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FUNCTIONAL INTERPRETATION OF ROOT DENSITIES IN THE FIELD FOR NUTRIENT AND WATER UPTAKE

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1 INTRODUCTION: HOW MANY ROOTS DOES A PLANT NEED?

Much field research on root systems has been performed in an agricultural context. After the time-consuming and tedious research necessary to answer the question "how many roots does a plant have?", always the next question is "how many does it need for maximum crop production?". As soon as variation in root pattern and root density is noted, the question of practical implications follows. Is a higher root density always better for crop production? Is the shoot/root ratio an important characteristic for cultivar selection? Such questions are common, but real answers scarce so far. For water balance studies a correct definition of "root depth" is critical; the "effective root depth" used so far for hydrological field studies in the Netherlands (the depth above which 80% of the roots are concentrated, RIJTEMA (1969)) is unsatisfactory as it is stated relative to the total root system instead of as an absolute value of a critical root density.

A more intensely branched root system can extract the plant's needs from a poorer soil than a smaller root system. In any situation where the soil-root system is not supplying the crop's needs, the farmers' choice is either to improve the soil fertility or to improve root density (by cultivar selection, soil tillage, stimulating mycorrhiza, etc.). The need for clear guidelines on functional interpretation of root densities as they occur in the field is apparent.

To a considerable extent the plant "knows" how many roots it needs. The roots' plasticity and regulation of the shoot/root ratio according to growing conditions are well-known (GOEDEWAAGEN 1942, BROUWER 1963, RUSSELL 1977). Functionally it is a matter of balance between active leaf area and active root surface area. The environmental resources light, water and nutrients act as the ultimate factors (providing the functional and evolutionary causative explanations), while the internal hormonal system of the plant may form part of the proximate factors (providing the physiological, directly causative explanations).

Three levels of control in the shoot/root system can be distinguished:

constraints: external limitations, such as a high penetration resistance or poor oxygen supply limiting root growth,

coarse control: morphological responses by differential growth of plant parts, inducing changes in the overall shoot/root ratio or local growth stimulation of roots in locally enriched zones,

fine control: physiological regulation of current processes, such as uptake rate.

The morphological and physiological response can be compared to the numerical and functional response respectively of predators to a change in the availability of prey, the first of each pair being slow but potentially unlimited, the second fast but limited in extent.

The general characteristics of the morphological response have been summarized by SCHUURMAN (this symposium) in Fig. 1. Both shoot and root growth show an optimum when plotted against growth factors such as water or nutrient supply, but their optima are different and generally shoot response is more pronounced than root response. Within a range of conditions that is common in agriculture the root system responds weakly positively, hardly at

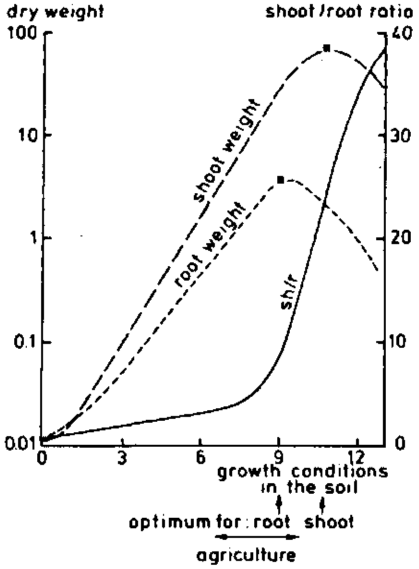

Fig. 1. The response of shoot weight, root weight and shoot/root ratio of annual plants to growing conditions, according to SCHUURMAN (1983). Present-day Dutch agriculture can be expected to be in the range of 7-10 of the (arbitrary) scale on the x-axis. Root weights in this figure probably need a correction of about 30% (VAN NOORDWIJK and FLORIS 1979, FLORIS and DE JAGER 1981).

all or negatively to fertilisation, while the shoot system continues to respond positively. Apparently the possibilities for uptake by the roots are used more fully after fertilisation, which shows that not the physiological capabilities of the root, but the supply to the root by the soil is limiting. The local response of root growth to local differences in fertility of the soil (GOEDEWAAGEN 1942, DREW 1976, DE JAGER 1979) can be explained along the same lines as the overall shoot/root regulation.

The physiological response of root activity according to the plant's nutrient requirements has received little attention from plant physiologists in the past. For water a physiological response clearly follows from the leaf water potential as suction causing water flow in the soil-root-system. For regulation of nutrient uptake according to shoot requirements, various possible mechanisms have been proposed (LONERAGAN 1979, for N: BEN ZIONI et al. 1971, CRAM 1973, for P: DE JAGER 1979, for K: GLASS 1975). The fact that a process such as nutrient uptake is regulated does not mean that it necessarily proceeds at a constant rate, independent of external conditions, but the variations in uptake rate are in fact much smaller than could be expected on the basis of Michaelis-Menten kinetics. Describing this physiological response adequately has been one of the major problems in modelling solute movement in the soil-root system (NYE and TINKER 1977). As a rough first approximation we assumed in the models presented here the regulation to be perfect for both water and nutrients, i.e. the plants' uptake is according to its needs for current growth, provided that conditions allow such uptake. Assuming a linear growth rate of the crop (in the Netherlands a reasonable estimate for the growth of a closed crop canopy is 200 kg DM.ha^{-1}.day^{-1} (SIBMA 1968) a constant daily nutrient requirement follows. In fact, in the field a constant daily nutrient uptake seems to be common, although the average nutrient content may fall gradually during the linear growth phase. In the case of water, potential evapotranspiration has become a standard meteorological measurement. Such values can be used as indications of the plants' water requirements for maximum growth, if taken on an hourly basis during daylight instead of on the more commonly used daily basis.

The question remains how to define root density. Root length, surface area, volume or weight may be chosen as the main parameter. Root dry weight is important for studies concerning the carbon-balance, but its use as the main parameter quantified in root research in the past (SCHUURMAN and GOEDEWAAGEN 1971) has hindered a more direct functional interpretation of root data. If transport in the soil towards the root is the rate-limiting step, root length per volume of soil seems the most appropriate parameter. If the soil-root interface (transport between soil in the rhizosphere and the apoplast of the root) is rate-limiting, root surface area would be the best choice. If uptake from root apoplast to root symplast or internal transport inside the root is the dominating step, root volume is the best parameter. If in field measurements both root length and diameter are recorded, we can do all the necessary calculations (although we need the complete frequency distribution of root diameters to transform root surface area into volume and vice versa). In this paper root length per volume of soil is used as the basis of comparison, with root diameter as secondary parameter.

2 MODEL CALCULATIONS ON WATER UPTAKE

2.1 Potentially versus actually available water

Three types of situations can be distinguished in which water stress occurs:

1 there is no water present in the profile at a water potential acceptable to the plant,
2 the plant's roots cannot penetrate the soil layers in which water is available,
3 roots are present in layers with available water, but root density is insufficient for uptake at the required rate.

The third type of water stress is the most interesting case for our present discussion. If the water potential of the leaves is lowered to -5 bar during moderate water stress or to -16 bar during severe water stress, soil water potential will remain higher than this value, depending on the resistance in the pathway. Fig. 2 shows the pathway of water transport, with the symbols used here.

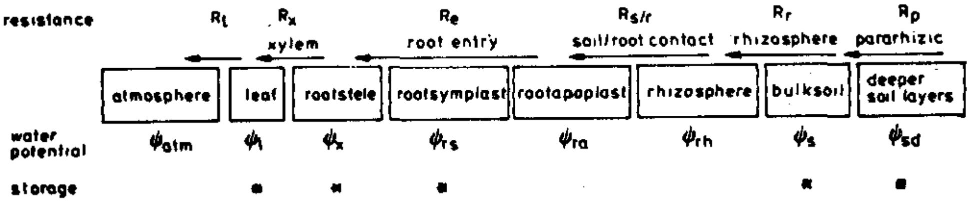

Fig. 2. The soil-plant-air continuum for water uptake, with the various resistances.

Neglecting temporary storage of water inside the plant, the transpiration rate T, per unit cropped area can be described (OERTLI 1976) by:

$$T = \frac{-\psi_{atm} + \psi_1}{R_1} = \frac{-\psi_1 + \psi_x}{R_x} = \frac{-\psi_x + \psi_{ra}}{R_e} = \ldots\ldots \qquad (1)$$

In this section we will discuss which of the resistances dominates the transport, and how much available water is left in the soil because of insufficient root density. Root entry resistance, rhizosphere resistance and soil/root contact resistance will be considered.

2.2 Root entry resistance

Published values for root entry resistance or its inverse, root conductivity L_p, (volume of water per surface area of root per unit time per pressure difference) vary within a considerable range. A much discussed topic is whether or not root conductivity varies with flux and/or water potential (FISCUS 1977).

At reasonable values for transpiration and water potential, Lp can be expected to be in the range of 5 to 500 10^{-3} cm day^{-1} bar^{-1}, with 70.10^{-3} as a midpoint value (NEWMAN 1976, FISCUS 1977).

The root entry resistance for the root system beneath 1 cm^2 cropped area is:

$$R_e = (w.h.2\pi\ R_o.L_p)^{-1} \qquad (2)$$

where w = root density (cm root.cm^{-3} soil)
h = root depth (cm)
R_o = root radius (cm)

The product w.h. may be called Total Root Length, the product w.h.2π R_o the Root Area Index comparable to the term Leaf Area Index. Rearranging part of equation (1) and substituting (2) we obtain a formulation of the required total root length.

$$w.h. = T/(L_p(-\psi_x + \psi_{ra})) \qquad (3)$$

or

$$\log(wxh) = \log T - \log L_p - \log(-\psi_x + \psi_{ra}) \qquad (4)$$

Fig. 3 shows some results for three levels of the transpiration rate and for cases of a moderate or severe water stress (- 5 or -16 bar). The range of values of L_p implies a range of required root area indices, partly overlapping the range actually found in the field. Apparently plant entry resistance cannot be neglected. A better knowledge of realistic values of L_p is necessary.

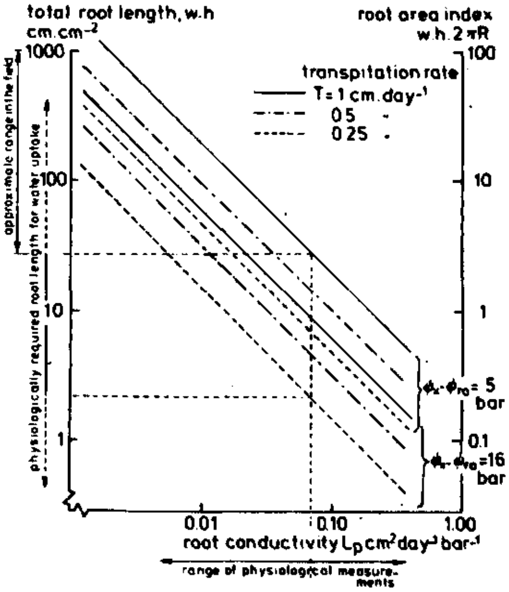

Fig. 3. Physiologically required root length for water uptake, as determined by the root conductivity Lp.

2.3 Rhizosphere resistance

Soil water diffusivity D decreases with water content, Θ, so possibly a dry rhizosphere could develop around a living root, restricting inflow of water from the bulk soil. A reasonable description of D as function of Θ is given by

$$D = D_o \, e^{\beta(\theta - \theta_o)} \qquad (5)$$

STROOSNIJDER (1976) listed the parameters D_o, β and θ_o for a range of Dutch soils, described earlier by RIJTEMA (1969).

PASSIOURA and COWAN (1968) presented steady state and steady rate solutions for water flow to a single root, assuming a constant D. A solution to the general diffusion equation for the D/θ relationship of (5), assuming no water flow across the cylinder of soil with radius R_1, can be specified for θ_{R_1}:

$$\theta_{R_1} = \theta_o + \frac{1}{\beta} \ln \left[\frac{q}{2\pi D_o} \left[\frac{R_1^2}{R_1^2 - R_o^2} \ln \frac{R_1}{R_o} - \frac{1}{2} \right] + e^{\beta(\theta_{R_o} - \theta_o)} \right] \qquad (6)$$

where

$$q = T/(w.h) \qquad (7)$$

is the water use per unit of root length, and

$$R_1 = (\pi w)^{-\frac{1}{2}} \qquad (8)$$

is the radius of a soil cylinder attributed to a single root of radius R_o.

Equation (6) describes θ_{R_1} the volumetric water content at the edge of the cylinder from which a single root extracts water (i.e. the bulk soil in the soil layer), as a function of root density, soil parameters, transpirational demand and θ_{R_o}, the water content of the soil corresponding with the water potential at the root surface.

In Fig. 4 results are presented for a range of soil types. $\theta_{R_1} - \theta_{pF4.2}$ indicates the amount of water potentially available to a plant of a water potential of -16 bar, but inaccessible because of rhizosphere resistance. The calculations given are for a case where T/h = 0.05 day^{-1} (e.g. T = 1 cm day^{-1} and h = 20 cm). For most soils rhizosphere resistance is negligible at root densities above 0.1 cm^{-2}. In certain loamy soils (7 and 11 in Fig. 4) rhizosphere resistance can be a real phenomenon, even at root densities of 0.3 - 3 cm^{-2}. As the lines approach the x-axis asymptotically, the last drop of water is extracted only at an infinitely high root density. As arbitrary boundary a value of 1% soil moisture has been indicated.

The effect of root radius R_o on the results is shown in Fig. 5 for soil type 7. When compared on a root length basis, thinner roots have a slight disadvantage; when compared on a surface area basis they are able to extract more water than thicker roots (on a volume or root weight basis this effect is even more pronounced). The calculations presented here support the general conclusion reached by NEWMAN (1969), that rhizosphere resistance is normally not important under field conditions.

2.4 Root soil contact resistance

FAIZ and WEATHERLEY (1977) have presented experimental evidence for a major resistance to water flow occurring at the soil-root interface. HERKELRATH et al. (1977) produced similar data and proposed a formulation for this contact resistance, proportional to the water content of the soil surrounding the root θ_{rh}, divided by the water content at saturation θ_{sat}:

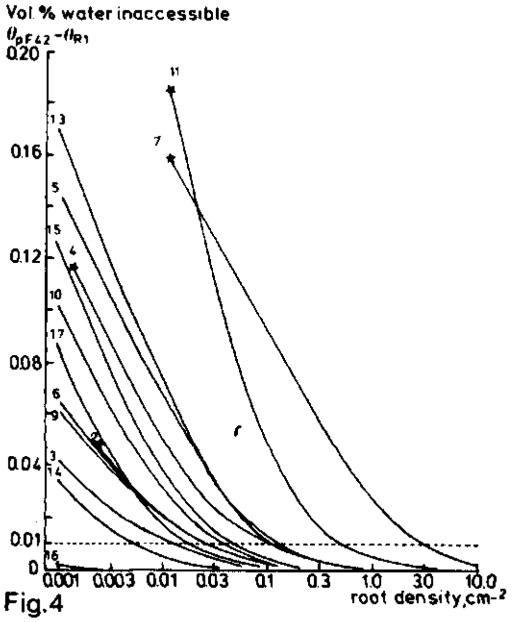

Fig.4

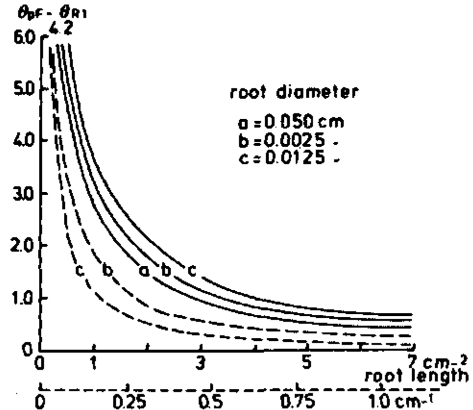

Fig.5

Fig. 4. Potentially available water remaining in the soil because of rhizosphere resistance, as a function of root density. The numbers indicate different soil types, based on measurements and nomenclature of RIJTEMA (1969). The asterix indicates the moisture content at pF 2.0. Calculations were done for T = 1 cm day^{-1} and h = 20 cm. soil type: 2 = medium coarse sand, 3 = medium fine sand, 4 = fine sand, 5 = humous loamy medium fine sand, 6 = light loamy medium coarse sand, 7 = loamy medium coarse sand, 9 = sandy loam, 10 = loess loam, 11 = fine sandy loam, 13 = loam, 14 = sandy clay loam, 15 = silty clay loam, 16 = clay loam, 17 = light clay.

Fig. 5. Effect of root diameter on amount of water left in the soil because of rhizosphere resistance. Root length and root surface area were scaled in such a way that the two graphs coincide for a root of 0.05 cm diameter. Calculations for soil type 7, T = 1 cm day^{-1}, h = 20 cm.

$$T = \frac{(-\psi_x + \psi_{rh})\ \theta_{rh}}{R_e\ \theta_{sat}} \qquad (9)$$

For solving this equation we need a θ/ψ relationship of the soil, i.e. the water retention curve. No generally applicable mathematical formulas of curve fits are available. By a graphical technique, however, we can solve the equation by taking the points of intersection of the soils water retention curve and a modification of (9):

$$\psi_{rh} = \psi_x + \frac{q\ \theta_{sat}}{2\pi\ R_o\ L_p\ \theta_{rh}} \qquad (10)$$

A similar graphical technique has been used by RAATS (1974) for modelling infiltration into crusted soils.

Fig. 6 shows an example of the Θ/ψ plane with water retention curves of two soils and solutions to (10) for several root densities. Other parameters being equal root density has a strong effect on q: more roots can work at a proportionally lower rate each. The interpretation of root densities has been given for $2\pi\ R_o\ L_p = 7.10^{-3}\ cm^2\ day^{-1}\ bar^{-1}$, $T = 1.0$ cm day^{-1} and h = 20 cm, but other interpretations can be constructed according to the grouping in equation 10. Each line shows a vertical asymptote for $\psi_{rh} = 0$:

$$\Theta_{rh} = \frac{-q\ \Theta_{sat}}{L_p\ \ \varphi_x} \tag{11}$$

and a horizontal approach to

$$\varphi_{rh} = \varphi_x - \frac{q}{L_p} \qquad \text{for } \Theta_{rh} = \Theta_{sat} \tag{12}$$

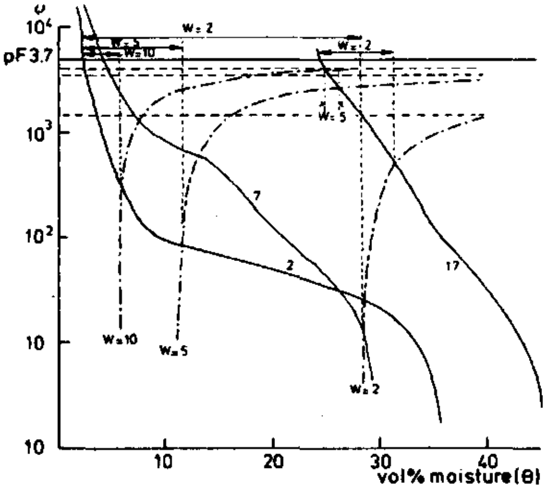

Fig. 6. Calculation of the effect of root-soil contact resistance on water uptake. Water retention curves are shown for three soil types (see Fig. 4). For three root densities (w = 2, 5 and 10 cm^{-2}) lines are given indicating the uptake possibilities (see text).

Equation (12) is equivalent to (3), showing the absence of soil-root contact resistance. The interpretation of Fig. 6 is that water can be taken up by a root following the water retention curve, up to the point of intersection with the Θ_{rh}/ψ_{rh} line for the given root density; the remaining water up to $\Theta_{\psi x}$ is potentially available at the plant's water potential, but not accessible because of the contact plus plant entry resistance.

Fig. 7 gives the results for six soils selected to show the range in the data of all soils in the data set. If the mathematical description of the contact resistance can be trusted, this resistance plays the dominant role in the transport process. Root densities of about 2 cm^{-2} in a 20 cm layer from which all the requirements of the plant are drawn, are needed when -16 bar is acceptable inside the plant, and root densities of around

5 cm^{-2} when -5 bar is taken as the limit for plant water stress.

We can take the analysis one step further by introducing a "marginal root efficiency". The water gained by the plant by having more roots can be used for keeping the stomata open for photosynthesis. Water use efficiency of photosynthesis is roughly 4 mg DM cm^{-3} water (DE WIT 1958), corresponding to 200 kg DM ha^{-1} day^{-1} and 5 mm transpiration day^{-1}. On the other hand, root growth implies the consumption and use of dry matter, roughly 0.09 mg DM cm^{-1} for roots of 0.04 cm diameter and 7% dry-matter content. Combining these two values, a marginal root efficiency of 0.02 cm^3 water cm^{-1} root follows, indicating the amount of water one centimeter of root has to extract to just pay for its own dry-matter investment. For each line in Fig. 7 the point is indicated where $d(\theta_{\psi x} - \theta_{Ro})/dw$ equals this value. As can be seen from the graph, most curves show a sharp transition around this point, making the analysis insensitive to moderate changes in marginal root efficiency.

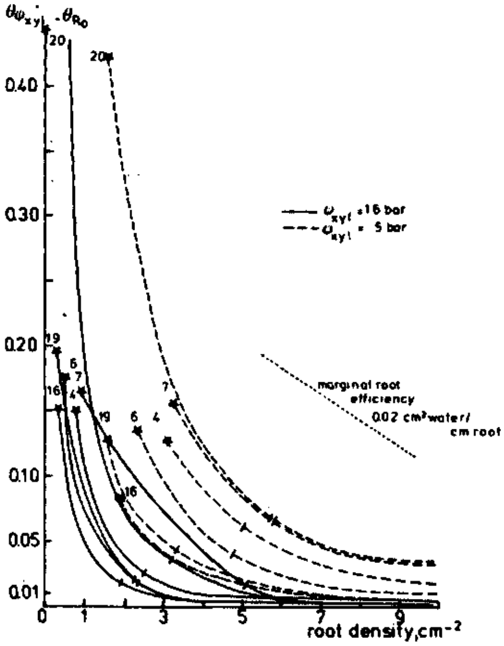

Fig. 7. The amount of potentially available soil water left in the soil because of soil-root contact resistance, as a function of root density. Solid lines indicate ψ_{xyl} = -16 bar, broken lines ψ_{xyl} = - 5 bar; the asterix indicates the moisture content at pF 2.0. Soil types as in Fig. 4, except for 19 = basin clay and 20 = peat. Calculations for T = 1 cm day^{-1}, h = 20 cm.

The conclusion of this discussion on water uptake is that a soil-root contact resistance, if acting along these lines, determines the root density required for water consumption, the root entry resistance being a modifying factor. Rhizosphere resistance plays a minor role. Root densities normally encountered in the plough layer under crops (0.5 - 10 cm^{-2}) seem to be required if almost all the available water has to be extracted from this layer at a fairly high transpiration rate and a low plant water potential.

Instead of the definition of root depth used in the water balance studies so far (RIJTEMA 1969), a more gradational definition could be based on Fig. 7. Instead of assuming all water above a certain root depth to be available and the water below the root depth unavailable, a partial availability can be quantified now for each root density.

3 MODEL CALCULATIONS ON NUTRIENT UPTAKE

3.1 Physiological requirements

When the nutrient supply to the root system is increased by fertilisation and maintenance of a favourable moisture content of the soil, a smaller root system will be sufficient. Theoretically one might expect that this is possible until the physiological limit of the root's activity has been reached. If conditions allow the roots to work at their maximum possible rate, according to physiological measurements the required root densities can be calculated by dividing the daily nutrient requirements by the maximum influx rates. Table 1 shows some results.

Table 1. Calculation of physiologically required root density for nutrient uptake. Required nutrient level based on EPSTEIN (1972); required uptake rate based on 200 kg DM ha^{-1} day^{-1}; values for maximum influx into roots taken from NYE and TINKER (1977).

	Required level $\mu mol\ mg^{-1}$	Required uptake rate $\mu mol\ cm^{-2}\ day^{-1}$	Maximum influx into roots $\mu mol\ cm^{-2}\ day^{-1}$	Required root area index $cm^2\ cm^{-2}$	Required total root length $cm\ cm^{-2}$
N	1.0	2.0	0.97 -6.1	0.33-2.1	3.5-22
P	0.06	0.12	0.078-0.49	0.24-1.5	2.5-16
K	0.25	0.5	0.26 -0.39	1.3 -1.9	14 -20

Of course the values chosen for this calculation are rather arbitrary, taken from a broad range of plant-specific values. Comparison with Fig. 3 shows that the root density required for water uptake, even when free water is available, generally exceeds the root density required for nutrient uptake. In this way the water supply acts as the natural limit to the reduction in root size possible by increased fertilisation. In horticulture, when nutrient solution culture on, for instance, rockwool is used, such a situation is approached. Pot experiments with tomato and cucumber tend to corroborate the hypothesis that water is the main limiting factor under such conditions (VAN NOORDWIJK, in preparation). Under agricultural conditions the supply of nutrients to the root surface is not always sufficient for the roots to work at their maximum capacity. The rate of mass-flow and/or diffusion determines the nutrient supply to the root in such situations. DE WILLIGEN (1981) has given a mathematical analysis of diffusion and mass-flow of solutes to a root assuming constant uptake. A comparison of a mobile nutrient, N, and one of the least mobile, P, indicates the range of root densities required for nutrient uptake.

3.2 Model calculations on N-uptake

The mathematical description by DE WILLIGEN (1981) shows that transport of N in the soil to the root normally involves very small gradients. This means that the concentration at the root surface will be nearly identical to the average concentration in the soil layer. If the water uptake by the roots is high, accumulation of nitrate in the rhizosphere may occur because mass-flow exceeds the daily uptake requirements. Uptake of nitrate can continue at the rate required by the plant until a certain minimum concentration is reached. This minimum concentration is determined by the root absorbing power compared with the required rate of uptake per root. Increasing the root density decreases the required rate of uptake per root and decreases the minimum concentration required, and thus results in a more complete utilization of the resources in the soil. The root absorbing power for nitrate can be expected to be in the range of 0.025 - 2 cm day^{-1} (NYE and TINKER 1977, α in their notation).

Fig. 8 shows the fractional depletion of soil nitrate as a function of root density, transpiration rate and root absorbing power. For normal values of the root absorbing power 90% of all nitrate in the soil can be used at root densities below 0.5-1.0 cm^{-2} in a 20 cm layer.

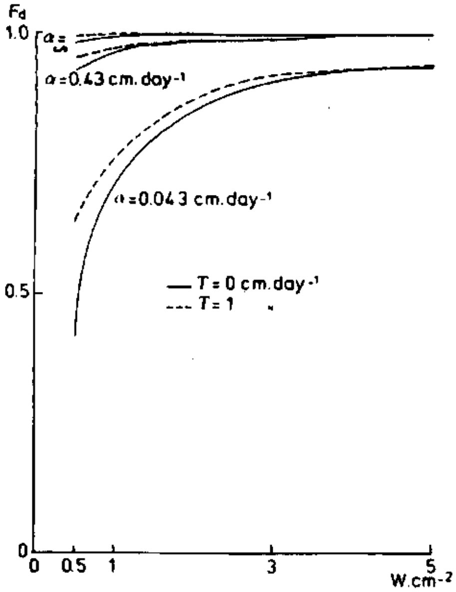

Fig. 8. Nitrate uptake as a fraction of available amount of soil nitrate, as a function of root density and root absorbing power with and without mass-flow (DE WILLIGEN 1981).

The assumption of a constant daily uptake rate is only an approximation of reality. Another approximation can be obtained by assuming that root uptake rate will always be maximum. If the root absorbing power is assumed to be infinitely high, this amounts to assuming the root to be a zero-sink.

A simple model for diffusion and mass flow of ions to a single root acting as zero-sink has been presented by VAN KEULEN et al. (1975). It applies to weakly or nonadsorbed ions, such as nitrate. A simple guideline is suggested of the form

$$t.D_o.w = 1 \qquad (13)$$

in which t = time required for 90% depletion of the soil (day)
D_o = diffusion rate ($cm^2\ day^{-1}$)
w = root density (cm^{-2})

For nitrate $D_o \approx 1\ cm^2 day^{-1}$. The root density required depends on t. For a continuous supply of N at a low level through N-mobilisation, uptake by the roots within 1 day may be necessary to reduce losses due to competition with microorganisms. This means w should be about 1 cm^{-2}. If more time is available, root densities of about 0.1 cm^{-2} suffice to utilize most of the nitrogen resources in the given soil layer.

3.3 Model calculations on P-uptake

A theoretical approach to the question what root density is required in soils of different P-status was outlined before (DE WILLIGEN and VAN NOORDWIJK 1978, VAN NOORDWIJK and DE WILLIGEN 1979). A diffusion model for transport to single roots was used to evaluate the possibilities for P-uptake from five different soil types at different fertility levels. The model is based on several simplifying assumptions, including:

+ P-"adsorption" isotherms are used as indicators of reversible, instantaneous exchange between soil and soil solution. Irreversible immobilisation reactions are neglected.
+ Complete physiological regulation of P-uptake is assumed, resulting in a constant daily P-requirement during the linear growth phase of the crop. The number of days during which such growth can be maintained is used as the main parameter for crop success. A higher root density implies a proportionally lower uptake requirement per root.
+ The root system is described as static, all roots having the same P-uptake.
+ No root hairs or mycorrhiza-hyphae are considered.
+ A constant moisture level of the soil is assumed.

Some results are presented in Fig. 9 a-e. The total amount of phosphate in the adsorbed plus solution phase has been translated into a potential (maximum) number of growing days. This number might be realised at an infinitely high root density. Differences among these maximum numbers for different soils at the same P_w-value of the soil reflect the various "adsorption" characteristics. Higher root densities can be seen to extract a higher proportion of the available phosphate, but according to the law of diminishing returns. On the fine sandy soil of low P-binding capacity (Fig. 9a) at P_w 30 (mg P_2O_5 l^{-1} soil) a root density of 2 cm^{-2} can extract 50% and a root density of 5 cm^{-2} 80% of available P; on the basin clay (Fig. 9e) these values are 20% and 50%. Apparently an increase in root density beyond 5 cm^{-2} is of limited use on the fine sand, while on the basin clay it would still result in a considerable increase in P-uptake by the plant.

Similar to the situation in the water uptake models, the main effect of an increased root density in this model is through the required P-uptake per root. The lower P-requirements of a root in a more extensive root system can be maintained by diffusion for a much longer time and with a smaller concentration gradient in the rhizosphere. This effect is more important than the smaller diffusion distances at higher root densities usually taken as the reason for a higher P-extraction. The effective depletion zones per root are larger for higher root densities (!).

P-extraction at a root density of 1 cm^{-2} is similar for the five soil types at the P_w values indicated. This result reflects the success and limitations of P_w as a method to describe the P-status of the soil for plant nutrition. P_w (a water extraction of soil with a soil-to-water volume ratio of 1 : 60) is a compromise between measuring capacity and intensity of P-supply, which was optimalized for pot experiments with young potato plants (VAN DER PAAUW 1971). For crops with a higher root density and/or lower P-requirement P_w may be expected to underestimate the fertility of strongly absorbing soils while overestimating the fertility of soils of weak P-adsorption. For crops with a poorer root development than potatoes ($w \approx 1$ cm^{-2} in the plough layer) and/or a higher P-requirement, the reverse may be true.

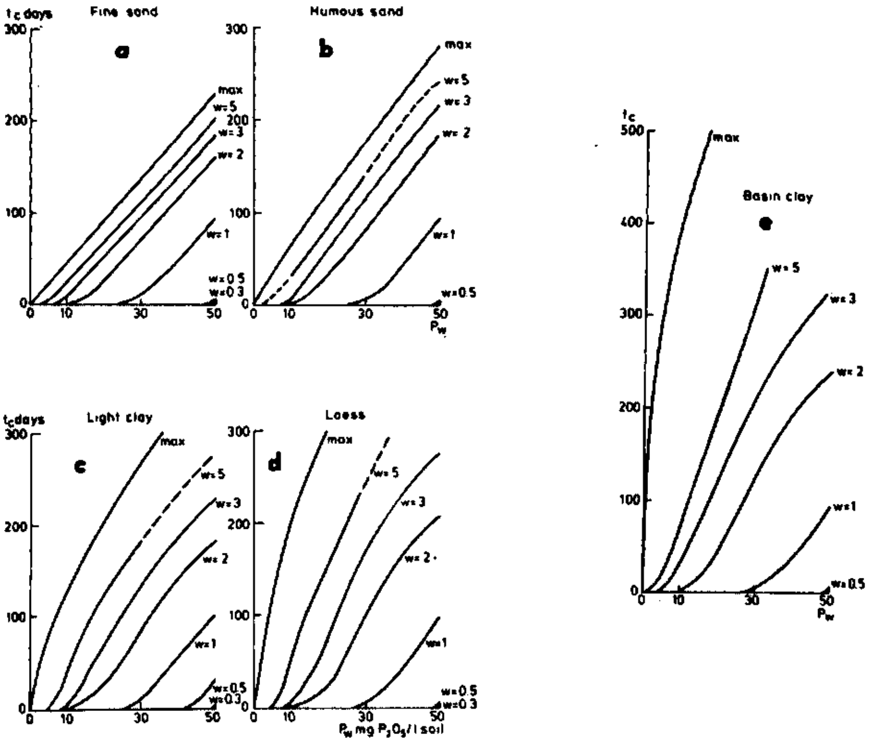

Fig. 9. The number of days, t_c, during which the P-requirements of a crop can be met, as a function of P_w and root density.

Fig. 10 presents the same data as Fig. 8, now with root density as the x-axis. The divergence of soil types at higher root densities can be noted, but the fact that they converge in a certain region is more remarkable, given the variations in the nature of the P-supply. For crops with a linear growth phase of 2-3 months a root density of about 1 cm^{-2} appears to be sufficient on a soil of P_w = 50; a root density of about 2 cm^{-2} would be required on a soil of P_w = 30, while root densities above 5 cm^{-2} would be needed on soils of P_w = 10 (on the two sandy soils even the potential supply is too low in such a case). Empirical results of the P-responsiveness of crops appear to coincide with such values. A sequence of crops of beans, potato, sugarbeet, cereals, grass shows an increasing root density in the plough layer and a decreasing P-responsiveness for an approximately constant P-demand.

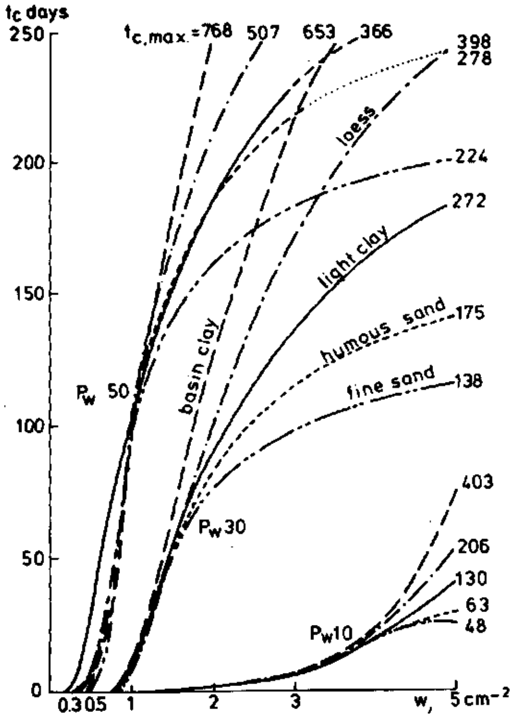

Fig. 10. Uptake time, t_c, as a function of root density on different soils at three levels of P_w. The numbers at the end of each curve indicate t_c max, i.e. the uptake time for an infinitely dense root system.

4 CONTAINER EXPERIMENTS ON P-UPTAKE

To test part of the theory presented above, a series of container experiments was carried out in which two clones of perennial ryegrass (Lolium perenne L) were used. Previous work on these clones (BAAN HOFMAN and ENNIK 1980) had revealed a marked difference in root production with a similar shoot production when the plants were tested in monoculture on nutrient so-

Fig. 11. Response of two clones of perennial ryegrass of different root density, to P_w value of the soil. Left: clone 39, with an average root density of 20 cm^{-2} in the plough layer; right: clone 40 with an average w = 12 cm^{-2}. The photograph at the bottom shows a difference in root depth of the clones accompanying a difference in root density in the plough layer.

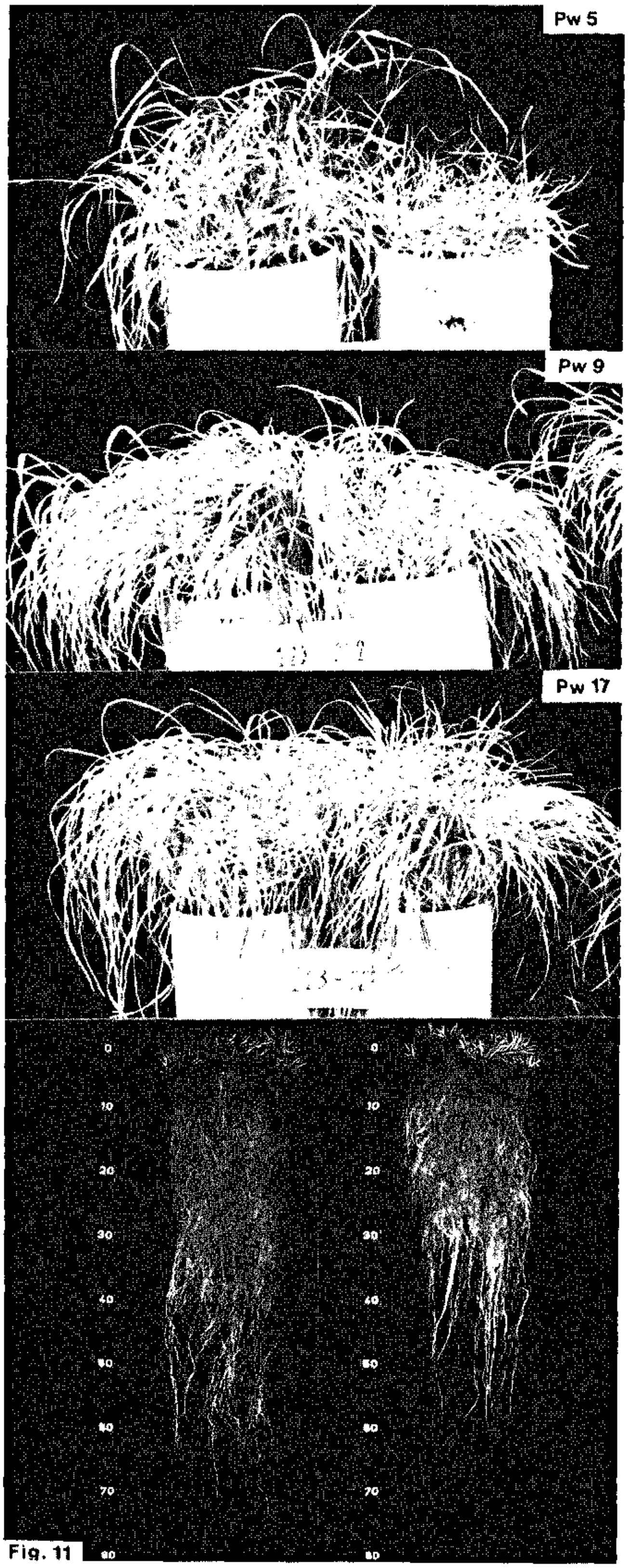

Fig. 11

lution. In competition experiments on soil or solution, clone 39 with its higher root weight proved to be far superior to clone 40.

In three successive experiments we compared the P-response of clone 39 and clone 40 on different soils, using filled-in PVC containers of 22 cm diameter kept at a constant water table. Fig. 11 gives an impression of the results. On poor soils clone 39 outyields clone 40; on richer soils the difference disappeared. Mycorrhiza (VAM) was present in the experiments, especially on the poor soils. The total length of hyphae was estimated to be half the root length at the end of the experiment (10 weeks). The development of the hyphae takes more time than root development, however, so a substantial contribution to the P-nutrition of the grass can only be expected after several weeks.

Further analysis of the results has to wait until all measurements have been completed.

5 DISCUSSION

The theory presented seems to indicate that the following root densities in a 20 cm layer are needed to supply the plant with the necessary resources:

water 0.3 - 1 or 1 - 5 cm^{-2} (without or with contact resistance)
nitrate 0.1 - 1 cm^{-2}
phosphate 1 - 10 cm^{-2}

Such root densities can be expected to occur in the plough layer (phosphate uptake), just below the plough layer (water uptake) or down into the subsoil (nitrate uptake). These guidelines are still very rough first approximations. The number of possible complicating factors seems to be unlimited.

One of the reasons for uncertainty is the lack of experimental methods to describe the soil/root interface in various situations. The importance of the suggested interface resistance for water was shown in section 2. Effects on oxygen uptake are possibly of a similar magnitude (DE WILLIGEN and VAN NOORDWIJK, in preparation), while effects on nutrient uptake remain uninvestigated.

Obviously the root density and pattern required depend on the seasonal resource availability, e.g. water regime, nitrogen movements in the soil profile, P-status of the soil and climatically determined growth potential. The question remains whether or not a root density can be too high, i.e. supra-optimal. If energy investment in the roots is considered as a cost (as in Fig. 7), root densities can certainly be too high. But the existence of "wasteful respiration" (LAMBERS 1979) has recently made the role of energy-bearing carbohydrates uncertain as a limiting factor within the plant, also under conditions where light seems to be the main environmental constraint. In certain special cases root densities may be too high for other reasons. PASSIOURA (1972) demonstrated that for wheat grown on a limited supply of stored water in the soil, a restricted root system induced a more even use of water throughout the life cycle of the plants and thus increased grain yield.

So far the discussion on plant strategies has essentially been concerned with crops grown in monoculture. In situations where interspecific competition occurs, the demands made on root densities are different. This is clearly demonstrated by the clones of perennial ryegrass. Clone 40 with a relatively weak root system can give a very high shoot production on fertile soils when grown in monoculture. But it loses the competition with clone 39 with its higher root density. In case of competition the higher root densities seem to have overall advantage. A certain degree of niche-specialisation among grassland plants has been demonstrated by BERENDSE (1981) to be based on a difference in root distribution pattern. Stable coexistence of plants is possible if each specialises in a root distribution in a specific layer. But such specialisation does not appear to have an adaptive value to the plant per se, when compared with an uniform deep root system. Genetically determined limitations to the plasticity of the roots apparently play a major role.

In an agricultural context an increased root density may be useful as it would create possibilities for uptake of the crop's demands from the soil at a lower fertility level. This can be relevant wherever losses from the soil are related to the levels maintained (as for leaching, immobilisation, volatilisation, etc.). Present-day agricultural practice with its heavy mechanisation causing a deterioration of soil structure seems to achieve the opposite. An increase in root density is, of course, only useful when the resources are potentially available in the soil.

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SUMMARY

The question "how many roots does a plant need?" has to be solved for various conditions of supply by the soil and demand by the crop, before we can hope to obtain guidelines for a functional interpretation of root densities in the field.

When evaluating the role of root density in models of plant water uptake, the strongest influence was found when a "soil-root-interface" resistance was incorporated. If this resistance acts in the way it is described by the model, root densities in the order of 1 - 5 cm root/cm^3 of soil are required for an adequate use of the available soil moisture.

Available theory on nitrogen transport in the soil indicates that root densities of 0.1 - 1 cm of root/cm^3 of soil are sufficient for nitrogen uptake from a specific soil layer.

Increasing the root density seems to have the highest beneficial effect on P-nutrition. In model calculations we tried to specify the relationship between P-nutrition of the crop, root density, soil type and P-status. In the range 1 - 10 cm root/cm^3 of soil in the plough layer, root density plays an important role in explaining the P-response of a crop.

A series of container experiments was started with two clones of Lolium perenne, to test the theory. Some results are presented.

ZUSAMMENFASSUNG

Funktionelle Deutung der Wurzeldichten im Feld für Nährstoff- und Wasseraufnahme

Die Frage "wie viele Wurzeln braucht eine Pflanze?" muß für die unterschiedlichen Standortbedingungen erst gelöst werden, bevor wir hoffen kön-

nen, Richtlinien für eine funktionale Erklärung von Wurzeldichte im Feld zu erhalten.

Die Erhöhung der Wurzeldichte scheint die beste Wirkung auf die Ernährung mit P zu haben. In Modellberechnungen versuchten wir, die Beziehung zwischen P-Ernährung der Feldfrucht, Wurzeldichte, Bodentyp und P-Gehalt anzugeben. Im Bereich 1-10 cm Wurzeln/cm^3 Boden in der Pflugschicht, spielt die Wurzeldichte eine große Rolle, um den Versorgungszustand einer Feldfrucht mit P zu erklären.

In einer Serie von Gefäßversuchen mit 2 Klonen Lolium perenne wurde die Theorie überprüft. Einige Ergebnisse werden vorgestellt.

Bei der modellhaften Abschätzung der Bedeutung der Wurzeldichte für die Wasseraufnahme der Pflanzen wurde der stärkste Einfluß gefunden, wenn der "Boden-Wurzel-interface"-Widerstand enthalten war. Wenn der Widerstand so wirkt, wie er im Modell beschrieben wird, werden Wurzeldichten von 1-5 cm Wurzeln/cm^3 Boden zur angemessenen Verwendung der verfügbaren Feuchtigkeit benötigt.

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