root and transport of nitrogen (NO_3^{-1}) from root to shoot. This can give a regulation of the growth of both.
The question of the influence of light on the roots can be split in the influence on root structure and direct on uptake of ions. By influencing the ratio young to old roots light influence indirectly the ratio of different ions. As earlier stated a different influence on nitrogen and potassium uptake on one side and phosphorus, calcium and magnesium uptake on the other side would be expected.
The transport of energy rich compounds like sugars is important. In soils it may be expected that about 30% of the energy, which the plant uses, is used for the roots. In a crop like pine this can be 50% of the total energy. In the case that water and nutrients are freely available it is reduced to 10-20%.
Light influences the (root:shoot)-ratio in the way as earlier mentioned. This can be seen in Figure 5 for different types of onion in experiments of Son et al, 1988.

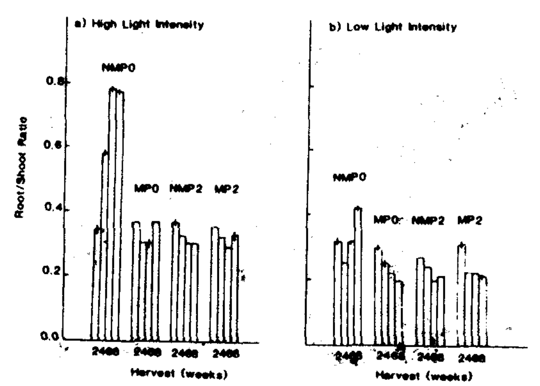

Fig. 5. Root:shoot dry weight ratios of plants grown over 8 weeks at (a) 600 umol m^{-2} s^{-1} and (b) 250 umol m^{-2} s^{-1}. From Son et al, 1988).

At the moment of alteration to an other ratio alters also the ratio between small and thicker roots. Sugars may play a large rol in the determination of the root-system. Thus found Stoffela et al (1988) that addition of sucrose in a tissue culture of bell pepper caused more formation of basal and lateral roots. Chermnykhaud and Kosobrukhov (1987) mention that between 300 and 700 $J.cm^{-2}.day^{-1}$ the alterations in photosynthesis are the largest. On the other side Bastow-Wilson (1988) assumes still another factor besides sugars which regulates root growth. Light influences directly or indirectly absorption rate and ratios of the nutrients. Mac Duff and Wild (1988) describe stimulation of the uptake of NO_3^{-1} and K^{+1} by more light in the region from less than 100 $J.cm^{-2}.day^{-1}$ to 800 $J.cm^{-2}.day^{-1}$. Tremblay (1988) found a different influence of different types of lamps on the uptake of calcium, iron and manganese. Results calculated from work of Kosobrukhov et al (1988) show that the intensity of the irradiation can change the ratios in the uptake of the nutrients (Figure 6).

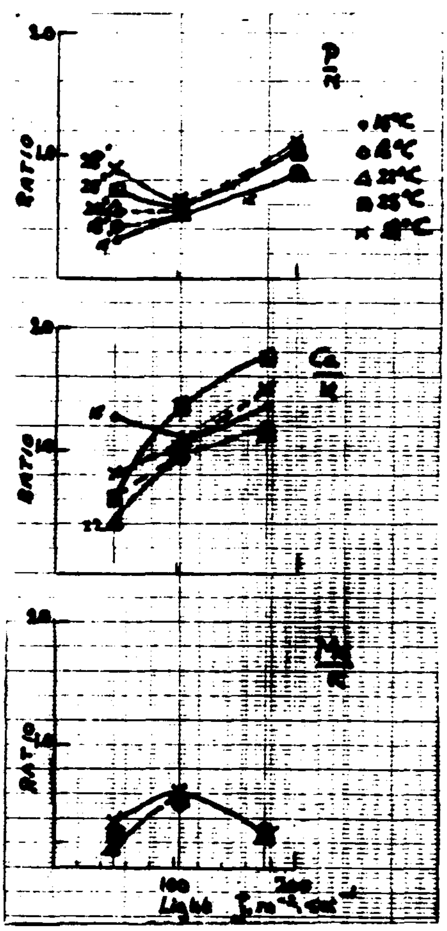

Fig. 6. Absorption ratios for tomato plants in relation to irradiation and root temperature. From Kosobrukhov et al, 1988.

There is a dependance of the root temperature. With low roottemperature the P/N ratio in the region of 0-200 $J.m^{-2}.sec^{-1}$, with higher root temperatures there is a minimum in the curves at about 100 $J.m^{-2}.sec^{-1}$. With calcium on the contrary there is a minimum for Ca/K at 15°C root temperature, while at the other root temperatures the ratio increases with higher irradiation. The curve for Mg/K has for all the root temperatures in the experiment a maximum at about 100 $J.cm^{-2}.sec^{-1}$. Knowledge about influence of level of irradiation and perhaps wavelength is still incomplete. More knowledge about this influence would perhaps give the possibility to steer the root structure and uptake better.

6.2. Carbondioxyde

Carbondioxyde stimulates, when light is not limiting, the formation of assimilates. It has been found that in general addition of carbondioxyde increases rootgrowth for that reason (Bastow Wilson, 1988).

Thornley (1972) mentions a formule for the increase of root volume (V_r):

$$\frac{dV_r}{dt} = \Theta\, Y_G V_r F(C_r, N_r) \qquad \text{Formule II}$$

In this formule the symbols has the following meaning:

Θ = conversionfactor from dry matter to volume

Y_G = conversionefficiency from nutrition in the substrate to plant dry matter

V_r = volume of the roots

C_r = carbon concentration in the roots

N_r = nitrogen concentration in the roots

Also does he gives a differential equation for the rate of increase of the total quantity of assimilates in the roots:

$$\frac{d(V_r C_r)}{dt} = \beta\, (C_s - C_r)/r_C - V_r . F(C_r, N_r) \qquad \text{Formule III}$$

In this formule the still not mentioned symbols are:

r_C = resistance between root and shoot

β = resistance scaling factor

N_r = nitrogen substrate concentration in the roots

C_s = carbon substrate concentration in the shoot

The rate for the total quantity of carbon is thus among others dependent on the difference between the assimilateconcentrations in shoots and roots, for the total context in the shoot.
Thornley gives the following formula:

$$\frac{d(V_s C_s)}{dt} = K_c V_s - (C_s - C_r)/r_C - V_s . F(C_s, N_s) \qquad \text{Formule IV}$$

In the last formula the still not mentioned symbols mean:
V_s = Volume shoot
K_c = specific shoot activity

The factor K_c is besides from the lightintensity dependent on the carbondioxyde concentration in the air. Via C_s are V_r and C_r also dependent with the CO_2 concentration in the air. Thus the rootgrowth dependence can be understood.
It is not possible at the moment to give the influence of carbondioxyde in the air on rootmorphology. It would however be expected that the increase of assimilate content would act in the first place on root elongation.

7. Indications in the composition of the shoot of the root morphology

Morphological differences in roots consist of differences in the portion of younger and older roots in the root system. As it is often difficult to do determinations on the root itselves in a system (for example rockwool) it would be important to indicate differences in the roots from ratios of nutrients in the shootparts of the crop determined for instance in newly formed leaves. The differences in behaviour of uptake of elements like nitrogen and potassium on one side and elements like calcium, magnesium and iron on the other side give possibilities to do that. An example of a relationship between the ratio for Ca:K is given for young teaplants in research of Chamuah (1988) as given in Figure 7.

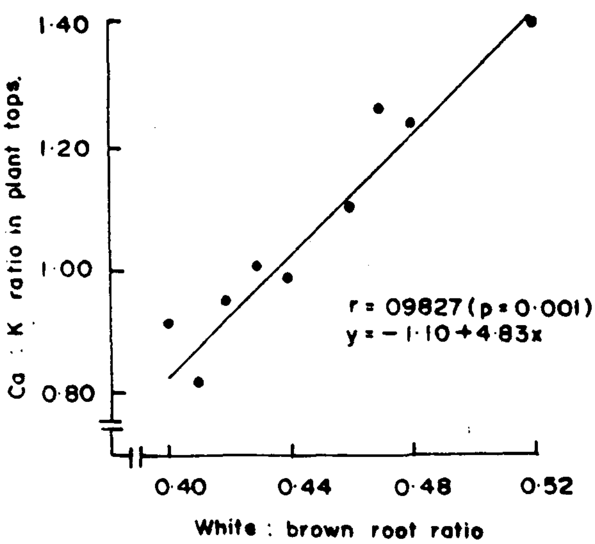

Fig. 7. Relationship between white:brown root ratio and Ca:K ratio in plant tops of teaplants. From Chamuah, 1988.

In soil the problem is more complex but also differences in behaviour between different elements can give information between what happens "under the soil surface" and "above the soilsurface". Thus use Glinski et al (1989) an aeration index I_0, which is the following quotient:

$$I_0 = \frac{N_{plant}:N_{soil}}{Mn_{plant}:Mn_{soil}}$$

Differences in behaviour in the soilchemistry and the uptakebehaviour in relation with aeration are the base of this formula.
In principle ratios like P:N,Ca:N,Ca:K,K:N, etc. can give information about the momentary influence on the rootsystem of factors like aeration, density, available substrate volume and so on. On literature or new experiments this approach can be tested.

8. Possibilities of using determinations of constituants of the root-system for estimating the mean age

It may be expected that the composition of a rootsystem with many roottips (much young tissue) is very different from a root system with much old root tissue. This can be used as an indirect method of estimation the mean age of the root system.

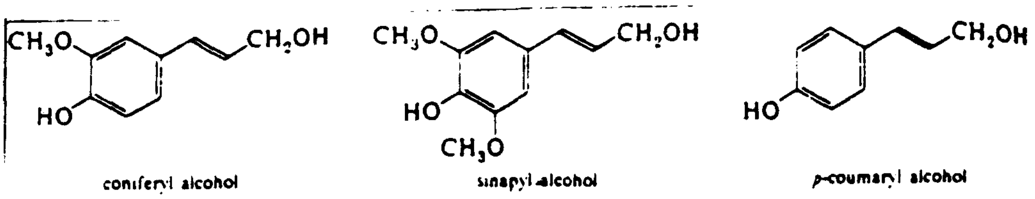

Fig. 8. Basic Building blocks of lignin. From Streitweiser and Heathcock, 1985.

In the differentation process from the dividing cells on the root tip to a cell at a large distance (p.e. 40 cm) from the root top the cells undergo large alterations. The cell in the root tip consists mainly of cell nucleus and protoplasm, while a differentiated cell further from the tip (in the parenchym) has a large vacuole with cell sap and less protoplasm and nucleus volume. In het meantime wood formation takes place in the vessels and further suberization in the endodermis.
A number of organic and also inorganic compounds can be used as determination of the age of the root system. Nucleic acids, proteins and pH of pressing-sap will be expected to be high in young tissue. Lignin (see figure 8) and cork will be higher in old tissue.
In general it will be important to determine nucleic acids, proteins, cellulose, lignin (wood), pH in pressing-sap and some inorganic elements like potassium, calcium and magnesium.
For the most compounds are standard analytical methods. For lignin there is a rather simple method of Morrison (1972 I + II) in which lignin reacts with acetylbromide and after that light absorption at 280 nm is measured.
Methods for nucleic acids or desoxyribonucleic acids were described by Kenis et al (1985), de Korte (1985), Schneider (1945) and Ogur and Rosen (1950). Extraction of nucleic acids occurs often with perchloric acid, which has the disadvantage of being rather agressive. Sometimes also trichloric acid was used as a extractant. Determination takes place in the uv at 260 or 320 nm. In other methods colouring reactions with diphenylamine or orcinol are used and light adsorption is measured at 675 nm.

9. Some preliminary experiments of applying alterations in the root-environment and the influence on root-structure and root-weight

The purpose of these experiments is to alter the physical circumstances around the rootsystem according to a gradient systematically.
Two methods were followed. In the first round glass beads with diameters varying from 10 to 0.1 mm were used to alter the root environment. In the second experiment the density of rockwool is changed by pressing the rockwool in plastic holders.
At the moment experimentation has been pointed still to improve the experimental circumstances because of the rather large differences of growth on pots with the same diameter of beads. Especially it seems to be important to ge a better and more regular drainage in the pots with beads.
Some indications of the influence on the form of the rootsystem and a root- and shootweights will be given. In future also experiments will be taken on the influence of root environment on uptake of different nutrients.
Experimental data:

1. Tomato plants were sowed in sand or perlite. After that the plants were planted out in 450 ml round glass beads in plastic pots of 600 ml. The diameters of the glass-beads were 10 mm, 5 mm, 2 mm, ..., 01 mm. As a comparison som horticultural substrates like rockwool, baked clay and sand were used.
   Nutrient solution was dropped on the beads three times an hour during 3-5 minutes. The nutrient solution had the usually used composition for tomato on recirculation culture (Sonneveld and Straver, 1989).
   The bottom holes of the pots were covered by cambric cloth. With this kind of cloth obstruction sometimes occurred. The upper sides of the pots were covered by black plastic to prevent formation of algae which are a problem.
   The plants were harvested when they had lengths of 30 - 75 cm, shoots and roots were then separated. The root system was described roughly. The roots were washed free from the glass beads.
   After that the weight of shoots and roots were determined. The roots were dried on filterpaper before weighing. Roots and sometimes also

the shoots were dried at 80°C. Dry weights were determined after that. "Shoot":"root"-ratios were determined as a measure for the effectivity of the roots.

2. Density of rockwool. Tomato plants were precultured in the same way as under 1. After that the plants were cultivated on rockwool as in plastic holders with a height of 20 cm and depth and width of 10 cm. In object 2 and 3 either the lower 2/3 part or the upper 2/3 part two times as much rockwool was pressed as in the other 1/3 part or the control. In the control and that 1/3 part trade rockwool blocks of normal density were used. After the experiments the rockwool with roots was pulled out of the holders. The rockwool was cut and the rootsystem was observed. Further the weight of the shoot was determined.

Some results and conclusions:

Probably by accidental differences in the drainage of the different pots differences between the repetitions are rather large. There are however some indications in the root-observations and the determinations of root and shoot weights. The last can be found in table 1.

In the experiments with the beads the differences in diameter lead to alteration of a number of factors. Thus with the larger beads the air-holes between the beads are large in relation to the root diameter. Further in the objects with larger beads oxygen-availability is larger, water-availability is lower and resistance to root growth is lower.

The morphology of the root-system has been altered by the treatments. With the larger beads (10,5 and 2 mm) roots can be found in a large part of the pot and some roots pass the cloth on the holes at the bottom of the pots. The roots grow then farther in the nutrient solution in the tray under the pots. In the smaller beads (1, 0.5, 0.2 and 0.1 mm) and the sand the roots penetrate in a smaller part of the pot. Especially the roots in the pots with the smallest beads the roots are more curved, brown and probably more branched. The pot wall is often a barrier where the roots begin to run around. The root-system on water culture has the form of a fish-bone (one time branching) and consist out of thin, white roots. Also on the more dense rockwool (especially 1/3 loose on 2/3 dense) more and thicker roots and more wood-formation takes place.

The shoot:root-ratio seems to be lower on the smaller beads (table 1).

Perhaps the energy and minerals which the roots have to use are larger in this situation. This can cause less possibilities for shoot-growth. Higher root dry weights were found with the smaller balls (0.1 and 0.2 mm), perhaps a result of the development of thicker roots and the increased root-formation. Shoot weights are the highest in the rockwool, proving that the circumstances for the roots around the beads are still not optimal.
This type of experiments will be continued with further technical improvements. Further the uptake-activity of the root-system will be determined.

10. Conclusions

This report has been made to get more knowledge about the behaviour of in different artificial substrates or in nutrient film technique. It would be possible to formulate the qualifications for artificial substrates better if there is more knowledge of an optimal root environment. Another possibility may be that it would become possible to steer the root system in a desired direction. Purpose will be further to prevent the presence of an unnecessary large root system or root-death during the cultivation. It may appear that it have advantages to alter the root-circumstances at a certain stage of the cultivation.
It became apparent from the literature-study that it is difficult to separate the different parameters which work in the root-environment. Also it appeared that quantitative data are scarce and that it is often only possible to give qualitative relationships.
The parameters can be separated in:

- Structure of the substrate (determining the way which the roots can follow).
- Physical parameters:
  - Density or resistance in the substrate
  - Oxygen supply of the root-system
  - Root temperature
  - Suction-pressure in the substrate and water-availability.
- Chemical parameters:
  - Macro- and microelements
  - Organic compounds:

    - Humic compounds
    - Exudates
    - Growth-regulators
  - Carbondioxyde in the root-environment.
- Influence of the environmental circumstances of the shoot indirectly on the root:
  - Light
  - Carbondioxyde in the air
  - Air temperature
  - Moisture percentage in the air.

About the influence of the spatial structure of the medium concrete results were found only in one publication. It can be learned from the results mentioned there that when the root meets a rigid barrier the angle of the rootgrowth can alter.
When roots meet a barrier perpendicular many roots die.
Further studies about the influence of the spatial structure of media like rockwool are desirable.
About density some quantitive results are available.
About 1 Mpascal resistance roots of many plants have been inhibited much in the growth. Branching and early lignification can be a result of resistance (50 kpascal).
Oxygen contents of 5-10 $mg.kg^{-1}$ are necessary for root growth in the nutrient solution. Less than 0.5 $mg.kg^{-1}$ oxygen becomes limiting. Shortage of oxygen can alter root morphology and gives shorter and more branched roots.
Still no exact data can be given about the influence of root-temperature on root-growth, root-morphology and uptake. Perhaps experiments under well-conditoned circumstances are necessary here.
Also the factor water is very complex. Variation of the water-content varies at the same time other factors like resistance of the substrate and the oxygen-content around the roots. Determination of the pF-curves of the media can give some exact information on the water availability. The root-system of very wet cultures or water-culture is probably rather typical. It is a "fish-bone"-like rootsystem of very white thin roots, which branch on time. When the medium becomes dryer probably more

wood-formation takes place and the roots are thicker and branch more. The influence of nutrients (concentrations and ratios) is also not quite clear. Especially this is valid for the quantitative aspects. Elements like nitrogen, calcium and phosphorus are of course necessary for root-growth. Their concentration can have an influence on root-morphology. Some indications can be obtained from what is known about optimal concentrations in solutions for soilless cultures. High electroconductivity (high total sal concentration) gave short, thick and much branced roots. With low iron-concentations a fine and strongly branched root-system was described.

More study of the literature is necessary about experiments in which the concentration of one element was varied systematically. Elements like calcium, phosphorus, iron and boron are interesting in relation to possibilities to steer the root-system.

Humic compounds are interesting because it has been found that they stimulate root growth in the concentration region of 10 - 300 $mg.l^{-1}$ in the nutrient-solution. Especially compounds with phenolic groups are interesting. Indirectly the can influence the roots by translocating nutrients to the root-surface. The question can be put if addition of humic compounds in soilless cultures can be useful.

Exudates of the roots have somtimes an active function in translocating ions to the roots, especially when the supply is limited. The phytositerophores found in German research have a function in iron translocation. A question which needs perhaps further research is if root-exudates when they concentrate to high contents in the nutrient-solutien with recirculation are inhibiting for the root-growth.

Growth-regulators may be used to steer the root-system, for instance when more or less root-surface becomes necessary in a certain stage of cultivation. Compounds like indolylacetic-acid and naphtylaceticacid in concentrations of 10^{-5} - 10^{-6} molar stimulate root-growth.

Factors as light, carbondioxyde in the air and air moisture percentage have an indirect influence on root-growth. It is however too early to give mathematical formations for these effects.

An important question is also how to get information about the contribution of young and old roots in the root-system during experiments without harvesting plants. As the uptake and translocation of different

elements in young and old roots is quite different it is possible to draw conclusions from analysis of a number of elements in newly formed leaves.
Calcium for instance is absorbed and translocated especially by the younger part of the root and potassium also by the older part. It can be expected and was also found that the Ca/K-ratio is relative high when there are many young roots.
When it is possible to analyse the roots the concentrations of certain compounds can be used as markers for the mean age of a root-system. Thus desoxyribonucleicacids (DNA) will be high in a relative young root-system and lignin (woodcompounds) will be low.
The ultimate purpose of this type of research is to find mathematical formulations for growth, root parameters or uptake on one side and the environmental circumstances of the roots on the other side. A formula as given in formula I is an example of this. There uptake has been related with root surfaces and with environmental factors like root-temperature and oxygen-content in the root-medium. Besides these type of formulae research is needed to obtain formulae about the relation between certain separate parameters in the root-environment and the active root-surface.
The first and preliminary results of experiments on the glass beads with diameters from 10 to 0.1 mm diameter suggest that in the substrate of the smaller balls the roots can elongate more difficultly. The roots become then more lignified, thicker and more branched. Relative to the rootmass more shoots were formed on the larger balls (5 mm as base).
When rockwool was pressed more densily more woodformation, branching and thicker roots were found. When it is possible to quantify this further it may be possible to give more qualifications for a certain type of rockwool. Knowledge about the meaning of a certain type of root-system for uptake and energy-usage is then still necessary.

Table 1. Some results of experiments with tomato plants on glass beads with as comparison some other substrates. Results expressed as % of the value of the plants on the "5 mm" beads.

Type substrate		("Shoot"-root)-ratio		Shootweight		Wet weigth roots		Dry weight roots	
No. exp.	Glass beads	I	II	I	II	I	II	I	II
1.	10 mm	97	81	133	112	173	139	112	126
2.	5 mm	100% (5.9)	100% (6.9)	100%	100%	100%	100%	100%	100%
3.	2 mm	84	110	112	119	162	97	112	77
4.	1 mm	90	-	119	-	157	-	112	-
5.	0.5 mm	65	87	59	79	81	110	75	115
6.	0.2 mm	65	89	71	61	90	74	137	115
7.	0.1 mm	65	74	100	80	183	104	237	153
8.	Rockwool	-	-	216	140	-	-	-	-
11.	Sand	59	86	127	78	234	71	175	85
12.	Free water culture	56	74	145	29	272	39	137	30

Value of the "5 mm beads" is set on 100%   I and II are two different experiments.

Between () (shoot:root)-ratio

Literature

Alwan, A.H. and P. Newton (1984). Dissolved oxygen, root growth, nutrient uptake and yields of tomatoes. ISOSC Proceedings Wageningen:81-112.

Bastow Wilson, J. (1988). A review of evidence on the control of shoot: root ratio, in relation to models. Ann. of Bot. 61:433-449.

Bandera, B.W. and D.D. Fritton (1986). Directional response of corn roots to physical barriers. Plant and Soil 96:359-368.

Bergmann, W. (1958). Ueber die Beeinflussung der Wurzelbehaarung von Roggenkeimpflanzen durch verschiedene Aussenfaktoren. 80:218-224.

Bugbee, B. and J. White (1984). Tomato growth as affected by root-zone temperature and the addition of gibberellic acid and kinetin to nutrient solutions. J. Amer. Soc. Hort. Scie. 109:121-125.

Burns, R.G. et al. (1986). Humic substances. Effects on soil and plants. Congress Milaan maart 1986, Reda, Milaan, 161 pp.

Brouwer, R. (1981). Effects of environmental conditions on root functioning. Acta Hort. 119:91-101.

Chamuah, G.S. (1988). The effect of nitrogen on root growth and nutrient uptake of young tea plants (Camellia sinensis L.) grown in sand culture. Fertilizer Research 16:59-65.

Chemnykaud, L.N. and A.A. Kosebrukhov (1987). Effects of environmental factors on optimum temperature and photosynthetic intensity of plants adapted to various conditions. Biotronics 16:1-11.

Clarkson, D.T. (1981). Nutrient interception and transport by root systems. In: C.B. Johnson. Physiological processes limiting plant productivity:307-330.

Dorp, F. van (1977). Simulatie van veranderingen in concentraties van voedingselementen rond plantewortels. Proefschrift L.U. Wageningen, PUDOC, Wageningen, 162 pp.

Feldman, L.J. (1984). Regulation of root development. Ann. Rev. Plant Physiol. 35:223-242.

Fitter, A.H., R. Nichols and M.L. Harvey (1988). Root system architecture in relation to life history and nutrient supply. Functional Ecology 2:345-351.

Gerard, C.J., H.C. Mehta and E. Hinojosa (1972). Root growth in a clay soil. Soil Science 114:37-49.

Glinski, J. et al. (1989). Characterization of the soil aeration status by plant and soil analyses. Z. Pflanzenernährung. Bodenk. 152:27-32.

Göhler, F. und M. Drews (1986). Sink-source-Beziehungen bei Gewächshaus-tomate und -gurke im NFT-Verfahren. Arch. Gartenbau, Berlin 34:109-117.

Harrison-Murray, R.S. and D.T. Clarkson (1973). Relationships between structural development and the absorption of ions by the root system of Cucurbita pepo. Planta (Berl.) 114:1-16.

Heins, B. and M. Schenk (1987). Root growth and nitrate uptake of vegetable crops. Journal of Plant Nutrition 10:1743-1751.

Heuvelink, E. (1984). Invloed van het bodemmilieu op ontwikkeling en activiteit van het wortelstelsel. L.U. Wageningen, Tuinbouwplantenteelt, Rapport, 39 pp.

Hurd, R.G. (1978). The root and its environment in the nutrient film technique of water culture. Acta Hort. 82:87-97.

Kageyama, Y. and K. Konishi, 1988. Mophological and physiological characteristics of tomato plants grown in nutrient solution in comparison with those grown in soil. J. Japan. Soc. Hort. Sci. 57:408-417.

Kenis, J.D., S.T. Silvente and V.S. Trippi (1985). Nitrogen metabolism and senescence-associated changes during growth of carnation flowers (Dianthus caryophyllus). Physiol. plant. 65:455-459.

Korte, F. (1985). DNA/RNA-Bestimmungen in pflanzlichen material. Methodicum Chemicum B: Analytik 1/2:1.9.3;1.9.4;1.2.2.

Kosobrukhov, A.A. et al. (1988). Photosynthesis and absorption of mineral nutrient in tomato plants under various root zone temperature and light conditions. Biotronics 17:21-28.

Kuiper, (1984).

Mac Duff, J.H., M.J. Hopper and A. Wild (1987). The effect of root temperature on growth and uptake of ammonium and nitrate by Brassica napus L in flowing solution Culture. J. Exp. Bot. 38:42-52.

Mac Duff, J.H. and A. Wild (1988). Changes in NO_3^- and K^+ uptake by four species in flowing solution culture in response to increased irradiance. Physiologia plantarum 74:251-256.

MacKay, A.D. and S.A. Barber (1984). Comparison of root and root hair growth in solution and soil culture. Journal of Plant Nutrition 7:1745-1757.

Marschner, H. (1986). Mineral nutrition of higher plants. Academic Press, London, 674 pp.

Marschner, H., Römheld, V. and I. Cakmak (1987). Root-induced changes of nutrient availability in the rhizospere. Journal of Plant Nutrition 10:1175-1184.

Morrison, I.M. (1972). A semi-micro method for the determination of lignin and its use in predicting the digestibility of forage crops. J. Sci. Fd Agric. 23:455-463.

Morrison, I.M. (1972). Improvements in the acetyl bromide technique to determine lignin and digestibility and its application to legumes. J. Sci. Fd Agric. 23:1463-1469.

Ogur, M. and G. Rosen (1950). The nucleic acids of plant tissues. I. The extraction and estimation of desoxypentose nucleic acid and pentose nucleic acid.

Protopapas, A.L. and R.L. Bras (1987). A model for water uptake and development of root systems. Soil Science 144:353-366.

Römheld, V. and H. Marschner (1986). Evidence for a specific uptake system for iron phytosiderophores in roots of grasses. Plant Physiol 80:175-180.

Schneider, W.C. (1946). Phosphorus compounds in animal tissues I. Extraction and estimation of desoxypentose nucleic acid and of pentose nucleid acid.

Schönwitz, R. and H. Ziegler (1982). Exudation of watersoluble vitamins and of some carbohydrates by intact roots of maize seedlings into a mineral nutrient solution. Z. Pflanzenphysiol 107:7-14.

Scotti, I.A., G. Frappetti and S. Silva (1983). Influenza di frazioni umiche sull'absorbumento di ^{59}Fe, ^{54}Mn, ^{58}Co, ^{65}Zn in piante di pomodore cresciute in idroponica ...:53-70.

Son, C.L., F.A. Smith and S.E. Smith (1988). Effect of light intensity on root growth, mycorrhizal infection and phosphate uptake in onion. Plant and Soil 11:183-186.

Sonneveld, C. (1984). De invloed van organische stof toediening aan de voedingsoplossing bij komkommers. Intern Verslag 1984-10, Proefstation voor de Glastuinbouw, 11 pp.

Sonneveld, C. and W. Voogt (1985). Studies on application of iron to some glasshouse vegetables grown in soilless culture. Plant and Soil 85:55-64.

Sonneveld, C. (1987). Magnesium deficiency in rockwool-grown tomatoes as affected by climatic conditions and plant nutrition. Journal of Plant Nutrition 10:1591-1604.

Stoffela, P.J. et al. (1988). Root morphology and development of bell peppers. Hort. Science 23:1074-1077.

Streitweiser, and Heathcock (1985). Introduction of organic chemistry, Mac Millan, ...

Sutton R.F. (1980). Root system morphogenesis. New Zealand Journal of Forestry Science 10:264-292.

Stutzel, H., D.A. Charles-Edwards and D.F. Beech (1988). A model of the partitioning of new above-ground dry matter. Ann. of Bot. 61:481-487.

Tachabana, S. (1988). Cytokinin concentrations in roots and root xylem exudate of cucumber and figleaf gourd as affected by root temperature. J. Japan. Soc. Hort. Sci. 56:417-425.

Thornley, J.H.M. (1972). A balanced quantitative model for root:shoot ratios in vegetative plants. Ann. Bot. 35:431-441.

Tremblay, N. et al. (1988). Influence of photosynthetic irridiance on nitrate reductase activity, nutrient uptake and partitioning in tomato plants. Journal of Plant Nutrition 11:17-36.

Veen, B.W. (1972). The influence of mechanical impedance on the growth of maize roots. Plant and Soil 66:101-109.

White, (1984).

Whittington, W.J. Root growth, Proceedings of the fifteenth Easter School in Agricultural Science, university of Nottingham, Butterworths, Londen.

Wiersum, L.K. (1980). The effect of soil physical conditions on roots and uptake. In: D. Atkinsen, J. Jackson, M. Sharples and W. Waller (eds.), mineral nutrition of fruit trees. Butterworths, Sevenoaks:111-121.

Willigen, P. and M. van Noordwijk (1987). Roots, plant production and nutrient use efficiency. Dissertation Agricultural University Wageningen, 282 pp.

Yoshida, S. and H. Eguchi (1988). Relationship between gas exchanges in intact roots and water uptake in response to leaf transpiration in hydroponics. Biotronics 17:59-68.

Young, (1988).