ROOTS, PLANT PRODUCTION AND NUTRIENT USE EFFICIENCY

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Abstract

De Willigen, P and M Van Noordwijk, 1987. Roots, plant production and nutrient use efficiency. PhD thesis Agricultural University Wageningen, the Netherlands, 282 pp, Dutch summary.

The role of roots in obtaining high crop production levels as well as a high nutrient use efficiency is discussed. Mathematical models of diffusion and massflow of solutes towards roots are developed for a constant daily uptake requirement. Analytical solutions are given for simple and more complicated soil-root geometries. Nutrient and water availability in soils as a function of root length density is quantified, for various degrees of soil-root contact and for various root distribution patterns. Aeration requirements of root systems are described for simultaneous oxygen transport outside and inside the root.

Experiments with tomato and cucumber are discussed, which were aimed at determining the minimum root surface area required in an optimal root environment. Experiments on P-uptake by grasses on various soils were performed to test model calculations. Model calculations on the nitrogen balance of a maize crop in the humid tropics suggested practical measures to increase the nitrogen use efficiency.

additional keywords: functional equilibrium, shoot/root ratio, root porosity, Lolium perenne, soil fertility index, sampling depth, synchronization, synlocalization.

Peter de Willigen is eerst verantwoordelijke voor de hoofdstukken 7 tot en met 13

Meine van Noordwijk is eerst verantwoordelijke voor de hoofdstukken 2 tot en met 6, 14 en 16

Hoofdstukken 1 en 15 vallen onder gezamenlijke verantwoordelijkheid.

Stellingen

1. Een uitgebreid wortelstelsel kan bijdragen aan een efficiënt meststoffengebruik, maar is geen vereiste voor het realiseren van maximale bovengrondse plantengroei.
   -dit proefschrift

2. De theorie over het functionele evenwicht tussen spruit- en wortelgroei speelt bij de ontwikkeling van de oecofysiologie van planten dezelfde rol als het "optimal foraging" concept in de dier-oecologie; het leidt tot zinvol onderzoek naar regelmechanismen en tot inzicht in de adaptieve waarde daarvan; de betreffende regulering kan echter op diverse mechanismen gebaseerd zijn.

3. Bij onderzoek van nutriënten-opname in een landbouwkundige of planten-oecologische context, dienen wortelmorfologische parameters en de waterhuishouding méér, en fysiologische parameters die het opnamemechanisme karakteriseren minder aandacht te krijgen dan thans gebeurt.

4. Nutriënt-opname modellen die geen rekening houden met de regulatie van de opnamesnelheid door de plant, zijn slechts toepasbaar zolang het betreffende nutriënt de plantengroei beperkt.

5. Stijging van het maximale productieniveau heeft een neutraal of negatief effect op de efficiëntie van stikstofgebruik en geen positief effect zoals door van Keulen en Wolf (1986) gesuggereerd wordt.
   -Keulen, H van and J Wolf, 1986, Modelling of agricultural production: weather, soils and crops. Wageningen, Pudoc.

6. "Maximalisering van de efficiëntie van meststofgebruik" als doelstelling van agrarische productie leidt tot andere landbouwkundige keuzes dan bij "maximalisering van opbrengsten" worden gedaan; met het huidige stelsel van heffingen en subsidies stuurt de overheid de boerenbedrijven teveel in de richting van de opbrengst-doelstelling; macro-economisch gezien en uit het oogpunt van de milieu-effecten op langere termijn is deze sturing te betreuren.

7. Bij de keuze van boomsoorten voor haag-teelt ("alley-cropping") in de tropen moet men accepteren dat bomen met het gewenste diepe-en-niet-oppervlakkige wortelbeeld een langzame begingroei hebben.
   -Hairiah K and M van Noordwijk, 1986, Root studies on a tropical ultisol in relation to nitrogen management. Instituut voor Bodemvruchtbaarheid Rapport 7-86.

8. Bij de renovatie van stedelijke riool-systemen zoals die thans gepland wordt, wordt de kans gemist om door betere scheiding van huishoudelijk en industrieel afval, tot voor hergebruik aanvaardbaar rioolslib te komen.
   -Nota riolering, Tweede kamer der Staten Generaal, vergaderjaar '86-'87, 19826 nr 1-3.

9. De Nederlandse kunstmest-hulp aan ontwikkelingslanden is het afgelopen decennium eenzijdig op stikstof-meststoffen gericht geweest; vanuit de doelstellingen van ontwikkelingssamenwerking zou juist een accent op fosfaatmeststoffen en hergebruik van organisch afval verwacht mogen worden.
   -Noordwijk, M van, 1986. De nadelen van kunstmesthulp. Landbouwkundig tijdschrift 98 6/7: 34-36.

10. Bij een gemiddelde stikstof-recovery in tropische landbouw van slechts 20-30% zoals de SOW gebruikt in berekeningen voor de FAO over de kunstmestbehoefte van enkele Afrikaanse landen, kan ontwikkelingsgeld beter besteed worden aan onderzoek en voorlichting over efficiënter meststoffen-gebruik dan aan het subsidiëren van kunstmest.

-Stichting Onderzoek Wereldvoedselvoorziening, 1985. Potential food production increases from fertilizer aid: a case study of Burkina Faso, Ghana and Kenya. A study prepared for FAO. Wageningen, 48 pp

11. Het getuigt van groot optimisme dat de Minister van Ontwikkelingssamenwerking verwacht met slechts één ecologisch geschoolde ambtenaar een verantwoord beleid met betrekking tot "milieu en ontwikkeling" gestalte te geven.

12. Bezinning van zowel Noord- als Zuid-Soedanezen op hun gemeenschappelijke historische wortels en culturele identiteit kan bijdragen aan een oplossing voor de burgeroorlog in Soedan.

-Francis Mading Deng, 1973. Dynamics of identification. Khartoum, Khartoum University Press.

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Roots, plant production and nutrient use efficiency
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CONTENTS

10. Depletion by roots partially in contact with soil

11. Effects of variation in root distribution pattern on depletion

12. Integration over a root system and growing season

13. Rooting depth, synchronisation, synlocalization and N-use efficiency under humid tropical conditions

14. P-uptake by grasses in relation to root length density

15. Indices of nutrient and water availability and fertilization schemes

16. Optimal root systems

1. QUANTITATIVE ROOT ECOLOGY AS AN ELEMENT OF SOIL FERTILITY THEORY

1.1 Roots and efficiency of nutrient and water use

Farmers through the ages and throughout all ecological zones have developed techniques for increasing plant production by modification of the root environment by manuring, fertilization, soil tillage, drainage and irrigation with little knowledge of roots. The enormous rise in crop yields of the past century has been based to a considerable extent on further manipulation of the root environment, guided by empirical results and qualitative, partly erroneous (chapter 2), ideas about root growth and function. Discussions on present-day possibilities for increasing plant production still often concentrate on manipulation of the root environment with limited consideration of roots (Van Keulen and Wolf, 1986).

For most crops, roots themselves are not of interest to the farmer; roots mediate between certain external growth factors and the plant as a whole. Considerable variation exists in the efficiency of different root systems in this respect. Extensive root systems are not a prerequisite for maximum plant production if water and nutrients are supplied ad libitum. Under restricted supply, however, larger root systems may absorb more nutrients and/or water. Thus, good root development may allow maximum production at lower current fertility levels or stabilize crop production in a variable environment. In so far as the rate of nutrient losses to the environment depends on current fertility levels, larger root systems may contribute to an increased nutrient use efficiency. Apparent nitrogen recoveries (extra crop uptake after fertilization divided by amount given) of 50%, common for many crops, may be acceptable on economic grounds; they are not acceptable from an environmental viewpoint if the remainder is lost to ground- or surface water. To improve nutrient use efficiencies a better understanding of root growth and function is required.

Fertilizer experiments have often shown that crops with a similar total nutrient demand, e.g. beans, potato, barley and wheat for phosphorus, require different levels of current soil fertility for maximum growth. Advisory schemes for fertilization reflect such differences by distinguishing several groups of crops as shown in figure 1.1 for phosphate.

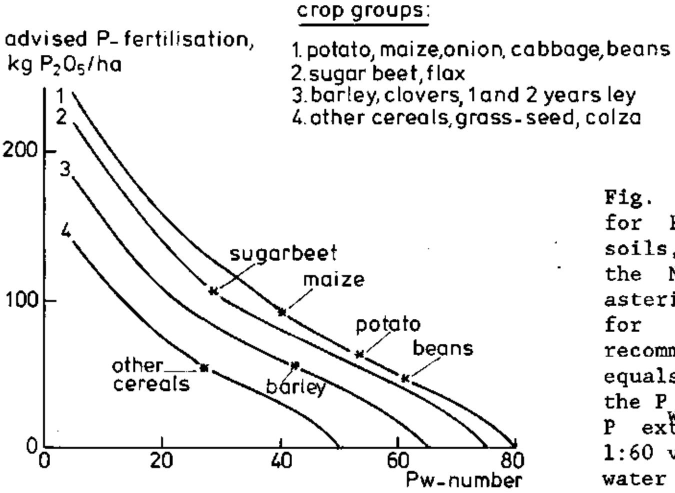


Fig. 1.1 Recommendation scheme for P-fertilization on sandy soils, basin clay and loess in the Netherlands (CAD, 1984); asterisks indicate the point for various crops where recommended fertilization equals expected crop P-uptake; the P_w number is the amount of P extracted from soil with a 1:60 volume ratio of soil to water [P_2O_5 mg/l].

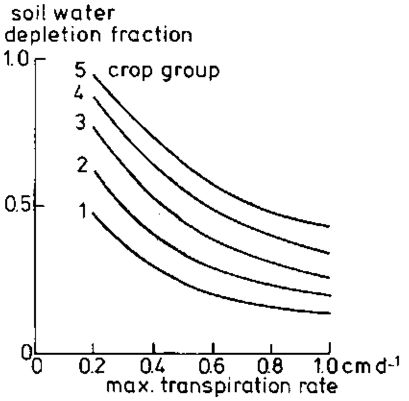


Fig. 1.2 Fraction of "available" soil water (stored in the soil between a matric potential of -0.01 and -1.6 MPa) which can be freely taken up by different crops at a given maximum transpiration rate; crops are classified in five groups according to relative uptake ability (table 15.3; Doorenbos and Kassam, 1979).

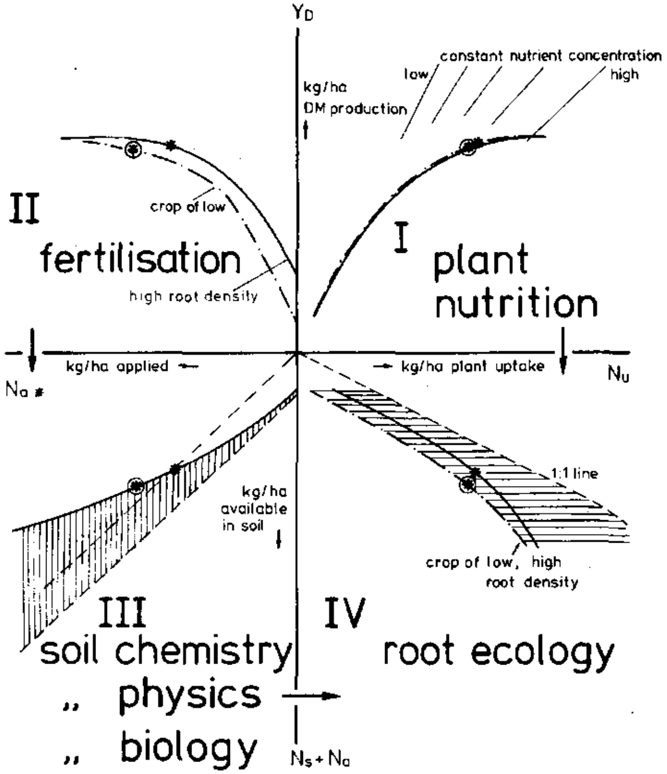


Fig. 1.3 Four-quadrant scheme for analysis of nutrient response of crops (for explanation see text); shaded areas indicate potential nutrient losses to the environment $N_{e,p}$; modified from three-quadrant presentation by De Wit (1953) in which quadrant III and IV are combined and axis $N_a + N_s$ is not used.

Experience in irrigation management shows that at similar transpiration rates different crops may effectively utilize different proportions of "available" soil water (figure 1.2; Doorenbos and Kassam, 1979). Such differences among crops in belowground resource utilization indicate differences among root systems, in size and/or in uptake rate per unit root. Analysis of such differences in efficiency is the object of this thesis.

1.2 Analysis of fertilizer experiments

The results of classical fertilizer experiments can be analyzed by a four-quadrant scheme (figure 1.3). The relation between nutrient application and dry matter production (quadrant II) is based on the nutrient balance of the soil (quadrants III and IV) and on the uptake pattern of the crop (quadrants IV and I). Nutrient balance and crop uptake overlap in quadrant IV, the domain of quantitative root ecology. The axis between quadrant III and IV indicates the size of the "available" pool, which consists of nutrients already present in the soil, N_s, and nutrients added by fertilization, N_a. The notation used is:

N_a = amount of nutrients applied in fertilizer or manure [kg/ha],
N_{a*} = addition to "available" pool by fertilization [kg/ha],
N_s = initial "available" pool in the soil [kg/ha],
N_u = nutrient uptake by the crop [kg/ha],
$N_{e,p}$ = pool of potential nutrient losses to the environment [kg/ha],
Y_D = dry matter yield [kg/ha],
Y_H = harvestable yield of dry matter [kg/ha],
$Y_{H,M}$ = maximum yield attainable by the crop under prevailing conditions apart from the nutrient tested [kg/ha].

Definition of this "available" pool $N_s + N_a$ in a way which is both theoretically and empirically satisfactory is no simple matter; in chapters 7 and 15 this will be discussed further. The main justification for recognising this pool and thus adding a fourth quadrant to the three-quadrant presentation by De Wit (1953) is that solubilization of fertilizer and mineralization of organic manures added to the soil are largely independent of root activity. Certain losses of nutrients to the environment have priority over uptake by the plant and can be included in quadrant III. In as far as such processes depend on root activities, the available pool cannot be defined unequivocally.

Quadrant III describes the relation between applied amount of nutrients and the size of the pool of available nutrients in the growing season. In this quadrant the initial amount of available nutrients in the soil determines the intercept with the vertical axis; the relation is not 1:1 as not all nutrients applied necessarily are available during the growing season: part may be lost to the environment directly after application for instance due to NH_3 volatilization, and another part may not enter the available pool in the first growing season (for instance part of nutrients in organic matter or P-fertilizer).

The processes in quadrant IV primarily depend on the size of the pool of available nutrients, not on their origin: a high initial amount plus a low level of fertilization may give the same result as a low initial amount and a high amount of fertilizer incorporated in the soil. Again, under certain conditions the definition of an available pool is not as clear-cut as presented in figure 1.3; several pools with variation in availability have to be distinguished in such a case.

The uptake pattern of the crop (quadrant IV) is related to crop demand, i.e. the incorporation of nutrients in tissue growth and dry matter production (quadrant I). Shaded areas in figure 1.3 indicate nutrients not taken up by the crop, which form the pool for potential losses to the environment. Part of these losses, those in quadrant III, are independent of plant activity as they occur before the growing season starts. Another part of the potential losses to the environment occurs during or after the growing season, from the pool of nutrients in the soil solution or easily exchangeable fractions. This part of the potential losses is indicated in quadrant IV; uptake by the plant and certain processes leading to losses to the environment, such as leaching, compete for nutrients in this pool.

For each of the four quadrants, the slope of the relation found in a particular situation indicates an aspect of the fertilizer use efficiency of the soil-plant system under consideration. Quadrant III describes the relative availability of a nutrient source: N_a/N_{a*}. This efficiency sometimes depends on the available amount in the soil after fertilization, $N_s + N_a$, for instance in the case of nonlinear adsorption reactions. Usually efficiency in quadrant III depends on the nutrient source, soil type, climatic conditions, time and method of application and on the soil ecosystem. Efficiency in quadrant IV can be described by the relative depletion of available nutrients by the crop: $N_u/(N_s + N_a)$. This efficiency depends on the root system of the crop, which is the central theme of this thesis, as well as on the uptake capacity of the crop at saturation, the size of the available pool and competition for this pool, for instance by microorganisms immobilizing nutrients. Efficiency in quadrant I depends on the nutrient concentration in total plant dry matter and on the harvest index, i.e. the fraction of total dry matter production harvested.

Efficiency in quadrant II, i.e. yield increase due to fertilizer addition, is determined by the respective efficiencies in each of the other quadrants. Presently, schemes for fertilizer recommendations take an economic efficiency into account in this quadrant: expected benefits due to yield increase divided by expected fertilizer costs. Due to widespread concern over negative effects elsewhere of nutrients lost from agro-ecosystems, losses to the environment nowadays should also be considered in constructing fertilization schemes.

In practice the apparent nutrient recovery fraction, which is based on quadrant IV and III together, tends to decrease with increasing yield and input levels. In a review of nitrogen utilization efficiencies of farming systems throughout the world (both past and present) Frissel (1977) concluded that up to a farm input (from natural as well as fertilizer sources) of 150 kg/(ha y) N-output (in harvested products) is about 66% of the input. For inputs above 150 kg/(ha y) outputs are about 50% of the input. Leaching of N is about 10% and about 20% of total N input, respectively. Leaching of N per unit of consumable output, however, showed no clear relation with input or yield level; it usually varies between 0.3 and 0.7 kg leached per kg nitrogen in consumable output. Considerable variation exists in efficiencies at each yield level; probably at every yield level efficiencies can be improved.

An increase of the overall nutrient use efficiencies and concurrent reduction of nutrient losses to the environment has to be based on improved partial efficiencies in quadrant III, IV and I. Processes in quadrant III and IV probably offer more opportunity for improvement than those in quadrant I. Minimum nutrient concentrations in plant dry matter may be decreased and harvest index may be increased by plant breeding to obtain higher efficiencies in quadrant I, but nutritive value and agronomic functions of the non-harvested plant residues may suffer from such a change. Efficiency in quadrant IV can be improved by obtaining a higher relative depletion by "better" root systems in relation to time and spatial aspects of nutrient availability and in quadrant III relative availability can be improved by adjusting fertilization techniques to soil and climatic conditions. In figure 1.3 a schematic indication is given of how a difference in efficiency of the root system may influence the soil fertility levels required for adequate nutrient uptake and consequently influence the possible nutrient losses to the environment (all other things being equal).

The fractional depletion of available nutrients in the soil as found at the end of the growing season is the outcome of the competition throughout the growing season between uptake by the crop and processes leading to losses to the environment, such as leaching, volatilization and denitrification. For some combinations of crop, soil, climate and nutrient concerned, the outcome of the balance between uptake and losses to the environment will primarily depend on the time course of uptake and availability, for others primarily on the exact localization of available resources in the root environment. The mobility of the nutrient concerned in the soil determines which aspect - time or space - is the most important and whether synchronization or synlocalization of nutrient supply and nutrient demand should form the major focus of agricultural interventions aimed at increasing nutrient use efficiency.

To obtain higher nutrient recoveries both supply of and demand for nutrients have to be predictable. In this thesis we will quantitatively evaluate the influence which root density (amount of roots per volume of soil) and other root characteristics have on water and nutrient uptake, in relation to water and nutrient mobility in the soil and crop requirements.

1.3 Utilization of below- and aboveground resources

Definition of the available resources is more complex for below- than for aboveground resources. Figure 1.4 shows the basic symmetry in the relations among roots, shoots and their respective environments. The amount of available external resources constitutes the ultimate constraint to plant production; the shoot and root surface area make up the interfaces with the above-

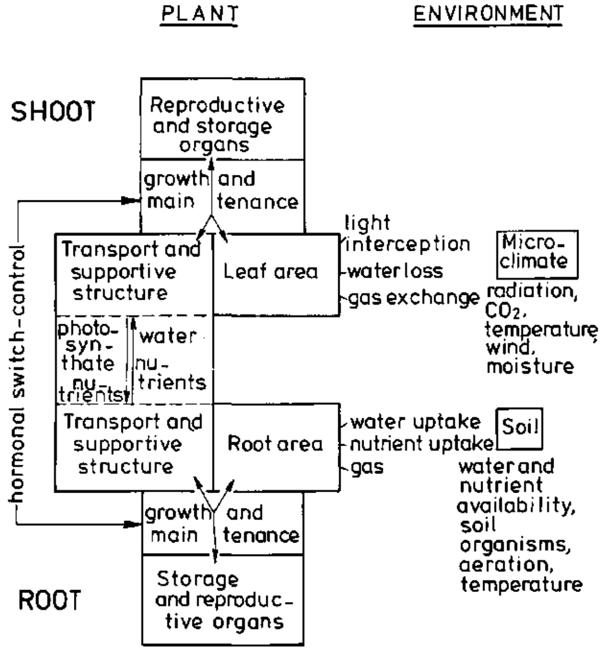


Fig. 1.4 Schematic representation of plant parts in their interaction with above- and belowground environment, emphasising the basic symmetry in relations.

and belowground environment, respectively, and determine the efficiency of obtaining external resources, such as light, carbon dioxide, water and nutrients. Much progress in understanding of plant production has been made in the past decades by quantification of the relationships between components of the microclimate-shoot subsystem shown in figure 1.4.

In the British tradition of growth analysis, starting with Gregory in 1918, (Evans, 1972; Hunt, 1982), a set of terms was developed to separate components of overall plant production: relative growth rate (RGR), leaf weight ratio (LWR), net assimilation rate (NAR) or unit leaf rate (ULR), specific leaf area (SLA), leaf area index (LAI), leaf area duration (LAD). A more mechanistic approach to CO_2 and water exchange between leaves and their environment was taken by others (De Wit, 1965; De Wit et al., 1979; Monteith, 1981). Light interception, photosynthesis and transpiration have been linked to microclimate and leaf area index, at vegetation and crop levels. Leaf area index has been linked to the transport and supportive structures in studies of "crop architecture" (Givnish, 1986).

Analogous studies in the soil-root subsystem of figure 1.4 are more fragmentary as yet. Comparable to the terminology of leaf growth and net assimilation rates, Williams (1948) introduced terms for describing the role of roots in total plant production, which in a modified and extended form are shown in table 1.1. The usefulness of such terms depends on the relative independence of functional (e.g. NAR and NUR) parameters from morphological ones (e.g. LAI and RAI). Descriptive work has been done to separate root growth (morphological aspect) and net uptake rates per unit root (physiological aspect) (figure 1.5).

As an example figure 1.6 shows the results of a P-application experiment by Goedewaagen (1937), in which the increased P-uptake and shoot growth at higher soil P levels is initially due to increased root growth and at higher P applications primarily due to increased uptake rates per unit root at constant or even diminishing total size of the root system.

The validity of the Root Area Index (RAI) as a concept depends on whether or not root systems of different geometry (e.g. root diameter or distribution of roots over the soil profile) will show similar uptake rates on a total root area basis. The concept of root area duration (RAD) is only useful if at a constant RAD the actual time course of root growth and decay over a growing season does not essentially influence uptake. The concept LAD does not survive a similar test, as LAI values above those of the "closed crop" hardly increase light interception and the product NAR x LAI remains constant with increasing

Table 1.1 Comparison of terms for growth analysis of roots and shoots.

Shoot	Root
LWR Leaf weight ratio (as part of total plant dry weight) [g/g]	RWR Root weight ratio (as part of total plant dry weight) [g/g]
SLA Specific leaf area (per unit leaf dry weight) [m^2/g]	SRA Specific root area (per unit root dry weight) [m^2/g]
NAR=ULR Net assimilation rate per unit leaf area [g/(m^2 day)]	NUR Net uptake rate of water or nutrients per unit root area [mol/(m^2 day)]
LAI Leaf area index (green leaf area per unit cropped area) [m^2/m^2]	RAI Root area index (living root area per unit cropped area) [m^2/m^2]
LAD (Green) leaf area duration (LAI integrated over the growing season) [days]	RAD (Active) root area duration (RAI integrated over the growing season) [days]

Plant requirement [mol/day]

|| ?

Uptake rate [mol/day] = Relative rate of depletion [mol/(mol day)] × Absolute supply [mol]

" = Root weight [g] × Specific root surface area [m^2/g] × Uptake rate per unit root surface area [mol/(m^2 day)]

Fig. 1.5 Simplified diagram for analysis of uptake rates.

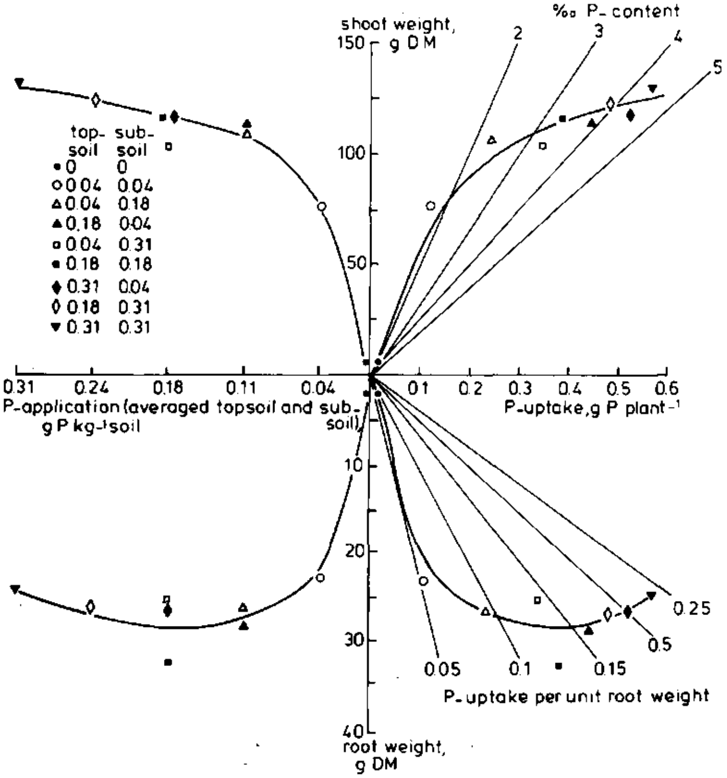


Fig. 1.6 Example of experiment on which the distinction between "morphological" and "physiological" response to fertilization by Goedewaagen (1937) was based: P-uptake, shoot and root weight of oats as influenced by P-fertilization of topsoil and subsoil.

LAI. For nutrients of low mobility, such as phosphate, interference between roots may be less severe, so the concept of a RAD may be more meaningful than that of LAD. Detailed quantification of processes determining nutrient and water uptake by root systems is required to test these concepts. Knowledge of the quantitative relations between water and nutrient uptake, root area index and soil fertility is in an initial stage. Both the resources themselves and the ways they can be obtained by the plant are more difficult to define for underground resources than for aboveground resources, for a number of reasons:

A. Generating flux: Photosynthesis by a leaf can be described as interception of an external resource; interception does not influence the "transport of light" towards the leaf. In gas exchange between leaves and surrounding air such interactions become apparent as stomatal control influences gas exchange with the environment, but the ratio between the inflow of CO_2 and the outflow of H_2O vapour to the crop canopy as a whole is dominated by climatic influences out of control by the plant. Water and nutrient uptake generate the flow of water and nutrients towards the root and the plant root can control water and nutrient uptake separately. In as far as roots may influence the pH of the rhizosphere, excrete enzymes or chelating substances or have symbiotic relationships with for instance N-fixing bacteria, roots may even alter the availability of nutrients. For light and CO_2 no comparable influences exist. Depletion of soil water in the root zone may generate capillary rise. These effects make it much more difficult to define availability of nutrients and water than to define availability of light and CO_2.

B. Dimensions and geometry: Aboveground resources (light, CO_2) usually vary in one direction only, which allows for relatively simple descriptions of leaf-leaf interactions (apart from turbulent CO_2 transport in leaf canopies). Simplification of the root environment to a one-dimensional system requires more rigourous assumptions than for the aboveground environment. Geometrical complications and root-root interaction in resource utilization are more complex. Belowground resources have to be considered in a three- (or sometimes two-) dimensional context. Concepts such as the "closed crop canopy", which considerably help in analyzing aboveground resource utilization, cannot be directly transferred to roots. Shoot height is important to the individual plant in obtaining aboveground resources in situations of competition between or within species, but not for total aboveground resource availability and total plant production in a cropped field. Rooting depth, however, may influence the size of the pool of available resources for both individual plant and total crop. Geometrical complications may arise for instance due to the interaction of root growth and soil structure. An inhomogeneous (e.g. aggregated) structure of the soil may lead to an inhomogeneous distribution of roots. The amount of actual contact between root surface area and the solid phase of the soil may vary as a consequence of differences in soil structure as well.

C. History: Belowground resources are stored, at least temporarily, in the root environment. In root functions therefore "history" plays an important role; photosynthesis by a leaf on day T does not influence light or CO_2 availability on day T+1, whereas for water and nutrient uptake such influences are important.

As each extra root may influence uptake by all other (present and future) roots, simple additive approaches are generally unsuccessful. Definition of typical roots, which may represent part of the root system as a whole, is in a way the crux of the problem. Various quantitative descriptions of water uptake from soils as a function of root density have been developed in the past decades, but macroscopic models of root functions at the crop level could hardly ever be derived from microscopic, single root models.

Nye, Barber and coworkers took a mechanistic, quantitative approach to nutrient uptake by roots in the soil (Nye and Tinker, 1977; Barber,1984). Starting from plant physiological concepts of the relation between nutrient uptake and external concentration, they described transport of nutrients towards a single root by diffusion and mass flow, as influenced by soil chemical and soil physical processes. When calculated uptake rates for all roots of a crop under normal agricultural conditions are added, unrealistically high nutrient contents in the crop are found (Barraclough, 1987). However, by adjustment of root physiological parameters in the model to values measured for the specific crop in the specific growth phase under specific climatic conditions, good agreement between calculated and experimental total uptake rates can be obtained (Silberbush and Barber, 1984).

In our view the major weakness in the approach of Nye and Barber is the neglect of internal regulation of nutrient uptake rates by the plant, which forms the background of the changing "physiological parameters" during the growth of a plant. In descriptions of plant water uptake it has been customary for a long time to start from transpirational demand and not from uptake potential by the roots, as transpiration clearly is the driving force for water uptake. Plant physiological experience shows that internal nutrient use by the crop may similarly regulate nutrient uptake rates (though not directly providing the "driving force"), as will be further discussed in chapter 3. Starting from such a description of nutrient and transpirational demand at the crop level we will formulate models of root function in this thesis which differ in essential aspects from the available theories.

1.4 Model approach

As a root system usually consists of branch roots of various orders, of varying age and of varying positions in the soil, a mechanistic approach is possible only by sufficient simplification. Starting from a very simple description of a single root supposedly representative of a whole root system in the soil, we will investigate the consequences of a number of complications such as the heterogeneous distribution of roots in structured soils and the variation in soil-root contact. The sets of conditions considered and the assumptions made will be mentioned in 1.5 and discussed in subsequent chapters.

To describe the soil-root-shoot system we have to consider:

1) the physico- chemical availability of water and nutrients in the soil,
2) the physiological uptake potential by roots, and
3) the relation of actual uptake rate to crop requirement.

Our first interest is to quantify critical situations where nutrient and water uptake are just sufficient to support the production level determined by aboveground conditions. We will assume that the crop is growing at this potential rate and evaluate for how long the required uptake rate can be maintained, as a function of root density and amount of available nutrients and water.

Limitations to plant growth due to shortage of nutrients are most likely to occur either at the start or towards the end of the growing season. Figure 1.7 shows the growth response of grassland on P-fertilization in a P-deficient soil: different fertilization rates resulted in differences in growth in the exponential phase; in the subsequent linear growth phase the absolute growth rates were the same and absolute differences in cumulative dry matter production remained unaltered; later, non-fertilized plots showed decreasing growth rates, while fertilized plots continued at an approximately constant growth rate. Insufficient uptake at the end of the growing season may have been caused by local depletion of soil resources by the root system. Our model calculations primarily aim at describing the period of unconstrained uptake, i.e. the period in which local depletion around the root does not restrict uptake.

The amount of water stored in the soil within reach of the root system is

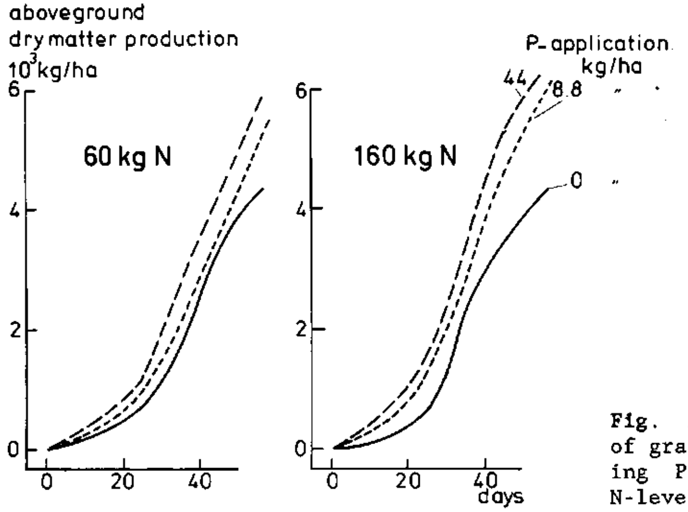


Fig. 1.7 Dry matter production of grassland in 50 days following P-fertilization at two N-levels (Mulder, 1949).

never sufficient to meet the transpirational requirements during a whole growing season; timely replenishment by rain, irrigation or capillary rise is required. Our calculations for water are aimed at determining which part of the available water can be taken up at the required rate, as influenced by root density (figure 1.2). Critical situations of water shortage at specific growth stages will affect flowering, fruit set and other transitions in the life cycle of a plant, apart from general effects on dry matter production. Our calculations end at the start of such critical situations.

Our models start from the assumption that a plant fully controls its uptake rate (for both nutrients and water) according to its needs in situations of adequate supply (De Willigen and Van Noordwijk, 1978; Van Noordwijk and De Willigen, 1979; De Willigen, 1981; Van Noordwijk, 1983a). This assumption contrasts with the starting point of Nye's and Barber's models, where uptake rates are governed by external concentrations at the root surface. In our models uptake rates are largely independent of external concentration. The following procedure is followed:

a) the total daily uptake requirement of the crop for nutrients and water and the total root length are used to obtain the required uptake rate per unit root length,

b) the soil-root system is characterized by one or more typical roots, which deplete a certain amount of soil,

c) soil resources are used up at the required rate, until depletion of the root environment (counteracted by transport towards the root) has resulted in a limiting concentration at the root surface. At this limiting concentration the physiological abilities of the root allow a just sufficiently high uptake rate. The limiting concentration is determined by plant physiological parameters and by the required uptake rate per unit root. As will be discussed later, the limiting concentration for nutrients can be taken as zero for most agricultural conditions at normal root densities. For water the limiting concentration is determined by the most negative plant water potential that is acceptable and by the hydraulic conductivity of roots.

d) when the limiting water content or concentration is reached, a certain amount of available water and nutrients still remains in the soil. For linearly adsorbed nutrients this amount is proportional to the integral of the

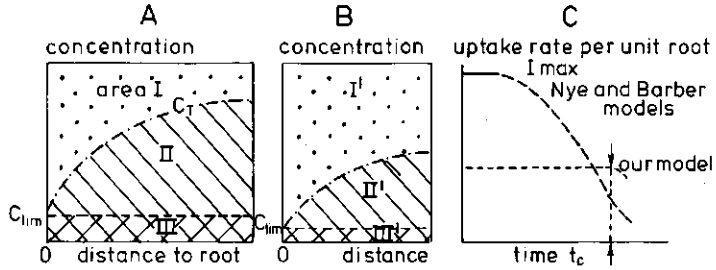


Fig. 1.8 Schematic representation of a model assuming a constant daily uptake; A. starting from a uniform initial concentration C_i, uptake proceeds till time T_c when the concentration at the root surface has reached a limiting concentration, C_{lim}; in the case of linear adsorption the area under the concentration profile at this point in time C_T indicates the part of available resources not usable at the required rate; area I, II and III are discussed in the text; B. the effect of a doubling of root density in our model (compare with A): required uptake rate is halved, so the concentration profile can be flatter, diffusion distances are reduced by $\sqrt{2}$ and the limiting concentration is lower; C. in comparison with Nye's and Barber's model descriptions, our model usually starts from an uptake rate lower than I_{max}, which remains constant over a much longer period.

remaining concentration profile over the relevant area (figure 1.8 A). Part of this area (area II) is due to physicochemical constraints to water and nutrient transport towards the root; the remaining part (area III) to physiological characteristics of the root determining the limiting concentration. In this figure we assume that the concentration decreases by uptake only during the period considered.

Knowledge of the size of areas I, II and III gives us two important answers we need: the length of time during which uptake may proceed at the required rate is found by dividing area I by daily uptake requirements; apparent nutrient recovery (relative depletion potential) is measured as the ratio of area I and area I + II + III. The main steps required now are to define a typical root with its volume of soil, to define the required uptake rate and to calculate the critical concentration profile. Formulation of the critical concentration profile for various root geometries forms the central part of our work. Increasing the root density affects all steps taken (figure 1.8 B).

Figure 1.8 C compares our approach with the models of Nye and Barber in which the uptake rate by a single root will decrease with the concentration at the root surface as soon as the <u>maximum</u> uptake rate (I_{max}) can no longer be maintained; most versions of the Nye models do not consider a maximum uptake rate at all. In our model we continue with a constant daily uptake rate per unit root until the <u>required</u> uptake rate can no longer be maintained.

Chapter 7 and 9 will present a mathematical formulation of the model outlined above. In chapter 9-11 analytical and numerical solutions to the differential equations formulated will be presented for situations of increasing geometrical complexity. For more complex situations, in which various classes of typical roots are distinguished within a single root system, the total required uptake rate has to be distributed over the respective classes of roots. This problem will be dealt with in chapter 12, using results of single root situations to estimate the performance of root systems of a heterogeneous nature. As we describe both water and nutrient uptake as governed by plant demand, the boundary conditions in the mathematical description of the transport processes are essentially the same. For some nutrients mobility in the soil is not influenced by their concentration (linear adsorption); for such situations analytical solutions to the relevant differential equations can be found. For the more complex problems of nutrients with nonlinear adsorption and for water (in both cases mobility depends on the concentration and water content in a way which is specific for each soil type) the analytical solutions may still form the basis for quantification (chapter 9).

1.5 Assumptions of our model approach

We will now outline the main groups of assumptions underlying our model, formulating specific questions for the discussion of the assumptions and estimation of typical parameter values in chapters 2 to 7. A basic assumption is that roots influence the performance of the whole plant primarily through their role in water and nutrient uptake (chapter 2). The relation between root and shoot growth in the field can be adequately analyzed in terms of external resource supply and a functional equilibrium between shoot and root growth instead of traditional explanations in terms of a morphological equilibrium ("the more roots the better...."). However, field evidence does not provide an unequivocal answer to the question whether nutrient and water uptake by the roots directly limits plant growth, or whether internal reflections of external conditions, for instance in hormone levels, modify plant growth before internal shortages of resources are felt. In chapter 4 experiments will be discussed in this context, describing the minimum size of root systems under optimal supply of water and nutrients. We will show that the critical size of the root system under these supposedly ideal conditions is in fact determined by the (physiological) possibilities for water and nutrient uptake per unit root.

A second group of assumptions relates to the description of nutrient and water uptake and more specifically to the amount of control a plant exerts over total nutrient and water uptake. In chapter 3 we will review literature on nutrient and water uptake to discuss the validity of the main concepts used and assumptions made in our models and to arrive at reasonable parameter estimates. The most important questions in this chapter are:

* how realistic is our assumption of complete regulation?
* how can the limiting nutrient concentration be defined?
* how can daily uptake requirements be defined?
* which distinctions between roots are required in defining typical roots, e.g. age, diameter, branching?
* how can the relation between plant water potential and water uptake rates be described?

The review of literature on physiological aspects of water and nutrient uptake in this chapter (3) will form a basis for the experiments in chapter 4 as well. On the physiological level water and nutrient uptake interact in a number of ways. In chapter 3 we will focus on the osmotic effects of ions accumulating around the root on plant water uptake. Accumulation of salts forms a major obstacle in obtaining acceptable nutrient use efficiencies in modern horticulture on soilless media (chapter 5). Required root volume in these artificial substrates strongly depends on the degree of synchronization between nutrient supply and nutrient demand.

A third group of assumptions is related to the geometry of roots and root systems (chapter 6). The relation between root length, surface area, volume and weight is important as root function probably is related to root length or surface area, while carbon costs of root formation and maintenance are related to root weight. A survey of values of the specific root length (m/g) and related parameters in the literature will be included here. Discussion of the geometry of root systems in the field leads to the definition of specific cases for which the depletion efficiency will be formulated in subsequent chapters.

The simplifications we make in describing nutrient and water mobility in the soil will be discussed in chapter 7, along with the formulation of the general transport equation and estimation of relevant parameter values. In our model calculations on water and nutrient uptake we assume that the aeration requirements of roots are satisfied. In chapter 8 we will investigate this assumption by describing transport of oxygen to all root cells by external as well as internal pathways.

Results of model calculations on nutrient uptake on a microscopic (single root) level obtained (chapter 9-12), will be compared with experimental results of nutrient recovery on a macroscopic (crop) level in chapters 13 and 14. In chapter 13 an example of the need for synchronization of nutrient supply and uptake demand by roots in situations of high nutrient mobility will be discussed for nitrogen in the humid tropics. In chapter 14 P-uptake by grasses will be discussed as an example of the importance of root length density for nutrients of low mobility. In chapter 15 we will review the extent to which our present theory may answer the questions raised in this introduction: can we relate fractional depletion of available nutrients and water to root density and other parameters and can we derive reliable methods for estimating available nutrient supply from our theory. In the final discussion, chapter 16, optimal root systems will be considered in view of the conflicting requirements for aeration and nutrition.

2. AGRICULTURAL CONCEPTS OF ROOTS: FROM MORPHOGENETIC TO FUNCTIONAL EQUILIBRIUM BETWEEN ROOT AND SHOOT GROWTH

2.1 Concepts of root growth and function

2.1.1 Introduction

A major assumption behind our models is that the main importance roots have for plant production is their role in nutrient and water uptake; thus we do not consider stability of the plant and specific hormonal interactions as critical root functions. We use the concept of a functional equilibrium between shoot and root growth (Brouwer, 1963). This concept has replaced older ones in which the balance between shoot and root growth was supposed to be based on morphological (form, size) or morphogenetic interactions. A consequence of the functional equilibrium concept is that the old maxim "the more roots, the better crop production" is no longer universally valid. The morphogenetic equilibrium theories predict effects of improved rooting on yield in any situation, while the functional equilibrium concept, as used here, predicts effects of improved rooting on fractional depletion of available resources and hence predicts only effects on yield in situations of suboptimal supply. Distinction between the two predictions is possible under optimal supply conditions. In this chapter we will review these concepts and summarize some agricultural experience on which a distinction between the two predictions can be made.

2.1.2 Morphogenetic equilibrium

In the older literature (Schulze, 1911) many attempts were made to directly relate rooting depth to plant height or, for trees, lateral root expansion to crown diameter. Shoot/root ratios expressed on this basis were very variable. Still, short-straw varieties of cereals were presumed to be shallow-rooted (Lupton et al., 1974). When the idea of a direct correspondence between root and shoot length (a morphological equilibrium or balance of form) was refuted, the concept of a morphogenetic equilibrium remained.

In the concept of a morphogenetic equilibrium the complete attainment of the potential aboveground production is supposed to depend on the full realization of the belowground growth potential. This was expressed by Hellriegel in 1883 in a "basic law of agriculture": "Das gesamte Wachstum der oberirdischen Pflanze ist streng abhängig von dem Entwicklungsgrade, den die Wurzel erreicht. Nur wenn die letztere sich zu ihrer höchsten Vollkommenheit auszubilden vermag, kann sich die oberirdische Pflanze in aller Üppigkeit entfalten. Es ist nicht möglich, das Wachstum der Wurzel zu beschränken, ohne die Entwicklung des Stammes und der Zweige zugleich zu hemmen. Es wird erlaubt sein zu vermuten, dass jede Pflanzenart bei der Anlage ihrer Wurzel so gut eine besondere und eigentümliche architektonische Idee verfolgt wie bei der Anlage ihres oberirdischen Teils. Ist aber diese Vermütung richtig, so wird man jeden Umstand, der geeignet ist, die Pflanze in der Verfolgung dieser Idee wesentlich zu hindern, als nachteilig für die Vegetation derselben zu betrachten haben; man wird schliessen mussen, dass jede Planzart so gut ihr bestimmtes Bodenvolum verlangt um den höchsten Grad ihrer Ausbildung zu erlangen, wie ihre bestimmte Menge von Kali und Phosphorsäure, ja dass sogar die Form des ihr zur Ausnützung verfügbaren Bodenkorpers nicht ganz gleichgültig ist." (Schulze, 1911). The main task for root research in this context was to separate the "ideal type" of root system of each crop or plant species from the environmental modification of this type found in any situation. This proved to be no simple task.

Quantitative measurements of root and shoot growth, however, raised doubt about the validity of Helriegel's law, which for agricultural practice could be simplified to "the more roots, the better shoot growth". Tucker and Von Seelhorst (1898) performed pot experiments in which root and shoot growth were recorded under different conditions of nutrient and water supply (fig. 2.1). The results clearly show that maximum shoot growth occurred in the wettest pots, while maximum root production was found in drier soil. The consequences of this falsification of Hellriegel's law were not fully accepted, however. For a long time the increase in root growth which can be observed when groundwater tables are lowered, was considered to be an inherently positive effect of drier soil conditions, even when susceptibility to drought was increased by such measures. Agricultural interventions such as lowering the groundwater table or deep soil tillage often result in better growth of both roots and shoots in the first year(s) after the intervention. On further analysis, this effect is not due to Hellriegel's law, but to a temporarily increased mineralization of soil organic matter, supplying extra nitrogen to the crop (see 2.2.2).

More recently, versions of the morphogenetic equilibrium concept are stated in the form of a hormonal equilibrium. According to this concept a continuous activity of hormone-producing root meristems is required for shoot growth and this hormone production function of roots, rather than their nutrient and water uptake, may limit plant growth. Evidence exists for effects of root-produced cytokinins on shoot growth and functioning, and of shoot-produced abscisic acid on root functioning. These effects may be regarded as the internal translation of information about the relation between the plant and the environment. Environmental conditions have to influence relevant parts of root or shoot (receptors) before a signal, possibly in the form of a hormone, can be produced. Response to the signal can only be functional to the plant (or adaptive), when it is related to the information the signal contains about cur-

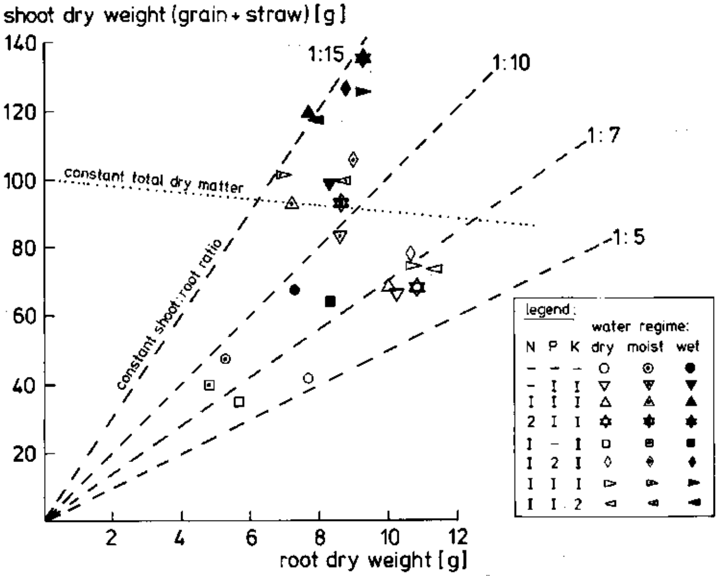


Fig. 2.1 Root and shoot dry weight of oats in pots maintained at three different soil water contents by frequent weighing and watering, with various fertilization levels (Tucker and Von Seelhorst, 1898).

rent conditions in the plant's environment and the rate with which external resources can be obtained. Neglect of the environmental information carried by plant hormones leads to the expectation that plant growth can be promoted by supplying extra hormones (or related substances) to the plants, in the form of organic manures, (bacterial) preparations or synthetic hormones. Although it is possible to overrule the internal regulation of root and shoot growth with such substances, the modified plants are seldom better adapted to utilize environmental resources, and externally applied hormones are often intended to act as herbicides. Positive effects of externally applied hormones on crop growth occur when it is desirable to switch the plant into a different growth phase; e.g. promotion of root initiation of stem cuttings, inducing a shift from vegetative to generative phase in the life cycle of the plant and influencing fruit set.

2.1.3 Environmental determinism

Agri cultura means cultivating land. The success of this manipulation of the soil, the root environment, has led to a form of environmental determinism. External influences are supposed to directly influence plant organs. "Phosphate stimulates root development" and "water attracts roots" (hydrotropism) are typical statements of this view. These statements were based mainly on observations that P-deficient plants develop extra branch roots near local phosphate supplies and that roots of water-stressed plants develop primarily in moist zones of the soil. Although experiments such as those of Goedewaagen (1932) showed that the local root response disappeared in plants well supplied with P, the misinterpretation that P will always stimulate root development led to recommendations to fertilize the subsoil with P in the presence of P-rich topsoil, to stimulate deep root development (see below). Wiersum (1958) and De Jager (1985) have shown that the local response is not specific for P, but can be observed for any nutrient (at least N, P, K and S) in short supply in the plant as a whole. The nutrient status of the plant, in combination with the heterogeneity of the external nutrient supply, determines whether or not a local root response will occur.

When the effects of variation in nutrient levels or water availability on root and shoot were investigated, a double-optimum curve usually was the result. Phosphate is no exception, as shown in figure 1.6 (Goedewaagen, 1937). The optimum for root growth generally occurs at a lower level of external supply than the optimum for shoot growth and root function (nutrient and water uptake). This effect was discussed by Goedewaagen (1937) for N and P and later presented in graphical form by Schuurman (1983) (figure 2.2). Although this observation in fact falsified the previous expectation that more roots will always give better crop growth, the negative effects on root growth at high external nutrient supply were usually seen as something inherently bad. The idea that this reduced root growth reflected a meaningful response of the plant to external conditions only gradually gained ground.

2.1.4 Functional equilibrium

Boonstra (1934, 1955) defined "root value" as the plant dry matter production per unit root weight and used this quantity for selecting cultivars with small but efficient root systems. This approach was an early attempt at quantification of root functions for the whole plant. Varieties with a high shoot/root ratio under fertile conditions gave a higher (shoot) yield than varieties with a low shoot/root ratio and absorbed more water and minerals per unit root dry weight (Goedewaagen, 1937). Such considerations and the demonstration of active regulation by the plant to restore shoot/root balance after disturbance

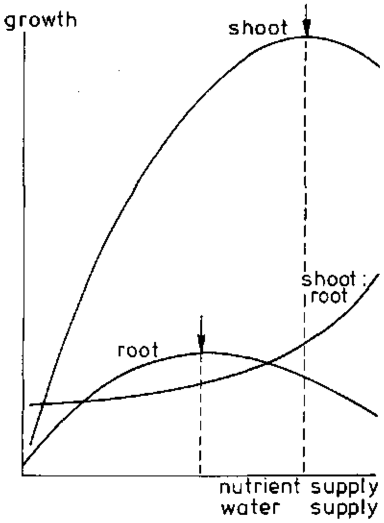


Fig. 2.2 Schematic response of root and shoot growth of annual plants to variation in the supply of water and nutrients (Schuurman, 1983).

by removing part of either organ led to the concept of a functional equilibrium between shoot and root growth, in response to environmental conditions (Brouwer, 1963; 1983). The essential difference from the morphogenetic equilibrium is that the shoot and root are not assumed to respond to the size of the other plant part, but to the effectiveness (rate) at which basic needs are acquired from the environment by the complementary organs. The main difference from the environmental determinism is that the response to external factors depends on the internal condition of the plant. In Brouwer's concept the proximate level of regulation, through competition between root and shoot for carbohydrate and nutrients, is directly coupled to the environmental factors which determine the ultimate sense or non-sense of the plant's growth response. Further studies have shown that internal control on the proximate level can be exerted in various ways (Lambers, 1983).

The functional equilibrium concept together with considerations of nutrient and water supply in the soil may account for two types of empirical evidence, not in agreement with the previous concepts: small root systems may be sufficient for maximum plant growth under conditions of optimum supply of water and nutrients, and manipulating the soil for more roots may be counterproductive.

2.2 Agricultural experience

2.2.1 Small root systems may be sufficient for maximum plant growth

The experiment of Tucker and Von Seelhorst shown in figure 2.1 demonstrated that a comparatively small root sytem under continuously moist and nutrient-rich conditions in the pots allowed a maximum shoot production. The presence of many roots does not necessarily coincide with a high uptake rate of water and nutrients and a weakly branched root system may sometimes achieve much more than one would expect. Other situations where small root systems are able to support (near-)maximum crop growth occurred:

- in recently reclaimed polders under constantly wet and fertile conditions (Goedewaagen, 1955; figure 2.3),
- under supplementary fertilization in compacted soils (Schuurman, 1971), and
- in nutrient solutions in artificial substrates in horticulture (chapter 4 and 5, figure 4.1).

Under certain conditions smaller root systems may even result in higher yields. Passioura (1972, 1983) reported a situation where crops have to complete their life cycle on the amount of water stored in the profile at the start of the growing season. In this case a lower rate of water consumption in the initial phase is positive for the harvest index and hence for the final yield. Cultivars have been selected with a lower xylem diameter which have a lower rate of water uptake. Root growth in such cases has to be in phase with the plant's water demand during its life cycle. Agricultural selection for growth in a monoculture may add a characteristic to the plant's genome which *is not viable in a multi-species environment.* In natural *situations* competition between and within species will hinder the evolution of such water saving behaviour (Wright and Smith, 1983), unless plants are strongly allelopathic. Cowan (1986) discussed optimal plant strategies in water use under uncertain rainfall conditions: restricted water use by stomatal closure in situations where there is no direct physical need to do so, may increase the amount of water available in a later period when it may be used more efficiently. Changes in relative sensitivity to water stress during the plant's life cycle complicate the choice of "optimal" root characteristics for

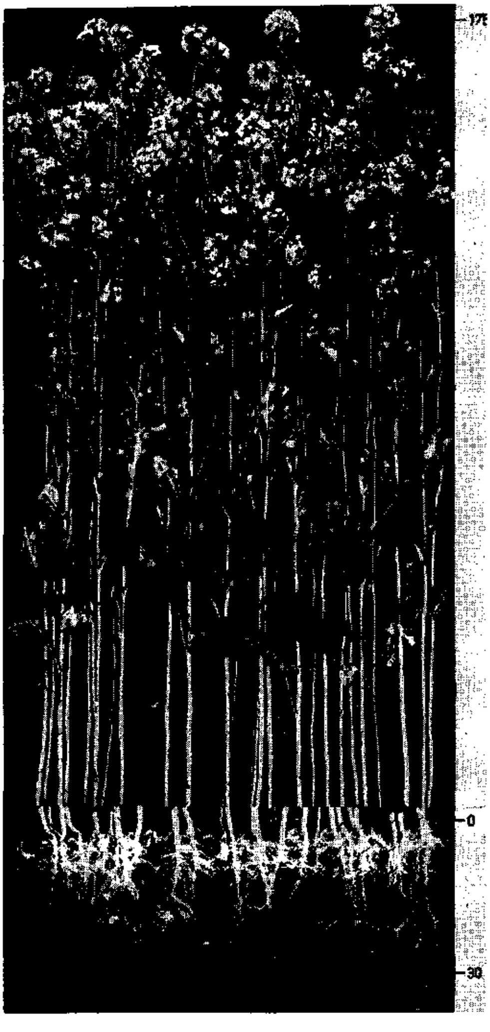


Fig. 2.3 Root and shoot of Colza (oilseed rape, Brassica napus) in a recently reclaimed polder (1948, Noordoostpolder). Poor aeration combined with ample supply of water and nutrients caused an extremely high shoot/root ratio (Goedewaagen, 1955).

such environments, but a restricted water use in early phases by a rather small root distribution and/or high internal resistance to water transport in combination with a deep root system and low internal resistance later on, have a positive effect on harvest index and hence on agricultural water use efficiency for plants growing on water stored in the soil.

2.2.2 Manipulating the soil for more roots may be counterproductive

2.2.2.1 Manipulating depth of water table

High water tables in the growing season restrict root development. Lowering the water table usually results in an increase of rooting depth. However, positive effects on crop yield of lowering the water table in many field experiments can be attributed to a temporary increase in mineralization of soil organic matter and possibly an increased N-recovery, providing extra nitrogen to the crop, and not to a direct effect on the maximum yield level of the increased root development as such. Especially on peat soils, lowering the water table results in mineralization of soil organic matter, providing N to the plant.

Van Hoorn (1958), discussing a field experiment with arable crops on a clay soil, went so far as to predict that all yield depressions caused by a shallow water table might be compensated by applying more fertilizer (nitrogen and other nutrients). For arable crops, Van Hoorn found that deeper groundwater tables resulted in an additional availability to the plant of some 100 kg N/ha. Sieben (1974) found a difference in soil N-supply of 30 kg N/ha between high and low groundwater tables. Minderhoud (1960) found similar effects on grassland on basin clay soils and peat soils. Van Wijk and Feddes (1975) stated that compensation of negative yield effects of high groundwater tables by extra N-fertilization was incomplete on grassland. The experiments they discussed did not allow such a conclusion, however, as the maximum N-level used in this experiment was not high enough to fully meet the N-demand of the crop.

In mechanized agriculture soil compacting effects of tractor wheels can be reduced by maintaining drier soil conditions. Thus the final economical evaluation for the farmer of reducing groundwater levels may be positive, even when effects on plant growth as such are negative (Boekel, 1974; Wesseling, 1974). Figure 2.4 shows results of a long-term soil column experiment with variation in the groundwater table in the absence of soil compaction by machinery (Schuurman et al., 1977). Negative effects of low groundwater tables on crop yield in dry years are larger than positive effects in wet years. A direct consequence of the lowering of groundwater levels in agricultural land improvement schemes in the Netherlands is an increased need for (sprinkler) irrigation in dry periods. The main effect of sprinkler irrigation may be to restore a sufficient water content in the topsoil to allow diffusion of nutrients to the roots (Garwood and Williams, 1967). The increased need for sprinkling irrigation as a consequence of lowering groundwater tables leads to conflicts between agriculture and both civic water use and the desire to maintain forests and nature reserves in their original condition.

Aeration problems, with direct effects on roots and indirect effects due to increased denitrification rates, mainly occur after heavy rainfall in summer. Aeration requirements and tolerance to temporary anaerobiosis vary considerably among crops, internal aeration of the roots by air channels in the root cortex playing an important role (Goedewaagen, 1942; Chapter 8). Drainage requirements to cope with high summer rainfall can be met by a dense, rather shallow drainage system or a deeper, more widely spaced system (Raadsma, 1974). In the Netherlands the choice has been for the latter, mainly for financial reasons. Fluctuations in groundwater level of the same absolute

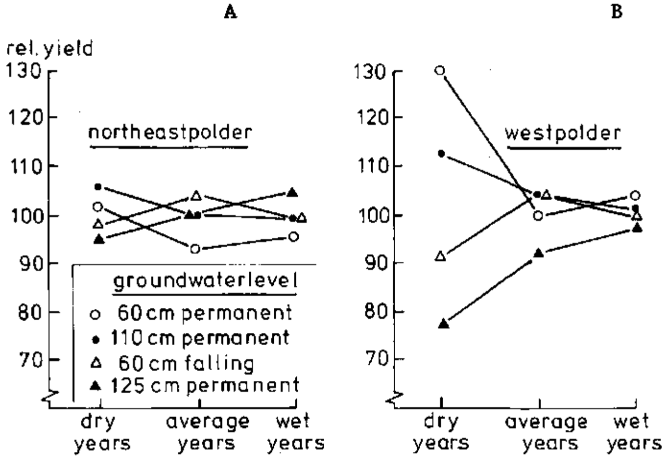


Fig. 2.4 Yield effect of groundwater levels on 9 loam/sand profiles in large columns with undisturbed soil profiles (A: 4 from Noordoostpolder; B: 5 from Westpolder, N. Groningen); relative yields are shown as the aggregate of a crop rotation for four groundwater levels (constant at -60, -110 and < -125cm, or starting at -60 and falling during the growing season); years were classified according to water deficit in the growing season; deep water tables gave deep rooting (Schuurman et al., 1977).

size may be much less problematic for the crop when they occur at lower depths in the soil profile, so drainage requirements can be lower for deeper systems. It is interesting to note that development in agriculture has been towards drier soil conditions by introducing deep drainage - followed by deep soil tillage to improve the drought resistance of crops, and by sprinkler irrigation to deal with dry periods (Van Ouwerkerk and Raats, 1986) - while glasshouse horticulture has switched to wetter conditions by implementing water culture techniques to obtain higher yields (Chapter 5). The main difference between modern agriculture and glasshouse horticulture in this respect is that in agriculture the root environment has to support the heavy pressures of tractors and harvest equipment, while in glasshouses root environment and traffic lanes are separated.

It is now widely acknowledged that the need for maintaining soil structure under the heavy machinery used (especially in spring and autumn), is the main reason for lowering water tables (alternatively leading to extension of the growing period if the same amount of damage to the soil structure is accepted), while from a point of view of plant production per se effects may be negative or at least depend on rainfall (Van Wijk and Feddes, 1986; Boekel, 1982; Cannell et al., 1986).

2.2.2.2 Deep soil tillage

Marcus Porcius Cato stated in his book "De Agri Cultura" in about 200 B.C.: "Quid est agrum bene colere? Bene arare. Quid secundum? Arare. Quid tertium? Stercorare. [What is good cultivation? Good plowing. What next? Plowing. What third? Manuring.] (Hooper and Ash, 1935). Cato's preference for plowing as a prime measure to improve crop yields was in accordance with agricultural practice in many situations around the world ("when the crop stands still, stir the soil"; Scott Russell, 1981). The explanation of the positive effects of plowing on subsequent crop growth has varied considerably. Weed control, stimulating mineralization of soil organic matter, modifying the soil water balance and improving conditions for root growth have all been considered as principal reasons. In a number of cases of (deep) soil tillage, however, negative yield effects were found, despite positive effects on root growth.

The agricultural need for plowing or other means of soil cultivation depends on climatological conditions and on the existing pressures on the soil leading to soil compaction. The availability of herbicides to control weeds has decreased the need for plowing under certain conditions and surprisingly positive yield responses have been obtained under zero-tillage, despite reduced root development under such conditions. Especially in England minimum tillage has been advocated for permanent cereal-growing areas; root functions in nutrient and water uptake may be unimpaired by the combination of a reduced and more superficial root system, the fact that phosphate fertilizers are not mixed through the soil and the fact that topsoil remains moist throughout most of the growing season (Scott Russell, 1977; Cannell et al., 1986). The severe damage to soil structure caused by heavy machinery and by harvesting procedures for potato and sugar beet under wet conditions have prevented application of such minimum tillage systems in the Netherlands (Westmaas research group on new tillage systems, 1984; Van Ouwerkerk, 1986). In tropical regions minimum tillage systems deserve special attention as they reduce the risk of soil erosion (Lal, 1984).

Deep soil tillage in situations where an impenetrable layer prevents deep root development may have positive effects on drought resistance of crops if it makes a deep groundwater table accessible to the root system. In other cases manipulation of the soil to increase root penetration has given neutral or negative effects on crop yields apart from first years N-effects (Alblas, 1984). Figure 2.5 shows results of a deep soil tillage experiment on grassland. Deep soil tillage in this experiment effectively reduced the penetration resistance of the soil and had the expected positive effects on root development. Deep P-fertilization had no effect on root development in the presence of P-rich topsoil. Positive effects on grass yield in the first year, however, could be completely compensated by extra nitrogen fertilization on control plots. In the subsequent years this nitrogen effect of soil tillage disappeared and the grass appeared to be more instead of less sensitive to drought as a result of the intervention. Measurements showed that water storage in the (sandy) soil was reduced by loosening the soil (Schothorst and Hettinga, 1983). In this case the extra nitrogen available to the crop in the first year was probably due completely to an increase of mineralization, not to improved recovery.

2.2.3 More roots may give better utilization of resources

From the examples given it may be clear that the statement "the larger a root system the better" is untenable as a generalization if maximization of yields is the primary criterion. Roots have no direct influence on maximum yields as supposed in Hellriegel's law; however, the size of the root system may have a positive effect on fractional depletion of available nutrients and water. The size of the root system always has to be evaluated along with the supply of water and nutrients. If a larger root system can only be obtained while reducing the effective supply of water and/or nutrients, plant production may decrease instead of increase. If the root system can be improved, however, without affecting the level of supply, better crop growth may be possible at moderate soil fertility, or maximum yields may be obtained at a lower input level. A safe method in this respect may be to make use of the genetic variation in root systems within and between crop species by plant breeding. Comparison of root systems of varieties of one crop has often shown

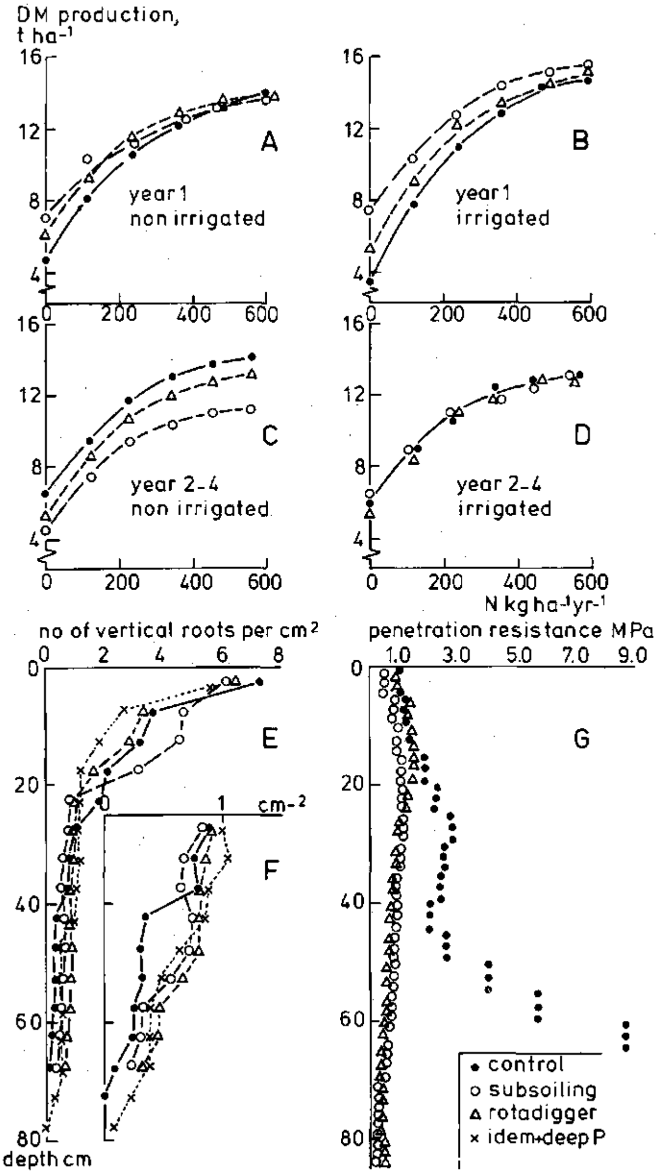


Fig. 2.5 Effects of deep soil tillage on grassland on a sandy soil at Heino: A-D grass yields in the first experimental year (1977) and subsequent years (average for 1978-1980) in relation to N-fertilization and sprinkler irrigation, E,F a. root development, G. penetration resistance (A-D and G based on Schothorst and Hettinga, 1983).

clear differences in root architecture and/or total size of the root system. Heritability for root characteristics is comparable to that for shoot morphological factors (Troughton and Whittington, 1968).

Comparison of root characteristics of different cultivars has shown that no ideal set of root characteristics exists, suitable for all conditions. El Bassam (1983) found evidence that some Ethiopian land races of cereals showed much better root penetration and consequently drought resistance than modern varieties, which give a higher yield under well-watered conditions. Weaver and Brunner (1927) already described the existence of three landraces of linseed in India, each one adapted to a particular soil type and not thriving in each others environment (deep-rooted, sparse root system in black-soil areas; superficial, intense root systems on wetter, alluvial soils and an intermediate type).

In selecting new crop varieties, however, little attention has been paid to root characteristics, and the fear has been expressed that by selection under fertile soil conditions in fact a selection for less developed root systems took place. Although some reasons exist for such fear for implicit selection on high shoot/root ratios (Boonstra, 1955), little experimental evidence is available. Pommer (1983) compared root systems of new and traditional varieties of temperate region cereals, under several input levels. Under mineral NPK fertilizer regimes new varieties of wheat, barley and oats had more roots than traditional varieties, but on manure treatments there was a tendency in the opposite direction. Lupton et al. (1974) found only small differences between root systems of semidwarf and traditional taller varieties of winter wheats. Similarly, Wright et al. (1983), comparing root growth of tall and dwarf Sorghum varieties, came to the conclusion that genetic control of root growth is apparently independent of genes for stem growth and selection on aboveground characteristics does not directly lead to a change in root system characteristics.

If root development is insufficient to reach all parts of the soil, extra root growth may have the same direct effect on yield as fertilization. Kuilman (1948) described a "disease" of paddy rice in Indonesia, Omo mentek, characterised by yellow leaves after transplanting the young rice plants. Varieties tolerant to this "disease" had a more finely branched root system. According to Kuilman the "disease" was K deficiency in the plant, despite reasonable K levels in the soil. Attention to root branching in programs for cultivar selection could solve the problem (no K fertilization was necessary in this case). Similarly, under conditions of low K mobility in the soil, root length density was positively related to potassium uptake and yield of corn in experiments of Kuchenbuch and Barber (1987).

For phosphate the influence of root length density on uptake is probably stronger than for potassium. Elsewhere, (Van Noordwijk and De Willigen, 1986, figure 4) we showed results of an unpublished experiment with mustard and potato by Van der Paauw in 1962, in which root length density in the soil was manipulated by varying the pot size and the number of plants per pot. In this experiment root length density, L_{rv}, was in the range 1 to 5 cm/cm^3. For each of the four soil P levels, a higher value of L_{rv} was correlated with a higher P-uptake per unit volume of soil. Only for mustard at the highest P level used in the experiment, still low in an absolute sense, saturation of P-demand could be seen at high L_{rv}. Otherwise both a higher L_{rv} value and a higher P-status of the soil correlated with a higher P-uptake.

Fungal hyphae as part of mycorrhiza ("fungus-root") may considerably enhance P uptake from (moderately) poor soils, acting as extended root systems (Ruyssen, 1982). As the optimum for mycorrhiza development is found to the left of the optimum for roots in figure 2.2 (Lamont, 1983), it is questionable, however, whether mycorrhiza can play a role of any significance at the required production levels of Dutch agriculture (Ruyssen, 1982; chapter 14).

As long as increased root growth was supposed to be positive for yield as such, and not for nutrient use efficiency, soil tillage experiments were done under high chemical soil fertility conditions - and rarely showed yield effects. Quantification of the interactions between nutrient supply, water content, root development and uptake requirements is needed. With that information, we may hope to better understand the effects of soil structure on crop growth. Negative yield effects of soil compaction can be due, at least in part, to reduced root growth. Prummel (1975) found that soil compaction on a basin clay soil lowered the potential production level of flax, barley and sugar beet. P-uptake was reduced by soil compaction in most cases, leading to a a need for a higher external P supply to obtain the P-uptake required for maximum growth. In comparable experiments Boone and Veen (1982) found that reduced P-uptake was largely due to reduced root growth, P-uptake per unit root being unaffected. Extra P-fertilization could in these experiments only partially compensate for negative yield effects of a poor soil structure.

On sandy soils, soil compaction affects the overall possibilities for root penetration. On clay soils, soil compaction in the field (in contrast with the experiments quoted before) mainly affects the soil structure, the size and shape of soil aggregates. Wiersum (1962) performed elegant experiments with artificially created soil aggregates of various sizes, and showed that P-uptake is seriously hindered when roots cannot penetrate large aggregates, when compared with small aggregates, while for N there is little effect of aggregate size on possibilities for uptake. Similar effects were described by Voorhees et al. (1971). To a certain extent the negative yield effects of a poor soil structure, i.e. low pore volume, high bulk density and/or coarse aggregates, can be compensated by extra N or P fertilization (N to compensate for increased denitrification losses, P to compensate for reduced accessibility of soil P); usually this compensation is not complete, however. Negative effects on plant growth of poor soil structure which cannot be compensated by extra fertilization or irrigation, may be due to insufficient aeration of the root system. Requirements for aeration of the roots may conflict with requirements for water and nutrient uptake, as will be discussed in more detail in chapters 8 and 10.

Coarsely aggregated soils, or soils which can only be penetrated by roots in cracks and fissures, result in an inhomogeneous root distribution. The effects of this root pattern on accessibility of nutrients, in relation to mobility of the nutrient, form the subject of chapter 11.

2.3 Discussion

We now return to the main question of this chapter, whether or not it is acceptable to start from the functional equilibrium theory and to describe water and nutrient uptake as the prime functions of roots for the plant as a whole. In a number of cases we have seen that not the size of the root system or root growth as such, but the possibility of obtaining more water and nutrients is critical for positive yield response to agricultural manipulation of the soil. In most cases a difference in the amount of roots coincided with a difference in nutrient and water supply. In chapter 4 we will discuss experiments in which root growth was directly manipulated without a change in nutrient and water supply, which provides a more direct test of the assumption we use in our model calculations. First we will consider physiological aspects of water and nutrient uptake in more detail in chapter 3.

3. WATER AND NUTRIENT UPTAKE

3.1 Introduction

In this chapter we will review literature on nutrient and water uptake to discuss the validity of the main concepts and assumptions in our models and to obtain reasonable estimates for the parameters used. The most important assumptions are:

1. Uptake of nutrients and water is regulated by internal demand,
2. Daily nutrient requirements of crops are constant throughout the main part of the growing season,
3. The limiting nutrient concentration at the root surface which enables the plant to absorb nutrients at the required rate is virtually zero under agricultural conditions, except for P at low root densities and/or soils of high buffer capacity; thus when transport of nutrients to the root limits uptake, the root may be described as a zero-sink,
4. Physiologically based maximum uptake rates for nutrients and water determine the minimum root surface area necessary in situations of high external supply; this minimum is determined by the possible water uptake per unit root,
5. Hydraulic conductance of roots to entry of water does not depend on the water potential at the root surface and/or the transpirational demand,
6. The limiting water potential at the root surface at which the plant root can just take up water at the required rate is determined by the hydraulic conductance, the reflection coefficient of solutes at the root surface, the external salt concentration and the required uptake rate,
7. If external supply allows, all roots of a root system will take up water and nutrients at the same rate, irrespective of age, distance to the root tip and root diameter (i.e. apart from "live" and "dead" roots no distinctions are necessary),
8. Turnover of roots during the growing season is negligible, i.e. roots may function for several months.

3.2 Assumption 1: Internal regulation of nutrient uptake

3.2.1 History of concepts

The gradual recognition that the plant controls the total rate of nutrient uptake can be marked by the following quotations:

Liebig (quoted by Russell, 1973) stated that "all substances in solution in a soil are absorbed by the roots of a plant, exactly as a sponge imbibes a liquid and all that it contains, without selection."

Van den Honert (1933, 1936) used an experimental setup in which low concentrations of phosphate in a nutrient solution could be maintained by high flow rates and found that rather low concentrations (0.4 - 0.7 μmol/l) of phosphate were adequate to meet the requirement of the plant. Van den Honert (1936) described nutrient uptake as an active, selective process, using a conveyor belt as analogy: "Evidently the ions adsorbed are transported to the interior at a constant speed, which removes its charge from the surface, deposits it inside and returns empty to be charged again. The more the belt conveyor is charged, the higher the rate of intake." Van den Honert (1933): "In the first experiments taken another kind of curves was obtained ... The explanation may be that a stock of phosphate, still existing inside the plant, hampers the absorption."

Broyer and Hoagland (1943) showed that the rate of potassium uptake of young barley plants is influenced by pre-treatment to a "low salt" or a "high salt" condition and that uptake is relatively independent of current conditions of light and humidity. Epstein (1972) reviewed the nutrient uptake research which took place in the subsequent three decades, confirming that nutrient uptake by roots is selective (although not completely ion-specific) and active. This research was not based on measurements on roots of intact plants in fast flowing, dilute nutrient solutions as used by Van den Honert but on Hoagland's techniques, using excised roots of plants which had grown on a depleted nutrient solution for several weeks: low-salt roots.

Williams (1948) stated that the intake of phosphate "was more controlled by internal factors of demand than by external factors of supply." Still, Nye and Tinker (1977) stated as opening sentence of their book on solute movement in the soil-root system: "It is now widely accepted that under given growth conditions uptake of a solute by roots is related to its concentration in the soil solution and the extent to which this is buffered by the soil". Later (in section 7.3.5) they state: "On the other hand, it is obvious that the roots do not function as a simple "pump" for nutrients, without regard for the conditions of the rest of the plant, since plants would otherwise have extremely large nutrient concentrations. .... in general there must be a strong feedback control on root activity from the rest of the plant. The mechanism of this feedback is not known. It may simply be a matter of the total amount of carbohydrate or inorganic nutrient in the root or the shoot, or a hormonal mechanism."

Clarkson (1985): "This application of ion transport kinetics [the work of Epstein and followers] must have encouraged public spirited laboratory workers to believe that their painstaking observations were actually useful in the real world ... Several facts about kinetic parameters seem to have been overlooked in the enthusiasm generated in this work. In a given cultivar I_{max} and/or K_m are likely to vary with plant age, the nutrient concentration to which the plant has been acclimatized and the nutrient status of the plant. In addition Imax may be directly dependent on the inherent vigor of a plant and vary inversely with the relative root size or the fraction of roots having access to the nutrient. In a variety of circumstances, steady state concentrations of nutrients in roots and shoots seem to be independent of external ion concentration and environmental variables such as temperature. The relative expansion of root surface will have the effect of reducing the flux necessary to sustain a given nutrient, it can also reduce the minimum concentration necessary to maintain the inflow (see Wild and Breeze, 1981)."

Considering this development of ideas and concepts it is remarkable that in the 1930's when plant physiological research of nutrient uptake started to become quantitative, there was more interest for whole plant relations than in much of the research work of the 1950's when isolated roots in "tea-bags" became a standard plant physiological preparation. In subsequent years research was aimed at understanding the mechanism of the "conveyor belt" (Van den Honert), "carrier" (Epstein) or "nutrient specific ATPases", rather than on the way it functions in the whole plant under normal conditions. Van den Honert (1936) concluded from the rather low P-concentration required for maximum growth in his experiment: "This agrees well with a critical concentration in the soil solution found independently by soil chemical research". Although this was a very promising statement for understanding soil fertility experiments, soil chemical and plant physiological research for a long time followed separate paths.

3:2.2 Experimental evidence for internal regulation of nutrient uptake

Figure 3.1 shows dry matter production and P-uptake of permanent grassland under adequate P-supply, in the period up to a cut of grass in spring or summer (Van Burg, 1968; 1970). Variation in the rate of dry matter production

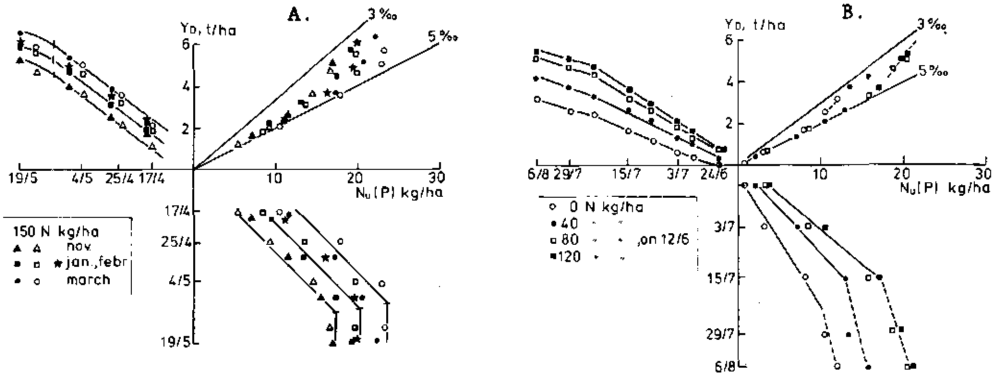


Fig. 3.1 Dry matter production and P-uptake in grassland with adequate P-supply, determined by frequent harvests during a growing period for a spring or a summer cut of grass; variation in dry matter production is reflected in variation in P-uptake by a constant P-content; A. results for two experimental fields in 1961 with N-fertilization of 150 kg/ha applied in autumn, winter or spring (data of Van Burg, 1968); B. results of one experiment in 1958 for a cutting period in summer with variation in N-level (data of Van Burg, 1970).

through variation in N-supply, directly leads to variation in P-demand, at constant internal P-contents. The fact that probably similar root systems under a constant P-supply take up different amounts of P, can not be easily explained by model descriptions, such as those of Nye and Tinker (1977) or Barber (1984), which are based on "physiological" parameters of the relation between external concentration and uptake rate. Experimental results such as shown in figure 3.1 can be easily accounted for when an efficient internal regulation of P-uptake is assumed.

The variation in internal nutrient contents of plants grown under widely

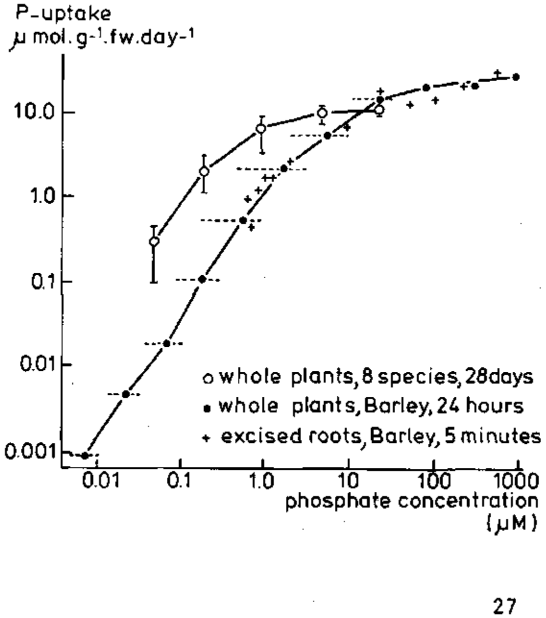


Fig. 3.2 Comparison of short- and long-term P uptake studies by Loneragan (1978)

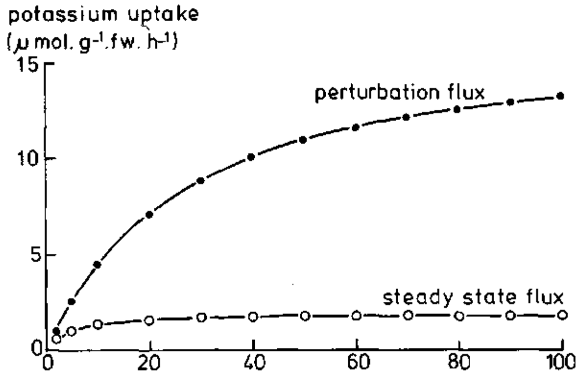


Fig. 3.3 Potassium uptake in relation to external concentration in long-term experiments (steady-state flux) and short-term measurements on low-salt roots (perturbation flux) (Glass and Siddiqi, 1984).

different external nutrient concentrations is small and certainly several orders of magnitude less than the range of conditions (external supply) under which plants can grow unimpeded. This simple observation shows that plants apparently have efficient homeostasis systems for nutrient uptake. This homeostasis implies that in the majority of situations nutrient uptake rates by roots are below the potential rate at the given external concentration. Loneragan and Asher (1967) were among the first in more recent time to use an experimental setup similar to that of Van den Honert: intact plants growing on solutions maintained at low concentrations by fast (re)circulation. They found the maximum uptake rate for phosphate to be lower and to be reached at a much lower concentration than in short-term "tea-bag" experiments (figure 3.2). Similar results were obtained for potassium (figure 3.3).

Although internal levels of nutrients in a plant clearly influence uptake rates by individual roots, observed uptake rates still are conventionally expressed as "root absorbing power" α [m/s], i.e. uptake rate per unit root surface area [mol/(m^2 s)] divided by the external concentration [mol/m^3]. Figure 3.4 shows how data on uptake rates by plants at different external concentrations presented in the form of α obscure the fact that after an initial stage net uptake rate [mol/(m^2 s)] varies very little over an external concentration range of a factor 100.

Various experiments have shown that manipulation of nutrient demand per unit root in fact leads to changes in uptake rate per unit root, although the response may not be immediate. Römer (1985) found that removing ears from wheat plants increased carbohydrate levels in leaves and roots, but sharply reduced P uptake per unit root. Caradus and Snaydon (1986) compared P uptake of 7 white clover populations and concluded that shoot characteristics determine P uptake: P uptake per unit root size was negatively correlated with root size; reciprocal grafting of genotypes indicated that shoot factors were decisive in P uptake; in split-root experiments P uptake per unit root could only be increased by internal shortage of P in the shoot.

Split-root experiments have yielded further evidence on regulation of nutrient uptake. Goedewaagen (1932) found that P-uptake per unit root weight from the same external supply was higher when only part of the roots were supplied with nutrients (figure 3.5). Jungk and Barber (1974) did not find an effect of root trimming on P-uptake in the first 8 hours after reducing the part of the root length of maize in contact with a P solution by 37-58%. After 4 days they found an increased P-uptake per unit root of 20-40%.

Split-root experiments on maize by De Jager (1985) showed that the uptake rate of N, P, K and S could be increased by localizing the supply of a particular nutrient to part of the root system, while uptake rates for non-locali-

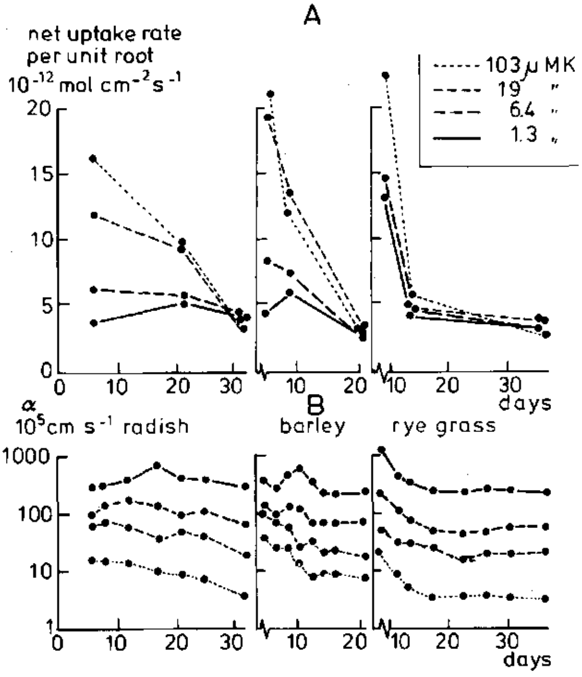


Fig. 3.4 Results of uptake experiments with intact plants on a fast recirculating nutrient solution maintained at constant concentrations; B. data were presented in the form of α by Wild and Breeze (1981) and have been recalculated to the original net uptake rates per unit root (A.).

zed nutrients remained constant. Regulation of nutrient uptake apparently is nutrient-specific. Specificity of regulation also follows from the ability of most plants to obtain an almost constant nutrient composition from a wide range of nutrient solutions (Steiner, 1984). General control systems, based on carbohydrate levels in the roots (Marschner, 1974) or hormone levels (Nye and Tinker, 1977) cannot explain specific regulation of the uptake of individual nutrients; internal carbohydrate or hormone levels cannot provide the root with sufficient information.

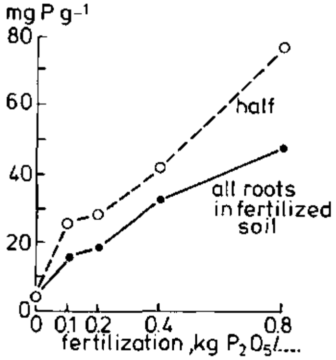


Fig. 3.5 P-uptake per unit root dry weight by oats in a split-root experiment in which plants received P-fertilizer on half or the whole rooted volume of soil (Goedewaagen, 1932).

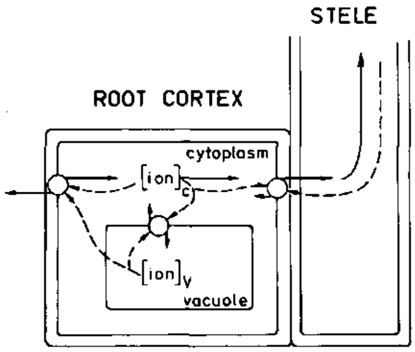


Fig. 3.6 Schematic presentation of relevant parts of the root in regulating nutrient uptake; solid lines indicate net flow of nutrients, broken lines indicate flow of information (Glass and Siddiqi, 1984).

3.2.3 Information required for regulation

The regulation problem can be presented schematically as in figure 3.6; the single root cell represents the symplastic pathway between epidermis and stele containing a large number of unconnected vacuoles. At three points on the interface between root symplast and apoplast/vacuole/stele active (energy consuming) transport occurs. Transport activity on these sites must be related to the nutrient status of the intact plant.

For each of the three sites control of the uptake and transport rate is possible through:

* differential synthesis and breakdown of carriers, according to the presence of nutrients in the cortical cells (coarse control),

* differential activity of the carriers, influenced by the internal nutrient concentration in the cortical cells (fine control); a simple allosteric mechanism has been suggested for this feedback (Glass, 1975),

* differential leakage or efflux from the cells dependent on the internal concentrations in the root, reducing net uptake rates at constant carrier activity (Deane-Drummond, 1986).

A majority of the authors on the mechanism of nutrient uptake and its regulation assume that active transport between apoplast and symplast and that between symplast and xylem are both directed towards the centre of the root. In the epidermis/cortex carriers are supposed to pump nutrients into the cell, in the stele out of the cell. Such a description attributes to active sites in cell membranes a sense of direction which cannot be easily explained. Dunlop (1974) explored the possibilities of a description in which leaky membranes, both in the epidermis/cortex and in the stelar parenchyma, actively pump nutrients into the symplasm. In the stele leakiness may predominate, especially in older roots, in the epidermis/cortex the active uptake predominates. Although this description may not be satisfactory as yet (De Boer, 1985; Drew, 1987), it is intriguing for its simplicity and focusses on the importance of passive leakage concurrent with active transport.

Various models have been developed for different nutrients, depending on internal metabolism of the nutrient in either root or shoot and on the amount of recirculation of the nutrient in ionic form in the plant via the phloem. Literature on this topic has been reviewed by Cram (1973), Glass (1983), Glass and Siddiqi (1984) and Clarkson (1985).

Probably the first schematic representation of regulation of P-uptake by an intact plant was given by Alberda (1948, fig. 3.7). He suggested that the uptake capacity of growing shoot tissues determined the net uptake rate by the roots, by an over-flow model for phloem loading; recirculated P and P newly taken up compete for sites in the stelar pump loading the xylem. The P

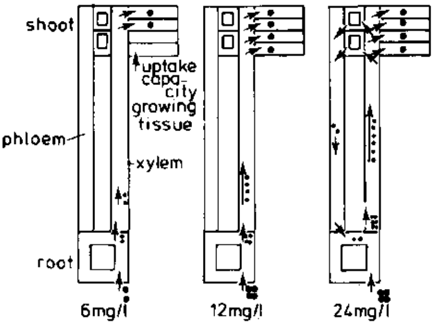


Fig. 3.7 Model of regulation of P-uptake (Alberda, 1948); uptake in the root, excretion to the xylem, use in the shoot, loading of phloem and redistribution to the roots are shown at three external concentrations.

concentration in phloem sap in this model contains the required information about P consumption in the shoot.

Recent estimates show that the amount of nutrients in (re)circulation in the plant (phloem - root - xylem - leaf - phloem) is considerable, even under stressed conditions (Simpson et al., 1982; Keltjens, 1981; De Jager, 1985). Recirculating nutrients in the plant probably contain all the information required for an efficient regulatory system. The degree of nutrient-specific regulation of the uptake rate according to the metabolic requirements of the intact plant is restricted by considerations of electroneutrality in the plant. The difference in charge between total cation uptake and total anion uptake has to be balanced by excretion of either H^+ or OH^- to the rhizosphere. Such considerations are mainly relevant for N uptake, as this largely determines the overal cation/anion balance (Dijkshoorn et al., 1968; Findenegg et al., 1986).

For calcium and magnesium, regulation of the uptake rate according to the needs of the plant is less pronounced. Recirculation of Ca and Mg in the phloem and passage through the root symplasm are both insignificant (Marschner, 1974; Wiersum, 1974, 1979; Van Goor and Wiersma, 1974). Sonneveld and Voogt (1985) showed that in modern horticultural situations, K levels in the plant are only slightly related to K concentration in the root medium, while for Ca and Mg such relations are very clear. Calcium and magnesium uptake may be confined to the youngest part of the roots, without suberization of the endodermis. In other parts of the root system considerable accumulation of Ca (and Mg) outside the root may be expected.

3.2.4 Discussion

As evident from this review of concepts and experimental evidence, the assumption we make in our models of a complete regulation of nutrient uptake according to crop demands, probably is a slight over-statement: the real regulation is less precise and allows more deviation from "set values". For calcium, magnesium and other divalent cations regulation hardly exists, which is understandable from the lack of information about Ca and Mg levels going from shoot to root. Still, for N, P and K our assumption of complete regulation probably is a safer starting point for describing crop nutrient uptake under agricultural conditions than the neglect of regulation typical of other models (Nye and Tinker, 1977; Barber, 1984). Models of nutrient uptake describing the real degree of regulation inside the plant would have to take into account several pools inside the plant and transfer between the pools. This is not possible yet as detailed physiological information of this kind is lacking.

3.3 Assumption 2: Daily nutrient requirements constant

The assumption we make in our model description of a constant daily nutrient uptake is more specific than the assumption of regulation of uptake discussed in section 3.2. The "set point" of the regulation might change with time, leading to changing daily uptake rates. The concentration of nutrients on a dry matter basis in many plants gradually decreases with their age. As total dry matter production for a closed crop canopy has a long linear phase of constant daily dry matter production (Sibma, 1968), the decreasing nutrient content does not seem directly reconcilable with a constant daily rate of nutrient uptake, but in fact that is the case, as shown by figures 3.8, 3.9 and 3.10 for P-uptake, N-uptake and K-uptake by potatoes.

Both dry matter production and nutrient uptake show a prolonged linear phase; the nutrient uptake curve precedes the dry matter production by about 3 weeks. The result is a two-phase line in the relationship between nutrient uptake and dry matter production in quadrant I. The first phase (up to a dry matter production of 1.5 a 2 t/ha) may be interpreted as production of "young" tissue of high nutrient content, the second phase as the production of "mature" tissue of lower nutrient content, at least when expressed on a dry matter basis, in the closed canopy stage. In the closed canopy stage daily nutrient uptake is a constant, although the average nutrient content decreases along with the proportion of "young" tissue. Towards the end of the growing season the amount of "young" tissue is reduced to zero; internal redistribution of nutrients in the plant is sufficient to meet the nutrient requirements in this final stage, so no further uptake is necessary.

The two-phase description of N-uptake versus dry matter production holds for other crops as well (figure 3.11). The two-phase line may indicate the "set point" for regulation of N-uptake under conditions of ample supply: apparently most crops grow with about 5% N (dry matter basis) up to a dry matter production of 2 t/ha, if the external supply allows and with about 1%

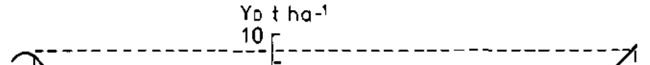


Fig. 3.8 Time course of dry matter production Y_D and phosphate uptake N_u(P) for various plant organs of potato in a situation of adequate nutrient supply in the field (data of Van der Paauw, 1948).

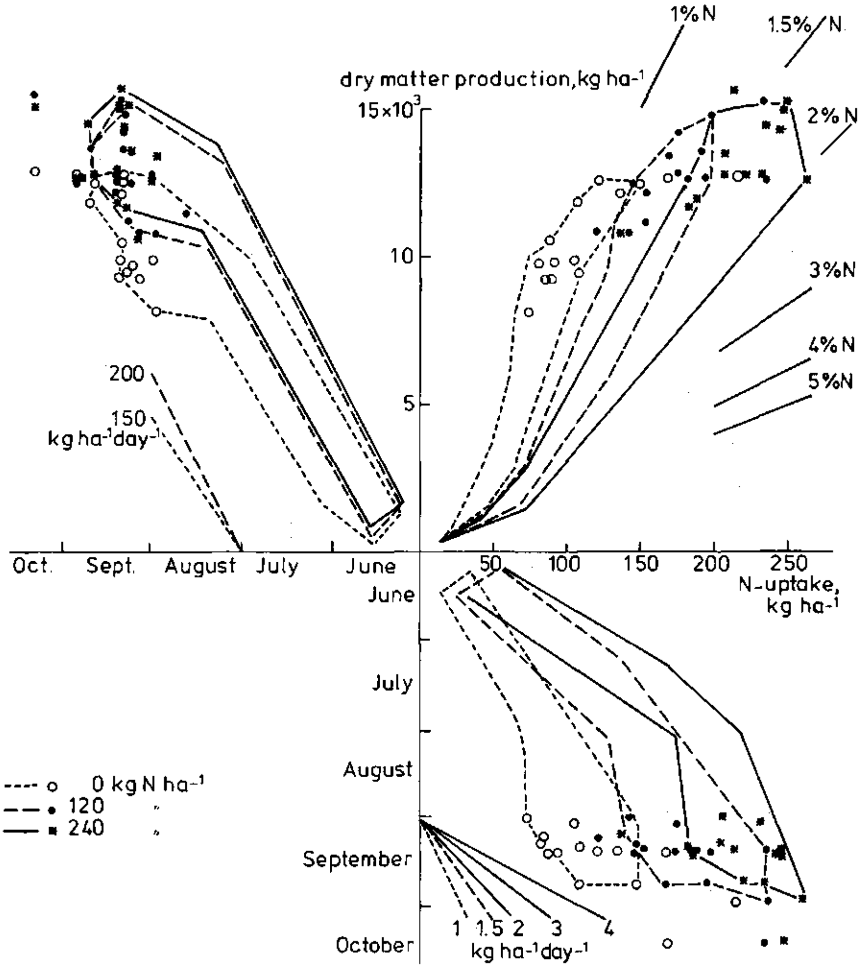


Fig. 3.9 Time course of aboveground dry matter production Y_D and nitrogen uptake $N_u(N)$ for potato in the field at three nitrogen fertilization levels; final yields are given for 14 experimental years and envelopes of the trajectories in 12 out of 14 years (two years of exceptionally high mineralization excluded; unpublished data of J.A. Grootenhuis, kindly supplied by J.J. Neeteson).

in the subsequent linear growth phase. In a zone to the left of this line dry matter production may proceed unhampered, but when the line of 1% N is approached, a growth reduction is found. At final yield the average N-content often is about 1.5%. If the external supply allows an N-content of 1.5% to be maintained, dry matter production may be unhindered. The extra uptake found under higher supply leads to a certain degree of buffering in the plant.

Figure 3.12 shows results for the three major nutrients N, P and K for a number of crops, as measured by Van Itallie (1937). In almost all cases a linear uptake phase occurs, at least covering the period in which 60% of the final nutrient content is taken up (horizontal lines in figure 3.12 indicate tration of 1.5% for N, 0.22% for P (table 3.1) and 1% for K. Daily nutrient requirement then is 3, 0.44 and 2 kg/(ha day) for N, P and K respectively.

3.4 Assumption 3: Critical nutrient concentrations are virtually zero

Experiments with rapidly recirculating nutrient solutions have shown the existence of a compensation point (C_{min}) at which no net uptake is possible. This concentration, C_{min}, at which leakage equals uptake, usually is very low when compared with concentrations in agricultural soils. For our present discussion we are interested in C_{lim}, the concentration at which required uptake rates can just be maintained. Van den Honert (1936) found that a P-concentration of 0.4 - 0.7 µmol/l in a rapidly flowing solution is sufficient for growth of sugar cane. This conclusion was much later confirmed for other species (Loneragan and Asher, 1967; Temple-Smith and Menary, 1977; Wild and Breeze, 1981). Jungk (1974) found a value of 0.1 µmol/l for P for four crop species, Breeze et al. (1984) found C_{lim} to be 0.1 - 0.4 µmol/l for P in older Lolium perenne plants. In figure 3.13 some literature values collected by Pitman (1976) are shown.

For N and K, values around 100 µmol/l and 10 µmol/l are reasonable estimates (compare figures 3.2 and 3.3) for plants growing in nutrient solutions with unrestricted root growth. Area III in figure 1.8 can now be specified. Table 3.2 gives estimates of the amount of available N, P and K remaining in the soil at this limiting concentration (the average values used for the adsorption constant K_a are discussed in chapter 7). Our conclusion from table 3.2 is in contrast with the conclusion of Robinson (1986) in his review of limits to nutrient inflow rates in roots: although critical concentrations are higher for N and K than for P, C_{lim} can be considered to be negligible for the functioning of root systems in soils for N and K but not for P.

For phosphate the amount of available P remaining in the soil at C_{lim} may be negligible on soils with a rather low adsorption constant K_a (100), but not on soils with high adsorption constants (compare figure 7.2). The amount remaining in the soil at C_{lim} is small when compared with the total amount of P present in the soil, but not when compared with the plant P-requirement. For such conditions C_{lim} has to be specified as a function of nutrient demand per unit root length.

The data quoted refer to plants with unimpeded root growth and consequently to situations with a rather low uptake requirement per unit root. In situations where demand per root is higher, limiting concentrations will be higher. A relationship may be formulated on the basis of short-term nutrient uptake

Table 3.2 Critical external nutrient concentration C_{lim} and amount of potentially available nutrients remaining in the soil at this concentration (at a water content $\Theta = 0.25$ v/v).

Nutrient	Critical external nutrient concentration C_{lim} [µmol/l]	Adsorption constant K_a	Depth [m]	Amount remaining in the soil at C_{lim} [kg/ha]
N	100	0	1	3.5
K	10	10	0.25	10.5
P	1	100-1000	0.25	7.8 - 78

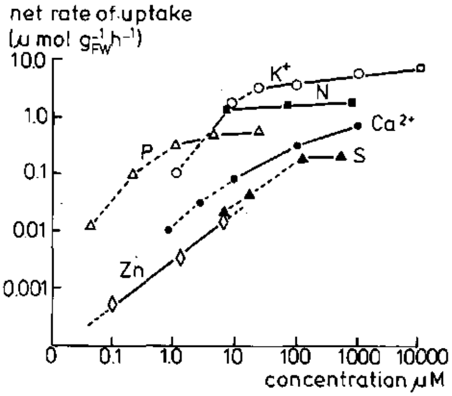


Fig. 3.13 Rates of net uptake of various elements in rapidly flowing, recirculating nutrient solutions of various concentrations (Pitman, 1976).

versus concentration studies for low-salt roots, which may reflect uptake potential under maximized demand. In the low concentration range the uptake capability can be expressed as maximum root absorbing power α (uptake rate per unit root surface area divided by the current external concentration). C_{lim} may now be estimated as α divided by the required uptake rate per root (figure 3.14). For phosphate, values of α are estimated at 0.7 to 7 x 10^{-6} m/s or 0.06 to 0.60 m/day (Nye and Tinker, 1977). As a conservative intermediate value we may take 0.17 m/day. P uptake requirements of 200 x 0.0022 = 0.44 kg/(ha day) lead to a required uptake rate per unit root surface area of 0.47 to 0.095 mmol/(m^2 day) for a root area indices in the range 3 to 15, respectively. Calculating C_{lim} according to this procedure results in 0.56 to 2.8 µmol/l for root area index of 15 and 3, respectively. Comparison with table 3.2 shows that the calculated C_{lim} cannot be neglected for estimates of P-availability to field crops, when low root length densities are considered.

3.5 Assumption 4: Maximum nutrient uptake rates are not relevant

Physiologically based maximum uptake rates for nutrients and water determine the required size of the root system in situations of high external

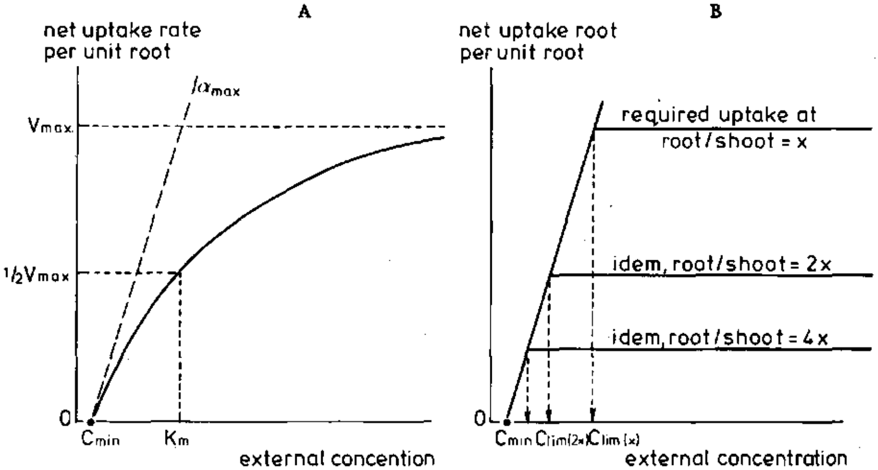


Fig. 3.14 Net uptake rate per unit root as related to external concentration in "tea-bag" experiments (A) and our interpretation of uptake dynamics at three root/shoot ratios (B).

supply. As will be discussed in chapter 4, the minimum value for the root surface area is determined by water uptake, not nutrient uptake, even in a nutrient solution where water is freely available. Maximum uptake rates for nutrients, if they exist at all, are therefore not relevant for describing roots grown in soil.

3.6 Assumptions 5 and 6: Constant hydraulic conductance

For the present discussion we are interested in the relation between plant water potential and the rate of water uptake in order to estimate the water potential required for the transpirational demand. Since Van den Honert (1948) introduced the electrical analog of a series of resistances for the catenary process of water uptake, such a description has been widely used. Water flow in each step of the chain is assumed to be proportional to a resistance and to the difference in water potential involved in this step. Usually steady state is assumed for water transport and capacitance for water in the plant is ignored; the simplest formulation for the volume flux of water F_w is:

$$(3.1)\quad F_w = \frac{-\psi_{atm} + \psi_{leaf}}{\Omega_{leaf}} = \frac{-\psi_{leaf} + \psi_{xylem}}{\Omega_{xylem}} = \frac{-\psi_{xylem} + \psi_{root}}{\Omega_{root}} = \frac{-\psi_{root} + \psi_{soil}}{\Omega_{soil}}$$

where ψ and Ω indicate water potentials and resistances, respectively.

The usefulness of this description depends on the relative independence of the resistance Ω_{root} (or its inverse, the hydraulic conductance L_p) on flow rates and plant water potential. The water potential mainly consists of hydrostatic and osmotic components, which interact near semi-permeable membranes (in fact the only place where osmotic components matter at all).

Actual measurements of water uptake by excised root systems normally yield nonlinear relations between applied hydrostatic pressure and observed volume flow (F_w). Such nonlinearities have for a long time been attributed to changes in hydraulic conductance (L_p) as a result of water flow, water potential and/or membrane composition (Newman, 1976a).

In 1975 two research groups independently published essentially the same mathematical description for the interaction of osmotic and hydrostatic driving forces in water uptake (Fiscus and Kramer, 1975; Dalton et al., 1975). According to these authors the observed nonlinearity may be explained by a gradual decrease of the osmotic pressure difference over the root membrane as the volume flow increases. In their opinion a constant hydraulic conductance may account for all available results.

In the past ten years this view has gradually become accepted, although some doubts are remaining (Michel, 1977; Newman, 1976b; Passioura, 1984). Some valid criticism of the initial single membrane model can be accomodated by a model of a single membrane with salt accumulation in front of the membrane (Raats, pers. comm.; appendix 3.2). The resulting equation for the volume flow of water is:

$$(3.2)\quad F_w = L_p \left(\Delta H_p - \frac{2\,\sigma_r^2\,\pi_0 - 2\,\sigma_r\,R_g\,T_k\,F_{s*}/F_w}{1 - \sigma_r + 2\,\sigma_r/W} \right),$$

where:

F_w = rate of volume flow of water per unit root surface area [cm³/(cm² s)],

L_p = hydraulic conductance per unit root surface area [cm³/(cm² s MPa)],

ΔH_p = H_{ps} - H_{pp} = difference in hydrostatic pressure between plant (xylem) and root environment [MPa],

σ_r = reflection coefficient for solutes at the root membrane [-],

π_0 = osmotic pressure of root environment [MPa],

R_g = gas constant [$8.3 * 10^{-6}$ cm³ MPa/(K mol)],

T_k = absolute temperature [K],

W = $(R_1/R_0)^{R_0 F_w/D}$,

D = diffusion constant for solutes around the root [cm²/s],

R_1 = radius of the outer boundary of the unstirred layer [cm],

R_0 = radius of the root [cm],

F_{s*} = active solute uptake per unit root surface area [mol/(cm² s)].

For the special case of a well-stirred solution ($R_1 = R_0$ and hence W = 1) equation (3.2) reduces to the form described by Dalton et al. (1975) and Fiscus (1975) (equation A3.5). A transition point between salt depletion and salt accumulation outside the root is found for $\sigma_r C_0 = F_{s*} / F_w$, when the "concentration of solutes reflected at the membrane" equals the "active uptake concentration"; only in that particular situation does the simple equation $F_w = L_p * \Delta H_p$ hold.

For high flow rates the terms with $1/F_w$ and 1/W vanish and a simplified form can be used:

$$(3.3)\quad F_w = L_p \left(\Delta H_p - \frac{2\,\sigma_r^2\,\pi_0}{1 - \sigma_r}\right) .$$

This equation shows that water uptake F_w can be approximately decribed by a linear function of ΔH_p, with an intercept with the x-axis determined by the osmotic value of the solution surrounding the roots and by the degree of reflection of solutes at the root surface. Accumulation of ions around the root, partly counteracted by diffusion away from the root, leads to increased osmotic effects with increasing reflection coefficients (appendix 3.2).

Of course single-membrane models cannot be used directly to calculate water uptake by whole root systems. Complications may arise from the fact that water has to pass two membranes (apoplast-symplast and symplast-xylem) rather than one, from the fact that solutes in the symplast maybe buffered by solutes in vacuoles and from the fact that excretion of solutes to the xylem is an active process under feedback control from internal nutrient levels in the plant, leading potentially to complicated patterns of nutrient and water uptake and release along the axis of a single root. Miller (1985) has given a two-membrane model for a root, considering salt accumulation effects between the two membranes (but not in front of the outer membrane). He performed detailed measurements in the region of low flow rates and could obtain exellent curve-fits for his data on the basis of this model. The number of parameters which cannot be estimated independently is so large, however, that such a curve fit appears always possible. For our present discussion detailed knowledge of all processes at low flow rates is not required and we may accept the single membrane in an unstirred solution (the unstirred solution may occur both outside the root and in the "free space" or apoplast) as an analogy for the whole root.

As our main interest is in situations of high flow rates we can assume that the rate of water uptake is linearly related to, but not proportional to the difference in hydrostatic pressure over the membrane (equation 3.3). The slope of this line depends on the hydraulic conductance L_p, which we assume to be constant, the intercept depends on the reflection coefficient σ_r and the osmotic pressure of the solution outside the membrane (π_0). In normal soils π_0 is negligible and (3.3) can be further simplified, as done in (3.1); for measurements in nutrient solutions and for horticultural practice π_0 is not negligible.

Estimated parameters for using such a model for whole root systems cannot be directly related to cell-physiological membrane parameters with the same name (such as L_p). Parameter estimates can be obtained from studies of excised root systems in pressure bombs or from measurements in intact plants (Passioura et al., 1984). When a pressure bomb technique is used with excised root systems the choice is between using low values of applied pressure (and getting involved in all parameters of the curvilinear response here) or using high values of applied pressure and running the risk of modifying the root by removing air from intracellular spaces with subsequent anaerobiosis (De Boer, 1985). A further complication is that the models assume equilibria to exist for solute concentrations both outside and inside the membrane; thus, to perform relevant measurements some time is required for the root to adjust to a new pressure applied, while in fact the root may start to deteriorate as soon as pressure is applied. Experimental procedures have to be a compromise and values obtained will be crude estimates of the real values in the intact plant. In view of these problems in obtaining reliable estimates of parameters, further sophistication in model description is not directly relevant. In table 3.4 some values from the literature for L_p are collected, which may represent a reasonable compromise between the desirable and the possible.

The importance of a correct estimate of hydraulic conductance L_p, can be seen from a simple calculation. The required uptake rate per unit root surface

Table 3.4 Literature values for hydraulic conductance L_p averaged over the whole root system; a root surface area of 0.1 cm^2/cm root length has been assumed (root diameter 0.36 cm) if no data were available.

Crop	Author	Hydraulic conductance L_p
		10^{-6} $cm^3/(cm^2$ s MPa)
Maize	Newman, 1973	2.2
,,	House and Findlay, 1966	1.8 - 6.8
Wheat	Andrews and Newman, 1969	0.36 - 6.7
,,	Lawlor, 1973	
,,	Jones et al., 1983	0.5
Barley	Steudle and Jeschke, 1983	0.3 - 4.3
Fescue	Burch, 1979	1.5
Onion	Anderson and Collins, 1969	4.3 - 9.0
Dwarf bean	Newman, 1973	0.56
Broad bean	Brouwer, 1954 (Michel, 1977)	11 - 22
,,	Newman, 1973	0.54
Soybean	Fiscus, 1977b	27
,,	Michel, 1977	4 - 13
Clover	Burch, 1979	1.5
Cotton	Taylor and Klepper, 1974	1.2
Tomato	Newman, 1973	6.1
,,	Morizet and Mingeau, 1976	10
Sunflower	Newman, 1973	0.7

area F_w [cm/s] can be calculated from the transpirational demand of a closed crop canopy (E, [cm/s]) and the root surface area per unit cropped area (Root area index, A_{ra}). Hence, for situations where π_0 is negligible:

$$(3.4) \quad F_w = E / A_{ra} = L_p \, \Delta H_p \ .$$

From (3.4) we can estimate the root area index required to meet a given transpirational demand, given L_p and given the difference in water pressure over the root membrane, ΔH_p. For $\Delta H_p = 0.1$ MPa and E = 0.5 cm/day = 5.8 10^{-6} cm/s, for a range of L_p values of 1 to 10 * 10^{-6} cm³/(cm² s MPa) values of the root area index are required of 58 to 5.8 respectively. For lower values of the root area index, a larger difference in water pressure between xylem and root environment is required and hence a larger amount of water will be left in the soil at the time the transpirational demand E can no longer be met at a given minimum water pressure in the xylem. For L_p values of about 1 * 10^{-6} cm³/(cm² s MPa), which have been reported by several authors, this effect is considerable. A similar conclusion was presented by Greacen et al. (1976). The majority of measurements of L_p have been done at laboratory temperatures; thus the hydraulic conductance in the field may be considerably over-estimated, as L_p is sensitive to differences in temperature (Kuiper, 1963; Dalton and Gardner, 1978).

3.7 Assumptions 7 and 8: Differences between roots, age effects, turnover of roots

In the classical textbook description of root functions nutrient and water uptake is supposed to be largely confined to the young zone directly behind the root tip and a high rate of turnover of fine roots is postulated (constant growth and decay throughout the growing season). The rate of uptake by the active zones according to this description is necessarily high to explain observed nutrient uptake by the plant as a whole. As an alternative, we assume here that nutrient and water uptake occur along the whole length of the roots, independent of root age, at a moderate rate. In this view turnover of roots is only necessary in so far as the root has depleted (or otherwise spoilt) its direct environment, not because its physiological abilities are no longer sufficient.

Observations leading to the first description were based on the application of radioactive isotopes to excised roots. The emerging view of uptake largely confined to the young root zones can now be ascribed to the experimental conditions. Measurements of uptake rates by isolated zones along the length of a root of an intact plant have shown that uptake is not much different between 5 and 44 cm from the root tip and translocation to the shoot is even higher for the latter zone, the higher uptake in the youngest zone apparently covering the nutrient requirements for the growing root tissue itself (Clarkson, 1981).

Significant changes in root morphology appear to have little effect on uptake rates. Drew and Saker (1986), Drew and Fourcy (1986) showed that aerenchymatous roots can still show virtually unimpeded uptake rates, even when only 20% of the mid-cortex is still intact; the critical site for uptake apparently is found at the endodermis, and integrity of tissues outside the endodermis is not required.

For water uptake the conventional interpretation of Brouwer's (1954) data on water uptake by various zones of broad bean roots of both age- and flux-dependent resistances, has been questioned by Fiscus (1977a). He showed that a difference in active salt excretion between various zones of the roots can account for the observed difference in flows, assuming an almost constant resistance ($1/L_p$) (i.e. independent of root age and flux). Other data on water

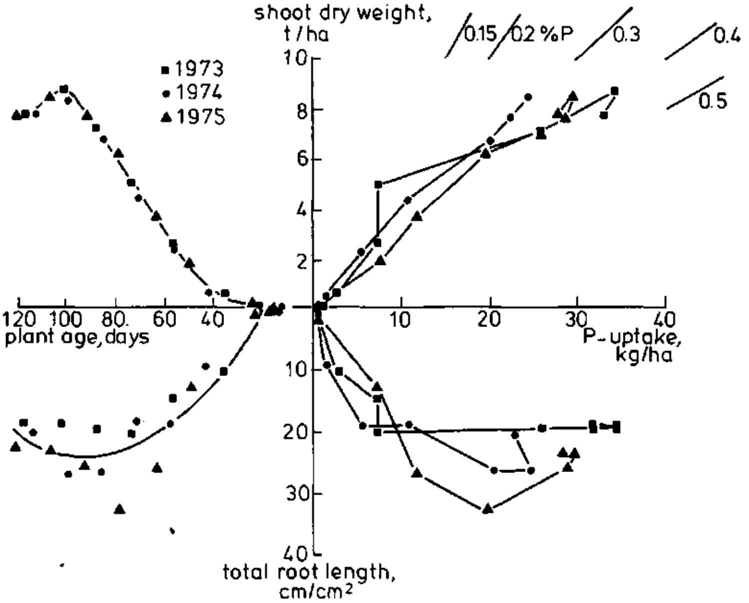


Fig. 3.15 Time course of root growth, P-uptake and dry matter production for field grown soybeans in three years (Barber, 1978).

uptake indicate differences between zones in some species and more homogeneous uptake in others (Hainsworth and Aylmore, 1986; Drew, 1987)

The concept of nutrient uptake being confined to root tips implies that a constant new root growth is needed to account for observed nutrient uptake patterns. Figure 3.15 shows the development of the root system in time for soybeans, as well as P-uptake and shoot growth. The largest part of total P-uptake occurs in the seed-filling stage, when no net root growth is found. Similarly, the root systems of most cereal crops reach their maximum net size early in the growing season, while uptake still continues for a considerable time. Such observations can only be explained by the root-tip uptake concept if a high turnover of fine roots at a constant net size is assumed.

With the recently introduced technique of mini-rhizotrons installed in the field, estimates for root turnover were obtained for Dutch agricultural conditions (section 6.4.2); turnover is not high enough to account for observed uptake if uptake would be confined to root tips. Troughton (1981) studied the ageing of grass plants when new root growth on tillers was inhibited; he concluded that ageing was probably due to problems with Ca and Mg uptake, while uptake of N, P, K and water continued without problems. Shone and Flood (1983) showed that in a dry period nutrient uptake from dry soil virtually stopped while fine roots died; upon rewetting the soil, the old seminal axis rapidly resumed uptake, despite a partial collapse of cortical cells in the dry period.

From this evaluation of the evidence for assumptions 7 and 8 it may be evident that our choice probably does not deviate too much from reality. The main exception probably is calcium and magnesium uptake, which may in fact be confined to the youngest roots and for which a constant rate of root growth is essential.

Appendix A3: Models for the interaction of water and salt uptake by a single membrane

A3.1 Single membrane in well-stirred solution

In the formulation of Fiscus (1975) which has been most widely followed, the model is as follows. For a semipermeable membrane, volume flow F_w (which is approximately equal to water flow) is related to both hydrostatic and osmotic pressure differences:

$$\text{(A3.1)}\quad F_w = L_p\,[\Delta H_p - \sigma_r\,\Delta\pi_0] = L_p\,[\Delta H_p - \sigma_r\,R_g\,T_K\,(C_{out} - C_{ins})]\ ,$$

where:

C_{out} = concentration of solutes outside membrane [mol/cm³],

C_{ins} = concentration of solutes inside membrane [mol/cm³].

Other symbols are explained in section 3.5. In an equilibrium situation, we may assume that the concentration inside the membrane equals solute uptake divided by water uptake:

$$\text{(A3.2)}\quad C_{ins} = F_s / F_w\ ,$$

where:

F_s = solute flow rate across the membrane [mol/(cm² s)].

For ideal semi-permeable membranes $\sigma_r = 1$ and $F_s = F_{s*}$, where F_{s*} = rate of active solute uptake across the membrane [mol/(cm² s)], so (A3.1) can be transformed into a quadratic equation in F_w from which F_w can be solved. For non-ideally semipermeable membranes (i.e. $\sigma_r < 1$), the salt flow across the membrane can be described as an active uptake term plus a drag (mass flow) term:

$$\text{(A3.3)}\quad F_s = C_m\,(1 - \sigma_r)\,F_w + F_{s*}\ .$$

For the effective concentration at the membrane C_m, we can use an approximation which is reasonable at least for $0.3 < C_{out}/C_{ins} < 3.0$ according to Fiscus (1975):

$$\text{(A3.4)}\quad C_m = (C_{out} + C_{ins})/\,2\ .$$

From the four equations (A3.1 to A3.4) we can eliminate two unknown parameters (C_{ins} and F_s), to arrive at an implicit equation for F_w:

$$\text{(A3.5)}\quad F_w = L_p\left(\Delta H_p - \frac{2\,\sigma_r^2\,\pi_0 - 2\,\sigma_r\,R_g\,T_K\,F_{s*}/F_w}{1 + \sigma_r}\right)\ .$$

The formula shows that for high values of F_w the relation between F_w and ΔH_p approaches asymptotically a straight line, with an intercept on the x-axis for:

$$\text{(A3.6)}\quad \Delta H_p = (2\,\sigma_r^2\,/(1 + \sigma_r))\ \ \pi_0\ .$$

As $0 < \sigma_r < 1$ this intercept is always to the left of π_0. The position of this intercept has been the subject of much subsequent dispute (see below).

An alternative formulation for the active uptake term F_{s*} has recently been given by Miller (1985), who used a saturation curve type of response:

(A3.7) $F_{s*} = K_u \, (C_\omega - C_{ins})$.

where:

C_ω = an internal equilibrium concentration [mol/cm³],
K_u = uptake efficiency [cm/s],

Solving F_w in such a case yields:

$$(A3.8) \quad F_w = L_p \left(\Delta H_p - \frac{2\, \sigma_r^2\, \pi_0 - 2\, \sigma_r\, R_g\, T_K\, K_u\, (C_\omega - C_{out})/F_w}{(1 + \sigma_r) + 2\, K_u \,/\, F_w} \right) .$$

For low values of F_w this solution differs from (A3.5); it introduces an extra parameter (C_ω and K_u instead of F_{s*}) which usually cannot be determined independently and with which better curve fits to experimental data can be obtained. For high values of F_w (and ΔH_p), however, this solution does not differ from (A3.5) and it gives the same intercept (A3.6) for the asymptote.

As Newman (1976b) pointed out, experimental results usually conform to the general shape as indicated by equation (A3.5), but the intercept on the x-axis often lies to the right of π_0, while the model predicts an intercept to the left of π_0. In reponse to this falsification of the model, Fiscus (1977b) proposed that salt accumulation in front of the membrane may lead to a higher effective C_{out}' than the measured external concentration C_{out} at some distance from the membrane. The process of salt accumulation in front of the membrane can be formulated as follows.

A3.2 Water uptake model for a single membrane, in non-stirred solution

If we consider the possibility of accumulation of solutes in front of the membrane, we have to deal with mass flow of solutes towards the membrane, back-diffusion of solutes and inflow through the membrane. In an infinitely large medium a steady state situation is possible in which the concentration profile in front of the membrane assumes a constant form. Steady state is possible when mass flow of solutes towards the membrane is just counteracted by diffusion and uptake. For a membrane which is not ideally semipermeable (i.e. $\sigma_r < 1$), such a situation is possible as solute inflow through the membrane will increase when solutes accumulate in front of the membrane. Under these conditions:

(A3.9) $F_s = F_w\, C + D\, (r/R_0)\, (\partial C / \partial r)$,

where:

C = concentration at radial distance R from the membrane (at $R=R_0$) ,
D = diffusion constant in liquid phase [cm²/s].

Solving for a constant concentration C_{out} outside the unstirred layer (at $R=R_1$):

(A3.10) $R = R_1 \,,\; C = C_{out}$,

and specifying for C_{out}' at $R = R_0$, yields:

(A3.11) $C_{out}' = F_s/F_w + (C_{out} - F_s/F_w)\, W$,

and

(A3.12) $W = (R_1/R_0)^{R_0 F_w / D}$.

From the four equations (A3.2, A3.3, A3.4 and A3.11) we can now eliminate three unknown parameters (C_{ins}, C_{out}' and F_s) to obtain equation (3.2). For (very) high values of F_w, 1/W will become negligibly small and again a linear relation between F_w and ΔH_p results, but now the intercept is:

(A3.13) $\Delta H_p = (2\,\sigma_r^2\,\pi_0)\,/\,(1 - \sigma_r)$.

For $\sigma_r > 0.5$ this intercept is to the right of π_0, confirming the explanation of Fiscus (1977). Passioura (1984) suggested that salt accumulation in front of the membrane will have stronger negative effects on F_w for increasing F_w. The relation between F_w and ΔH_p according to Passioura deviates exponentially from a straight line. This conclusion was obtained by considering the special case of $\sigma_r = 1$. This special case cannot be treated in this way, however, (Raats, pers. comm.) as the assumption of a steady-state concentration profile in front of the membrane is invalid under these conditions. In the case considered by Passioura the apparent resistance (flow rate/ applied pressure) will increase both with time and with applied pressure, both leading to a higher salt accumulation in front of the membrane. The only possibility for a steady-state situation in this case is when F_{s*}/F_w is exactly equal to C_{out} so uptake equals the amount of solutes brought to the membrane by mass flow.

Table 4.1 Estimates of physiologically required root surface area $A_{r,n}$ and root volume $V_{r,n}$ (assuming all roots to have a root diameter of 0.020 cm) for tomato. Nutrient contents based on Nederpel (1975) and Steiner (pers. comm.), growth rates per plant for a plant density of 2.2/m² after Steiner (1967) and Roorda van Eysinga (pers. comm.): 3 g vegetative and 6 g generative dry matter production per plant per day; F_{max} values after Brewster and Tinker (1972); $A_{r,n}$ calculated according to eq. (4.1).

Nutrient	N	P	K	Ca
M_v $({}^0/_{00})$	25	5	50	30
M_g $({}^0/_{00})$	25	5	50	2
Required uptake (mg/day)	225	45	450	100
per plant (mmol/day)	16	1.5	11	2.4
F_{max} (mmol/ (m² day))	6.0	0.5	3.5	0.6
$A_{r,n}$ (m²)	2.7	2.9	3.2	4.0
$V_{r,n}$ (dm³)	0.14	0.15	0.16	0.22

4.2 Initial estimate of physiologically required root volume

The "physiologically required minimum root surface area" per plant can be defined as the minimum of the required root surface areas for each of the essential nutrients and that for water. For water and each nutrient this root surface area can be estimated from uptake rates per plant required for maximum production at a given plant density, divided by the maximum uptake rates per unit root area. Here we will concentrate on tomato and cucumber production under glasshouse conditions in the Netherlands. For the linear growth phase of a closed canopy, in which both vegetative and generative tissue are formed at a constant daily rate, the equation is:

$$(4.1)\quad A_{r,n} = \frac{\dot{Y}_{D,v}\, M_v + \dot{Y}_{D,g}\, M_g}{N_p\, A_i\, F_{max}},$$

where:

$A_{r,n}$ = physiologically required minimum root surface area per plant for nutrient uptake [m²],
$\dot{Y}_{D,v}$ and $\dot{Y}_{D,g}$ = dry matter production per plant of vegetative and generative parts respectively [kg/(ha day)],
M_v and M_g = required composition of plant dry matter (vegetative and generative) [g/kg], supposed to be constant,
N_p = plant density [./ha],
A_i = atomic (or molecular) weight of the nutrient studied [g/mol],
F_{max} = maximum uptake rate per unit root surface area for the nutrient studied [mol/(m² day)],

Table 4.1 shows estimates of $A_{r,n}$ and the corresponding root volume $V_{r,n}$.

Assuming constant hydraulic conductance we may formulate the minimum root surface area for water uptake from a simplified version of equation [3.3]:

$$(4.2)\quad A_{r,w} = \frac{E_p}{L_p\, [\Delta H_p - 2\, \pi_0\, \sigma_r^2/(1-\sigma_r)]},$$

where:
$A_{r,w}$ = minimum root surface area required for water uptake [m²/plant],
E_p = transpiration rate per plant [cm³/s].

For a maximum transpiration E_p corresponding to 2 l per 6 hr period (4.4 mm per 6 hr for the plant density used), a root conductance $L_p = 5 * 10^{-6}$ cm³/(cm² s MPa), a reflection coefficient $\sigma_r = 0.7$, an osmotic potential of the solution of 0.03 MPa and an acceptable root water potential of -0.5 MPa, $A_{r,w}$ can be estimated to be 4.6 m²/plant, equivalent to 0.23 dm³ root tissue/plant.

These preliminary estimates show that for normal plant spacing and growth rates, a minimum root surface area of several m² per plant may be expected for glasshouse tomatoes and cucumber and that Ca uptake and water uptake may be the first root functions which become limiting when the size of the root system is reduced. The estimates for Ca are rather uncertain as F_{max} values reported in the literature for Ca are more variable than those for other nutrients, due to the fact that Ca-uptake is mainly restricted to young root tissue while possibilities for uptake of N, P and K are relatively independent of root age (chapter 3).

4.3 Experiments

4.3.1 Methods

Plant growth on pots with a total pore volume corresponding to the minimum root volume, as calculated in table 4.1, was compared with that on a range of larger pots. Experiments were aimed at quantifying:

- the relation between pot size and root growth as affected by a continuously recirculating nutrient solution,
- the critical root size as indicated by shoot growth, and
- the critical root function in this situation; main emphasis was placed on quantification of nutrient and water uptake rates, to test whether shoot growth is affected by restricted root growth before effects on nutrient or water status can be observed.

Plants were grown in a system with continuously recirculating nutrient solution, as shown in figure 4.3. The number of tricklers per pot varied per pot from 1 to 4 in order to keep the top layers moist in each pot size. The rate of flow per trickler was about 300 ml/hour. Aeration of the nutrient solution occurred during the free fall of the return flow into the storage tank and between the trickler and the pot. Oxygen content of the nutrient solution draining from the pots was measured on a number of occasions; all measurements showed a partial O_2 pressure of at least 12% and usually above 15%.

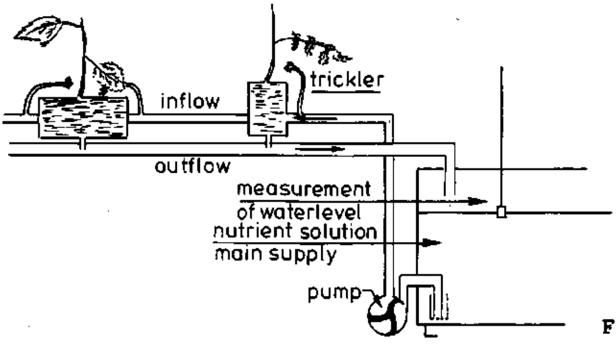


Fig. 4.3 Recirculation system.

The composition of the nutrient solution used was: 10.2 me/l NO_3^-, 1.2 me/l $H_2PO_4^-$, 4.8 me/l SO_4^{2-}, 4.5 me/l K^+, 7.0 me/l Ca^{2+} and 4.8 me/l Mg^{2+} as macro-elements and 10 mg/l Fe, 1 mg/l Mn, 0.13 mg/l Zn, 0.36 mg/l B, 0.04 mg/l Cu and 0.04 mg/l Mo. The solution had a pH of 6.5, an electrical conductivity (EC) of 1.5 mS/cm and an osmotic pressure of 0.064 MPa (from $\pi_0 = R_g * T_k * C = 0.083*293*0.026$ (i.e. 0.017 mol/l monovalent and 0.009 mol/l divalent ions/l)).

The reservoir contained 200 l of nutrient solution, which means about 3, 5 and 7 l/plant as the experiments proceeded and part of the plants were harvested. The reservoir was refilled daily with water, half- or full-strength nutrient solution in such a way that the electrical conductivity of the solution remained between 50 and 100 % of the original value. The pH of the solution was controlled on a daily basis. Once a week all nutrient solution was removed and replaced. Fluctuations of nutrient concentration could usually be kept to less than a factor of 10; NO_3^- and K^+ showed the strongest depletion, while Ca^{2+} and SO_4^{2-} showed the strongest accumulation. Because of the relative increase in divalent ions the ratio of osmotic value and electrical conductivity gradually changed from 0.042 MPa cm/mS to 0.037 MPa cm/mS. Maintenance of an approximately constant EC of the culture solution thus led to an approximately constant osmotic value of the solution and acceptable fluctuations in the concentration of the major nutrients (compare minimum concentrations in table 3.2). Water and nutrient consumption was recorded for all plants together by analysis of the remaining solution at the time of the weekly replacement.

A wide range of pot sizes was used in each experiment. Pots were filled either with (washed) coarse sand or with a rockwool block sheathed in black polyethylene. All pots were covered by a layer of black alkathene pellets to reduce evaporation from the pot surface. Pot height and diameters used in the various experiments are listed in table 4.2.

Plants were grown in a glasshouse with temperature controlled by heating and ventilation (target temperature (20)-25-(30), in reality 18-35 °C; relative humidity aimed at 0.80-0.90, in reality sometimes lower). All pots were placed on a table as shown in figure 4.4. In three harvest periods one third each of the pots was removed, so space and light available to every single plant (in the remaining regularly spaced planting pattern) gradually increased. Plants were supported by strings from the top of the glasshouse. By regular pruning only one stem was maintained in the tomato experiments; plants were decapitated beyond the 8th truss. In the cucumber experiments only fruits on the main stem above 80 cm were maintained; plants were detopped when the stem length was 2 m and two side branches were maintained thereafter.

Table 4.2 Details of pot size for the four experiments; tomato cv Moneymaker and cucumber cv Farbio were used in all experiments.

Experiment number	1 (IB 5037)	2 (IB 5047)	3 (IB 5065)	4 (IB 5065)	
Crop	tomato	cucumber	cucumber	tomato/cucumber	
Pots filled with sand:					
Pot height (cm)	15	15	5-15	15	15
Pot volume (dm^3)	0.5/1.5/6	0.5/1.3/3.8	3.1/6.2/12.3/19	1.25	6
Pore volume (dm^3)	0.2/0.6/2.4	0.2/0.5/1.5	1.3/2.5/4.9/7.6	1.3	2.4
Pots with rockwool:					
Pot volume (dm^3)	0.5/1.5/6	0.2/0.5/1.5/6			
Pore volume(dm^3)	0.5/1.5/4.8	0.2/0.5/1.5/4.8			

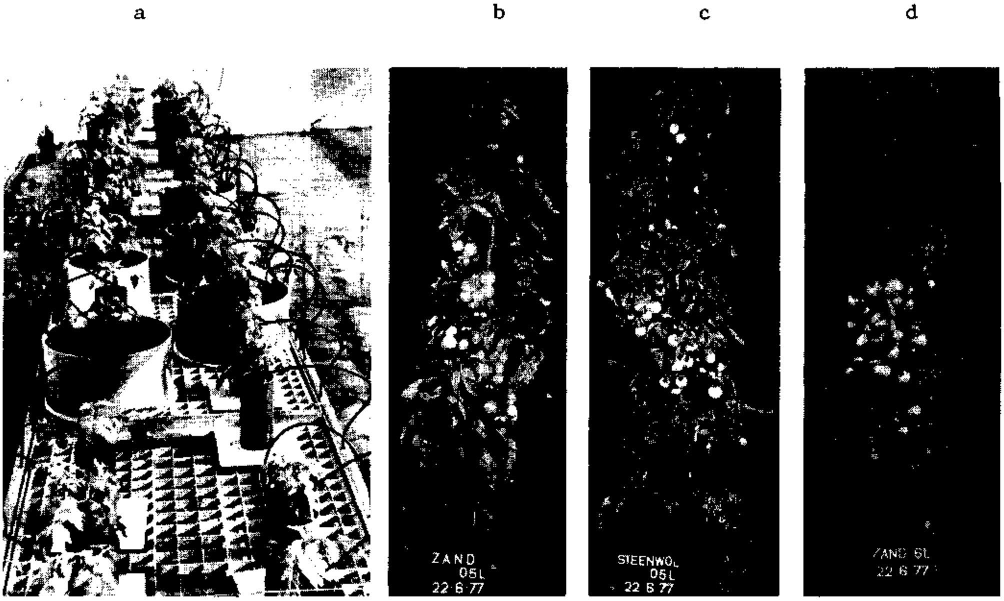


Fig. 4.4 Tomatoes growing in pots of various sizes in a recirculating nutrient solution; a. just after planting; b-d when the first truss ripens (b: 0.5 l sand, c: 0.5 l rockwool, d: 6 l sand).

Fruit abortion was recorded and all ripe fruits were picked regularly. In each sampling period aboveground parts were divided into stems, petioles, leaves and generative organs and weighed separately. Leaf area was determined by subsampling for specific leaf area (m^2/g) and checked by measurements on photocopied leaves. Root systems could be washed directly from the sandy pots, the rockwool pots required pretreatment in 2% HCl overnight (Brouwer and Van Noordwijk, 1978). After cleaning, root samples from rockwool were still contaminated with 3-6% dry weight of rockwool (determined by dry matter loss on ignition; for sand pots only 0.3% contamination was found). Corrections were made for the losses of dry weight by handling and storage of roots, for each growth stage and method used, according to results of a separate experiment shown in figure 4.5. In experiment 3 and 4 all plants were grown on sand to facilitate root measurements. Root length and frequency distribution of root diameters were measured on subsamples to obtain estimates of specific root length (m/g) and specific root surface area (m^2/g) for each pot, which were used to calculate total root length and total root surface area per pot.

In every sampling period the root entry resistance to water uptake was measured for each pot in a pressure bomb (figure 4.6). The whole pot was immersed in well-aerated water of (19)-20-(21) °C and measurements started within ten minutes after cutting the stem of the plant. Rate of water flow through the cut end of the stem was recorded at various levels of applied pressure to the water (0 = "bleeding", 0.05, 0.1 or 0.5 MPa) or suction to the stem (0.05 MPa). For each pot a sequence of applied pressures was used with a measuring period of about 10 minutes at each pressure. Longer measuring periods imply a risk of changes in hydraulic conductance of the roots by anaerobiosis as water infiltrates cortical air spaces under the pressures applied. In experiment 4 analysis was made of the effect of the time of day at

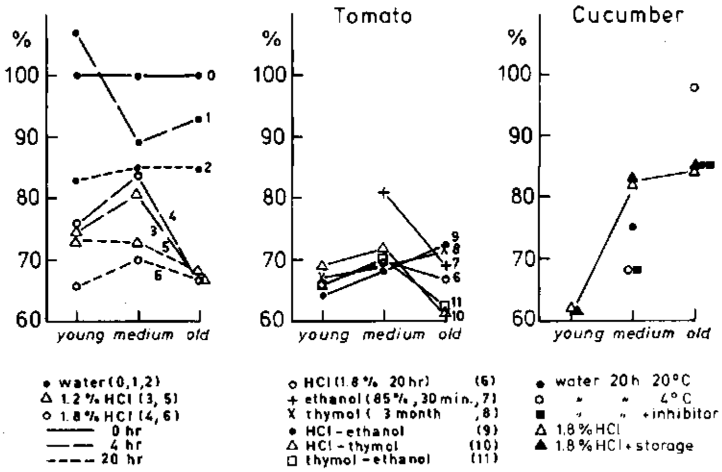


Fig. 4.5 Relative dry matter content of tomato and cucumber roots grown on a nutrient solution, after simulated washing and storage procedures; dry matter content of root samples is expressed as a percentage of dry matter content of root samples dried directly after sampling; young, medium and old approximately correspond with the three sampling stages in the main experiments; in the cucumber experiment a respiration inhibitor (0.1 mM KCN + 25 mM salicyl-hydroxamate at pH 6.5) was used, but it did not reduce dry matter losses.

which plants were cut and put in the pressure bomb and of the exudation pattern in the case of a more prolonged application of a given pressure. In some experiments estimates of leaf and fruit water potential were made by a modified Scholander pressure bomb technique, using leaves, young side shoots or young cucumber fruits which had been covered (while on the plant) with aluminum foil since the previous day.

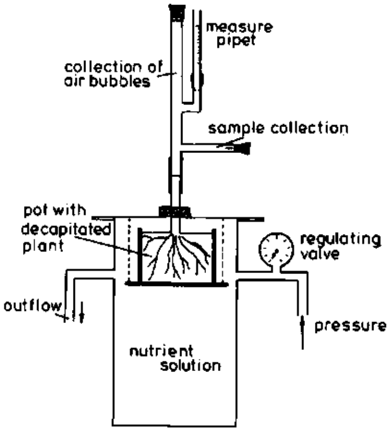


Fig. 4.6 Pressure bomb used to measure hydraulic conductance of roots.

4.3.2 Results

4.3.2.1 Pot size and root growth

Root development was physically obstructed by the smaller pots. In the upper zone of sand-filled pots a dense mat of roots was formed, causing a rise in the level of sand in the pot of up to 1 cm. Directly under the trickler a lump of roots was formed. Towards the end of the experiment this caused problems in some pots as the infiltration of nutrient solution into the pot was impeded. In the smallest sand-filled pots the flow rate from the tricklers had to be reduced, in accordance with the drainage rate possible.

In the tomato experiment all adventitious roots were classified according to their length. For the smallest pot size (ϕ 6.5 cm), the average length of 58 roots originating on the stem base was 6 cm (with a maximum of 15 cm), for the middle-sized pots (ϕ 11.2 cm) 71 roots were recorded to have an average length of 9 cm (maximum 40 cm) and for the largest pot size (ϕ 23 cm) the average length of 65 adventitious roots was 13 cm (maximum 50 cm) at final harvest. At the first sampling period 85% of the final number of adventitious roots was already present as well as 80% of the final length of the main axis of adventitious roots.

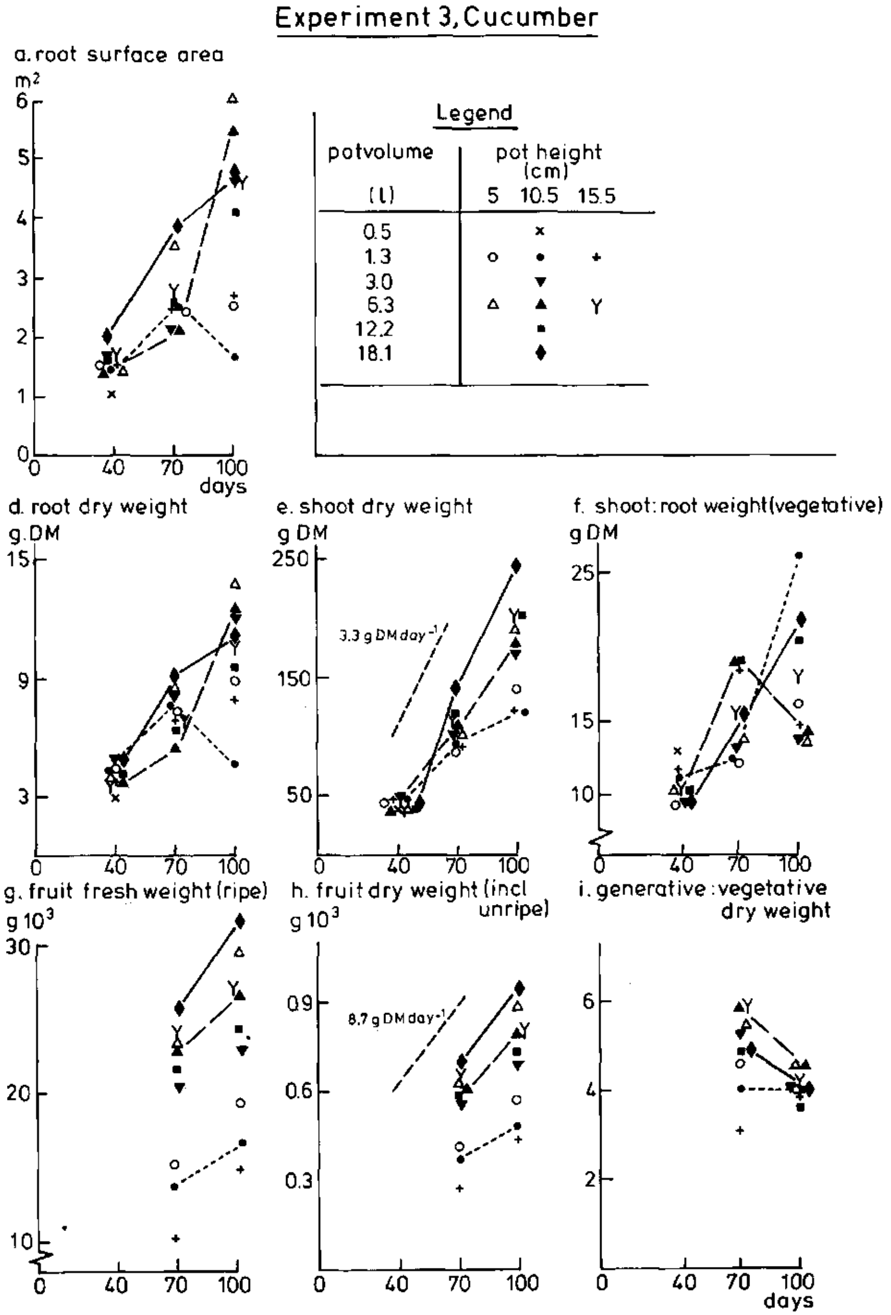
Cucumber roots were mostly restricted to the top 5 cm of the pot. For this reason pot height was varied for two pot volumes in experiment 3. In rockwool pots, roots were concentrated mostly on the sides of the blocks, between the plastic sheet and the rockwool block.

The ratio between root surface area and root dry weight was influenced by pot size and was also different for sand and rockwool. Tomato started off at about 0.28 m^2/g in sand pots and shifted to about 0.20 m^2/g in the smaller pots. In rockwool all tomato roots had a specific root surface area of about 0.18 m^2/g. For cucumber on sand-filled pots the figure was 0.35 m^2/g; data for roots washed from rockwool varied from 0.15 to 0.25 m^2/g. Total root surface area varied from 0.8 to 2 m^2 per plant in tomato and 1 to 4 m^2 per plant in full-grown cucumber plants. For cucumber, however, much larger pots are required to allow this root surface area to develop. Cucumber roots do not use the whole pot volume in narrow and relatively high pots. In experiment 3 pot height had no influence on total root surface area in the 4.9 dm^3 pore volume pots, but in the 2.5 dm^3 pore volume pots wide and shallow pots more root growth was possible than in narrow and deep ones.

4.3.2.2 Shoot growth and fruit production

Figure 4.4 shows tomato plants of three pot sizes at harvest time (experiment 1). Harvest data for this experiment are summarized in figure 4.7. In the tomato experiment, only the smallest, sand-filled pot caused a clear deviation from the growth pattern of the other pots: these plants developed a smaller leaf surface area and showed the first ripe fruits on the first truss. Of the tomatoes on the first truss, however, 30% showed blossom-end-rot, which was not observed in the other treatments.

Leaf/root ratio on a surface area basis varied between 3 and 1. The smallest pots gave the highest ratio. The root surface area obtained in the smallest sand pots, which under the conditions of the experiment was not sufficient for optimal growth of the shoot, was 0.8 m^2. The first plant with normal growth had a total root surface area of 1.2 m^2. The dry matter production per plant was of the order of 4 g per day of vegetative shoot tissue and 7 g per day of generative tissue. Both these values are slightly above the values used in table 4.1, probably due to the wider plant spacing used in the experiment. Vegetative shoot/root ratios on a dry weight basis were in the range of 16 to 32. At final harvest dry matter production of



Legend

potvolume (l)	pot height (cm) 5	10.5	15.5
0.5		×	
1.3	○	●	+
3.0		▼	
6.3	△	▲	Y
12.2		■	
18.1		◆	

Fig. 4.9 Harvest data cucumber experiment 3.

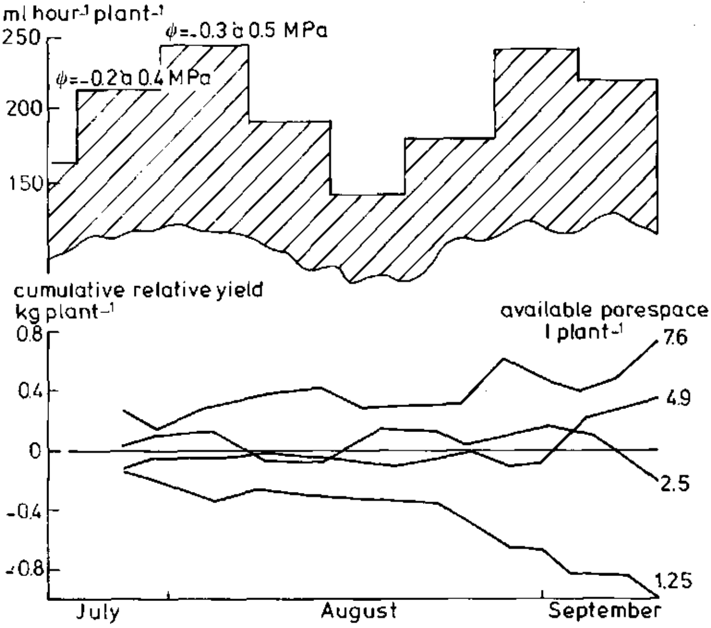


Fig. 4.10 Average water consumption for all cucumber plants in the course of experiment 3 and cumulative differences in fruit production (fresh weight) from plants grown on pots of four sizes (total available pore space per pot in dm^3); cumulative production per plant is given minus the average value). In the upper graph some measurements of leaf and young fruit water potential are presented.

generative tissue was about equal to that invested in vegetative tissue. The experiment was stopped when the first ripe fruits had just been picked.

In the cucumber experiments (figures 4.8 and 4.9) much more pronounced effects of pot size on plant growth were evident. In experiment 2 (figure 4.8) the largest pot used gave the highest production, and so the question remained whether or not this pot was large enough to show maximum plant development. Experiment 3, in which larger pot sizes were used, still was not completely conclusive. Dry matter production per plant in vegetative and generative tissue was very high in experiment 3, with 3.3 g vegetative and 8.7 g generative per day. Leaf/root area ratio varied from 1.0, vegetative shoot/root dry weight ratio varied from 10 to 20. Plants growing in sub-optimal pot sizes generally had higher fruit abortion rates and higher dry matter contents of the fruits. At final harvest the ratio between vegetative and generative tissue was fairly constant, showing that most plants had adjusted fruit load to the size of the vegetative shoot. Critical root surface area, as far as it could be established, was around 2 m^2 per plant in experiment 2 and around 4 m in experiment 3. From daily harvest data of ripe cucumbers, a more detailed analysis of the origin of yield differences is possible. Figure 4.10 shows cumulative differential yields for four pot volumes as developed in time; average water consumption by all plants may serve as an indicator of effective

4.3.2.4 Water uptake

Figure 4.14 shows that a suction of 0.05 MPa applied to a cut stem produced flow rates comparable to those obtained with an external pressure of 0.05 MPa to the roots. Initial measurements (experiment 1 and 2) with the pressure bomb indicated that the time of day affected the measured flow rates. Figure 4.15 shows results of part of experiment 4 aimed at analyzing such effects. Plants were cut at two times of day and measurements were continued for the whole day. Measured flow rates after an initial rise generally declined after the first hour of cutting. In tomato little influence of the time of cutting on the results was evident. Plants which were left bleeding in the glasshouse often showed a peak in the bleeding rate around noon, which is probably due to the rising temperature.

The measurements on cucumber showed a considerable effect of the time of collecting the plants from the glasshouse for cutting on measured flow rates at a constant external pressure of 0.5 MPa. The flow rate per unit root surface area of plants collected from the glasshouse and cut at 11 a.m. was 2 to 3 times as high as that of plants collected from the glasshouse and cut at 8 a.m.. From the absence of such an effect at 0.1 or 0 MPa external pressure we may conclude that this effect cannot originate from variation in F_{s*} or σ_r alone, but may do so from variations in L_p at constant other variables, if we accept the description in equation 3.3. Such differences in apparent L_p might be due to the higher temperature of the root system in the glasshouse previous to the measurement. In the pressure bomb we tried to maintain a constant temperature of 20°C, but we cannot exclude temperature effects during the measurements.

Because of the rapid decline of flow rates after cutting, measurements were normally performed within the first hour after cutting; rates of flow at 0, 0.05 and 0.1 MPa pressure were compared for half the plants, flow rates at 0, 0.1 and 0.5 MPa pressure for the other half. For every pot two cycles of applied pressure were completed (e.g. 0, 0.1, 0.5, 0, 0.1, 0.5, 0 MPa). Occasionally plants had to be discarded, being apparently leaky when after measurement at high external pressure subsequent measurement of bleeding showed no or negative flow rates. Especially in small sand-filled pots with tomato significant amounts of air bubbles were recorded, indicating that air-filled cavities in the cortex were immersed. The possibility exists that in such cases part of the observed flow occurred in air-channels in the cortex rather than through the natural pathway in the xylem. For this reason measurements of plants which showed air bubbles in the exudate were discarded. The most reliable set of data was obtained in experiment 4. Rates of flow per unit root surface area at various pressures are given in figure 4.16 for

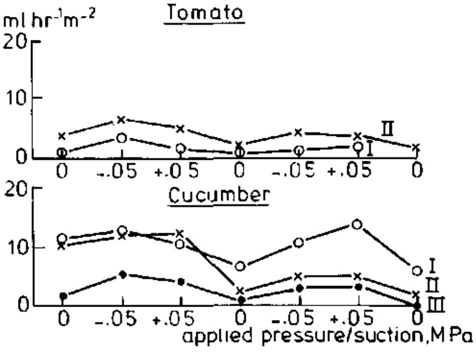


Fig. 4.14 Comparison between suction and pressure on rate of water flow in tomato.

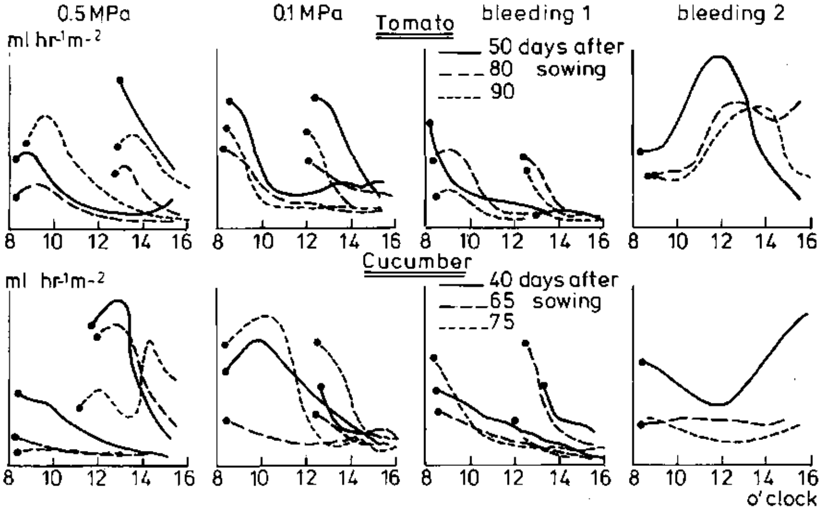


Fig. 4.15 Daily pattern in water flow per unit root area under various pressures; plants were collected at two times from the glasshouse; scale differs for various applied pressures.

tomato and cucumber at three harvest periods (results for 0, 0.05, 0.1 and 0.5 MPa are averages of 4, 2, 4 and 2 replicates, respectively). Root hydraulic conductance L as estimated from the slope of the line between applied pressures of 1 and 0.5 MPa was higher for tomato than for cucumber: about 9 and 12 * 10^{-6} cm/ (s MPa), respectively (according to (3.2) this is an underestimate of the true value). The age of the plant had remarkably little effect on the hydraulic conductance, averaged over the whole root system. The position of the intercept of the extrapolated straight line with the x-axis discussed in the appendix to chapter 3 was found to be close to π_0 for tomato, and at low or even negative x-values for cucumber; these positions of the intercept suggest that the reflection coefficient σ_r was less than 0.5.

4.4 Water balance of tomato and cucumber

Observed values for the critical root surface area in our experimental conditions are lower by a factor of 2 to 3 than the initial estimates in table 4.1, despite the slightly higher dry matter production per plant. Experiment 1 indicated that the critical root surface area for tomato was 1 m^2/plant, experiment 2 gave a value of about 2 m^2 for cucumber and experiment 3 (under conditions allowing a higher growth rate) a value of about 4 m^2. Observed uptake rates for nutrients per unit root surface area in the experiments were higher than estimated "maximum" values F_{max} from the literature used in table 4.1, up to a factor of 4 for N, 5 for P, 2 for K and 7 for Ca. Thus nutrient uptake was not a limiting root function in our experiment, with the possible exception of calcium uptake in the tomato experiment, as evident from the occurrence of blossom-end-rot in the smallest pots.

Water uptake probably was a limiting factor for shoot growth in the experiments, as will be discussed next. Figure 4.10 shows that yield effects due to the pot size in cucumber experiment 3 were found mainly in two periods of high insolation and hence transpiration. This circumstantial evidence can be substantiated by a quantification of all parameters of the water balance (4.2).

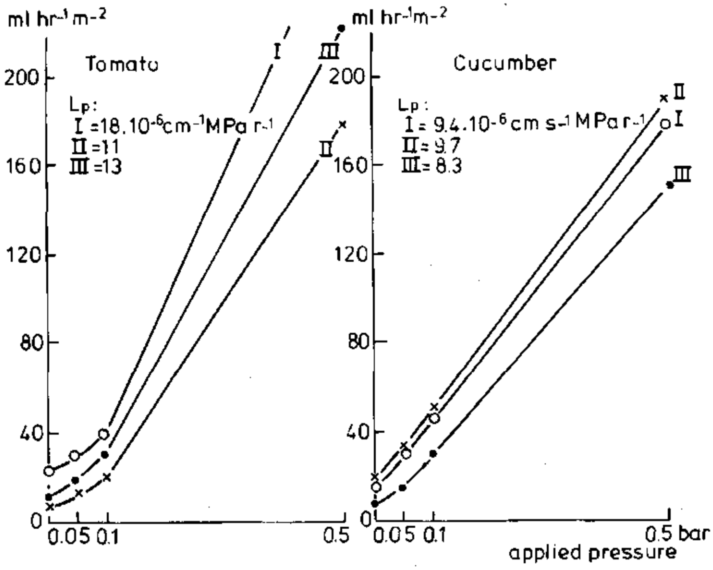


Fig. 4.16 Flow rate per unit root surface area as a function of applied pressure to the root system for tomato and cucumber in experiment 4 at three stages of the life cycle of the plant: I during the exponential growth phase, II at the start of flowering, III when first trusses ripened (tomato).

Hydraulic conductance L_p

Measurements of hydraulic conductance of roots grown in medium-sized sand-filled pots in experiment 4 (figure 4.16) showed a value of 12 and 9 $* 10^{-6}$ cm/(s MPa) for tomato and cucumber, respectively, instead of 5 as used in paragraph 4.2. Apparent hydraulic conductivities of roots grown in rockwool were higher than of roots grown in sand, especially on small pots, probably because of an extra resistance in the latter situation due to densely packed sand, blocking part of the root epidermis (data not shown here).

Transpiration per plant E_p

Total water use per plant per day in the experiments was in the range of 2 to 4 l; in the daytime (8 a.m. - 5 p.m.) the transpiration rate was approximately twice as high as the evening + nighttime value (5 p.m. - 8 a.m.). Average maximum daytime transpiration rates per plant were about 200 ml/hour for tomato (experiment 1) and about 300 ml/hour for cucumber (experiment 3).

Difference in hydrostatic water potential ΔH_p

Both the literature and our own experiments suggest that -0.5 MPa is a reasonable estimate for ΔH_p for tomato; for cucumber a value of -0.4 MPa was found at the start of yield differences in experiment 3.

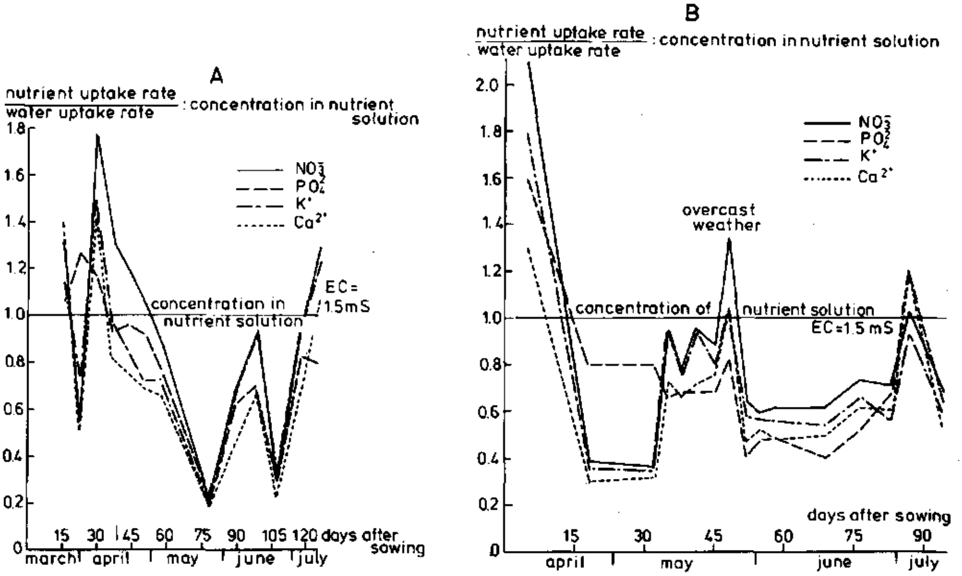


Fig. 4.17 Nutrient and water uptake by tomato (A, experiment 1) and cucumber (B, experiment 2); C_u = uptake concentration = nutrient uptake rate/water uptake rate [mol/l]; C_s - nutrient concentration in the solution [mol/l]; for C_s the initial composition of the nutrient solution has been used; extended periods of overcast weather are indicated.

Osmotic pressure π_0

The osmotic pressure of the nutrient solution was 0.03 - 0.07 MPa, so we may use an average of 0.4.

Solute reflection coefficient σ_r

No independent estimates of σ_r could be made as the procedure we used to collect root exudate was not sufficiently precise for a detailed analysis. A possibility exists to estimate the reflection at the root surface from a comparison of the "uptake concentration" $C_u = F_n/F_w$ (rate of nutrient uptake/ rate of water uptake), with the concentration C_s around the root. Figure 4.17 shows the ratio C_u/C_s in experiment 1 and 2. The dimensionless quantity C_u/C_s varied from 2.0 in the initial growth phase to 0.2 occasionally in later growth phases. Values above 1 indicate depletion of the nutrient solution, values below 1 accumulation of salts in the solution. C_u/C_s varies for individual nutrients, but as an overall average over the whole growing period a value of 0.7 seems to be reasonable. This value may be tentatively translated into a reflection coefficient of 0.3 if we want to use the simplified equation (4.2), neglecting active nutrient uptake F_{s*}. This value of σ_r is much lower than the values usually reported for non-nutritional ions such as Na and Cl, for which 0.8 - 1.0 is commonly found. Strictly speaking this use of a reflection coefficient for nutritional ions is not in agreement with the assumption of concentration-independent nutrient uptake (chapter 3); the value found is valid only for the concentration used in the experiment.

Minimum root surface area for water uptake $A_{r,w}$

Using the above-mentioned values in (4.2), $A_{r,w}$ can be estimated at about 1.0 m^2 for tomato and about 2.4 m^2 for cucumber for the conditions of our experiments. The fact that the actual hydraulic conductance was double the value initially estimated roughly corresponds with the fact that the critical root surface area was half the value estimated. Thus we may conclude that the observed minimum root surface area, as indicated by unrestricted shoot growth, closely agrees with the root surface areas required for water uptake under the experimental conditions, as evident from independent measurements of the potential for water uptake of the root systems.

4.5 Discussion

The critical root surface area as evident from the experiments agrees quantitatively with estimates of the required total water uptake and potential water uptake per unit root surface area. In this respect our experiments agree with the functional equilibrium theory, predicting that the required size of the root system is determined by the rate at which external resources (water and nutrients) can be obtained; internal functions of the root system such as hormone production apparently act within the limits of direct resource availability. Experimental results such as the shift to early fruit production in tomato and increased fruit abortion in cucumber may be caused on the proximate level by differences in levels of absisic acid (ABA) and/or cytokinins. The first step in such a causative chain is a difference in internal water status of the plant due to a reduced root system at ample external supply, which has to invoke an internal response in the plant.

Some aspects of the experiments and especially C_u/C_s for horticultural practice will be discussed in chapter 5 in relation to the nutrient use efficiency of horticulture on artificial substrates. At this stage we may conclude that the hypothesis can be corroborated that at a certain stage of improved supply of water and nutrients, physiologically determined maximum uptake rates limit a further reduction in the size of the root system. For tomato and cucumber at least, the maximum uptake rate for water determines the size of the root system in a nutrient solution (the osmotic pressure of which can hardly influence these results). No evidence for real maximum nutrient uptake rates could be obtained.

For a model description of nutrient uptake in the field, under situations where supply to individual roots by diffusion and mass flow is the rate-limiting step, the simplified approach (neglecting "physiological parameters") outlined in chapter 1 may be sufficient.

5. MINIMAL ROOTED VOLUME AND NUTRIENT USE EFFICIENCY IN MODERN HORTICULTURE

5.1 Introduction

In modern horticulture on artificial substrates (figure 4.1) the smallest possible root environment is desirable, for practical and economic reasons. Results discussed in chapter 4 suggest that the rooted volume can be greatly reduced before the physiological limits to root functions are reached due to physical obstructions to root growth, provided the supply of water and nutrients to the roots is continuously maintained. The latter condition, however, is not easily met, especially when recirculating systems (as in the experiments of chapter 4) are avoided for fear of spreading diseases. The majority of horticultural systems on soilless media involve relatively small root systems associated with a low nutrient use efficiency. This association, however, is not based on a direct causative chain. In these horticultural systems with a very small buffering capacity of the root environment for water and nutrients, the relative depletion fraction is determined by the degree of adjustment of nutrient supply to the current needs of the crop, rather than by the ability of the plant to obtain nutrients from the root environment. In this chapter the nutrient use efficiency obtained in commercial practice will be discussed and analyzed; possibilities for improving the nutrient use efficiency of relatively small root systems will be indicated. Consideration of this soilless situation helps in formulating functions normally performed by soils.

The smaller buffering capacity of the root environment for nutrients and water in soilless cultures compared with conventional ways of growing plants in soil offers possibilities for manipulating and rapidly changing the root environment. The small buffering capacity imposes a need for frequent replenishment as well as a need for regulating the nutrient content of the solution. As a plant rarely takes up water and the various nutrients according to the external supply, it is continuously changing the composition of the nutrient solution. The smaller the rooted volume, the more these disturbances are felt. Problems in maintaining an ideal root environment in these weakly buffered systems make it difficult to obtain maximum plant production as well as a high nutrient use efficiency.

In this chapter root development in rockwool culture under conditions as exist in commercial practice will be discussed in relation to salt accumulation in the root environment, leaching of nutrients and nutrient use efficiency. Improvements of the low nutrient use efficiency obtained so far primarily depends on a better synchronization of nutrient supply with nutrient demand.

5.2 Root development in rockwool

5.2.1 Research methods

The geometry of rockwool culture systems for tomato and cucumber is shown in figure 5.1 (compare also figure 4.1 D). Usually four plants are grown on one piece of rockwool (length x width x height = 180 x 30 x 7 cm^3) with one trickling point near each plant. The rockwool slab is sheathed in polythene foil with drainage slits in one or more places. Nutrient solution is supplied several times a day, excess nutrient solution is lost through the slits to the glasshouse soil. The 10 l of rockwool per plant holds about 5 l of nutrient solution, i.e. about twice the average daily transpirational demand.

The composition of the nutrient solution is based on crop-specific recipes. Total salt content of the nutrient solution used is frequently (daily)

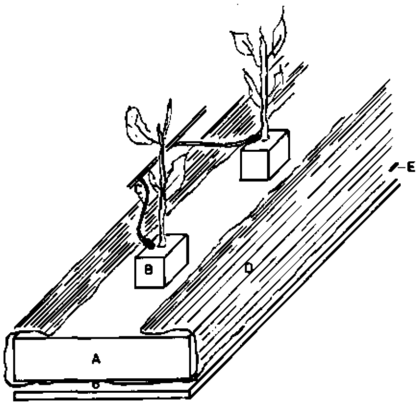


Fig. 5.1 Schematic presentation of rockwool-grown tomatoes: A = rockwool slab, B = planting cube, C = trickler, D = polythene sheath and E = drainage slit.

adjusted on the basis of the pH and the electrical conductivity (EC) of a sample of nutrient solution. Nutrient ratios are adjusted on the basis of complete analysis of samples of solution collected from the rockwool slab twice a month for macro-elements and monthly for trace elements.

Root development was recorded in two rockwool-culture experiments under semi-practical conditions: a tomato experiment in 1977 and a cucumber experiment in 1978. In both cases the rockwool slabs were cut into subsamples of 10x10x 2.5 cm³ from which nutrient solution was collected for measurement of EC and pH and from which roots were washed (see section 4.3.1 for methods).

5.2.2 Results

Figures 5.2 shows the spatial variation in root surface area and EC of the nutrient solution in rockwool slabs with tomato. Highest root densities were

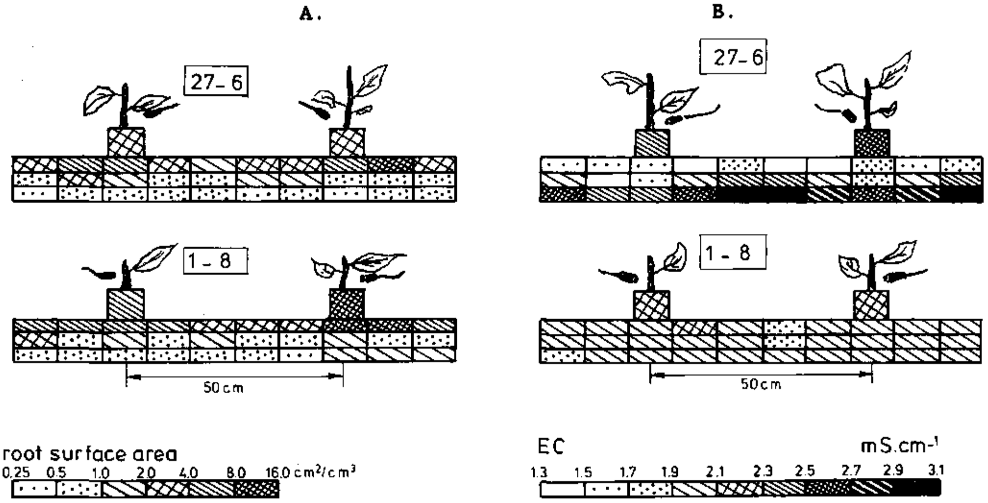


Fig. 5.2 Distribution of root surface area (A) and total salt content (B) of the nutrient solution as indicated by electrical conductivity (EC) for a tomato experiment on two harvesting dates (Van Noordwijk, 1978).

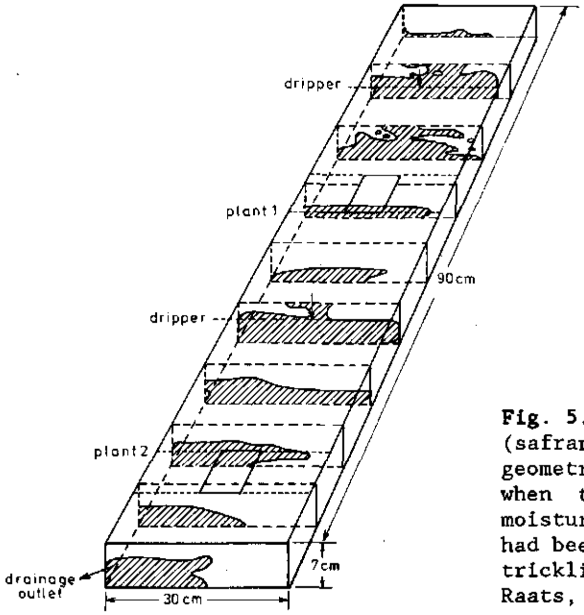


Fig. 5.3 Distribution of a red dye (safranine) in a rockwool slab in the geometry used for growing cucumbers, when the equivalent of 1.7 x the moisture holding capacity of the slab had been infiltrated through the two trickling points (Van Noordwijk and Raats, 1982).

found in the upper zone of the rockwool slab. Small-scale differences in EC occurred: over 5 cm distance EC varied by a factor of 2. Relatively high EC values were found in the lowest zone of the slab, in-between two plants and in between tricklers. Recognition of such local differences in EC and of the existence of so-called dead corners with high salt contents has subsequently led to better instructions for sampling the nutrient solution, avoiding the dead corners. Ions accumulating in the dead corners mainly are Cl^-, SO_4^{2-}, Ca^{2+} and Mg^{2+}.

At a plant density of 2.2/m², total root surface area was 1.1 m² per plant for a 2-month old cucumber crop in March and 2.0 m² per plant when the crop was 5 months old. For tomato a total root surface area of 2.2 m² per plant was found. These values agree with the size of the root systems in the experiments discussed in chapter 4 in non-limiting pot sizes.

Figure 5.3 shows that nutrient solution from the tricklers does not mix well with the solution present. Large parts of the rockwool slab are not incorporated in the major flow lines. As discussed before (Van Noordwijk and Raats, 1980, 1982) this infiltration pattern may predict where salt accumulation will occur; recommendations were made to adjust the geometry of infiltration and drainage points to make full use of the buffering capacity of the rockwool. The cause of salt accumulation lies in incomplete synchronization of nutrient supply and demand, as will be discussed now.

5.3 Nutrient use efficiency

Van Noordwijk and Raats (1982) showed that in the cucumber experiment of figure 5.3 a large part of all fertilizer used was washed to the drains: only about 30% of N, P, Mg and K and about 10% of Ca and Mg applied during the growing season was actually taken up by the crop in this experiment. Data on nutrient and water use by 15 tomato and cucumber growers collected by Van der Burg and Hamaker (1984) are shown in figure 5.4. In commercial practice 30 -

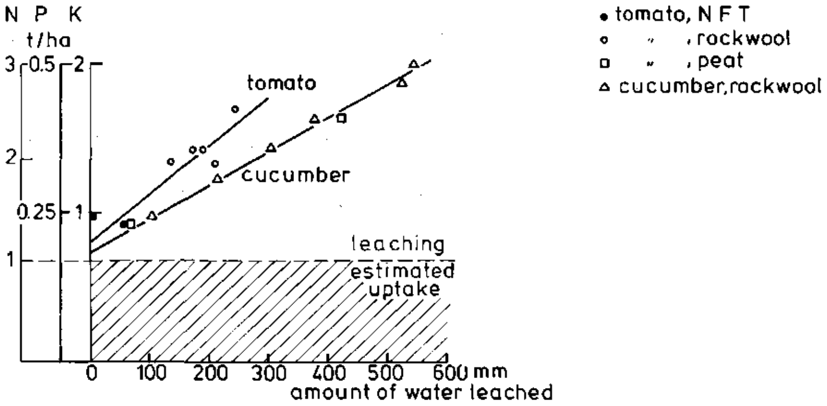


Fig. 5.4 Fertilizer use in 15 glasshouses in one growing season in relation to the amount of water leached (after Van der Burg and Hamaker, 1984); total fertilizer use; estimated nutrient uptake for both cucumber and tomato is indicated.

60% of N, P and K supplied is taken up by the crop. The relatively low efficiencies and the large amounts of nutrients lost (up to 1000 kg N/ha) deserve further analysis. Losses of water and nutrients are partly due to uneven delivery of solution by the tricklers and uneven growth and uptake of the plants, which cause leaching of excess nutrient solution when the water supply is adjusted to the most-demanding plant with the slowest trickler (Van Noordwijk, 1983b).

Even in completely homogeneous systems, however, an apparent need for leaching of nutrient solution stems from the salt accumulation which would otherwise occur. If irrigation water is used which contains NaCl, accumulation of salts in the system cannot be avoided; leaching requirements for such a case were described by Van Noordwijk and Raats (1982). Even without NaCl or other undesirable salts in the system, salts often accumulate, due to difficulties in adjusting nutrient ratios to current demand.

In the recommended composition of a nutrient solution Ca and Mg are supplied in higher concentrations relative to plant demand than K, to maintain suitable K/Ca and K/Mg ratios for adequate uptake. The necessity to maintain a K/Ca ratio in the root environment which differs from the uptake ratio may be due to the fact that different parts of the root are involved in uptake of Ca (only the young parts) and K (the whole root length, compare chapter 3). For the young root parts the K/Ca uptake ratio may be equal to the ratio supplied; around the older roots Ca accumulates, unless the nutrient solution is thoroughly mixed. SO_4^{2-} serves as a counter ion for the necessary excess of Ca and Mg in the nutrient solution and is supplied in excess of plant demand as well. To maintain the pH of the nutrient solution part of the nitrate is supplied as HNO_3. Alternatively a NH_4 : NO_3 ratio can be found at which nutrient uptake has no effect on pH. In a root medium such as a rockwool slab where the nutrient solution is not thoroughly mixed continuously, local depletion and accumulation of the nutrient solution and change in pH can hardly be avoided.

As figure 4.17 showed, the relative depletion of the nutrient solution, C_u/C_s, may vary from week to week and in fact from day to day, as transpirational demand fluctuates. The optimal concentration of all nutrients in the nutrient solution for maximum yields (and/or quality) has been established for many plant species in experiments in which many concen-

Table 5.1 Estimated daily uptake concentration, C_u, of nutrients (figure 4.17) by a tomato crop compared to the recommended composition of the nutrient solution in the rockwool slab (Sonneveld and Van der Wees, 1980). Three system concentrations are shown for each nutrient: lowest $C_s(\ell)$, desired $C_s(d)$ and highest $C_s(h)$. The range of concentrations tolerated is defined as $C_s(h)/C_s(\ell)$. Uptake concentration C_u calculated for a daily transpiration of 2.5 l/plant is compared to the desired system concentration $C_s(d)$ in the last column.

Daily uptake mg/(plant day)		Uptake conc. C_u mg/l	System concentration C_s $C_s(\ell)$	$C_s(d)$ mg/l	$C_s(h)$	Tolerance $C_s(h)/C_s(\ell)$	Utilization $C_u/C_s(d)$
N	225	90	84	130	210	2.5	0.69
P	45	18	15	31	47	3.0	0.58
S	50	20	32	64	160	5.0	0.31
K	450	180	160	200	270	1.75	0.90
Ca	100	40	160	200	280	1.75	0.20
Mg	30	12	24	48	72	3.0	0.25

tration levels, maintained throughout the growing season, were tested (Sonneveld and Voogt, 1985). If in such an experiment a concentration C_s would be tested which equals the average C_u over the whole growing period, the plants would receive insufficient nutrients during some parts of the growing season. As soon as $C_s > C_u$ the concentration around the root C_s will tend to rise further, as soon as $C_s < C_u$, C_s will decrease further. For this reason it is understandable that the recommended C_s exceeds the average C_u (Table 5.1). As a consequence, nutrients will accumulate in the root environment during large parts of the growing season and may cause difficulties with the water uptake by the plant as well as imbalance in K/Ca ratio of the nutrient solution. Leaching of nutrient solution is a simple way out for the grower, but this results in a low nutrient use efficiency.

The relationship between leaching of water and nutrients and the fractional uptake (C_u/C_s) can be formulated simply for a perfectly mixed system such as a rapidly recirculating nutrient solution (NFT-system, figure 4.1). For imperfectly mixing systems of low buffering capacity, such as rockwool slabs, this algebraic description may still be a reference. For the water and nutrient balance of a perfectly mixed system (Raats, 1980) we may write:

$$N_a = N_u + N_\ell \quad , \tag{5.1}$$

$$W_a = W_u + W_\ell \quad , \tag{5.2}$$

where:

N_a and W_a = input of nutrients and water, respectively,

N_u and W_u = uptake of nutrients and water, respectively,

N_ℓ and W_ℓ = leaching of nutrients and water, respectively.

When we define "leaching fractions" ℓ_n and ℓ_w for nutrients and water, respectively, as:

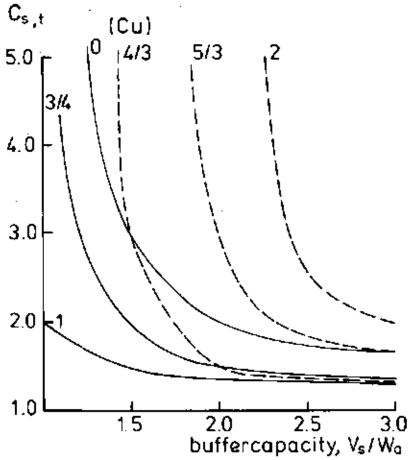


Fig. 5.7 Required storage capacity V_s/W_a of a nutrient solution system, assuming water uptake during the day only and constant nutrient uptake, and replenishment with an ideal solution once a day; solid lines for accumulation, $c_u < 1$, broken lines for depletion, $c_u > 1$ (Van Noordwijk and Raats, 1982).

5.4 Discussion: Synchronization requirements and buffering capacity

The physiological limit to the root/shoot ratio, discussed in chapter 4, is not reached in practical rockwool culture: due to difficulties in maintaining an "optimal" supply of water and nutrients the size of the rooted volume has to be considerably larger than the volume minimally required for root development as such. In substrate culture, the present association of small root systems with low nutrient use efficiencies is not a necessity. As shown in figure 5.6, the leaching fraction for nutrients could be considerably reduced if a better synchronization of nutrient supply with current demand would be achieved, with c_u as close to 1.0 as possible (e.g. $c_u = 0.8$ leads to 22% losses).

If the replacement solution is regulated in an ideal way and such that the effect of nutrient uptake by the crop on pH is neutral, no leaching is required. While in all cases the replacement solution C_n should, ideally, equal the (current) uptake solution C_u, the system concentration C_s may be different from C_u in a well-mixed system. This makes it possible to supply cations (K^+ and Ca^{2+}) in a ratio which differs from their uptake ratio. In such a case, however, perfectly mixed systems (such as the rapidly recirculating nutrient solution in the NFT-system, figure 4.1) are to be preferred to non-mixing systems such as rockwool.

Reduction of the buffering capacity in the immediate environment of the root in soilless culture increases the possible degree of human control over both plant nutrition and losses to the environment. To obtain the desired - and possible - nutrient use efficiencies a considerable change of present-day practices is needed.

In agricultural systems important functions of the soil in natural ecosystems have been replaced by technical means. In soilless cultures this can be seen in the clearest form. Rain water is collected from the roofs of the glasshouse and stored in a basin next to the glasshouse for daily use. In field-grown crops water is stored in the soil between rains, preferably within reach of the root system. On a macro-scale, agricultural water management in the Netherlands has become similar to that in the glasshouse: excess water from runoff and drainage is collected in ditches and pumped out of agricultural areas to large lakes; during dry periods surface water has to be returned to agricultural areas for (sprinkler) irrigation of the crop. The necessity of such measures depends on the size of the effective water buffer capacity in the rooted zone and hence on water depletion efficiency of the crop.

As water acts as a carrier for nutrients manipulation of the water supply has several consequences for the nutrient supply of the crop, both favourable and unfavourable. Nutrients for the soilless cultures are stored in a concentrated form in basins inside the glasshouse; the amounts given daily have to meet actual requirements on that day as the buffering capacity of the root environment is low. In field-grown crops, nutrients are added once or at most in a few split applications of fertilizer. Buffering capacity of the soil (as influenced by organic matter and clay content, rooting depth, biological and chemical factors) is necessary to obtain reasonable nutrient use efficiencies under such poor synchronization of supply and demand and to (partly) protect nutrients from leaching during periods of excess rainfall. A direct consequence of this buffering is a reduced mobility of the nutrient in the root zone and hence transport distances to the root surface become important. Higher root densities may reduce transport distances as well as uptake requirement per unit root length. For soil grown plants the geometry of the system is of considerable importance as it determines the transport distances involved in nutrient and water uptake. As a further step towards our model description, chapter 6 will consider the geometry of soil-root systems and chapter 7 physical and chemical aspects of buffering and mobility in the soil.

6. GEOMETRY OF THE SOIL - ROOT SYSTEM

6.1 Introduction

In this chapter we will define representative situations of the geometry of soil-root systems, for which transport equations will be solved in chapter 8 to 11. In section 6.2 we will analyze the geometry of roots and derive an expression for specific root length and specific root surface area, as defined in chapter 1; literature values are presented to obtain standard values for use in later chapters. In section 6.3 literature data on root length density L_{rv} (root length per unit volume of soil) will be reviewed.

Section 6.4 will describe the dynamics of root growth and decay in the field, as a further discussion of assumption 8 in chapter 3. In section 6.5 we will concentrate on the distribution pattern of the roots, in section 6.6 on the degree of physical contact between soil and root. In section 6.6 we will define the geometry to be used in the models of chapter 8 to 11.

6.2 Relations between basic root parameters

Geometry of roots

Generally roots can be assumed to be cylindrical in shape and hence simple relationships exist between length, surface area and volume:

$$(6.1) \quad V_r = \pi R_0^2 L_r = A_r R_0/2 \qquad [\mathrm{cm}^3],$$

where :
V_r = root volume [cm³],
A_r = root surface area [cm²],
L_r = root length [cm],
R_0 = root radius [cm].

Root volume is related to root fresh weight via the specific weight and root porosity; root dry weight is related to root fresh weight via the dry matter content:

$$(6.2) \quad Y_{D,r} = M_{d,r} F_r = M_{d,r} (1-\epsilon_r) S_r V_r ,$$

where:
$Y_{D,r}$ = root dry weight [g],
F_r = root fresh weight [g],
$M_{d,r}$ = dry matter content of roots [-],
ϵ_r = air filled root porosity as fraction of V_r,
S_r = specific weight of non-airfilled root tissue [g/cm³].

A root system consists of a set of partly interconnected cylinders of various lengths and diameters. The relationships between root system values of basic dimensions such as length, surface area and volume are similar to those for single roots, except for the definition of the average root radius. If the root system consists of k classes of roots, each with root radius $R_0(j)$ and root length per class $L_r(j)$, or if n random measurements of root radius $R_0(\underline{i})$ are made, we may define two types of average root radius, a linear average $\overline{R}_0$ and a quadratic average R_0:

$$(6.3)\quad \bar{R}_0 = \{\sum_{j=1}^{k} L_r(j)\, R_0(j)\} / \sum_{j=1}^{k} L_r(j) = \sum_{i=1}^{n} R_0/n \qquad [cm],$$

$$(6.4)\quad \tilde{R}_0^2 = \{\sum_{j=1}^{k} L_r(j)\, R_0(j)^2\} / \sum_{j=1}^{k} L_r(j) = \sum_{i=1}^{n} R_0(i)^2/n = var(R_0) + \bar{R}_0^2 \;,$$

with $var(R_0)$ as the variance in the usual statistical definition.
The specific root surface area, $A_r/Y_{D,r}$, and the specific root length, $L_r/Y_{D,r}$, can now be formulated as (Van Noordwijk, 1987):

$$(6.5)\quad A_r/Y_{D,r} = \{M_{d,r}\,(1-\epsilon_r)\, S_r\, (\bar{R}_0/2)\, (\tilde{R}_0/\bar{R}_0)^2\}^{-1} \qquad [cm^2/g],$$

$$(6.6)\quad L_r/Y_{D,r} = \{\pi\, M_{d,r}\,(1-\epsilon_r)\, S_r\, \tilde{R}_0^2\}^{-1} \qquad [cm/g].$$

Figure 6.1 shows commonly found values for the $A_r/Y_{D,r}$ and $L_r/Y_{D,r}$ ratio, as influenced by the parameters of (6.5) and (6.6).

Survey of specific root length data

Equation (6.6) shows that specific root length cannot be directly obtained from estimates of average root diameter. Data for various crops as reported in the literature are summarized in figure 6.2; details and literature references can be found in appendix 6. Considerable variation in values occurs; possibly part of this variation is due to a lack of standardization in methods of handling root samples and collecting quantitative root data. No consistent difference exists between Monocotyledonae and Dicotyledonae. Although most references show a range of values for the same crop under different conditions or for different genotypes of the same crop, standard values relevant to a majority of situations can be found. Specific root length for various crops and situations usually is in the range 100 - 300 m/g, for roots with an average root diameter of 0.2 - 0.3 mm.

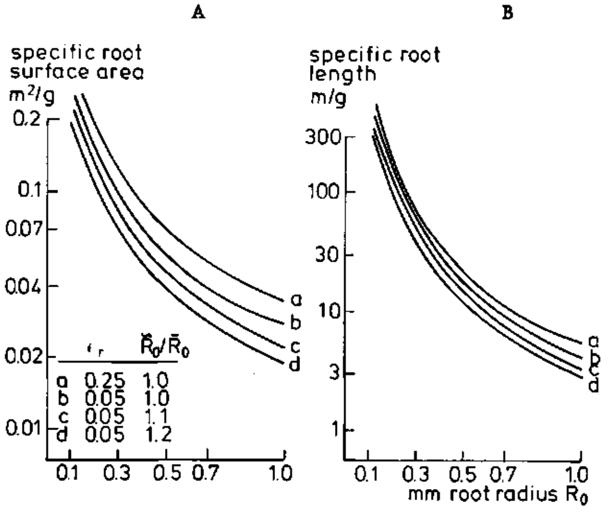


Fig. 6.1 Specific root surface area (A) and specific root length (B) as a function of average root diameter (equations 6.5 and 6.6); parameters used $M_{d,r}$ = 0.075, ϵ_r = 0.05 or 0.25, S_r = 1.0; the lines for ϵ_r = 0.25 can also be interpreted as $M_{d,r}$ = 0.059, ϵ_r = 0.05.

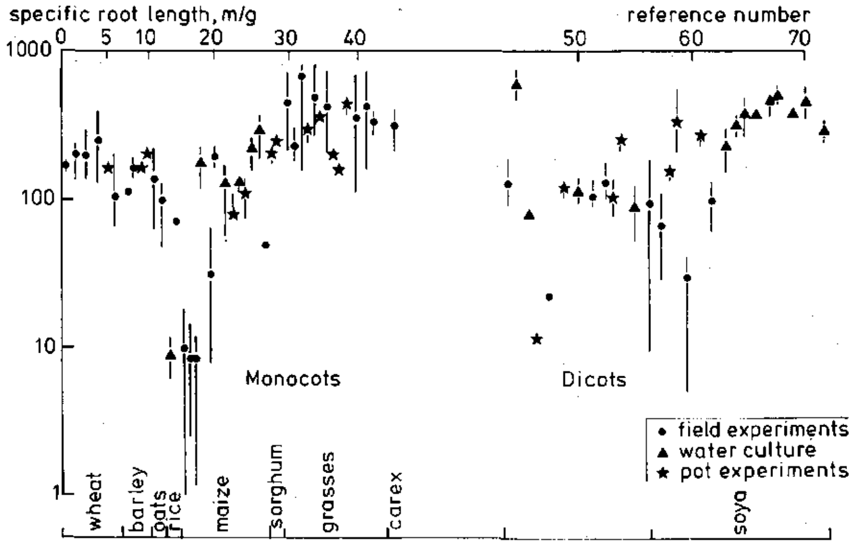


Fig. 6.2 Summary of literature data on specific root length; plant species arranged in taxonomic order; numbers refer to appendix 6.

Air-filled root porosity ϵ_r

The parameter ϵ_r in (6.5) and (6.6), the root porosity, can be measured by comparing the specific weight of roots as such with that after grinding (Jensen et al.,1969) or evacuation, when all pores may be expected to be water-filled. Results of this technique are in agreement with visual in-

Table 6.1 Data on root porosity, ϵ_r, reported in the literature and unpublished results.

Crop	Root porosity [%]	Reference
Wetland grasses and rushes	8 - 45	Crawford, 1982
Rice	27 - 36	Jensen et al. 1969
Maize	8 - 10	Jensen et al. 1969
,, adventitious roots	3 - 19	IB-unpublished
Barley	4	Jensen et al. 1969
,,	2 - 4	Yu et al. 1969
Wheat cv "inia", susceptible	3 - 8	Yu et al. 1969
,, cv "pato", tolerant	5 -15	Yu et al. 1969
Onion	5	Jensen et al. 1969
Wetland dicots	2 - 19	Crawford, 1982
Tomato	6	Jensen et al. 1969
,,	4 - 9	IB-unpublised
Sunflower	5 - 11	Yu et al. 1969
Bean, Pea	4	Jensen et al. 1969
Gerbera	2 - 8	IB-unpublished
Bouvardia	0 - 1	IB-unpublished

spection of microscope slides (Van Noordwijk et al., in prep.). Data on root porosity for some agricultural crops are summarized in table 6.1. For a quantification of the aeration status of roots, the air-filled porosity of a root is important (Chapter 8).

6.3 Root length density and root area index

Unit soil area

Root parameters may be expressed per plant, per unit soil volume or per unit cropped soil area. The first way is most relevant for studying shoot/root relationships, the second for studying relative depletion of nutrients and water present in the soil and the third for studies on a crop level, for instance of dry matter input into soil ecosystems by roots. These three bases of comparison may be distinguished by a second subscript : L_{rp} [cm], L_{rv} [cm/cm³] and L_{ra} [cm/cm²] respectively (similarly for A_r, etc.). L_{rv} is called root length density. The dimensionless A_{ra} has previously been defined as Root Area Index, in analogy to the Leaf Area Index (Barley, 1970). When considering root systems under closed crop canopies roots of neighbouring plants usually are intermingled and an individual plant may not be a convenient basis for expressing root parameters. The size of the root system of an "average" plant corresponds to the amount of roots under a "unit soil area", U_a, as defined in figure 6.3A.

The unit soil area equals the reciprocal of plant density. Figure 6.3B shows that it may be expected that an equal number of roots of the central plant will be found outside the unit soil area, as roots of neighbouring plants enter this volume of soil. Relationships between the various bases of comparison are simple:

$$L_{ra} = L_{rp} / U_a \qquad [\mathrm{cm/cm^2}], \tag{6.7}$$

$$L_{ra} = \int_0^{Z_r} L_{rv}(z).\, dz \qquad [\mathrm{cm/cm^2}], \tag{6.8}$$

where z = depth and Z_r = depth of rooted zone. The unit soil area may be divided into four quarters of equal size, which form the smallest representative area of the field, except for different exposure of the soil surface to the sun.

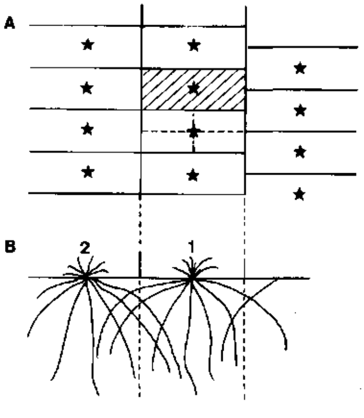


Fig. 6.3A. Top view of the "unit soil area", U_a, for row crops; plants are indicated by an asterisk, U_a by the shaded area. B. Side view of the root system under the unit soil area.

t_ℓ = turnover of root length during a growing season [-],

$L_r(e)$ = standing root length in the observation plane at the end of a growing season [cm/cm^2],
$L_n(e)$ = cumulative length of new roots since the start of the growing season [cm/cm^2],
$L_t(e)$ = cumulative length of roots observed during a growing season [cm/cm^2] for annual crops $L_n(e) = L_t(e)$,
$L_d(e)$ = cumulative length of dead and/or disappeared roots at the end of the growing season [cm/cm^2].

The root length replacement ratio r_ℓ can be calculated for both annual and perennial crops. For perennial crops it gives information on the average longevity of individual roots. If $r_\ell = 1$ we may conclude that the average longevity of a root is 1 year, provided that $L_r(e)$ is constant from year to year. The frequency distribution of individual root longevities cannot be estimated this way.

Table 6.3 presents data for four sets of observations; for winter wheat on average only 13% of the root length formed during the growing season had disappeared by the end of the growing season; for sugar beet this value is about 50% and for grassland 40%. Although we do not have enough data for generalization to all agricultural situations, for model calculations neglect of root turnover during the growing season (assumption 8, chapter 3) seems to be acceptable as a starting point.

Table 6.3 Root length replacement ratio r_ℓ and turnover t_ℓ of fine roots of field-grown crops during a whole growing season, as observed in minirhizotrons in the field; for grassland two irrigation regimes are compared, (1 = irrigated when soil water pressure fell below -200 cm; 2 = non-irrigated), for sugar beet sown (1) and planted (2) crops are compared, for winter wheat two farming systems (1 = "conventional"; 2 = "integrated"); depths: a = 0 - 10, b = 10 - 30, c = 30 - 60 cm; for sugar beet and wheat a = 0 - 30 cm (Grzebisz et al., in prep).

		Treatment		Depth		
	average	1	2	a	b	c
r_ℓ						
Grassland 1983	0.99	0.92	1.07	1.99	1.22	0.53
Grassland 1984	0.76	0.61	0.91	1.21	0.68	0.58
Sugar beet	2.12	2.03	2.20	2.62		1.76
Winter wheat	1.12	1.09	1.15	1.22		1.09
t_ℓ						
Grassland 1983	0.53	0.55	0.51	0.69	0.39	0.33
Grassland 1984	0.31	0.33	0.30	0.34	0.33	0.23
Sugar beet	0.53	0.52	0.54	0.62		0.44
Winter wheat	0.13	0.11	0.15	0.17		0.09

6.5 Root distribution pattern

Root anisotropy

An important aspect of variation in root distribution, related to root orientation, is described by the degree of anisotropy. A normalized anisotropy factor a_n can be defined, modified from Lang and Melhuish (1970), from the number of roots N_x, N_y and N_z intersecting three mutually perpendicular planes X, Y and Z, respectively (Z horizontal, X and Y vertical perpendicular to and along the crop rows, respectively):

$$(6.10) \quad a_n = \sqrt{(N_x - N_m)^2 + (N_y - N_m)^2 + (N_z - N_m)^2 \; / \; 6\, N_m^2} \;,$$

where:

N_m = average number of roots seen per unit sample area = $(N_x + N_y + N_z) / 3$,

and N_x, N_y and N_z are the number of roots seen per unit sample area.

Root-plane intersections can be counted in various ways. The two main sampling approaches used are: counts of N_z on auger samples which are broken for inspection (Schuurman and Goedewaagen, 1971), or counts of N_x on smoothed profile walls on which roots are made visible by removing some soil by spraying (Böhm, 1979). Roots can be counted in grids directly or after mapping on polythene sheets. Horizontal planes can be mapped as well (N_z). The profile wall method shows spatial arrangement of roots, for instance in relation to soil structure. As a third, less practicable method, blocks of soil hardened by resins can be inspected (Lang and Melhuish, 1970).

The average number of roots seen per unit area for three planes, N_m, can be related to the length of roots in a volume of soil by:

$$(6.11) \qquad L_{rv} = 2 \;\lambda_r\; N_m \;,$$

where $\lambda_r = 1$ for $a_n = 0$. For root distributions which are not anisotropic the correction factor λ_r can be estimated (Van Noordwijk, 1987) from:

$$(6.12) \qquad \lambda_r = 0.5 \;\; a_n^2 \; + 1 \;,$$

$$(6.13) \qquad \lambda_r = 0.8 \;\; a_n^2 \; + 1 \;,$$

for the "linear" and the "planar" situation, respectively, with (0,0,1) and (1,1,0) roots in the three planes in the extreme case.

In the usual application of both the profile wall and the core-break method roots are counted in one plane only. For counts in the horizontal plane N_z the relationship with L_{rv} can be formulated as follows. If root densities in the two vertical planes are equal, we may write $N_x = N_y = \ell_r\, N_z$. For roots with a preferentially vertical orientation $\ell_r < 1$. From (6.12) and (6.10) we can eliminate λ_r and N_m in (6.11):

$$(6.14) \qquad L_{rv} = N_z \;\; (3\; \ell_r^{\,2} + 2\; \ell_r + 1) \;/\; (2 \;\; \ell_r + 1) \;,$$

and for roots with preferentially horizontal orientation, $\ell_r > 1$, from (6.13) and (6.10) we can eliminate λ_r and N_m in (6.11):

$$(6.15) \qquad L_{rv} = N_z \; (16\; \ell_r^{\,2} + 8\; \ell_r + 6) \;/\; (10\; \ell_r + 5) \;,$$

For $\ell_r = 1$ these equations reduce to $L_{rv} = 2\, N_z$; for $\ell_r = 0$ it follows from (6.14) that $L_{rv} = N_z$; for large ℓ_r (6.15) can be approximated by (Van Noordwijk, 1987) $L_{rv} = N_x (1.6\ \ell_r + 0.8)$.

When root counts are made in one plane only and no knowledge of ℓ_r is available, as is usual in both the core-break method and the profile wall method, calibration is necessary by correlating N in the plane of observation and L_{rv}. Values for L_{rv}/N found in this way may differ from theoretical values because of errors in counting all roots, for instance overlooking roots or counting dead remains of roots which are distinguished as such in washed samples.

Calibration factors L_{rv}/N_z for the core-break method usually vary with sample position, sample depth and time, as we may expect from the strong influence of factor ℓ_r. Core-break methods thus can only give a rough indication of root distribution in the field. Available estimates of ℓ_r, the ratio between root counts on horizontal and vertical planes are in the range 0.5 - 4.

Distribution pattern

When considering L_{rv} on a small scale (small volumes of soil) part of the variation is due to the fact that roots occur as discrete events, branch roots originating on main roots. Root distribution on this scale deviates from randomness either in the direction of regularity or in the direction of clustering. Definitions of such patterns are given in plant ecology (Pielou, 1969; figure 6.5). The pattern can be quantified by measuring "nearest neighbour distances" between roots, and between soil and root, i.e. by classifying all soil according to the distance to the nearest root (figure 6.6). Root distribution pattern can be influenced by soil factors (e.g. structure) as well as plant factors (e.g. branching).

On the basis of a comparison of point-root and root-root nearest neighbour distances (figure 6.7A), statistical tests of randomness are possible (Diggle, 1983). The description of nearest neighbour distances on root maps is not only a technique for tests of randomness, it may also provide insight into the frequency distribution of real diffusion distances involved in nutrient and water depletion by a root system. In the three-dimensional reality (figure 6.7B), however, diffusion distances will be shorter than in our two-dimensional maps. The difference may be quantified as follows.

For a two-dimensional map of the Z-plane, the frequency distribution of point-root distances in case of a random distribution of roots, can be derived from a Poisson distribution as (Pielou, 1969; Marriot, 1972):

$$(6.16) \qquad P[d < D_2] = 1 - \exp(- \pi N_z D_2^2) \ ,$$

where:

D_2 = two-dimensional distance,

d = distance of a point on the map to the nearest root,

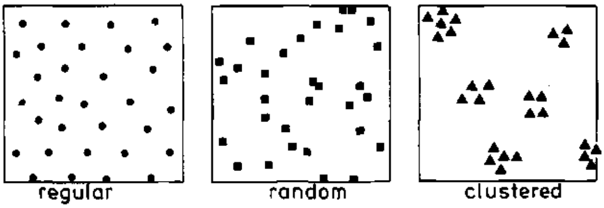

regular random clustered

Fig. 6.5 Three basic types of spatial distribution: regular, random and contiguous (clustered).

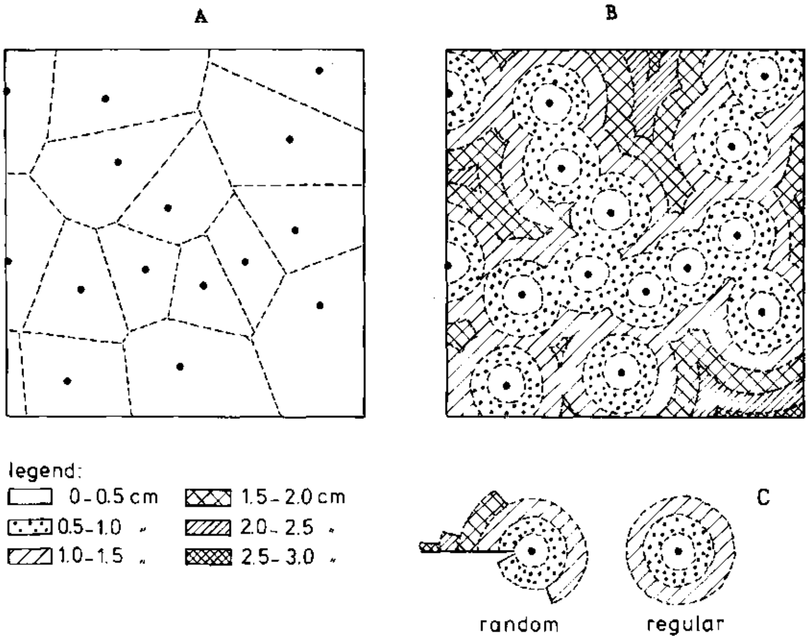


Fig. 6.6 A. Division of area according to the nearest root (Dirichlet tesselation); **B.** Classification of area on a root map according to the distance to the nearest root; **C.** Distribution of distances around an "average" root for a random and for a regular pattern.

N_z = number of roots per circle of unit radius ($= \pi$ cm^2).
For randomly oriented roots (6.11) shows:

(6.17) $$L_{rv} = 2 N_z .$$

For three-dimensional distances of points to randomly oriented and spaced lines Ogston (1958) and Barley (1970) derived that:

(6.18) $$P[d < D_3] = 1 - \pi L_{rv} R_0^2 - \exp(- \pi L_{rv} (D_3^2 + 4/3 \Lambda D_3^3)) ,$$

where:
D_3 = three-dimensional distance,
Λ = number of root tips per unit root length.

The second term in (6.18) is a correction for the volume occupied by the roots, which normally is negligible. As figure 6.7B shows, Λ in (6.18) is of considerable importance. Its role follows from the possibilities of end-point contact for a half sphere around the root tip, added to the tangential contact for cylinders around the root.

For $\Lambda = 0$ we may compare equation (6.16) to equation (6.18) and relate D_2 to D_3:

(6.19) $$D_3 = D_2 / \sqrt{2} = 0.71 * D_2 .$$

This result strictly depends on random orientation of the roots with regard to the plane in which two-dimensional distances are measured. If D_2 is measured in a plane perpendicular to a parallel root system D_3 will equal D_2. In no case will D_3 be larger than D_2 measured in any plane.

Appendix A6. Quantitative information on specific root length and root length density, L_{rv}, in literature and unpublished results of the Institute for Soil Fertility (IB); Nr= number in figure 6.2; L/Y_D = specific root length, [m/g]; $2R_0$ = average root diameter, [mm]; L_{ra} = total root length per unit soil surface area, [cm/cm²]; L_{rv} = root length density, [cm/cm³]: I. average over rooted zone, II 0-30, III 30-60 and IV 60-90 cm depth.

REFERENCE	CROP/cv.	AGE	METHOD	DEPTH(cm)	*	Nr	L/Y_D	$2R_0$	L_{ra}	L_{rv}I	L_{rv}II	L_{rv}III	L_{rv}IV
MONOCOTYLEDONAE													
WHEAT													
Barraclough,1984	cv.Hustler	june80	core	100	SD	01	163	--	272	2.7	6.2	1.7	0.9
Barraclough,1984	cv.Hustler	june80	core	100	SD	02	196	--	240	2.4	5.3	2.0	0.55
Barraclough,1984	cv.Hustler	june81	core	100	SD	03	195	--	283	2.8	3.7	1.5	0.75
Barraclough,1984	cv.Hustler	june81	core	100	SD	04	243	--	380	3.8	7.6	1.9	0.2
Cumbus,1985	cv.Gamenya	17days	watercul.	--	F	05	162/159	--	--	--			
Gregory,1979	--	may/ju.	endoscope	100		*	--	--	60/90	1.0/2.0			
Gregory,1978	--	17june	core	150		*	--	--	223	1.5	4.6	1.7	0.8
Stankov,1976	--	--	core	50		*	--	--	--	4.65			
Alston,1980	Halberd	maturi.	core	34		*	--	--	--	3.6	3.3	--	--
Proffitt,1983	cv.SST33	126day	core	160		*	--	--	--	0.23	0.46	0.27	0.07
Chaudhary,1985	--	70days	--	90		*	--	--	--	1.6	8.6	3.7	1.95
Welbank,1974(2)	--	38/94d.	--	100		*	--	--	--	--	0.4/2.2	0/1.1	0/0.3
Andrews,1969(4)	--	--	soil	--		*	--	0.18	--	26			
IB-unpubl.	cv Arminda	20/6/86	core	20		06	70/101	0.33	--	--			
IB-unpubl.	cv Arminda	15/8/86	core	70		*	268	--	--	4.2			
BARLEY													
Drew,1980	spring barley	30/65-Zadoks	core	20	TF	07	112	--	56	2.8			
Drew,1980	spring barley	30/65-Zadoks	core	20	TF	08	162	--	104	5.2			
Aboulroos,1979	barley	35days	pot	--		09	165	--	--	--			
Soileau,1973	barley	31days	pot	--		10	202	--	--	12	12	--	--
Stankov,1976	--	--	core	50		*	--	--	--	4.7			
Kirby,1971(2)	--	ripe	--	140		*	--	--	--	--	1.6	0.7	0.3
OATS													
IB-unpubl.	--	20/9/86	monolith	40		11	21	0.22	--	8.75			
Köpke,1979	--	5wk.	monolith	50		12	97	0.22	1.7	0.34	1.08	0.55	0.03
Ehlers,1980	--	18-5/22-6	profile	100		*	--	--	--	--	0.59	0.47	0.01
Ehlers,1983	cv.Leande	june	profile	75		*	--	--	14/64	0.16/0.71	1.0/1.8	0.2/?	0.1/?

REFERENCE	CROP/cv.	AGE	METHOD	DEPTH(cm)	*	Nr	L/Y_D	$2R_0$	L_{ra}	$L_{rv}I$	$L_{rv}II$	$L_{rv}III$	$L_{rv}IV$
OATS(continued)													
Steinhardt,1981	--	71days	core	90		*	--	--	--	0.49	0.16	0.06	0.02
Stankov,1976	--	--	core	50		*	--	--	--	0.08	.		
RICE													
Rao Niranjan,1977	cv.Earlirose	21days	watercul.	--		13	12	--	--	--	.		
Hairiah,1986	cv.ITA 307	3,5,9,16 wk	pinb.	70		14	71	--	--	0.34	1.2/.7	0.2/sp	sp/-
MAIZE													
Follett,1974	cvPioneer3935	2.5mths	monolith	91	W	15	9.7	--	--	--	.		
Follett,1974	cvPioneer3935	2.5mths	monolith	91	W	16	8.2	--	--	--	.		
Follett,1974	cvPioneer3935	2.5mths	monolith	91	W	17	8.3	--	--	--	.		
Nielson,1978	16.genotypes	21days	watercul.	--		18	169	--	--	--	.		
Allmaras,1975	cvDeKalb XL-4	5august	monolith	145		19	30	--	--	--	.		
Mengel,1974	--	90days	core	75		20	101	--	112	1.5	26	3.0	1.6
Mackay,1984	cvPioneer3369A	28days	watercul.	--		21	127	0.19	--	--	.		
Robertson,1980	MC Nair508	--	core	150		*	--	--	75	0.50	1.4/4.4	.1/.7	.1/.4
Shierlaw,1984	Kretek	18days	pot	--		*	--	--	--	5.7	.		
Reid,1981	--	25days	pot	--		*	--	--	--	9.5	.		
Schenk,1979	5 cultivars	23days	pot	--		22	81	--	--	2.8/8.7	5.0---12.0		
Jungk,1974	--	12days?	watercul.	--		23	131	--	--	--	.		
Schenk,1979	Pioneer 3369A	23days	pot	--		24	108	0.21	--	5.0/12	.		
Warncke,1974	--	18-81d.	watercul.	--		25	214	--	--	--	.		
IB-unpubl.	cv.Brutus	35days	watercul.	--		26	280	--	--	--	.		
Carithers,1981(1)	--	60-100d.	APlayer	--		*	--	--	--	1.4	1.4/.9	1.4/1.7	--
Grimes,1975	pag sx-17	12wk.	core	183		*	--	--	--	2.0	4.2/8.2	3.0/.88	2.1/.41
Schenk,1980	3 cultivars	68days	core	70		*	--	--	--	2.75	2.89---2.28		
Foth,1962(2)	--	37/100d.	--	45		*	--	--	--	--	0.9/5.2	0.1/0.6	0/0.1
Hairiah,1986	--	2,4,8,14 wk.	monoli.	40		27	50	--	--	1.3	1.3	--	--
Taylor,1973(3)	--	--	--	180		*	--	--	--	3.9	7.4	4.1	3.5
SORGHUM													
Merrill,1979	cv.Pioneer887	80days	lysimeter	--		28	201	--	906	8.4	16	10	6.5
Hackett,1973	cvTexasRS-610	17days	pot	--		29	281	0.20	182	1.8	.		
Gardner,1964	Milo	--	pot	120		*	--	--	59	0.49	0.83	0.46	0.31
GRASS													
Clapp,1984	Festuca arund.	5years	core	75		30	428	--	197	2.6	5.4	1.1	0.4
Garwood,1979	Festuca arund.	1-2year	core	60		31	223	--	804	13.4	21.2	5.6	--
Burch,1979	Festuca arund.	--	pot	--		*	--	0.19	--	0.7	.		
Clapp,1984	Poa pratensis	5years	core	75		32	662	--	203	2.7	6.1	0.6	0.7
Reid,1981	Lolium Ryegr.	42days	pot	--		*	--	--	--	25.6	.		

REFERENCE	CROP/cv.	AGE	METHOD	DEPTH(cm)	*	Nr	L/Y_D	$2R_o$	L_{ra}	L_{rv}I	L_{rv}II	L_{rv}III	L_{rv}IV
COTTON													
Taylor,1974	Auburn 623b	10-14wk.	rhizotron	180		62	96	--	--	0.9	2.9/.3/.6	1.8/.9/.6	.6/1.6/-
Grimes,1975	Acala SJ-1	19wk.	core	183		*	--	--	185	1.01	2.33	1.99	1.50
Cappy,1979(1)	Rex 713	4stages	scope	126		*	--	--	--	.42	0.42		
Klepper,1973	Cotton	29juli	--	180		*	--	--	--	1.3/1.8	2.3/1.1	1.6	1.3/1.6
Taylor,1975(4)	--	--	soil	--		*	--	0.25	--	2.7	.		
POTATO													
IB-unpubl.	--	--	monolith	20		63	234	0.28	--	--	.		
IB-unpubl.	--	12/7/82	core	60		*	--	--	--	.	1.61	0.71	--
Vos,1986	cv Bintje	--	core	100		*	--	--	40	0.8	1.5	0.7	0.2
TOMATO													
Chapt.4 expt4	cv.Moneymaker	9-19wk.	watercul.	--		64	312	--	--	--	.		
Chapt.4 expt1	cv.Moneymaker	7-16wk.	watercul.	--		65	372	0.22/0.16		--	.		
IB-unpubl.	cv.Moneymaker	115days	watercul.	--		66	378	--	--	--	.		
CUCUMBER													
Chapt.4 expt4	cv.Corona	6-12wk.	watercul.	--		67	437	--	--	--	.		
Chapt.4 expt3	cv.Corona	5-14wk.	watercul.	--		68	494	0.24	--	--	.		
Chapt.5	--	adult	rockwool	--		69	382	--	--	--	.		
Chapt.4 expt2	cv.Corona	5-14wk.	watercul.	--		70	444	0.12/0.23	--	--	.		
FLAX													
Stankov,1976	--	--	core	50		*	--	--	--	5.5	9.2		
IPOMOEA, TALL MORNINGGLORY													
Scott,1976	--	12wk.	core	100		*	--	--	--	2.13	4.74	0.73	1.14
LETTUCE													
IB-unpubl.	cv.Plevanos	5weeks	watercul.	--		71	284	0.37	--	--			
Rowse,1974	cvBorough Won.	68days	core	55		*	--	--	--	0.62	0.77	0.2	--

(1)= as quoted in Brown and Scott (1985), (2)= as quoted in Nye and Tinker (1978), (3)= as quoted in Brown and Biscoe (1985), (4)= as quoted in Burch (1979).

* column indicates the main source of variation in each publication:
S = Soil type, D = date, F = fertility status, T = soil tillage,
V = Cultivar, W = Watering regime.

7. AVAILABILITY AND MOBILITY OF NUTRIENTS AND WATER

7.1 Introduction

The early research workers looking for procedures to assess the availability of a nutrient aimed at chemical methods by which the amount of available nutrients could be measured, searching for extractants which could simulate the uptake by plant roots (Dyer, 1894), e.g. 1 or 2% citric acid, 1% acetic acid etc. (Sjollema, 1904). Rather recently some soil scientists (Melsted and Peck, 1973) still considered it one of the major tasks of soil fertility research to develop methods by which the amount of available nutrients in the soil can be assessed: "To us (one of) the objectives of soil testing (is) to accurately determine the available nutrient status of the soil.....". A major problem is how to define "available nutrient status" in this context. According to Russell (1973) it was soon realized that all that was needed for fertilizer recommendation schemes was a standardized chemical extraction technique which gives a good correlation with the yield or nutrient uptake of a crop and gives a fair indication of the amount of fertilizer to be applied. The requirement that a soil test for a particular nutrient should more or less give the absolute available amount was also in the Netherlands abandoned long ago (Van der Paauw, 1938; Sluijsmans, 1965). In fact for fertilizer recommendation the result of a soil test is often recast into a number, which though being a measure of availability, frequently only remotely is connected with an absolute amount of the nutrient concerned. Moreover, the dimension of such numbers makes it very difficult, if not impossible, to comprehend any mechanistic relation between the achieved soil fertility index and the yield or nutrient uptake. In this view the knowledge of the mechanisms involved is considered to be of minor importance only: "Agronomic science is a practical science which benefits more by increasing knowledge about relations than about mechanisms determining a process......" (Ferrari, 1965).

Although it cannot be denied that considerable successes were obtained by applying this pragmatic point of view - it has been said that the Dutch fertilizer recommendations are among the most sophisticated in the world (De Wit, 1968; Van der Paauw, 1973) - also large disadvantages are connected with it. The soil fertility index used in one country is generally not transferable to other countries with other climatic conditions or soils, and it takes a very long time (30-40 years; Van der Paauw, 1973) before a soil test or whatever index derived from it, is thought to be adequately calibrated. And even in the country where the index has been developed extensive field trials have to be initiated for new calibration when agricultural practice has changed (e.g. new crops are introduced, mechanization is intensified, rotation narrows, yield levels increase). Insight in the chemical, physical and biological processes involved in nutrient supply and uptake can contribute substantially in the selection of suitable soil tests and in interpretation of results of soil analysis. In chapter 15 we will return to this. The interest then shifts from indexes of soil fertility back to absolute amounts of nutrients present, and quantification of the relative depletion of this amount by specific crops under specific conditions. Knowledge on underlying mechanisms nowadays seems of prime, rather than of secondary importance. Yet direct influence of the mechanistic approach on fertilizer recommendations is still rare.

In this chapter we will discuss the basic principles to be used in later chapters, where transport through and uptake from the soil by plant roots will in some detail be described and evaluated quantitatively. This will be done by developing models in which the processes thought to be most important are incorporated.

7.2 Availability

It is difficult to define availability of nutrients and water in an unequivocal way because it depends on plant and soil properties, as well as on meteorological conditions, and on their interactions. Eventually the total amount of a nutrient present in soil can be withdrawn by plants, so, to make any sense, a definition of availability should involve an uptake period and/or an uptake rate. We define the available pool of nutrients and water as that part of the total amount present in the root zone which can be taken up by a crop within a single growing season, when transport through the soil is not limiting (root density infinitely high). Within the root zone during the uptake period many processes can occur which render part of the originally available pool, at least temporarily, unavailable (chemical fixation, microbial immobilization), or transform former unavailable fractions into a readily available form (mineralization, release from minerals). When relevant, considerations about crop uptake have to take into account these amounts released or fixed.

Because of its finite root density and because transport rates in soil are finite, the plant can take up only a fraction of the available pool. The amount that can be taken up at the required rate, will be indicated as the unconstrained uptake capacity. Then the total uptake capacity is that amount which will be taken up in a certain period, e.g. a growing season, with a rate less than or equal to the required rate. The difference between total uptake capacity and available pool is the amount remaining in the soil due to transport limitations (see figure 1.8).

The concept of availability is easiest explained in the case of water.

7.2.1 Water

The first to discuss the availability of soil water in quantitative terms apparently were Viehmeyer and Hendrickson (1927). The water retained by a soil between its permanent wilting point (a concept first used by Briggs and Shantz, 1912) and field capacity was believed to be completely available for plant uptake, irrespective of plant or soil properties, or evapotranspiration. Though it is now understood (Hagan et al., 1959; Hillel, 1980) that this definition does not describe actual uptake capacity by most crops, the concept of Viehmeyer and Hendrickson can be employed to describe the availability of soil water. Accepting here for a fact that there exists a limiting value of the plant water potential below which the plant cannot function properly, this limiting value can be used to establish the lower boundary of soil water available. When root density is infinite, all water in the root zone in excess of that at the limiting plant water potential can be extracted. If, as usually is the case in non-saline soils, the matric potential is the major component of soil water potential, and there is a unique relation between matric potential and water content, the above reasoning also defines the limiting soil water content.

It thus seems possible to establish the amount of water available in the root zone, viz. the water held by the soil in excess of that present at the wilting point. Actual uptake capacity by crops, with finite root density, is a fraction of this available amount.

7.2.2 Nutrients

We will confine ourselves to the three major nutrients: potassium, nitrogen and phosphorus. These are taken up by plants in inorganic form from the soil solution. To quantitatively assess the availability of nutrients is more complicated than in the case of water, as here usually more sinks and sources within the root zone play a role. Moreover, the plant root not only decreases the chemical potential (concentration) in the rhizosphere merely by taking up the nutrient (as it decreases the potential of water in the rhizosphere by taking up water) but may completely change the chemical environment of the soil in the vicinity of the root, as well as stimulate or restrain the microbial activity there. The term availability will be used in the way it was defined before: the amount of nutrients in a state which permits them to be taken up by plants in a single growing season. This amount then comprises the nutrients in the soil solution, which are "directly" available, diminished or augmented by the amount which can - by whichever mechanism - appear in or disappear from the soil solution during the uptake period. The availibility thus depends on the rate of required uptake, and on the rate of replenishment from the organic nutrient pool, slowly dissolving minerals, nutrient adsorbed at clay surfaces or by organic matter etc.

Potassium

For potassium three fractions in the soil can be recognized which in principle can be taken up: the fraction contained in minerals, that adsorbed by clay or organic matter and that in the soil solution. The release of potassium from minerals, though not completely insignificant, is normally so slow, that it only contributes a rather small amount to the requirement of the plant (Grimme, 1974). On the other hand, the adsorption/desorption reaction is so rapid that, at least for our purposes, instantaneous equilibrium between potassium in solution and that adsorbed can be assumed (Bray, 1954; Hissink, 1920). Moreover, this equilibrium, though fundamentally governed by complicated exchange reactions (Bolt and Bruggewert, 1979), can to a fair degree be described by a linear adsorption isotherm (Grimme et al., 1971; Nemeth, 1975), the adsorption constant of which is approximately proportional to the inorganic cation exchange capacity, as figure 7.1 shows. The adsorption constant is a function of the conditions, especially the soil pH plays an important role (Nemeth, 1975). The available potassium is thus given by the sum of the amount adsorbed and that in the soil solution.

The fertility index used in the Netherlands in case of potassium is the so-called K-value, which for clay soils is constructed by dividing the amount of potassium extracted by 0.1 N HCl and 0.4 N oxalic acid (called K-HCl and expressed in mg K_2O/100 g), by a linear function of the pH of the soil mea-

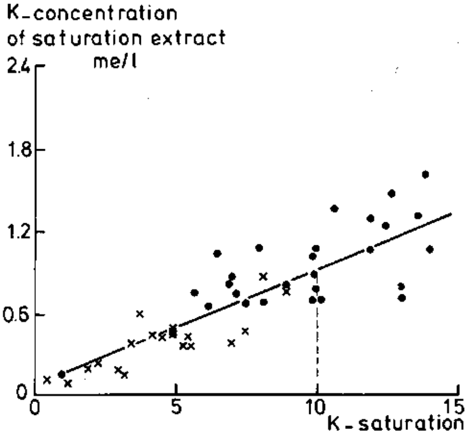


Fig. 7.1 Potassium concentration in the soil solution as a function of the potassium saturation of the inorganic adsorption complex (after Grimme et al., 1971).
Dots: sands - silty sands.
Crosses: silty sands - loams.

sured in 1 N KCl, and multiplying the result by a factor depending on clay content, the higher the clay content the lower the factor (Van der Paauw and Ris, 1955). For sandy soils the K-value is calculated as 20xK-HCl/(10 + percentage organic matter).

Nitrogen

In most soils in the temperate region all nitrate occurs in ionic form in the soil solution, so all of the nitrate present at any moment can be said to be available to plants. That part of ammonium which is, just like potassium, reversibly adsorbed by clay or organic matter is available as well.

During the growing season there generally is a continuous replenishment of mineral nitrogen by mineralization of organic nitrogen. That fraction of organic nitrogen which will be mineralized during the growing season is also available to the plant. In Western Europe a zero-order mineralization rate can be assumed (Addiscott, 1982; Greenwood et al., 1985; Verbruggen, 1985). The range of nitrogen mineralization in West European soils amounts to 0.2-1 kg/(ha.day) (Mengel and Kirkby, 1978; De Willigen, 1985b) for normal rotation and in the absence of extra input of organic matter, whereas the uptake rate of a crop growing at the optimum is of the order of 2-4 kg/(ha.day) (Beringer, 1985), so mineralization on the average is not rapid enough to replenish nitrogen in the soil solution at a sufficient rate, but the total amount mineralized in a growing season of 100 days, between 20 to 100 kg/ha, is not negligible.

When fresh organic matter has been added to the soil, it depends largely on its C/N ratio whether mineral nitrogen will be fixed or be liberated. Immobilization of mineral nitrogen by biomass will be temporary, in due course this nitrogen will be mineralized again, but it depends on environmental conditions and the nature of the added organic matter whether this will happen in the first growing season after application, or in subsequent growing seasons.

Phosphorus

As with potassium, the inorganic phosphorus in the soil can be thought to consist of three fractions (Mengel and Kirkby, 1978): phosphate in the soil solution, phosphate in the labile pool and nonlabile phosphate. The labile phosphate mainly consists (Olsen and Khasawneh, 1980) - we shall assume exclusively - of adsorbed phosphate. The nonlabile phosphate is that fraction of soil inorganic phosphate contained in poorly soluble minerals, and as in the case of potassium transfer from the nonlabile to the labile pool occurs very slowly (Barber, 1984). The relation between labile phosphate and phosphate in solution can be given by an adsorption isotherm, which in contrast to the situation with potassium, is usually nonlinear, even at low concentrations. Figure 7.2 gives some examples of phosphate adsorption isotherms of Dutch soils.

A good mathematical description of these isotherms can be given by a two-term Langmuir equation (De Haan, 1965; Holford and Mattingly, 1975; De Willigen and Van Noordwijk, 1978) as is shown in figure 7.2. This equation reads:

$$(7.1)\quad C_a = \frac{B_1A_1C}{1+B_1C} + \frac{B_2A_2C}{1+B_2C} ,$$

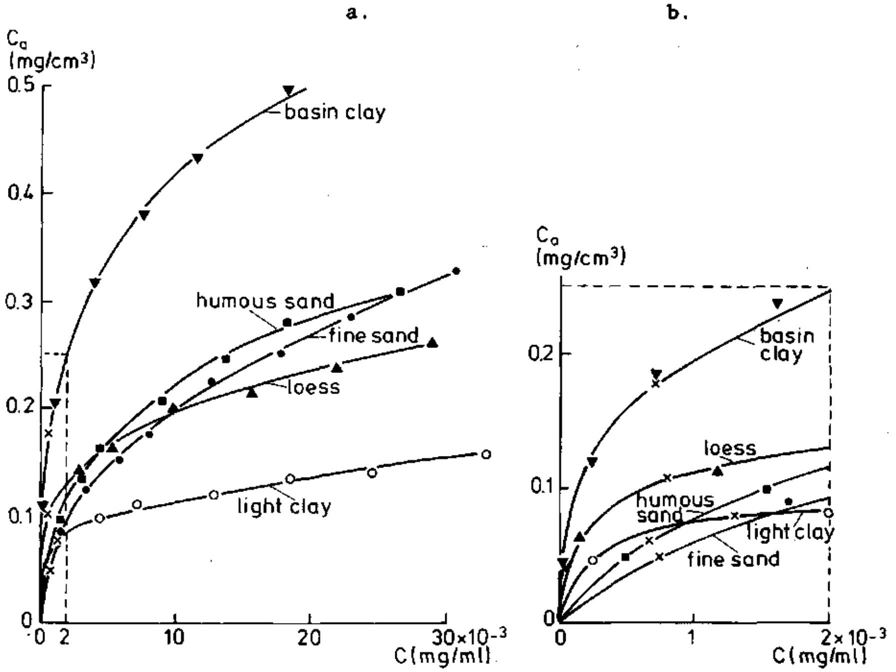


Fig. 7.2a and b. Phosphorus adsorption isotherm of five Dutch soils. The agriculturally relevant range is given in figure 7.2b.

where

C_a is adsorbed phosphate in mg P per cm³ soil,
C is the concentration of phosphate in the soil solution in mg P per ml,
B_1 and B_2 are parameters in ml/mg,
A_1 and A_2 are parameters in mg/cm³.

Although in the Langmuir equation the parameters have a physical meaning, it is used here without any such interpretation. In table 7.1 the parameters of the adsorption isotherms of figure 7.2 are given.

In the Netherlands recommendations for P application on grassland are based on the P_{Al}-value. It is obtained by extracting the soil with 0.1 N ammonium lactate and 0.4 N acetic acid. On arable soils the P_w-value is used. It gives the amount of phosphate extractable by water, at a volume ratio water/soil

Table 7.1 Parameters of the adsorption isotherms of the five soils of figure 7.2.

Soil type	B_1	B_2	A_1	A_2
	ml/mg		mg P/cm³	
light sand	500	8.5	0.16	0.91
humous sand	820	35	0.15	0.37
light clay	5000	20	0.087	0.18
loess	6600	44	0.12	0.26
basin clay	16000	130	0.15	0.49

express the potential in cm water. The flux equation then becomes:

$$(7.8) \qquad \vec{V} = -K_H(\vec{\nabla}H_p - \vec{\nabla}Z) \ ,$$

where
H_p = the pressure head [cm^3/cm^2] = $P_m/(M_w g)$,
K_H = the hydraulic conductivity [cm/day].

Substitution of (7.8) into (7.6) results in:

$$(7.9) \qquad \frac{\partial S}{\partial T} = \vec{\nabla}.K_H C(\vec{\nabla}H_p - \vec{\nabla}Z) + U \ .$$

As $S = \Theta C$, where Θ is the volumetric water content of the soil and C can be assumed to be constant because of the low concentration of solutes, one finally obtains:

$$(7.10) \qquad \frac{\partial \Theta}{\partial T} = \vec{\nabla}.K_H(\vec{\nabla}H_p - \vec{\nabla}Z) + U/C \ .$$

To solve (7.10) the relation between P_m (or H_p) and Θ should be known, this relation is usually called the water retention curve. Now the water diffusivity $D_w(\Theta)$ can be defined as:

$$(7.11) \qquad D_w = K_H \frac{dH_p}{d\Theta} \ .$$

For some soils the relations between D_w and Θ can reasonably well be approximated by convenient mathematical functions. Stroosnijder (1976), for instance, found that for some types of Dutch soils, the relevant data of which were collected by Rijtema (1969), the diffusivity could be given as an exponential function of water content:

$$(7.12) \qquad D_w = D_{w,s}\exp\{b_w(\Theta-\Theta_s)\} \ ,$$

where Θ_s is the water content at saturation and $D_{w,s}$ the corresponding diffusivity. We will confine ourselves here to those soils where (7.12) holds. These are shown in table 7.2, where also the relevant parameters are given.

Table 7.2 Hydraulic parameters of some Dutch soils. After Stroosnijder (1976) and Rijtema (1969).

Soil	$D_{w,s}$	b_w	Θ_s	Θ	Θ
	cm^2/day			(H_p = -10^2 cm)	(H_p = $-5*10^3$ cm)
medium coarse sand	$8.6*10^4$	45.6	0.395	0.10	0.03
loess loam	$7.2*10^3$	25.9	0.455	0.26	0.13
silty clay loam	$1.4*10^3$	22.7	0.475	0.375	0.20
light clay	$3.6*10^3$	20.3	0.453	0.354	0.25
clay loam	$4.3*10^3$	66.8	0.445	0.417	0.30

Substitution of (7.11) into (7.10) leads to :

$$(7.13)\qquad \frac{\partial\Theta}{\partial T} = \vec{\nabla}.D_w\vec{\nabla}\Theta - \frac{\partial K_H}{\partial Z} + U/C \ ,$$

where use is made of the fact that the gravitational potential has a component only in the vertical (Z) direction. Because of the nonlinear relations between $D_w(\Theta)$ and Θ, and K_H and Θ, a solution of (7.13) can usually be found only by numerical methods.

Some doubts exist as to the validity of Darcy's law at the scale where it is applied in microscopic models, i.e. at a scale of a few mm and less (Passioura, 1985; Klute and Peters, 1968). A recent detailed study on water uptake of single plant roots (Hainsworth and Aylmore, 1986), however, revealed that the profile of water content around a root could be reasonably well simulated with a model of Hillel et al. (1975), which is based on Darcy's law. This is at least an indication that flow of water also at a small scale can be adequately described by Darcy's law, as we have assumed.

7.3.3 Solutes

For a nutrient that is adsorbed by the solid phase the bulk density is the sum of the bulk density of the nutrient in solution and of that bonded by the solid phase:

$$(7.14)\qquad S = C_a + \Theta C \ .$$

When the adsorption/desorption reaction proceeds so fast that instantaneous equilibrium can be assumed, the bulk density of adsorbed nutrient is at any moment a function of the concentration:

$$(7.15)\qquad C_a = f(C) \ .$$

Those conditions will be considered here where $\vec{V}$ and D are constant, substitution of (7.16) into (7.6) then yields:

$$(7.16)\qquad \frac{\partial C}{\partial T} = -\vec{V}^*.\vec{\nabla}C + D^*\nabla^2 C + U^* \ .$$

where the effective flux $\vec{V}^* = \vec{V}/(f'+\Theta)$ with $f' = df/dC$,
the effective diffusion coefficient $D^* = D/(f'+\Theta)$,
and the effective production term $U^* = U/(f'+\Theta)$.

It is to be understood that the coefficient of hydrodynamic dispersion, which is a consequence of the distribution of flow velocities of the soil solution at a microscopic level (Bear, 1972), and has the effect of an extra diffusion, is incorporated in D. The dispersion coefficient is a function of the macroscopic flow velocity V^*; for some soils a simple proportionality between V and the dispersion coefficient has been established (Frissel et al., 1970).

When the adsorption isotherm is linear then $f(C) = K_a.C$, and $f'(C)$ is constant and so are V^* and D^*. If U is either a linear function of C, a constant or a known function of T and the space coordinates, (7.16) is a linear equation which can be solved analytically by classical mathematical techniques. In case of linear adsorption it follows that V^* and D^* are a factor $(K_a + \Theta)$ smaller than V and D, or the greater the adsorption the more transport to the root is retarded. This will be discussed somewhat more

8. OXYGEN REQUIREMENTS OF ROOTS IN SOIL

8.1 Introduction

An important condition for proper functioning of root systems is a sufficient supply of oxygen to all root cells. Although roots of some plant species can cope with temporary anaerobic conditions by switching from aerobic to anaerobic forms of metabolism, a sustained supply of molecular oxygen seems to be essential to support the active growth and functioning of roots of plants (Armstrong, 1979). The source of oxygen is the atmosphere and for diffusive flow of oxygen from the atmosphere to a certain location in the root two pathways, or combinations thereof are possible:

a. through the soil to the soil/root interface and then radially through the root tissue (the external pathway),

b. through the aboveground plant parts (leaves, stem), and longitudinally through the root (the internal pathway).

In this chapter the relative importance of both pathways in fulfilling the aeration requirements of roots will be discussed.

8.2 Transport by the external pathway

Except for plants with special structures (i.e. aerenchyma), the external pathway is generally thought to be the most important (Drew, 1983; Luxmoore et al., 1970). In experiments in well-stirred nutrient solutions, critical values of oxygen partial pressure at the root surface have been found to be around 1% (Brouwer and Wiersum, 1977; Drew and Lynch, 1980; Greenwood, 1969). Critical values of oxygen pressure in soil air vary widely, but values of 10-15% are not uncommon (Brouwer and Wiersum, 1977). The explanation for the contrast between the values - 1% at the root surface, and about 10% in soil air - can probably be found in the diffusion pathway involved. The plant root in a normally moist soil is believed to be covered with a water film, the thickness of which has been estimated to range from 0.01-0.1 cm (Luxmoore et al., 1970). A water film of 0.1 cm is four (or more) times larger than the radius of a typical plant root and probably applies only to very moist conditions. In a rapidly moving nutrient solution the water film (the unstirred layer close to the root) can be expected to be 10^{-3} - 10^{-2} cm (Helfferich, 1962 in Nye and Tinker, 1977). The water film forms an extra resistance for transport of oxygen from the soil atmosphere to the root, and moreover due to the respiration of micro-organisms, it also forms a sink for oxygen. Next to this, part of the root surface can be blocked from contact (via the water film) with the soil air by a soil aggregate, as is depicted in plate 6.1. For both situations, complete contact with soil air and partial blockage, the required oxygen concentration in the soil air will be estimated.

The discussion here is a summary of two earlier papers (De Willigen and Van Noordwijk, 1984; Van Noordwijk and De Willigen, 1984), where the derivation of the equations employed and the justification of the assumptions can be found. In the calculations to be discussed the following values for the parameters were chosen:

— The diffusion coefficient of root tissue for oxygen was taken as 0.7 cm^2/day (Kristensen and Lemon, 1964).

— From the reviews of Brouwer and Wiersum (1977), and Grable (1966), it appears that the range of respiration rate U_0 can be considerable viz. 1-60 mg/(cm^3.day), but the majority of the data is in the range 10-20 mg/(cm^3.day). In our calculations a value of 10 mg/(cm^3.day) was used, considering the fact that soil temperatures in temperate regions are usually lower than the temperatures at which oxygen consumption has been measured.

— Root radius R_0, varies from 0.01 to 0.05 cm and more for roots with secondary thickening. In the calculations we used a range of 0.01-0.03 cm.

8.2.1 Complete contact with the soil atmosphere

De Willigen and Van Noordwijk (1984), extending the theoretical reasoning of Lemon and Wiegand (1962), presented a steady-state solution of the distribution of the concentration of oxygen in the water film and the root. With this solution one can calculate which concentration in the soil air is required to ensure sufficient supply for all cells in the root. A water film of 0.01 cm is, as stated above, an upper value of the minimum thickness of the water film around a root. The effect of a water film appears stronger for thicker roots. For a root with a radius of 0.025 cm, 10% oxygen pressure is required when the water film is of about the same thickness as the root. The presence of rhizosphere respiration in the water film modifies the situation only to a small extent. Rhizosphere respiration of an additional 30% increases the needed oxygen concentration by 0.5-1%. If the rhizosphere respiration is subtracted from the root respiration, the required oxygen concentration in the soil air is lowered by 1-3%.

8.2.2 Partial contact with soil air

De Willigen and Van Noordwijk (1984) calculated isoconcentration lines of oxygen in the root when part of the root surface is blocked by a soil aggregate. The form of the isoconcentration lines was shown to change from partly circular curves when a small part of the root perimeter is blocked to almost straight lines when the greater part of the perimeter is blocked.

The required oxygen concentration is of course higher when part of the surface is blocked. As figure 8.1 shows the degree of soil-root contact is a critical factor, as is root radius. The effects of the presence of a water film and of partial blocking on the oxygen requirement are more than additive because the soil-root contact has two effects. These are: the total oxygen requirement of the root has to pass through a smaller root surface area and the diffusion distance is increased. As a first approximation of the first

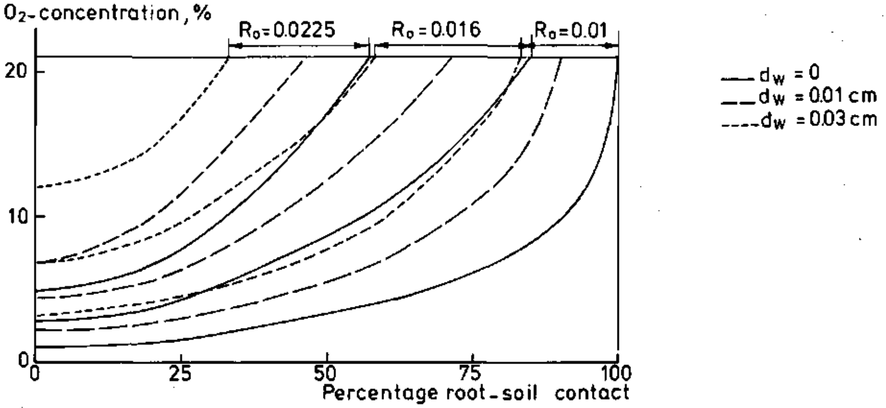


Fig. 8.1 Oxygen concentration required in soil air for aerobic respiration by all root cells as a function of the percentage root-soil contact, root radius R_0 and thickness of water film d_w.

effect the required oxygen concentration can be estimated as being proportional to $1/(1-f_B)$, where f_B is the fraction of the root perimeter blocked; from figure 6.9: $f_B = \psi_1/2\pi$. If for example 2/3 of the perimeter is blocked, the required oxygen concentration is tripled due to the first effect, and at most doubled due to the second effect.

8.3 Transport by the internal pathway

Continuity of gas-filled pores is a prerequisite for longitudinal transport to be of significance. Continuity of air channels exists when aerenchyma is present. Luxmoore et al. (1970) have presented a mathematical treatment of longitudinal transport from shoot to root through such channels. Calculations showed that a considerable part of the oxygen requirement of the root can be provided by the aboveground parts in species adapted to permanently wet soil, e.g. rice. For such conditions those properties which limit gaseous exchange between the root and its environment, i.e. large root radius and thick water film, improve the supply to the root tip. Aerenchyma is not found in roots of non-wetland species growing in aerated conditions, but usually gas-filled pores form a continuous pathway in longitudinal direction in roots of these species as well (Armstrong, 1979). Even with an effective porosity of no more than 3%, which can be considered a low value for such roots (Armstrong, 1979; see table 6.1) there are situations where longitudinal transport of oxygen contributes significantly to the respiratory demand of the root, as will be shown below. Moreover when roots of some important non-wetland crops such as maize (Konings, 1983; Yu et al., 1969), wheat, barley (Yu et al., 1969) are growing in a more or less permanent anaerobic environment, porosities can increase up to 17%. This can enhance longitudinal transport to a large extent.

We will derive some equations by which, at least approximately, the relative contribution of the internal and external pathways with respect to total root oxygen demand can be estimated. Moreover, the theory allows to estimate the maximum length a root can attain as far as its aeration status permits.

8.3.1 Mathematical formulation

The derivations pertain to transport and consumption of oxygen in a cylindrical root in vertical position in the soil. Because of the values of the parameters involved a steady-state situation will soon be attained as was shown by De Willigen and Van Noordwijk (1984). In such a situation the mass balance expressed in terms of axisymmetric coordinates is given by (as follows from (7.21)):

$$(8.1) \qquad \epsilon_{r*} D \frac{\partial^2 C}{\partial Z^2} + \frac{D_\ell}{R} \frac{\partial}{\partial R} R \frac{\partial C_\ell}{\partial R} = U(Z)(1 - \epsilon_r) \ ,$$

where ϵ_{r*} is the effective porosity of the root [cm^3/cm^3], i.e. the root porosity ϵ_r corrected for tortuosity,

C is the concentration of oxygen in the gas phase [mg/cm^3],

D is the diffusion coefficient in the gas phase [cm^2/day],

C_ℓ is the concentration in the liquid phase [mg/cm^3],

D_ℓ is the diffusion coefficient in the liquid phase [cm^2/day],

Z is the vertical coordinate [cm],

R is the radial coordinate [cm],

$U(Z)$ is the volumetric respiration rate of the root [$mg/(cm^3.day)$].

U(Z) is taken to be constant throughout the length of the root, save for the root tip with length ΔZ cm, where it usually is higher (Luxmoore et al., 1970):

(8.2a) $0 < Z < Z_r - \Delta Z$, $U(Z) = \text{constant} = U_0$,

(8.2b) $Z_r - \Delta Z < Z < Z_r$, $U(Z) = pU_0$,

where Z_r is the root length in cm, and p is a constant factor.

When equilibrium exists between oxygen in the gaseous and in the liquid phase, the concentration in the liquid phase is proportional to that in the gaseous phase (see (7.19)). Substitution of (7.19) into (8.1) leads to:

$$D_Z \frac{\partial^2 C_\ell}{\partial Z^2} + \frac{D_R}{R} \frac{\partial}{\partial R} R \frac{\partial C_\ell}{\partial R} = U(Z)(1 - \epsilon_r) \ , \tag{8.3}$$

where:

$$D_Z = \frac{\epsilon_{r*} D}{k_g} \ , \tag{8.4}$$

and D_R, the diffusion coefficient in radial direction, is identical to D_ℓ. It thus is assumed, in accordance with what has been said in chapter 7, that the component of the flux in the axial direction is entirely in the gaseous phase, whereas the component of the flux in the radial direction is entirely in the liquid phase. The plane Z=0 coincides with the soil surface where it is assumed that in the root, or rather at the root/stem junction, the concentration in the gas phase equals the atmospheric concentration C_A :

(8.5) $Z = 0$, $C = C_A$, i.e $C_\ell = k_g C_A$.

To account for possible effects of a water film and/or root wall permeability, the boundary condition chosen at the radial root surface allows for transfer of oxygen from the soil air to the root and vice-versa:

$$R = R_0 \ , \quad -D_R \frac{\partial C_\ell}{\partial R} = L(C_\ell - k_g C_{so}) \ , \tag{8.6}$$

where L is a conductance in cm/day, in which permeability of the root wall and effect of the water film is incorporated, C_{so} is the concentration of oxygen in the soil air [mg/cm³]. For a soil with an uniform diffusion coefficient D_s and uniform respiration rate U_s, the course of C_{so} with depth Z can be given (Greenwood, 1967):

$$Z < Z_\ell \ , \quad C_{so} = \frac{U_s}{2D_s} (Z - Z_\ell)^2 \ , \tag{8.7a}$$

$$Z > Z_\ell \ , \quad C_{so} = 0 \ , \tag{8.7b}$$

where $Z_\ell = \sqrt{\dfrac{2D_s C_A}{U_s}}$.

The boundary condition at the apical end of the root (where $Z=Z_r$) states that no transport of oxygen over this boundary can take place:

$$(8.8) \qquad Z=Z_r, \qquad \frac{\partial C_\ell}{\partial Z} = 0 \ .$$

From the solution of (8.3), subject to (8.5), (8.6), and (8.7), by iteration that value of Z_r is sought for which the minimum concentration in the root is zero. This value Z_{max} is the maximum length the root can attain. The procedure is explained later in more detail.

It is convenient to use dimensionless variables and parameters according to the definitions given in table 8.1. These definitions transform the differential equation (8.3) with conditions (8.5), (8.6) and (8.8) into:

$$(8.9) \qquad \kappa^2 \frac{\partial^2 c}{\partial z^2} + \frac{1}{r}\frac{\partial}{\partial r} r \frac{\partial c}{\partial r} = u(z) \ ,$$

$$(8.10) \qquad z = 0 \ , \ 0<r<1 \ , \quad c = 1 \ ,$$

$$(8.11) \qquad z = \pi \quad , \ 0<r<1 \ , \quad \frac{\partial c}{\partial z} = 0 \ ,$$

$$(8.12) \qquad 0<z<\pi \quad , \ r = 1 \ , \quad \frac{\partial c}{\partial r} = -\lambda(c - c_{so}) \ ,$$

where $$c_{so} = \left\{\frac{z}{z_\ell} - 1\right\}^2 .$$

Table 8.1 Dimensionless variables and parameters.

Dimensionless concentration	$c=C_\ell/(k_g \cdot C_A)$
" vertical coordinate	$z=\pi Z/Z_r$
" radial coordinate	$r=R/R_0$
" length of root tip	$\gamma=\pi\Delta Z/Z_r$
" thickness of aerobic soil layer	$z_\ell=\pi Z_\ell/Z_r$
" conductance	$\lambda=LR_0/D_R$
" respiration rate root	$u(z)=\dfrac{(1-\epsilon_r)U(Z){R_0}^2}{\epsilon_{r*}D_R k_g C_A}$
" ratio of diffusion coefficients	$\kappa^2=\left\{\dfrac{\pi R_0}{Z_r}\right\}^2 \dfrac{D_Z}{D_R}$

It can be shown (details can be found in the appendix A8), that the solution of (8.9)-(8.12) is given by:

$$(8.13a)\quad c = 1 + \frac{u_0}{2\kappa^2}z(z-2\pi) - \frac{u_0(p-1)\gamma z}{\kappa^2} + \frac{2}{\pi}\sum_{n=1}^{\infty} a_m I_0(m\kappa r)\sin(mz),\ \text{for } z<\pi-\gamma\ ,$$

$$(8.13b)\quad c = 1 + \frac{pu_0}{2\kappa^2}z(z-2\pi) + \frac{u_0(p-1)(\gamma-\pi)^2}{\kappa^2} + \frac{2}{\pi}\sum_{n=1}^{\infty} a_m I_0(m\kappa r)\sin(mz),\ \text{for } z>\pi-\gamma\ ,$$

where

$$(8.14)\quad a_m = \frac{\lambda(\hat{c}_{so} - 1/m + \hat{u}/(\kappa^2 m^2))}{m\kappa I_1(m\kappa) + \lambda I_0(m\kappa)}\ ,$$

and $m = n - 1/2$, $n=1,2,3,\ldots$
I_0 and I_1 are modified Bessel functions of the first kind and zero and first order respectively, and

$$(8.15)\quad \hat{c}_{so} = \int_0^{\pi} c_{so}\sin(mz)dz\ ,$$

$$(8.16)\quad \hat{u} = \int_0^{\pi} u\sin(mz)dz\ .$$

The first three terms of (8.13a and b) constitute the solution of (8.9), when radial gradients are absent ($\lambda=0$). From (8.13b) the value of Z_r can be calculated for which $c=0$, where $r=0$ or $r=1$. When $z_\ell < \pi$ the root can grow for some length into the anaerobic zone of the soil. In this zone oxygen will flow from the root to the soil, accordingly the minimum concentration will occur at the root wall, where $r=1$. When, on the other hand, $z_\ell > \pi$, oxygen flows from the soil to the root and the minimum concentration is found at the root centre, where $r=0$.

When Z_{max} is known the contribution of the external pathway to the root respiratory demand can be calculated. The flux at the root wall is given by $D_R\partial C_\ell/\partial R$ and the total flow F_R over the radial surface of the root is found by integrating the flux over this surface:

$$(8.17)\quad F_R = \int_0^{Z_{max}} 2\pi R_0 \left\{D_R\frac{\partial C_\ell}{\partial R}\right\}_{R=R_0} dZ = 2D_R k_g C_A Z_{max}\int_0^{\pi}\left(\frac{\partial c}{\partial r}\right)_{r=1} dz\ .$$

When (8.13a) or (8.13b) is differentiated with respect to r, evaluated at r=1, the result substituted in (8.17), and the integration is performed, one obtains:

$$(8.18) \qquad F_R = 4R_0\sqrt{(D_Z D_R)}\,k_g C_A \Sigma a_m I_1(m\kappa) \; ,$$

where a_m is defined earlier (8.14). When $Z_{max}>Z_\ell$ ($z_\ell<\pi$), the flux over that part of the radial surface, for which $0<Z<Z_\ell$ will be from the soil to the root, for the remaining part the flux will be from the root into the soil.

The contribution of the internal pathway is found likewise as the integral of the flux at Z=0, over the cross section of the root:

$$(8.19) \qquad F_Z = \int_0^{R_0} 2\pi R\left\{-D_Z \frac{\partial C_\ell}{\partial Z}\right\}_{Z=0} dR = \frac{-2\pi^2 R_0^2}{Z_{max}} D_Z k_g C_A \int_0^1 r\left(\frac{\partial c}{\partial z}\right)_{z=0} dr \; .$$

Again performing the integration, F_Z is found as :

$$(8.20) \qquad F_Z = \pi R_0^2 Z_{max}(1-\epsilon_R)U_0+\pi R_0^2 \Delta Z(p-1)(1-\epsilon_r)U_0 +$$

$$-4R_0\sqrt{(D_Z D_R)}\,k_g C_A \Sigma a_m I_1(m\kappa) \; .$$

The first two terms of the right hand side of (8.20) give the total respiration, so that the sum of F_R and F_Z gives the total respiration as it should.

As a reference the maximum length the root can attain when no transport within the root in longitudinal direction occurs will be used. In that case the relevant differential equation at the root tip reads:

$$(8.21) \qquad \frac{1}{r}\frac{d}{dr}\, r \, \frac{dc}{dr} = pu_0 \; .$$

The solution, with boundary condition (8.12), is:

$$(8.22) \qquad c = c_{so} + \frac{pu_0 r^2}{4} - \frac{pu_0(\lambda+2)}{4\lambda} \; .$$

When it is required that for r=0, c=0 it follows:

$$(8.23) \qquad c_{so} = \frac{pu_0(\lambda+2)}{4\lambda} \; .$$

Or using the relation between c_{so} and z:

$$(8.24) \qquad z_{max} = z_\ell\left\{1 - \frac{pu_0(\lambda+2)}{4\lambda}\right\} \; .$$

8.3.2 Parameter values

Values of the respiration rate, diffusion coefficients and root radius are the same as mentioned in section 8.2.

Luxmoore et al. (1970) found that the respiration rate of the apical centimeter of a maize root was about two times larger than in the remaining part of the root. Accordingly we put p=2, and $\Delta Z=1$ cm.

The diffusion coefficient of oxygen in air is 10^4 cm²/day.

The diffusion coefficient D_s for gases in the soil is a function of the gas-filled porosity. For different soil types in the Netherlands it was found (Bakker et al., 1982) that the relation between D_s and ϵ_s was quite satisfactorily described by

$$(8.25) \quad D_s(\epsilon_s) = D_s(1)*(\epsilon_s)^b \; .$$

In table 8.2 one finds some typical values of $D_s(1)$ and b for Dutch soils, in our calculations the parameters of soil 4 from table 8.2 were used.

Table 8.2 Parameters $D_s(1)$ and b from equation (8.25) for some Dutch soils.

Soil	$D_s(1)$ cm²/day	b
1. Loamy sand	$21\cdot{*}10^{-4}$	2.7
2. Loess	$2.6{*}10^{-3}$	1.6
3. Sandy loam Compacted by tractor wheel	$4.4{*}10^{-3}$	1.64
4. Sand	$1.9{*}10^{-5}$	4.02
5. Heavy clay	10^{-4}	1.77

For a soil at field capacity in the Netherlands one can expect ϵ_s to vary between 0.1 and 0.3 (Boekel, 1962, 1963). We used the range 0.05-0.2.

The soil respiration rate depends, for given environmental conditions, on amount and decomposition rate of soil organic matter, root respiration, and root density. We used a value of $1.8{*}10^{-3}$ mg O_2/(cm³.day). This value has to be augmented with the contribution of root respiration, which was calculated using the above-mentioned value for root respiration U_0, taking into account root radius and porosity, while root density was assumed to be 1 cm/cm³.

The porosity of roots of non-wetland plants varies from 3-18% (Armstrong, 1979; Yu et al., 1969; see table 6.1), depending on species and conditions. We used the range 0.1-15%, taking into account tortuosity.

The conductance L, which is called root permeability by Luxmoore et al. (1970) and Armstrong (1979), has been estimated by the former at $5{*}10^{-3}$ cm/s, or 40 cm/day. If a linear gradient of the oxygen concentration in the water film (with thickness d_w cm) adhering to the root can be assumed, the conductance can be estimated as D_ℓ/d_w. As the diffusion coefficient for oxygen in water is about 0.85 cm²/day and the water film thickness is assumed to be $5{*}10^{-3}$ to 0.1 cm, L should be in the range 8.5-170 cm/day.

8.3.3 Results and discussion

Earlier, two other models on longitudinal transport of oxygen through roots were designed (Luxmoore et al., 1970; Armstrong, 1979). The most important differences with the model presented here are the way the boundary conditions were formulated, and the method of solving the differential equation.

Luxmoore et al. (1970) developed a numerical model for the steady-state concentration of oxygen within the root. In their model the root with a given length was surrounded by a water film which at its outer boundary is in contact with soil air with constant oxygen concentration of 18%, or 0% when wetland conditions were considered.

Armstrong and Wright (1976) presented an electrical analogue model, designed for simulation of oxygen transport in a root growing in anaerobic conditions. At a given distance from the root the oxygen concentration was assumed to be zero. Later their model was adapted in such a way that different soil respiration rates and non-zero oxygen concentration in the soil could be accounted for (Armstrong, 1979).

The model discussed here allows for change of oxygen concentration with depth. The boundary condition at the apical end of the root, together with the requirement of zero concentration at that point, make calculation of the potential length of the root possible. Figures 8.2a and b show the effect of root porosity on the maximum length the root can attain, i.e. that length where the minimum concentration in the root is precise zero. The calculations were made for a moderately and a well aerated soil (ϵ_s =0.1 resp. 0.2 cm^3/cm^3), a thin and a rather thick root (radius 0.01 resp. 0.03 cm), and a low and a high conductance (10 resp. 200 cm/day). Both roots had the same volumetric respiration rate (10 mg/(cm^3.day)). The thickness of the aerobic zone of the soil was for the thin root 47 cm (ϵ_s=0.1) resp. 185 cm (ϵ_s=0.2), for the thicker root these values were 19 cm and 75 cm. The influence of root porosity is highest when transfer between soil and root is restricted.

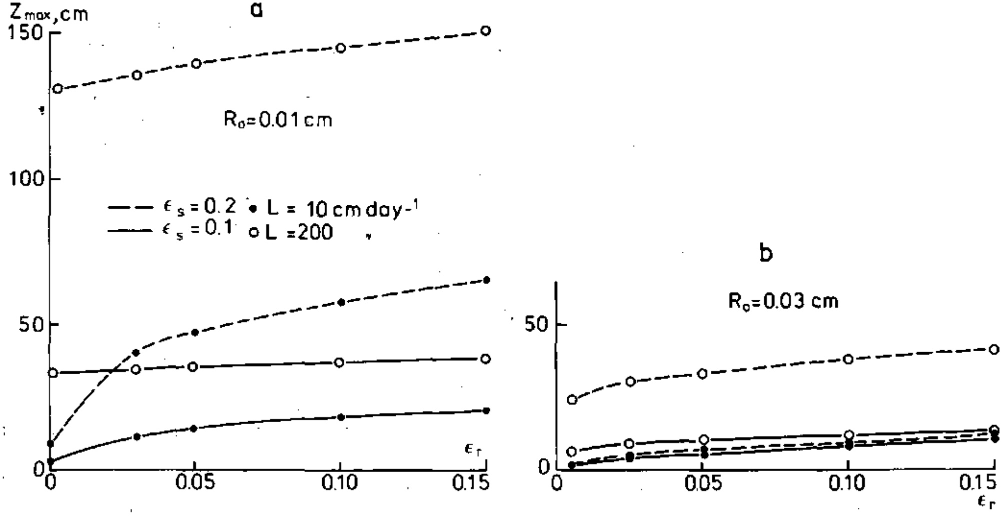


Fig. 8.2a and b Maximum attainable rootlength (Z_{max}) as a function of root porosity (ϵ_r), root thickness (R_0), gassfilled soil porosity (ϵ_s), and conductance (L). Other parameter values: root respiration rate 10 mg $O_2/(cm^3.day)$, soil respiration rate $1.8*10^{-3}$ mg $O_2/(cm^3.day)$.

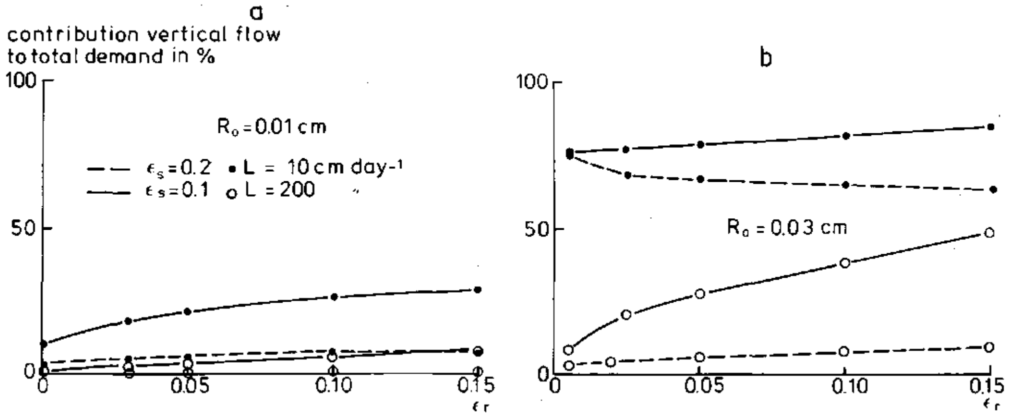


Fig. 8.3a and b Contribution of vertical oxygen flow to total oxygen demand of the root. Respiration parameters as in figure 8.2.

For a root radius of 0.01 cm and a soil porosity of 10%, the potential root length increases 7-fold, from 2.8 cm at a root porosity of 0.1% to 20 cm at a root porosity of 15%, when L is only 10 cm/day. For the higher conductance these lengths are resp. 33 and 39 cm. For the well aerated soil these increases are about the same. In case of the thicker root (figure 8.2b) a better exchange between root and soil is more important than a better aeration status of the soil.

The contribution of vertical flow (flow along the internal pathway) to the root respiratory demand is shown in figure 8.3a for the thin root. The highest contribution (up to 30% for a root porosity of 15%) of course occurs when the soil is poorly aerated and exchange between soil and root is limited. In other cases vertical transport contributes less than 10% of the total demand. Oxygen supply via the internal pathway is much more important for thicker roots, as is shown in figure 8.3b. With a low conductance at least 60% of the demand is satisfied by vertical transport. In that case the relative contribution of the internal pathway to satisfying the oxygen demand decreases with increasing root porosity, from 75% (ϵ_r=0.5%) to 63% (ϵ_r=15%). Absolutely the contribution increases, as the root length increases from 1.4 to 4.3 cm.

Another way of evaluating the influence of root porosity is to compare the limiting concentration in the soil air (i.e. the concentration in soil air which is just sufficient to keep the root aerated) without and with internal longitudinal transport. The former is calculated with (8.23). In figure 8.4a and b the ratio of these concentrations is plotted as a function of root porosity.

For increasing porosity this ratio decreases. In case of the thin root (radius 0.01 cm) the limiting concentration can be about half of what it should amount to when oxygen diffuses only radially in the root. For the thicker root (radius 0.03 cm) the limiting concentration can be 2-10 times lower.

The influence of soil porosity on attainable root length is shown in figure 8.5. Again it can be seen that in the case of thick roots a better aeration status of the soil does not strongly enhance the possibilities of deeper penetration, as long as the transfer between soil and root is restricted: when L = 10 cm/day the potential root length increases from 6.7 to 9.1 cm when the gas-filled porosity increases from 0 to 20%, whereas the thickness of the

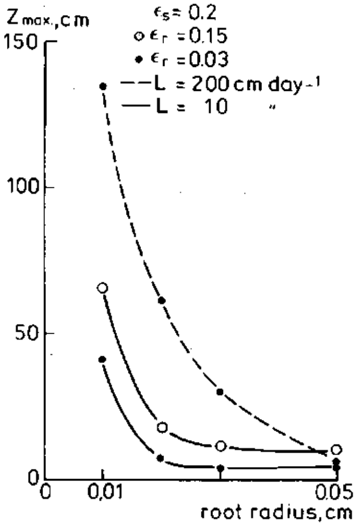


Fig. 8.8 Maximum attainable root length as a function of the root radius. Respiration rate as in figure 8.2.

fusion coefficient in the cortex, which has a thickness about half the radius of the root, was assumed to be 30 times larger than that in the stele. Because of the high diffusion coefficients, calculated radial gradients in the cortex were found to be practically zero. This then implies that as far as diffusion of oxygen is concerned, one can approximately neglect the cortex, i.e. assume that the effective root radius is the real radius diminished with the thickness of the cortex. With figure 8.8 the effect of high diffusion in the cortex can be estimated. For thick roots ($R_0 > 0.04$ cm) with low conductance (thick water film) the maximum length to be attained is only slightly increased when it is assumed that the effective root radius is half of the real root radius. When the root conductance is high, the effect of the high transport rate in the cortex is considerable.

In the models on nutrient uptake to be discussed in the next chapters, we assume that aeration of the root system is not limiting any of its functions. In the uptake models the value of the root radius is taken to be 0.025 cm on average, which is somewhat higher than the average root radius expected under field conditions (see appendix A6). Roots of this thickness would be able to reach a depth of 25 cm or more (figure 8.2b) on a sandy soil, where ϵ_s at field capacity is about 0.2, as can be estimated from moisture retention curves (Woesten et al., 1986), when the conductance L is of the order of 200 cm/day, which one would expect on a relatively dry soil. In case of a heavy clay the ϵ_s would be of the order of 0.1, the aerobic zone in the soil then can be estimated at 55 cm (with equation (8.7a) and the parameters of soil 5 in table 8.2). The maximum length of the root would be somewhat less than in case of the sand, but one would still expect the root to be able to grow to the lower boundary of the plow layer, the more so the higher the root porosity.

When the root surface is partly blocked from contact with soil air, the required oxygen concentration in the soil air can be quite high. From figure 8.1 for example the required concentration for a root with radius of 0.23 cm and 50% of its surface blocked, can be estimated at 15%. But here also, especially when the blocking does not occur over the complete length of the root, transport via the internal pathway can be expected to satisfy the oxygen demand at lower concentrations of the soil air. From figure 8.5b one can estimate that for a root porosity of 5% the required oxygen concentration drops to 10%, and for a porosity of 10% to 8%.

Appendix A8. Simultaneous longitudinal and radial diffusion of oxygen in a respiring root.

The modified Fourier sine transformation with respect to z of a function G(z) is defined as (Churchill, 1972):

$$g(m) = S_m\{G(z)\} = \int_0^\pi G(z)\sin(mz)dz, \quad m=n-1/2, \; n=1,\ 2,\ 3,\dots$$

The inverse transform, denoted by $S_m^{-1}\{g(m)\}$ is given by:

$$G(z) = \frac{2}{\pi}\sum_{n=1}^{\infty} g(m)\sin(mz) \ .$$

If the transformation $S_m(c)$ of c is denoted by $\hat{c}$, and that of u by $\hat{u}$, then (8.9) becomes after transformation:

$$\text{(A8.1)} \qquad -m^2\kappa^2\hat{c} + m\kappa^2 + \frac{1}{r}\frac{d}{dr}\, r\,\frac{d\hat{c}}{dr} = \hat{u} \ .$$

The solution of the homogeneous part of (A8.1) is:

$$\hat{c}_h = a_m I_0(m\kappa r) \ ,$$

and a particular solution is:

$$\hat{c}_p = \frac{1}{m} - \frac{\hat{u}}{m^2\kappa^2} \ ,$$

so:

$$\text{(A8.2)} \qquad \hat{c} = \hat{c}_p + \hat{c}_h = \frac{1}{m} - \frac{\hat{u}}{m^2\kappa^2} + a_m I_0(m\kappa r) \ ,$$

where $\hat{u} = \int_0^\pi u\sin(mz)dz = \frac{u_0}{m} + \frac{u_0(p-1)}{m}(-1)^{n+1}\sin(m\gamma)$.

The boundary condition at r=1 transforms into:

$$\text{(A8.3)} \qquad r=1,\ d\hat{c}/dr = -\lambda(\hat{c} - \hat{c}_{so}) \ ,$$

where $\hat{c}_{so} = \int_0^\pi c_{so}\sin(mz)dz$

Substitution of (A8.2) into (A8.3) yields:

$$a_m\{m\kappa I_1(m\kappa) + \lambda I_0(m\kappa)\} = \lambda\left(\hat{c}_{so} - \frac{1}{m} + \frac{\hat{u}}{\kappa^2 m^2}\right) \ ,$$

9.2 Geometry and boundary conditions

Consider an uniformly distributed parallel root system with root density L_{rv} cm/cm³, and suppose all roots have the same length H cm and radius R_0 cm (Table 9.1 gives a list of symbols). To each root thus a hexagonal cylinder can be assigned, which can be approximated by a radial cylinder of height H and radius R_1, the latter given by (cf. (6.20)):

$$(9.1) \qquad R_1 = 1/\sqrt{(\pi L_{rv})} \ .$$

From the assumed geometry it follows that the boundary condition at the outer boundary is that of vanishing flux:

$$(9.2) \qquad R = R_1 \ , \quad \vec{F} = 0 \ .$$

The boundary condition at the root surface follows from the demand for nutrients or water. If the plant demand for water and nutrients amounts to (water) E ml/(cm².day) and (nutrient) A mg/(cm².day), each root has to take up E/L_{rv} ml/day resp. A/L_{rv} mg/day. The condition at the root surface accordingly reads:

$$\begin{array}{lll} (9.3a) & & |\vec{F}| = E/(2\pi H R_0 L_{rv}) \ , \\ & R = R_0 & \\ (9.3b) & & |\vec{F}| = A/(2\pi H R_0 L_{rv}) \ . \end{array}$$

Another consequence of the root geometry chosen is that transport occurs in radial direction only, it is therefore convenient to use radial coordinates. The divergence operator ∇. in these coordinates reads:

$$(9.4) \qquad \nabla\cdot = \frac{1}{R}\,\frac{\partial}{\partial R}\,R\frac{\partial}{\partial R}\cdot \quad .$$

9.3 Nutrients

One of the goals of this section is to theoretically investigate the influence of combined transport by mass flow and diffusion as opposed to transport by diffusion only. To this end a steady-state situation with respect to radial flow of water is considered, where the loss of water due to uptake by the root is instantaneously, uniformly and continuously replenished. This represents a rather sweeping simplification of a situation where losses of water are replenished by rain or irrigation. The radial distribution of the flux of water in such a situation is given by:

$$(9.5) \qquad V = \frac{E}{2\pi H L_{rv}(R_1{}^2-R_0{}^2)}\left\{\frac{R^2-R_1{}^2}{R^2}\right\} .$$

The derivation of (9.5) can be found in appendix A9. Even with this simplification an analytical solution for the transport of solutes towards a root remains very complicated, so a further simplification was explored. It appears that the system depicted above, i.e. steady-state with replenishment uniform over the soil cylinder, can, as far as transport of solutes is concerned, be approximated by a steady-state situation where the replenishment occurs from outside the outer boundary of the soil cylinder. This means that the imposed condition at this boundary is that of constant water content. As is shown in appendix A9, the differences between concentration profiles generated by steady-state water flow with uniform replenishment, resp. replenishment at the outer boundary, are very small amounting to a few percent at the most. Accordingly the steady-state situation with replenishment at the outer boundary will be considered in the following.

If transpiration amounts to E ml/(cm^2.day) and a steady-state situation exists with respect to radial movement of water, the rate of water transport in the soil cylinder at any distance R from the root midpoint ($R_0<R<R_1$) is E/L_{rv} ml/day. So the flux of water at distance R is given by:

$$(9.6) \qquad V = - E/(2\pi HRL_{rv}) \ .$$

When the soil is not too dry (matric potential > -0.3 MPa) diffusivity generally is so high, that if root-density is not too low (L_{rv}>0.5 cm/cm^3), small gradients in water content suffice to transport water to the root at the required rate (Greacen, 1977, see also section 9.4). Hence the water content will be taken constant in the following. Equation (7.16) with (9.4) then assumes the form:

$$(9.7) \qquad (K_a+\Theta)\ \frac{\partial C}{\partial T} = \frac{D}{R}\ \frac{\partial}{\partial R}\ R\ \frac{\partial C}{\partial R} - V\ \frac{\partial C}{\partial R} + U \ .$$

while the boundary conditions (9.2) and (9.3 b) become:

$$(9.8) \qquad R = R_1 \ , \quad -2\pi HR_1D\ \frac{\partial C}{\partial R} + 2\pi HR_1VC = 0 \ ,$$

$$(9.9) \qquad R = R_0 \ , \quad -2\pi HR_0D\ \frac{\partial C}{\partial R} + 2\pi HR_0VC = \frac{-A}{L_{rv}} \ .$$

The initial condition chosen is that of constant concentration:

$$(9.10) \qquad T = 0 \ , \qquad C = C_i \ .$$

Equations (9.7) with (9.8)-(9.10) mathematically formulate the problem we wish to solve.

9.3.1 Linear adsorption

If the adsorption isotherm is linear and if also the release term U is constant, a linear function of C, or a function of R and T, the problem is completely linear. To facilitate notation and to show the interrelation between the various parameters and variables the dimensionless quantities given in table 9.1. are defined. Variables and parameters with dimension are denoted by capital Roman letters, dimensionless variables by lower case Roman letters, and dimensionless parameters by Greek letters. Use of dimensionless variables and parameters transform (9.7)-(9.10) into:

$$(9.11) \qquad \Theta\beta\ \frac{\partial c}{\partial t} = \frac{1}{r}\ \frac{\partial}{\partial r}\ r\ \frac{\partial c}{\partial r} - \frac{2\nu}{r}\ \frac{\partial c}{\partial r} + \upsilon \ ,$$

Table 9.1 List of symbols

Symbol	Name	Dimension	Dimensionless symbol
R_0	root radius	cm	-
D	diffusion coefficient	cm²/day	-
T	time	day	$t=DT/R_0^2$
T_c	period of unconstrained uptake	day	$t_c=DT_c/R_0^2$
$T_{c,max}$	maximum T_c	day	$t_{c,max}$
R	radial coördinate	cm	$r=R/R_0$
R_1	radius soil cylinder	cm	$\rho=R_1/R_0$
H	root length	cm	$\eta=H/R_0$
S_i	initial available amount of nutrient	mg/cm³, or kg/ha	-
S	available amount of nutrient	mg/cm³, or kg/ha	$s=S/S_i$
A	uptake rate	mg/(cm².day) kg/(ha.day)	$\omega=-\rho^2\Theta\beta/(2\phi\eta)$
ϕ	supply/demand parameter	-	$\phi=DS_i/(AR_0)$
C_i	initial nutrient concentration	mg/ml	-
C	nutrient concentration	mg/ml	$c=C/C_i$
C_a	bulk density of adsorbed nutrient	mg/cm³	-
Θ_i	initial water content	ml/cm³	-
Θ	water content	ml/cm³	$\theta=\Theta/\Theta_i$
K_a	adsorption constant	ml/cm³	-
$\Theta\beta$	buffer capacity	ml/cm³	$\beta=(K_a+\Theta)/\Theta$
U	production rate	mg/(cm³.day) kg/(ha.day)	$\nu=UR_0^2/(DC_i)$
E	transpiration rate	cm/day	-
V	flux of water	cm/day	$2\nu=RV/D=-E/(2\pi HDL_{rv})$
Q_ν	unconstrained uptake capacity	mg/cm³ or kg/ha	-

$$(9.12) \quad r = \rho \ , \quad -\frac{\partial c}{\partial r} + \frac{2\nu}{\rho}\, c = 0 \ ,$$

$$(9.13) \quad r = 1 \ , \quad -\frac{\partial c}{\partial r} + 2\nu c = -\frac{\rho^2\Theta\beta}{2\phi\eta} = \omega \ ,$$

$$(9.14) \quad t = 0 \ , \quad c = 1 \ .$$

Ranges of values of parameters chosen are given in table 9.2. The value of the limiting concentration C_{lim} is put at zero, for the nutrients considered here, i.e. nitrogen, phosphorus, and potassium. For N and K the zero value of C_{lim} has been motivated in chapter 3. Though for P the limiting concentration is not negligible for low root densities, as has been discussed in chapter 3 also, here and in the chapters 10-12 a zero value will be assumed, in order to

Table 9.2 Range of parameter values.

Parameter	Symbol	Dimension	Range
transpiration rate	E	cm/day	0-1
adsorption constant	K_a	ml/cm³	0 (N) 5-25 (K) 100(P)
water content	Θ	ml/cm³	0.3
diffusion coefficient	D	cm²/day	0.1
root density	L_{rv}	cm/cm³	0.5-5
initial available amount of nutrient	S_i	mg/cm³ kg/ha	0.1(N) 200 0.2(K) 400
uptake rate	A	kg/(ha.day)	3(N) 2(K) 0.44(P)
root radius	R_0	cm	0.025
root length	H	cm	20
production rate	U	kg/(ha.day)	1(N) 0.1(P)
Dimensionless parameters			
radius soil cylinder	ρ		10-32
root length	η		800
flux of water	$\|\nu\|$		0.-0.04
supply/demand	ϕ		13.3(N) 40(K)
buffer capacity	$\Theta\beta$		0.3(N) 5.3-25.3(K) 100.3(P)

facilitate comparison with the other nutrients. In chapter 15, where soil fertility status is evaluated, the real non-zero value of C_{lim} is taken into account.

If not explicitly mentioned otherwise, results shown pertain to a root density of 1 cm/cm³, and to the uptake and supply parameters of potassium. As was mentioned before (in chapter 7) the adsorption isotherm of phosphate is nonlinear, results concerning phosphate only serve as a reference, nonlinear adsorption being treated in section 9.3.2. Generally attention will be focused on effects of transpiration, adsorption, and especially root density. The parameters D, H, A and R_0 are usually taken to be constant, and so is η as a consequence. Effect of water content and root radius are considered in separate sections.

Two cases will be dealt with here: no release of nutrient from previous unavailable forms (section 9.3.1.1), and release a known function of time (section 9.3.1.2). For each case two situations will be distinguished: one in which transport is by diffusion only, the other where transport is both by diffusion and mass flow. For both situations the development of the concentration profile around the root, the period of unconstrained uptake and the fractional depletion will be discussed.

9.3.1.1 No release of nutrients
Transport by diffusion only

Though the case where transport is both by diffusion and mass flow is the more general, it is worthwhile to first treat the simpler case where transport is by diffusion only. The solution of (9.11), subject to (9.12)-(9.14), with $\nu=0$, was derived by De Willigen and Van Noordwijk (1978). It reads:

$$(9.15a) \quad c = 1 +$$

$$(9.15b) \quad \omega \left\{ \frac{2}{\rho^2-1}\,\frac{t}{\Theta\beta} + \frac{r^2-\rho^2}{2(\rho^2-1)} - \frac{\rho^2}{\rho^2-1}\ln r + \frac{\rho^4 \ln\rho}{(\rho^2-1)^2} - \frac{1+\rho^2}{4(\rho^2-1)} \right\} +$$

$$(9.15c) \quad \pi\omega \sum_{n=1}^{\infty} \frac{J_1(\alpha_n)\,J_1(\rho\alpha_n)}{\alpha_n} F_0(r,\alpha_n)\,\exp(-\alpha_n{}^2 t/\Theta\beta) \ ,$$

where $F_0(r,\alpha_n) = \dfrac{Y_1(\rho\alpha_n)\,J_0(r\alpha_n) - Y_0(r\alpha_n)\,J_1(\rho\alpha_n)}{J_1{}^2(\alpha_n) - J_1{}^2(\rho\alpha_n)}$,

α_n the n-th root of $Y_1(\rho\alpha)\,J_1(\alpha) - Y_1(\alpha)\,J_1(\rho\alpha) = 0$,
J_0, J_1 Bessel functions of the first kind and order 0 and 1, and
Y_0, Y_1 the modified Bessel functions of the first kind and order 0 and 1.

The concentration profile

The solution (9.15) consists of three parts, all of which satisfy the partial differential equation, but with different initial and boundary conditions. Part (9.15a) gives the steady-state solution when no uptake occurs. Together with (9.15a), part (9.15b) gives the steady-rate solution which will be reached for large t in due course, when the series part (9.15c) can be neglected. In the series part, time occurs in the exponent with a negative coefficient, so that its contribution will ultimately become vanishlingly small, the later the larger the buffer capacity. When the series part can be ignored, the rate of decrease of c is independent both of time and distance (hence the term "steady-rate"):

$$(9.16) \quad \frac{\partial c}{\partial t} = \frac{2\omega}{(\rho^2-1)\Theta\beta} = \frac{-\rho^2}{(\rho^2-1)\eta\phi} \ .$$

Figure 9.1 shows the time course of the absolute value of the the rate of change of concentration $|\partial c/\partial t|$ as a function of time for different locations and buffer capacities, demonstrating the eventual convergence of $|\partial c/\partial t|$ to the value given by (9.16), regardless of position and buffer capacity. When a steady-rate situation has developed the concentration profile around the root will maintain its then established shape, which will conformly move downwards with time. Figure 9.2 displays the contributions of the steady-rate and the series part to the complete solution, after 1 and after 10 days. After 1 day for distances greater than about 5 radii part b and c cancel each other, which means that the concentration does not yet decrease beyond this point, after 20 days this is the case only at distances greater than 18 times R_0.

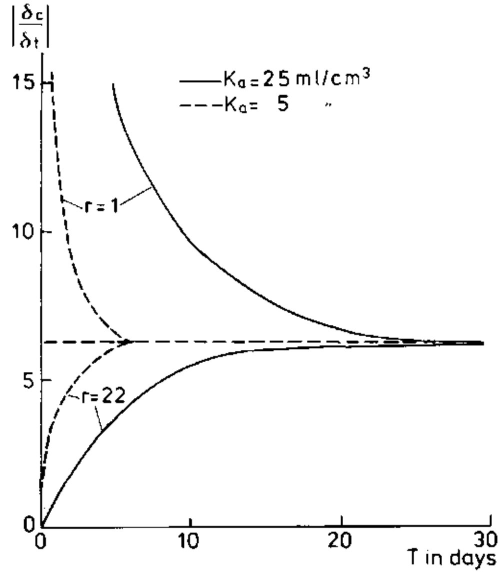


Fig. 9.1 Rate of change of concentration at the root surface (r=1) and at the boundary of the soil cylinder (r=22) as a function of time and adsorption constant. Parameters: root density 1 cm/cm³, uptake 2 kg/(ha.day), supply 400 kg/ha, root length 20 cm, diffusion coefficient 0.1 cm²/day. Transport by diffusion only.

The period of unconstrained uptake

An important characterization of the possibilities of the soil-root system with respect to uptake is given by the period during which the concentration at the root surface exceeds the limiting concentration. During this period - in dimensionless form denoted by the symbol t_c - uptake is completely in accordance with plant demand. The maximum time a root system of infinite root density can take up the nutrient at the required rate is simply the available amount divided by the uptake rate:

$$(9.17) \qquad T_{c,max} = \frac{H(R_1{}^2 - R_0{}^2)}{R_1{}^2 A} S_i \ ,$$

or in dimensionless form:

$$(9.18) \qquad t_{c,max} = \frac{DT_{c,max}}{R_0{}^2} = \frac{\rho^2 - 1}{\rho^2} \phi\eta = \frac{(\rho^2-1)\Theta\beta}{-2\omega} \ .$$

If it can be assumed that when t equals t_c, the series part of (9.15) can be neglected, it is easy to make t_c explicit:

$$(9.19) \qquad t_c = \frac{\rho^2 - 1}{\rho^2} \eta\phi - \Theta\beta \, G(\rho,0) \ ,$$

with G a function of ρ and ν, (ν=0 in case of transport by diffusion alone):

$$G(\rho,0) = \frac{1}{2} \left\{ \frac{1-3\rho^2}{4} + \frac{\rho^4 \ln\rho}{\rho^2 - 1} \right\} .$$

Transport by mass flow and diffusion

The solution of (9.11) with (9.12)-(9.14), when $\upsilon=0$, was derived by De Willigen (1981) and reads:

$$c = \frac{(\rho^2-1)(\nu+1)r^{2\nu}}{\rho^{2\nu+2}-1} + \tag{9.25a}$$

$$\omega \left\{ \frac{2(\nu+1)r^{2\nu}}{\rho^{2\nu+2}-1}\,\frac{t}{\Theta\beta} + \frac{r^{2\nu}(r^2-\rho^2)}{2(\rho^{2\nu+2}-1)} + \frac{\rho^2(\rho^{2\nu}-r^{2\nu})}{2\nu(\rho^{2\nu+2}-1)} + \right. \tag{9.25b}$$

$$\left. \frac{\rho^2(\rho^{2\nu}-1)r^{2\nu}(\nu+1)}{2\nu(\rho^{2\nu+2}-1)^2} + \frac{r^{2\nu}(\nu+1)(1-\rho^{2\nu+4})}{(2\nu+4)(\rho^{2\nu+2}-1)^2} \right\} +$$

$$(\omega-2\nu)r^{\nu}\,\pi \sum_{n=1}^{\infty} \frac{J_{\nu+1}(\alpha_n)\,J_{\nu+1}(\rho\alpha_n)}{\alpha_n}\,F_\nu(r,\alpha_n)\,\exp(-\alpha_n{}^2\,t/\Theta\beta) + \tag{9.25c}$$

$$\frac{2\nu r^{\nu}\pi}{\rho^{\nu+1}} \sum_{n=1}^{\infty} \frac{J_{\nu+1}{}^2(\alpha_n)}{\alpha_n}\,F_\nu(r,\alpha_n)\,\exp(-\alpha_n{}^2\,t/\Theta\beta)\ , \tag{9.25d}$$

with

$$F_\nu(r,\alpha_n) = \frac{Y_{\nu+1}(\rho\alpha_n)\,J_\nu(r\alpha_n) - Y_\nu(r\alpha_n)\,J_{\nu+1}(\rho\alpha_n)}{J_{\nu+1}{}^2(\alpha_n) - J_{\nu+1}{}^2(\rho\alpha_n)}\ ,$$

and α_n the n-th root of $Y_{\nu+1}(\rho\alpha)\,J_{\nu+1}(\alpha) - Y_{\nu+1}(\alpha)\,J_{\nu+1}(\rho\alpha) = 0$.

By taking the limit as $\nu \longrightarrow 0$ from (9.25) the solution when transport is by diffusion only can be obtained (equation (9.15)). As in section 9.3.1.1 we will discuss the development of the concentration profile around the root, the period of unconstrained uptake and the fractional depletion. Next also relevant differences with the situation where transport is by diffusion only will be treated.

Concentration profile

In (9.25) four parts can be distinguished, each as in (9.15) giving a solution of (9.11), with different initial and boundary conditions. The first part gives the steady-state situation when no uptake occurs ($\omega=0$). When transport is by diffusion only, this steady-state situation is identical to the initial situation. When flow of water contributes to the transport of the solute and $\omega=0$, the concentration is a decreasing function of the distance, as the derivative of c with respect to r:

$$\frac{\partial c}{\partial r} = \frac{2\nu(\rho^2-1)(\nu+1)}{\rho^{2\nu+2}-1}\,r^{2\nu-1}\ , \tag{9.26}$$

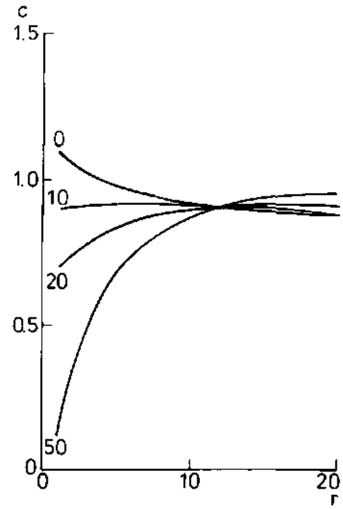


Fig. 9.4 Concentration profile around the root after an uptake period of 20 days for different values of the adsorption constant (the numbers at the curves), and a transpiration rate of 1 cm/day. Other parameters as in figure 9.1.

is negative for all r. In this situation the diffusion away from the root just cancels the transport by mass flow towards the root or:

$$(9.27) \quad \frac{\partial c}{\partial r} = \frac{2\nu}{r} c \ .$$

When mass flow plays an important role in transport, $\partial c/\partial t$ will eventually become independent of time, but will nevertheless stay a function of distance, so no steady-rate situation will develop:

$$(9.28) \quad \frac{\partial c}{\partial t} = \frac{2\omega(\nu+1)r^{2\nu}}{(\rho^{2\nu+1}-1)\Theta\beta} \ .$$

Calculation of values of c when the infinite series cannot be ignored, requires the use of a computer, an example of the type of computer program employed can be found in De Willigen (1981). Figure 9.4 shows the concentration profile around the root after 20 days. In the early stages of uptake at low values of the adsorption constant the concentration is highest at the root surface in the case of high transpiration as the nutrient is driven towards the root by mass flow at a higher rate than is required for uptake. Later as the average concentration is continously diminished because of uptake, the concentration profile changes from a concave into a convex form also in the case of low adsorption. As buffer capacity $\Theta\beta$ only appears in (9.25) in combination with t (in the denominator), it follows that a particular concentration profile found after a short time, when buffer capacity is high, will be found after a long time for low buffer capacity.

It is interesting to analyze the contributions of the four components of (9.25) to the value of c. Figure 9.5 shows these components as a function of distance for two different times, an adsorption constant of 50 ml/cm³ and a transpiration of 1 cm/day. As can be seen the components containing the series (c and d) play a less prominent role as time proceeds. For t=10 days part d is everywhere smaller than 0.01. Ultimately only the terms a (which is invariable with time) and b remain.

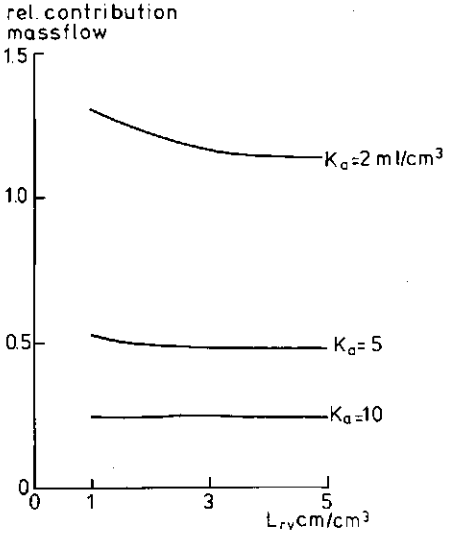


Fig. 9.7 Relative contribution of mass flow to total uptake in the period of unconstrained uptake, as a function of root density and adsorption constant. Transpiration 1 cm/day, other parameters as in figure 9.1.

The contribution of mass flow to the unconstrained availability is higher the higher the buffer capacity of the soil. It is approximately proportional to the adsorption constant, for subtraction of $f_{d,0}$ from $f_{d,\nu}$, and noting that according to table 9.1 $\Theta\beta = K_a + \Theta$, yields:

$$(9.33) \qquad f_{d,\nu} - f_{d,0} = \frac{(K_a+\Theta)\rho^2}{(\rho^2-1)\phi\eta} \{ G(\rho,0) - G(\rho,\nu) \} .$$

Figure 9.8 shows the interaction of adsorption constant and the root density with respect to the advantages of combined mass flow-diffusion transport above transport by diffusion alone. For a given amount of nutrient available the increase in unconstrained availibility due to mass flow is more important the higher the adsorption constant, or equivalently the lower the concentration of

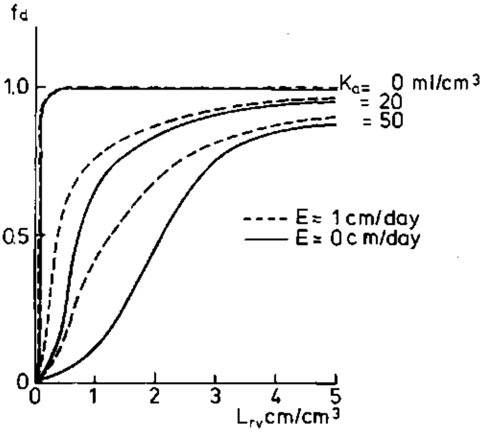


Fig. 9.8 Interaction of adsorption contact, mass flow, and root density for fractional depletion. Other parameters as in figure 9.1.

the soil solution, contrary to what commonly is inferred (Grimme et al., 1971). Generally, the unconstrained uptake capacity Q_ν in absolute units is given by:

$$(9.34) \quad Q_\nu = f_{d,\nu}.S_i = S_i - \frac{A(K_a+\Theta)}{DH} R_0^2 \frac{\rho^2}{\rho^2-1} G(\rho,\nu) \ .$$

The unconstrained uptake capacity thus equals the available amount S_i diminished by a term e.g. depending on the root density. This last term represents the amount which cannot be taken up atthe required rate.

For a given root density, plant demand, diffusion coeffient and transpiration, the unconstrained uptake capacity depends in a linear fashion on available amount and the adsorption constant K_a.

9.3.1.2 Release of nutrients a known function of time

Transport by diffusion only

Again it is profitable to start with the case where transport is by diffusion only. The solution of (9.11)-(9.14) in this case is simply found as:

$$(9.35) \quad c^* = c + \int_0^t \frac{\upsilon}{\Theta\beta}\, dt \ ,$$

where c is the solution without production of nutrient, i.e. (9.15). If the release rate is constant, i.e. $\upsilon = \upsilon_0$, the concentration thus is:

$$(9.36) \quad c^* = c + \frac{\upsilon_0 t}{\Theta\beta} \ .$$

The coefficient of t now is: $\left\{ \dfrac{2\omega}{\rho^2-1} + \upsilon_0 \right\} \dfrac{1}{\Theta\beta}$.

Eventually thus a steady-state situation - in which an invariable concentration profile is generated - will develop whenever:

$$\upsilon_0(\rho^2-1) = -2\omega = \rho^2\Theta\beta/\phi\eta \ ,$$

i.e. when the rate of production in the soil cylinder equals the uptake rate of the root. When the production rate is lower than plant demand, as generally will be the case for nitrogen and phosphate, a steady-rate situation might be reached in due course. The steady rate profile does not differ from that when no production occurs, as follows from (9.36)

The period of unconstrained uptake

Obviously the period of unconstrained uptake t_c^* will be increased when nutrient in available form is released from formerly unavailable forms. When the rate of release exceeds the uptake rate the period of unconstrained uptake will theoretically be infinite. In the more realistic event that uptake rate is greater than production rate, t_c^* can be calculated as:

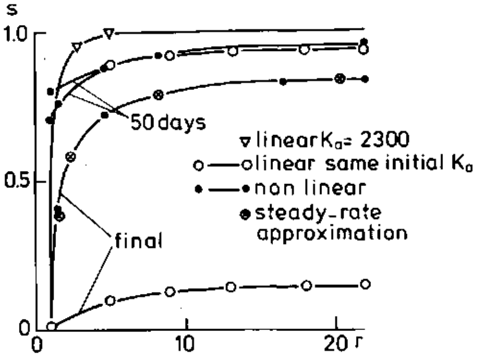


Fig. 9.10 The profile of dimensionless bulk density of available phosphate around the root after 50 days, and when the concentration at the root surface equals zero, for linear and nonlinear adsorption. Parameters as in figure 9.9.

of the adsorption isotherm at the initial concentration, are depicted. Initially thus in both cases the buffer capacity is the same, as was the amount of available phosphate. The rate of change of S in the neighbourhood of the root surface can be seen to decrease in the beginning more or less at the same rate for linear and nonlinear adsorption. Later however in the case of nonlinear adsorption the rate of change increases again, while in the case of linear adsorption it approaches the steady-rate value, as does the rate of change near the outer boundary of the soil cylinder. At this position the rate of change in the case of nonlinear adsorption increases first, though it does not reach the steady-rate value, to decrease slightly in a later stage. This implies that much more of the nutrient taken up by the root originates from its immediate vicinity when adsorption is nonlinear, and - which is the case normally - the adsorption isotherm is concave, i.e. stronger adsorption at lower concentration.

The profile of S around the root accordingly is in the neighbourhood of the root much steeper than in the linear case (figure 9.10), when the concentration at the root surface is zero. The profile of the concentration bears, when $t=t_c$, much resemblance with the steady-rate profile as is shown in figure 9.11. The same is true when mass flow is contributing to transport.

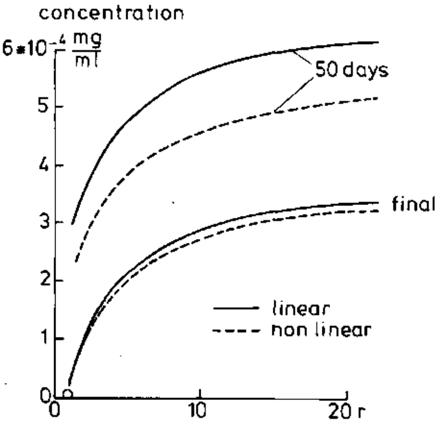


Fig. 9.11 Profile of phosphate concentration around the root after 50 days, and at the end of the period of unconstrained uptake. Parameters as in figure 9.9.

Period of unconstrained uptake

The period of unconstrained uptake t_c depends on the shape of the adsorption isotherm. It is much larger when the adsorption isotherm is linear as can be inferred from figure 9.10 .

The fact that the concentration profile approximates the steady-rate profile when the concentration at the root surface is zero, can be used to calculate t_c without using the numerical model. When the concentration at the root surface is zero, and the concentration profile follows a steady-rate profile, using (9.15) and table 9.1 the concentration in absolute units can be given as:

$$(9.43) \qquad C(r,t_c) = \frac{\rho^2}{2\eta}\,\frac{AR_0}{D}\left[\frac{\rho^2 \ln r}{\rho^2-1} - \frac{r^2-1}{2(\rho^2-1)}\right] .$$

The bulk density of available phosphate can then be calculated ((7.1) and (7.14)) as:

$$(9.44) \qquad S = \frac{B_1A_1C}{1+B_1C} + \frac{B_2A_2C}{1+B_2C} + \Theta C .$$

The course of S around the root can be given quite satisfactorily in this way as is shown in figure 9.10

The period of unconstrained uptake T_c in absolute units can likewise be approximated as:

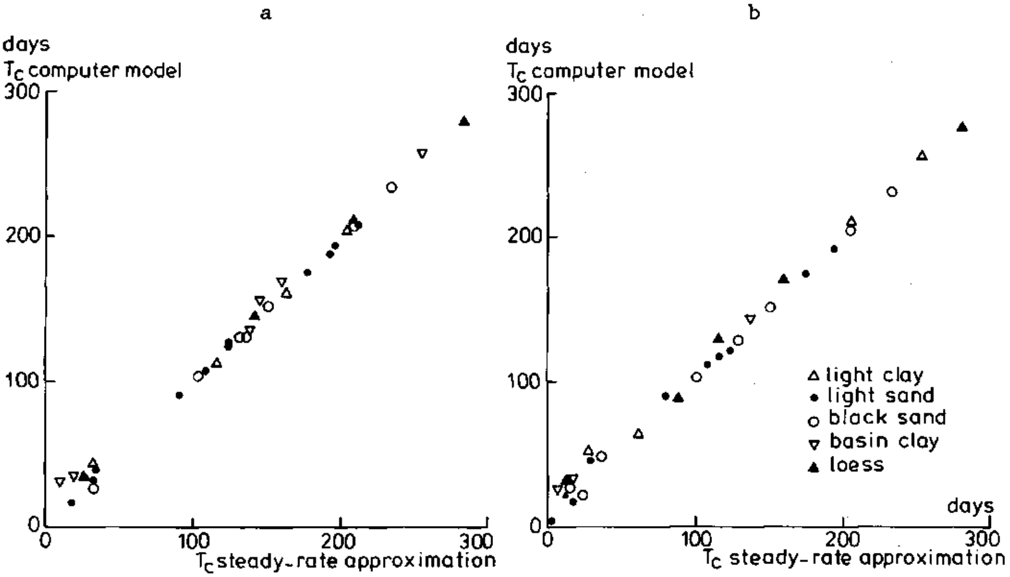


Fig. 9.12 Comparison of T_c computed with a numerical model with that computed by the steady-rate approximation. **Fig. 9.12a** Transport by diffusion only. **Fig. 9.12b** Transport by diffusion and mass flow. Initial amounts of available phosphate corresponding to P_w-values of 10, 30 and 50 mg P_2O_5 per liter soil and a root density of 1, 3 and 5 cm/cm³. Other parameters as in figure 9.9.

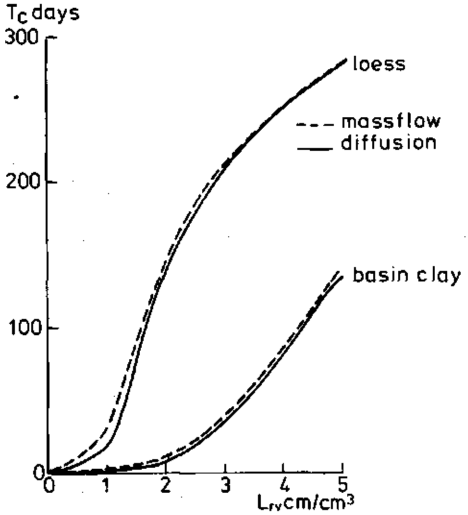


Fig. 9.13 Effect of mass flow (transpiration of 1 cm/day) on period of unconstrained uptake of phosphate for two soils. Initial available amount 0.08 mg/cm³. Other parameters as in figure 9.9.

$$(9.45) \qquad T_c = \left\{ H(R_1{}^2-R_0{}^2)\ S_i - \int_{R_0}^{R_1} 2HRS(R,T_c)\ dR \right\} / R_1{}^2A \ .$$

The first term in the numerator of the right hand side of (9.45) gives the initial amount, the second the amount left, when the concentration at the root surface is zero. T_c calculated is this way is a good approximation of T_c calculated by numerically solving the nonlinear partial differential equation, as is demonstrated in figure 9.12a.

As in the case for linear adsorption the beneficial effect of mass flow is relatively stronger the higher the adsorption and the lower the root density, but in absolute sense it enhances the extraction of phosphate from the soil only sligthly (figure 9.13)

Also when mass flow plays a role the approximation of the concentration profile by the analytical expression derived before (9.25 a and b), was found to be satisfactory. Figure 9.12b shows T_c calculated on the basis of (9.25a and b), (9.44) and (9.45).

The influence of buffer capacity can be demonstrated in the same way as done for figure 9.6, i.e. plotting the amount of available phosphate required to guarantee an actual uptake period of 100 days, as a function of root density (figure 9.14). For a root density of 1 cm/cm³ the amount of phosphate available should be more than seven times larger than the amount actually required in a period of 100 days for basin clay, for light sand only a little more than twice the required amount should be present. Mass flow is more important for low root densities and strong buffering.

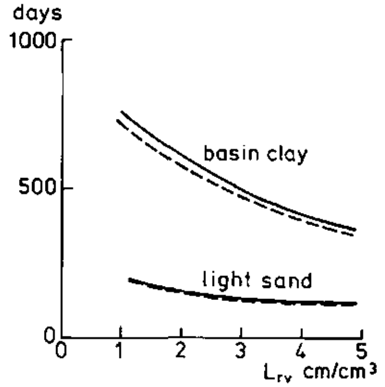


Fig. 9.14 Required supply of available phosphate, expressed in days like in figure 9.6, to ensure an unconstrained uptake period of 100 days as a function of root density. Interrupted lines: transport by diffusion and mass flow (transpiration 1 cm/day). Uninterrupted lines: transport by diffusion only.

Fractional depletion

Figure 9.15 shows the fractional depletion as a function of the root density, for an initial available amount S_i of 0.15 mg/cm³, or a potential uptake period of 682 days. This figure again shows the influence of buffer capacity and root density. It also demonstrates that the available amount (S) is not a good criterion for the unconstrained availability of phosphate. For a root density of 1 cm/cm³ only 10% of the available amount is available for unconstrained uptake in the case of basin clay, whereas this figure is 85% for the light sand. At higher root densities the differences become progressively less.

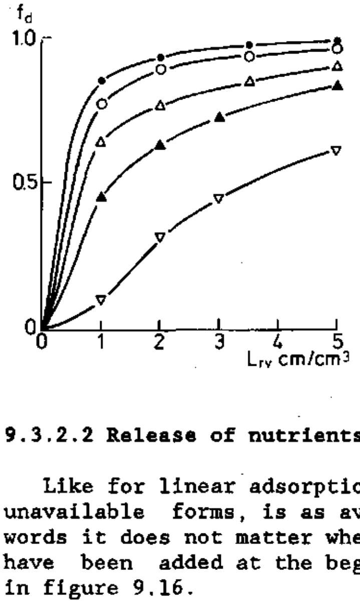


Fig. 9.15 Fractional depletion of available phosphate as a function of root density for different soils (the points have the same meaning as in figure 9.12). Initial available amount for all soils 0.15 mg/cm³.

9.3.2.2 Release of nutrients a function of time

Like for linear adsorption, here also the nutrient released from originally unavailable forms, is as available as the amount originally present; in other words it does not matter whether the nutrient is released gradually or would have been added at the beginning of the uptake period. This is demonstrated in figure 9.16.

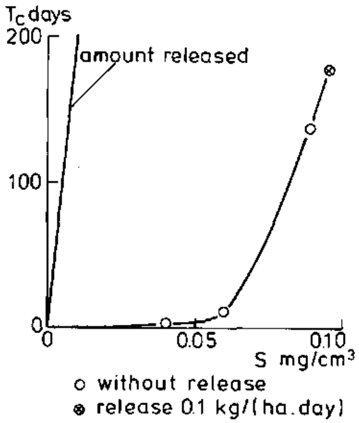


Fig. 9.16 Period of unconstrained uptake T_c as a function of supply of available phosphate, with and without production of 0.1 kg/(ha.day). Soil: light clay. Parameters as in figure 9.9.

9.3.3 Effect of water content

Changes in average water content can have profound influence on physical and chemical soil processes, and indirectly also on (micro)biological processes. We will consider here the changes in physical properties as far as these are relevant for transport of nutrients in the soil.

The diffusion coefficient D in the soil can be written as (Nye and Tinker, 1977):

$$D = D_0 \Theta f_\ell \quad , \tag{9.46}$$

where D_0 is the diffusion coefficient in free water [cm²/day],
Θ is the water content,
f_ℓ is an impedance factor.

The impedance factor f_ℓ depends on water content as shown in figure 9.17, taken from Barraclough and Tinker (1981). The impedance factor is seen to

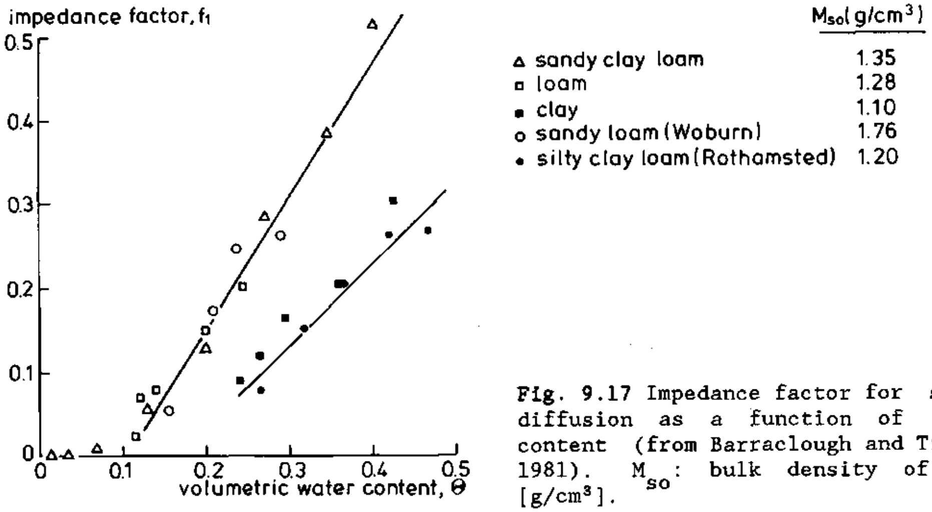


Fig. 9.17 Impedance factor for solute diffusion as a function of water content (from Barraclough and Tinker, 1981). M_{so}: bulk density of soil [g/cm³].

depend linearly (at least for a large range) on the water content, the diffusion coefficient accordingly being a quadratic function of Θ. Clearly diffusive fluxes will be severely restricted when the water content decreases below 0.1-0.15 ml/cm^3. When transport is by diffusion only a low value of the diffusion coefficient is equivalent to a large value of the buffer capacity $\Theta\beta$.

This can be seen by expressing the period of unconstrained uptake in absolute units:

$$(9.47) \qquad T_c = R_0{}^2 \left\{ \frac{(\rho^2-1)}{\rho^2} \eta \frac{S_i}{AR_0} - \frac{\Theta\beta}{D} G(\rho,0) \right\} .$$

Also the amount of nutrient actually taken up at the required rate (9.34) and the fractional depletion are linearly related to the quotient $\Theta\beta/D$. Figure 9.18 shows the influence of the water content via the diffusion coefficient on the fractional depletion of nitrate.

When mass flow also contributes to transport, the situation is more complicated, as D occurs now not only in combination with buffer capacity, but also in the parameter ν where D is weighted with respect to flow of water (see table 9.1). The function $G(\rho,\nu)$ is a positive and decreasing function of $|\nu|$, but not proportional to $|\nu|$, or inversely proportional to D. From the expression for T_c:

$$(9.48) \qquad T_c = R_0{}^2 \left\{ \frac{(\rho^2-1)}{\rho^2} \eta \frac{S_i}{AR_0} - \frac{\Theta\beta}{D} G(\rho,\nu) \right\} ,$$

it follows then, that a lower value of D also in case of mass flow has a disadvantageous effect on availability, be it of course to a lesser extent than when diffusion is the sole transport mechanism.

When drying out of the soil around the root can be adequately described by a sequence of steady-rate situations (see section 9.4), then down to a certain value of the average water content, Θ will be a constant function of the distance from the root. The drying out of the soil will have the effect on the availability on the one hand as if adsorption of the nutrient will be stronger, and on the other hand as if transpiration will be higher.

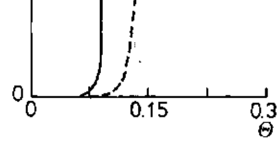


Fig. 9.18 Fractional depletion of nitrate as a function of water content. Transport by diffusion only. Uptake and supply parameters of nitrate as in table 9.2. Other parameters (except diffusion coefficient) as in figure 9.1.

and that Θ can be neglected with respect to K_a. The steady-rate solution of (9.11) with (9.12)-(9.14), when transport is by diffusion only, now is (appendix A9):

$$(9.52) \qquad c = 1 + \frac{\omega m}{2}\left[\frac{2t}{K_{a,0}(\rho^m-1)} + \frac{4}{m^2}\left\{\frac{r^m-\rho^m}{2(\rho^m-1)} - \frac{(1+\rho^m)}{4(\rho^m-1)} - \frac{m\rho^m}{2(\rho^m-1)}\ln r + \frac{m\rho^{2m}}{2(\rho^m-1)^2}\ln\rho\right\}\right] ,$$

where now

$$(9.53) \qquad K_{a,0} = p_a(R_0)^q , \qquad \omega = -K_{a,0}\rho^2/2\eta\phi ,$$

$$(9.54) \qquad m = q+2 ,$$

and S_i, implied in the definition of ϕ, is the bulk density of initial available nutrient at the root surface. The similarity between (9.52) and (9.15a and b) is clear. From (9.52) the period of unconstrained uptake t_c can be derived:

$$(9.55) \qquad t_c = \frac{2(\rho^m-1)}{m\rho^2}\eta\phi - \frac{2K_{a,0}}{m^2}\left\{\frac{1-3\rho^m}{4} + \frac{m\rho^{2m}}{2(\rho^m-1)}\ln\rho\right\}$$

$$= \frac{2(\rho^m-1)}{m\rho^2}\eta\phi - \frac{4K_{a,0}}{m^2}G(\rho^{m/2},0) .$$

The first term of the right hand side of (9.55) gives the maximum period of unconstrained uptake $t_{c,max}$. In figure 9.20 T_c in days is given as a function of q for a nutrient with an adsorption constant in the bulk soil of 10 ml/cm³ ("potassium") and one for which the adsorption constant is 100 ml/cm³ ("phosphate"). The supply of available nutrient was chosen such, that T_c amounted to 100 days when q=0, and the adsorption constant at the boundary of the soil cylinder was taken to be the same, irrespective of the course of adsorption with distance. For high adsorption the benefit of lowering the adsorption strength near the root can be significant, more than doubling the period of unconstrained uptake.

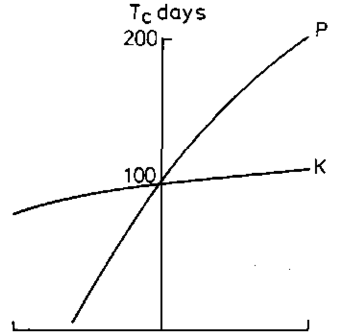


Fig. 9.20 Period of unconstrained uptake T_c as a function of power q, in equation (9.51). Adsorption constant in bulk soil 10 (K) resp. 100 (P) ml/cm³. Other parameters as in figure 9.1.

9.4 Water

9.4.1 Introduction

The problems treated above for transport of nutrients were linear or mildly nonlinear, as the transportparameters involved - the diffusion coefficient and the flux of water - were independent of the concentration so that at least the boundary conditions had a linear form. This is not the case for transport of water in the soil. The hydraulic conductivity usually is a strongly nonlinear function of the matric potential, which is in a mathematical sense analogous to the concentration of a nutrient in the soil solution, the water content being analogous to the bulk density of the nutrient.

Apart from the degree of nonlinearity of the transport process, other differences exist between water and nutrients as far as transport to and uptake by plant roots are concerned. The amount of water available in the root zone usually can satisfy the demand of a crop maximally for only a few weeks. Moreover the water content corresponding to the matric potential at which the plant root will no longer be able to extract water at the required rate can be still considerable (see table 7.2). This limiting potential will here be put at -5000 cm (-0.5 MPa).

Finally the rate of uptake of water shows a clear diurnal rythm, reflecting the transpirational demand. This periodicity in uptake will here be ignored, in order to show clearly the differences and similarities between nutrient and water transport.

The nonlinearities prohibit the finding of complete analytical solutions, nevertheless it will appear that approximations can be found, which allow calculation of the relevant variables T_c, the period of unconstrained uptake, and f_d, the fractional depletion, in a relative simple way.

Using radial coordinates and neglecting the production term the partial differential equation which describes transport of water becomes:

$$(9.56)\qquad \frac{\partial\Theta}{\partial T} = \frac{1}{R}\frac{\partial}{\partial R} RK_H \frac{\partial H_p}{\partial R} .$$

When, as will be assumed here, the water retentivity curve is unique (non hysteretic), (9.56) can also be written as:

$$(9.57)\qquad \frac{\partial\Theta}{\partial T} = \frac{1}{R}\frac{\partial}{\partial R} RD_w \frac{\partial\Theta}{\partial R} ,$$

where D_w is the diffusivity defined in (7.11). The boundary conditions (9.2) and (9.3b) now assume the form:

$$(9.58)\qquad R = R_1 , \quad \frac{\partial\Theta}{\partial R} = 0 ,$$

$$(9.59)\qquad R = R_0 , \quad D_w \frac{\partial\Theta}{\partial R} = \frac{E}{2\pi HR_0L_{rv}} .$$

Making the variables and parameters dimensionless, as indicated in table 9.1 and 9.3, changes (9.57)-(9.59) into:

Substitution of (A9.2) into (A9.3) yields (9.5).

Figure A9.1 show concentration profiles calculated with flux of water given by (9.5) and (9.6). Differences can be seen to be small, less then a few percent.

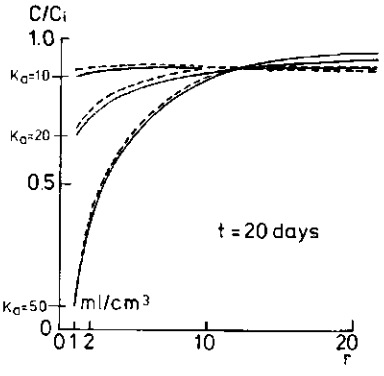


Fig. A9.1 Profiles of relative concentration around the root, when transport is by diffusion and mass flow. Uninterrupted lines give the solution when replenishment of water is uniform in the soil cylinder. Interrupted lines implies replenishment from outside the soil cylinder. Root density 1 cm/cm³, uptake and supply parameters are those of potassium given in table 9.2. Transpiration 0.5 cm/day.

A9.2 Diffusion of a nutrient to a root, when the adsorption constant is a function of distance from the root

If the adsorption constant K_a is a function of distance as given by (9.51) and Θ is neglected with respect to K_a, the partial differential equation (9.11), without the release term and in absence of mass flow, becomes:

$$\text{(A9.4)} \quad K_{a,0}r^q \frac{\partial c}{\partial t} = \frac{1}{r}\frac{\partial}{\partial r} r \frac{\partial c}{\partial r} .$$

Taking the Laplace-transform of (A9.4), with respect to t and with transformparameter s, and using initial condition (9.14) yields:

$$\text{(A9.5)} \quad K_{a,0}r^q(s\hat{c} - 1) = \frac{1}{r}\frac{d}{dr} r \frac{d\hat{c}}{dr} ,$$

where $\hat{c}$ is the Laplace-transform of c. Let:

$$\hat{c} = \hat{c}_h + \hat{c}_p ,$$

where $\hat{c}_h$ is the solution of the homogeneous part of (A9.5) and $\hat{c}_p$ is a particular solution. The solution of the homogeneous part is given by (Kamke 1943, page 440, 2.162 1a):

$$\hat{c}_h = AI_0(2\sqrt{(K_{a,0}s)}r^{m/2}/m) + BK_0(2\sqrt{(K_{a,0}s)}r^{m/2}/m) ,$$

where m is given by (9.54), and I_0 and K_0 denote modified Bessel functions of the first and second kind, and of order 0.

A particular solution of (A9.6) is:

$$\hat{c}_p = \frac{1}{s} ,$$

so:

$$\text{(A9.7)} \qquad \hat{c} = \frac{1}{s} + AI_0\{2\sqrt{(K_{a,0}s)}r^{m/2}/m\} + BK_0\{2\sqrt{(K_{a,0}s)}r^{m/2}/m\} \ .$$

The boundary conditions (9.12) and (9.13) (with ν=0) transform into:

$$\text{(A9.8)} \qquad r=\rho, \quad AI_1\{2\sqrt{(K_{a,0}s)}/m\} - BK_1\{2\sqrt{(K_{a,0}s)}/m\} = \frac{-\omega}{s\sqrt{(K_{a,0}s)}} \ ,$$

$$\text{(A9.9)} \qquad r=1, \quad AI_1\{2\sqrt{(K_{a,0}s)}\rho^{m/2}/m\} - BK_1\{2\sqrt{(K_{a,0}s)}\rho^{m/2}/m\} = 0 \ ,$$

from which A and B can be solved. Eventually $\hat{c}$ is found to be:

$$\text{(A9.10)} \qquad \hat{c} = \frac{1}{s} - \frac{\omega}{s\sqrt{(K_{a,0}s)}} \, \frac{M_1(\rho,s)N_0(r,s)+N_1(\rho,s)M_0(r,s)}{M_1(1,s)N_1(\rho,s)-N_1(1,s)M_1(\rho,s)} \ ,$$

where:

$$M_n(r,s) = I_n\{2\sqrt{(K_{a,0}s)}r^{m/2}/m\},$$

$$N_n(r,s) = K_n\{2\sqrt{(K_{a,0}s)}r^{m/2}/m\}, \text{ with } n = 0 \text{ or } 1 \ .$$

The inverse transform of 1/s is 1. The inverse transform of the second term of the RHS of (A9.10), which for convenience will be denoted by T_2, can be found by applying the complex inversion theorem (Churchill, 1972). This amounts to the finding of the residues of the product of this term and exp(st). The residues can be found as was outlined in De Willigen and Van Noordwijk (1978) and De Willigen (1981). The residue for s=0, which corresponds to the steady-rate solution is found by writing the Besselfunctions in the nominator and denominator of the second term of (A9.10) as summation series (Abramowitz and Stegun, 1970, page 375 9.6.10 resp. 9.6.11), which results in:

$$T_2\exp(st) = \frac{-\omega}{s\sqrt{(K_{a,0}s)}} \exp(st) \frac{m}{\sqrt{(K_{a,0}s)}} \left\{ \frac{a_1+a_2s+O(s^2)}{b_1+b_2s+O(s^2)} \right\} \ ,$$

where

$$a_1 = \frac{1}{\rho^{m/2}} \ , \qquad b_1 = \left\{ \frac{1-\rho^m}{2\rho^{m/2}} \right\} \ ,$$

$$a_2 = \frac{4K_{a,0}}{m^2} \left[\frac{\rho^m + r^m}{4\rho^{m/2}} + \frac{\rho^{m/2}}{2} \left\{ \frac{m}{2}\ln(\rho/r) - 1 \right\} \right],$$

$$b_2 = \frac{4K_{a,0}}{m^2} \left[\frac{1}{2\rho^{m/2}} \left\{ \frac{1}{8} + \frac{\rho^m}{4} \right\} - \frac{\rho^{m/2}}{2} \left\{ \frac{1}{4} + \frac{\rho^m}{8} \right\} + \frac{\rho^{m/2}}{4} \ln\rho^{m/2} \right],$$

and $O(s^2)$ stands for all terms in s of degree two or higher.
From (A9.11) it can be seen that $s=0$, is a double pole, the residue of $T_2\exp(st)$ at such a singular value is given by (Churchill, 1972):

$$\lim_{s\to 0} \frac{d}{ds} = s^2 T_2 \exp(st) = -\omega \lim_{s\to 0} \frac{d}{ds} \frac{\exp(st)}{K_{a,0}} \frac{m}{2} \frac{(a_1+a_2 s+\ldots)}{(b_1+b_2 s+\ldots)}$$

$$= \frac{-\omega m}{2K_{a,0}} \left\{ \frac{a_1 t}{b_1} + \frac{a_2}{b_1} - \frac{a_1 b_2}{b_1^{\,2}} \right\} .$$

Substitution of a_1, a_2, b_1, and b_2 as given above results in the expression for c given in (9.52).

10. DEPLETION BY ROOTS PARTIALLY IN CONTACT WITH SOIL

10.1 Introduction

In chapter 9 the influence of root density on realised uptake for a regular distribution of parallel roots was investigated. In developing the theory for such a system, it was assumed that the root over its total (active) surface had direct contact with either the soil solution or the soil solid phase. However, inspection of root-soil contact in the field, both macroscopically (figure 6.8), and microscopically by observing thin sections (Altemüller and Haag, 1983), reveals that complete contact between the root and the soil liquid and solid phases may be the exception rather than the rule, especially for heavy soils. Herckelrath et al. (1977) were the first to quantitatively evaluate the effects of limited root-soil contact for water uptake. Faiz and Weatherly (1978) performed an interesting experiment in which it was shown that increased soil-root contact could lead to enhanced uptake of water.

It is clear that partial contact between root and soil will limit the availability of nutrients as well, as gradients in the vicinity of the root have to be higher than when there is complete contact. In this chapter the influence of limited root-soil contact on nutrient and water uptake will be analyzed, the consequences for the aeration status being discussed in chapter 8. Like in chapter 9, attention will be focused on three aspects: the distribution of water and nutrients near the root, the period of unconstrained uptake t_c, and the fractional depletion f_d.

As far as soil root contact is concerned, two different situations can be distinguished. Firstly the root can lose contact with the soil water continuum due to its own shrinking or that of the soil in dry conditions (Sanders, 1971 in Tinker, 1976). On the other hand, as figure 6.8a shows, roots can grow in cracks, partially embedded in a soil aggregate. Both situations will be treated here, be it in a simplified way.

10.2 Nutrients

10.1.2 Limited soil/root contact due to shrinking

This situation can be schematized into that of figure 10.1. When only a part of the root surface, given by the contact-angle ψ_1 of figure 10.1, is in contact with soil the boundary condition for this part can be given by (using dimensionless variables as defined in chapter 9, table 9.1):

$$(10.1a)\quad r = 1\ ,\quad \left.\begin{array}{r} 0 < \psi < \psi_1 \\ 2\pi\text{-}\psi_1 < \psi < 2\pi \end{array}\right\} \frac{\partial c}{\partial r} = \frac{\pi \rho^2 \Theta \beta}{2\psi_1 \eta \phi} = -\frac{\pi \omega}{\psi_1}\ ,$$

where the flux is assumed to be uniform over the area of contact. The required flux is now a factor π/ψ_1 greater than in case of contact over the complete perimeter. Over the remaining part of the root surface the flux vanishes:

$$(10.1b)\quad r = 1\ ,\quad \psi_1 < \psi < 2\pi\text{-}\psi_1\ ,\quad \frac{\partial c}{\partial r} = 0\ .$$

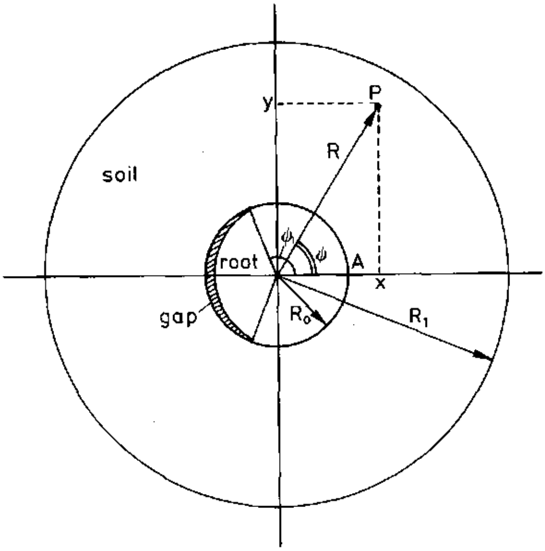


Fig. 10.1 Schematic representation of the position of a root in a soil cylinder. The location of the point P in the cylinder is given either by rectangular (x,y) or polar (R,ψ) coordinates. The degree of soil-root contact is given by the angle ψ_1.

The partial differential equation describing transport, the other boundary condition, and the initial condition retain the same form as presented earlier (i.e. equations (9.11), (9.12) and (9.14)), be it that here only diffusive transport will be considered, the flow of water, given by ν, being set at zero. As was shown in chapter 9, sooner or later a steady-rate situation will develop; then the solution for the concentration can be obtained (Appendix A10) as:

$$(10.2) \qquad c = 1 + \omega \left\{ \frac{2t}{\Theta\beta(\rho^2-1)} + \frac{r^2-\rho^2}{2(\rho^2-1)} + \frac{\rho^4 \ln\rho}{(\rho^2-1)^2} - \frac{\rho^2 \ln r}{\rho^2-1} - \frac{1+\rho^2}{4(\rho^2-1)} \right.$$

$$\left. + \frac{2}{\psi_1} \sum_{k=1}^{\infty} \frac{(r^{2k}+\rho^{2k})}{r^k(\rho^{2k}-1)} \; \frac{\sin k\psi_1 \; \cos k\psi}{k^2} \right] .$$

The only difference from the solution when the complete circumference partakes in uptake (9.15a and b) is in the last term of (10.2), the summation series.

The parameter values employed in the calculations are as usual, i.e. the root density is 1 cm/cm^3, uptake and supply parameters are those of potassium, given in table 9.1, where also the values of the other parameters can be found. With this choice of parameter values the maximum value of unconstrained uptake $T_{c,max}$ is 200 days.

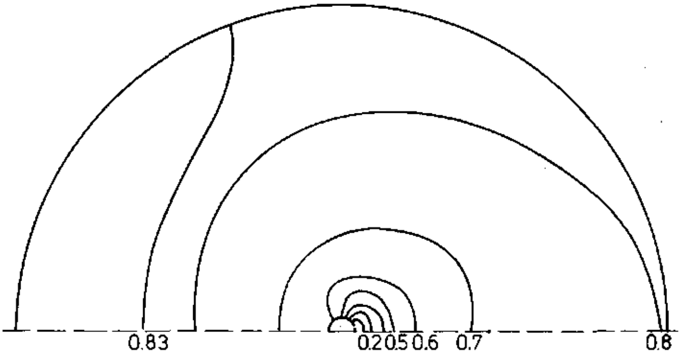


Fig. 10.2 Isoconcentration lines in the soil cylinder at $t=t_c$, root density of 1 cm/cm³, supply and uptake parameters of potassium as in table 9.2, adsorption constant K_a is 10 ml/cm³. Soil/root contact over 1/4 of the root perimeter.

The concentration distribution

In figure 10.2 isoconcentration curves are given for a root of which 1/4 of its surface is in contact with the soil. Radial symmetry does not exist anymore. As a consequence of the boundary conditions the isoconcentration curves are perpendicular to the boundary of the soil cylinder and to that part of the root perimeter not in contact with the soil.

Period of unconstrained uptake

The minimum concentration will always be found at point A in figure 10.1, i.e. at the point $r=1$, $\psi=0$, opposite the "gap". When the concentration at A becomes zero, uptake can no longer proceed at the required rate. Other parts of the root then have to increase uptake in order to satisfy the demand of the plant, which will lead to a stronger decrease of concentration, so very soon the concentration will become zero at any point of the root surface partaking in uptake. The period of unconstrained uptake t_c thus can be calculated by setting $c=0$, $r=1$, and $\psi=0$ in (10.2), and making t_c explicit:

$$(10.3)\qquad t_c = \frac{\rho^2-1}{\rho^2}\,\eta\phi - \Theta\beta G(\rho,0) - \frac{\Theta\beta(\rho^2-1)}{\psi_1}\sum_{k=1}^{\infty}\frac{\rho^{2k}+1}{\rho^{2k}-1}\,\frac{\sin k\psi_1}{k^2}\ .$$

In figure 10.3 t_c is shown as a function of ψ_1/π for different values of the root density. A higher degree of root-soil contact is more important the lower the root density. But also the extent to which the nutrient is bonded by the soil plays a role. When the nutrient is not adsorbed by the soil, even at low root densities small contact angles result in nearly the same t_c as more complete contact. As a reference also the curve for complete contact, but with the flux larger than under the standard conditions by a factor π/ψ_1, is given. This is of course much more unfavourable, as now the steady rate $\partial c/\partial t$ is also larger by a factor π/ψ_1.

In figure 10.4 the supply (measured in units of plant demand like in figure 9.8) to ensure an uptake period of 100 days is shown as a function of the degree of soil/root contact for a nutrient which is strongly adsorbed ($K_a =$

$$(10.6)\qquad c(r,\psi) = 1 + u_0 - \frac{t}{\phi\eta} - \frac{\rho_2{}^2\Theta\beta}{4\pi\eta\phi}\int_0^{2\pi} I(r,\lambda)d\lambda + $$

$$ - \frac{\Theta\beta r^2}{4\phi\eta} - \frac{\rho_2\Theta\beta\rho^2}{2\pi\phi\eta}\left[\sum_{k=0}^{n_R-1}\int_{p(n_R)}^{q(n_R)} I(r,\lambda)d\lambda\right] ,$$

where $p(n_R) = (2k\pi/n_R)-(\Delta\psi/2)$ and $q(n_R) = (2k\pi/n_R)-(\Delta\psi/2)$, n_R is the number of roots per aggregate, u_0 is an integration constant, $I(r,\lambda)$ is defined as

$$I(r,\lambda) = \ln\{\rho_2{}^2-2r\rho_2\cos(\lambda-\psi)+r^2\} ,$$

and λ is a dummy variable of integration.

The number of roots n_R is related to aggregate radius R_2, and root density L_{rv}:

$$(10.7)\qquad n_R = \pi R_2{}^2 L_{rv} = R_2{}^2/R_1{}^2 = \rho_2{}^2/\rho^2 ,$$

where R_2 is the aggregate radius, dimensionless $\rho_2=R_2/R_0$, and R_1 is $1/(\pi L_{rv})$ as before. Though u_0 can be evaluated by considering the average concentration (Appendix A10), this is not necessary here, as our interest is focused on t_c and fractional depletion, and on the relative position of the isoconcentration lines. For that reason the concentration is written with respect to the minimum concentration in the aggregate which will be met at point A (and similar points) in fig. 10.5:

$$(10.8)\qquad c(r,\psi) = c(\rho_2,0) + \frac{\Theta\beta}{4\phi\eta}(\rho_2{}^2-r^2) + \frac{\rho^2\Theta\beta}{\phi\eta}\ln\rho_2 - \frac{\rho_2{}^2\Theta\beta}{4\pi\eta\phi}\int_0^{2\pi} I(r,\lambda)d\lambda + $$

$$ - \frac{\rho_2\Theta\beta\rho^2}{2\pi\phi\eta}\left[\sum_{k=0}^{n_R-1}\int_{p(n_R)}^{q(n_R)}\{I(\rho_2,\lambda)-I(r,\lambda)\}d\lambda\right] .$$

Period of unconstrained uptake

With (10.8), the amount of nutrient left, when the concentration at point A has become zero, can be calculated by integration of the concentration over the soil cylinder. Then also the amount taken up, and by dividing this by the uptake rate, the period of unconstrained uptake can be computed.
In dimensionless units:

$$(10.9)\qquad t_c = \phi\eta - \frac{\phi\eta}{n_R\pi\rho_2{}^2}\int_0^{\rho_2} r\int_0^{2\pi} c\; d\psi\; dr .$$

Obviously the location of a root at the edge of an aggregate rather than in its centre will be disadvantageous for the availability of nutrients. The required flux through the root surface will be higher, and the average path length for diffusion longer. For instance with the parameter values usually employed (i.e. an uptake rate of 2 kg/(ha.day), a supply of 400 kg/ha, a root density of 1 cm/cm^3, and a diffusion coefficient of 0.1 cm^2/day), and an adsorption constant of 2 ml/cm^3, the period of unconstrained uptake is 195 days when roots are regularly distributed and in complete contact with soil, whereas it decreases to about 150 days when the root is situated at the perimeter of an aggregate with a diameter of 1.13 cm, corresponding to a root density of 1 cm/cm^3. When the aggregate diameter increases, but the root density remains the same, leading to more roots per aggregate, the situation improves, at least initially, the more so the higher the adsorption constant, as figure 10.6 shows. As a reference t_c values for complete contact and for contact of half the surface (situation 1) are given in figure 10.6 as well. The position at the edge of an aggregate is more unfavourable than the position within an aggregate (figure 10.1) with the same degree of contact. Figure 10.7 shows t_c as a function of the aggregate diameter and root density.

When the aggregate size increases t_c first also increases, and decreases later, as then the unfavourable effect of mutual competition of the roots exceeds the favourable effect of shorter diffusion distances. For a certain value of aggregate radius, the perimeter is completely covered with roots. Then:

$$(10.10) \quad n_R \pi R_0 = 2\pi R_2 = 2\pi R_1 \sqrt{n_R} \ ,$$

or :

$$(10.11) \quad n_R = 4\rho^2 \ .$$

When the root density is not very high, this can only occur, at least with the chosen value of the root radius, for very large aggregates. For instance, when the root density is 1 cm/cm^3, complete coverage would require an aggregate diameter of 50 cm, for a root density of 5 cm/cm^3 it would be 10 cm. Carslaw and Jaeger (1959, page 329 eq. (11)) present the solution for diffusion in a cylinder with constant flux at its outer boundary, i.e. the situation of complete coverage. From the steady-rate part of this solution, t_c can be calculated as :

$$(10.12) \quad t_c = \phi\eta - \frac{\Theta\beta\rho^4}{2} \ .$$

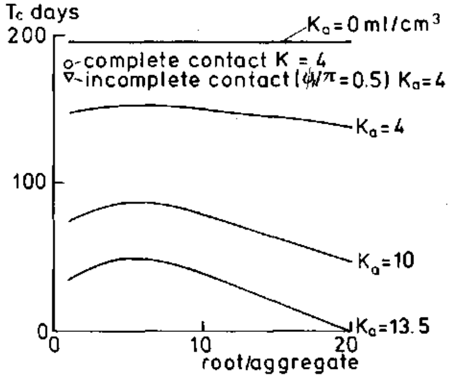


Fig. 10.6 Period of unconstrained uptake T_c as a function of the number of roots per aggregate, for a root density of 1 cm/cm^3, uptake and supply parameters of potassium (table 9.2)

10.3.2 Limited soil/root contact due to growth in cracks

We assumed that the steady-rate approximation would hold in this situation also. Accordingly the basis for our calculations is formed by equation (10.8), with matric flux potential w instead of concentration c.

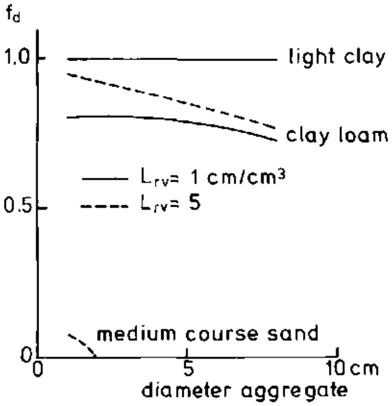


Fig. 10.10 Fractional depletion of water as a function of aggregate diameter and root density.

Period of unconstrained uptake and fractional depletion

The period of unconstrained uptake can be computed with an equation similar to (10.8):

$$(10.14)\quad t_c = \phi_w\eta - \frac{\phi_w\eta}{\pi\eta\rho_2{}^2}\int_0^{\rho_2}\int_0^{2\pi} r\Theta\, dr\, d\phi \ .$$

The fractional depletion is shown in figure 10.10, for three soils. In the case of light clay, the position of the roots at the edge of an aggregate hardly affects the availibility of water. In clay loam less water can be extracted, for L_{rv} = 1 cm/cm^3 about 65-75% compared to 85% in the "normal" situation (figure 10.9), but aggregate diameter plays a minor role. In the case of medium coarse sand finally, very much less water can be taken up (7% vs 55%) and only at small aggregate diameter, and high root density. However, the probability of finding aggregates of any appreciable size in such a soil seems very slight.

Appendix A10.

A10.1 Limited soil/root contact due to shrinking

The partial differential equation pertaining to transport by diffusion only reads in dimensionless variables:

$$(A10.1)\quad \Theta\beta\frac{\partial c}{\partial t} = \nabla^2 c \ .$$

When steady rate is attained the rate of decrease of concentration c is constant everywhere in the soil cylinder (cf.(9.16)):

$$\text{(A10.2)}\quad \frac{\partial c}{\partial t} = \frac{2\omega}{(\rho^2-1)\Theta\beta}\ .$$

The solution of (A10.2) is:

$$\text{(A10.3)}\quad c = \frac{2\omega t}{(\rho^2-1)\Theta\beta} + f(r,\psi),$$

where $f(r,\psi)$ denotes the dependence of c on the position in the soil cylinder, and r and ψ are cylindrical coordinates. When cylindrical coordinates are usedsubstitution of (A10.3) in (A10.1) yields:

$$\text{(A10.4)}\quad \frac{1}{r}\frac{\partial}{\partial r}\, r\, \frac{\partial f}{\partial r} + \frac{1}{r^2}\frac{\partial^2 f}{\partial \psi^2} = \frac{2\omega}{(\rho^2-1)}\ .$$

When a new variable v is defined as:

$$\text{(A10.5)}\quad v = \ln r,$$

(A10.4) transforms into:

$$\text{(A10.6)}\quad \frac{\partial^2 f}{\partial v^2} + \frac{\partial^2 f}{\partial \psi^2} = \frac{2\omega}{\rho^2-1}\exp(2v)\ .$$

The boundary conditions (10-1a) and (10-1b) read in terms of f,v and ψ:

$$\text{(A10.7a)}\quad v = 0\ ,\quad \left.\begin{array}{r} 0 < \psi < \psi_1 \\ 2\pi-\psi_1 < \psi < 2\pi \end{array}\right\} \frac{\partial f}{\partial v} = \frac{\pi\rho^2\Theta\beta}{2\psi_1\eta\phi} = -\frac{\pi\omega}{\psi_1}\ ,$$

$$\text{(A10.7b)}\quad v = 0\ ,\quad \psi_1 < \psi < 2\pi-\psi_1\ ,\quad \frac{\partial f}{\partial v} = 0\ .$$

the boundary condition at $r = \rho$ transforms into:

$$\text{(A10.8)}\quad v = \ln\rho\ ,\quad 0 < \psi < 2\pi\ ,\quad \frac{\partial f}{\partial v} = 0\ .$$

As the problem is symmetric with respect to the x-axis (see figure 10.1), it suffices to limit attention to the region $y>0$,or equivalently to $0<\psi<\pi$, which lead to two more boundary conditions:

$$\text{(A10.9a)}\quad \psi = 0\ ,\quad 1 < v < \ln\rho\ ,\quad \frac{\partial f}{\partial \psi} = 0,$$

Performing the integration indicated in (A10.17), and equating (A10.16) with (A10.17) yields eventually:

$$B = \frac{\omega}{\rho^2-1}\left\{\frac{\rho^4 \ln\rho}{\rho^2-1} - \frac{\rho^2}{2} - \frac{\rho^2+1}{4}\right\} + 1 \ .$$

Thus, the concentration is ultimately found as given in (10.2) in the main text.

A10.2 Limited soil/root contact due to growth in cracks

Consider an aggregate with radius R_2 cm, and root density L_{rv} cm/cm^3, then the number of roots per aggregate is:

$$\text{(A10.19)}\quad n_R = \rho_2{}^2/\rho^2 \ ,$$

where

$$\rho_2 = R_2/R_0 \ .$$

When the roots are taking up at constant rate, eventually a steady-rate situation will develop, in which by definition:

$$\frac{\partial C}{\partial T} = \text{constant} = Q \ .$$

Now:

$$\text{(A10.20)}\quad \frac{d}{dT}\, H \int_0^{2\pi} \int_0^{R_2} R\Theta\beta\, d\psi = -\pi R_1{}^2 A n_R \ .$$

Equation (A10.20) gives a balance, equating the totale decrease of the nutrient in the aggregate with the uptake rate of the n_R roots.
It follows then that:

$$\text{(A10.21)}\quad Q = -\frac{R_1{}^2 A n_R}{R_2{}^2 \Theta\beta H} \ ,$$

or dimensionless:

$$\text{(A10.22)}\quad \frac{\partial c}{\partial t} = \frac{R_0{}^2}{DC_i}\, Q = \frac{-1}{\eta\phi} \ .$$

Thus as before (cf. A10.3):

$$\text{(A10.23)}\quad c = 1 - \frac{t}{\phi\eta} + f(r,\psi) \ ,$$

and

(A10.24) $\nabla^2 f = \frac{-\Theta\beta}{\phi\eta}$.

If half of the perimeter of each of the roots is in contact with the aggregate, the flux over this part of the aggregates perimeter is given by:

$$\frac{\partial C}{\partial R} = \frac{-R_1{}^2 A}{R_0 H} ,$$

or

(A10.25a) $\frac{\partial c}{\partial r} = \frac{-\Theta\beta\rho^2}{\phi\eta} = \frac{\partial f}{\partial r}$.

When $\Delta\psi$ gives the angle corresponding to the arc of contact between the aggregate and the root (see fig. 10.5), and there are n_R equidistant roots, condition (A10.25a) holds for those parts of the aggregate perimeter for which:

$$0 < \psi < \Delta\psi/2 \quad , \quad 2\pi - \Delta\psi/2 < \psi < 2\pi \ , \text{ and}$$

$$\frac{2k\pi}{n_R} - \frac{\Delta\psi}{2} < \psi < \frac{2k\pi}{n_R} + \frac{\Delta\psi}{2} \quad \text{for } k=1,2,\ldots.,n_R-1.$$

Over the remaining parts the flux is zero:

(A10.25b) $\frac{\partial c}{\partial r} = 0$.

In order to solve the problem we make yet another transformation:

(A10.26) $u = f(r,\psi) + \frac{\Theta\beta r^2}{4\phi\eta}$.

This transforms (A10.24) into:

(A10.27) $\nabla^2 u = 0$,

and the boundary conditions into:

(A10.28a) $$\left.\begin{array}{l} r = \rho_2 \\ 0 < \psi < \Delta\psi/2 \\ \frac{2k\pi}{n_R} - \frac{\Delta\psi}{2} < \psi < \frac{2k\pi}{n_R} + \frac{\Delta\psi}{2} \\ 2\pi - \Delta\psi/2 < \psi < 2\pi \end{array}\right\} \frac{\partial u}{\partial r} = \frac{\Theta\beta}{\phi\eta}\left\{\frac{\rho_2}{2} - \rho^2\right\} ,$$

and

$$\text{(A10.28b)} \quad \left.\begin{array}{l} r = \rho_2 \\ \dfrac{2k\pi}{n_R} + \dfrac{\Delta\psi}{2} < \psi < \dfrac{(2k+2)\pi}{n_R} + \dfrac{\Delta\psi}{2} \end{array}\right\} \frac{\partial u}{\partial r} = \frac{\Theta\beta\rho_2}{2\phi\eta} \; .$$

The problem now is to find a solution to Laplace's equation (A10.27) within a circle, with prescribed flux (A10.28a and b) over its perimeter. The solution is given by an integral formula (Churchill et al., 1974, page 276-278):

$$u(r,\psi) = -\frac{\rho_2}{2\pi} \int_0^{2\pi} \ln(\rho_2{}^2 - 2\rho_2 r\cos(\lambda-\psi) + r^2)F(\lambda)d\lambda + u_0 \; ,$$

where u_0 is a constant, λ is a dummy variable of integration, and $F(\lambda)$ denotes the prescribed flux. In our case:

$$\text{(A10.29)} \quad u(r,\psi) = \frac{-\rho_2\Theta\beta}{2\pi\phi\eta}\left[\frac{\rho_2}{2} - \rho^2\right] \left\{ \int_0^{\Delta\psi/2} + \int_{2\pi-\Delta\psi/2}^{2\pi+\Delta\psi/2} + \sum_{k=1}^{n_R-1} \int_{p(n_R)}^{q(n_R)} \right\} +$$

$$- \frac{\rho_2}{2\pi} \frac{\Theta\beta\rho_2}{2\phi\eta} \sum_{k=0}^{n_R-1} \int_{q(n_R)}^{p(n_R)+2\pi/n_R} + u_0$$

$$= - \frac{\rho_2{}^2\Theta\beta}{4\pi\phi\eta} \int_0^{2\pi} + \frac{\rho_2\theta\beta\rho^2}{2\pi\eta\phi} \left\{ \sum_{k=0}^{n_R-1} \int_{p(n_R)}^{q(n_R)} \right\} + u_0 \; ,$$

where for convenience the integrands are omitted, and $p(n_R)$ and $q(n_R)$ stand for $(2k\pi/n_R - \Delta\psi/2)$ and $(2k\pi/n_R + \Delta\psi/2)$ respectively.

The concentration can be calculated with (A10.23) and (A10.26):

$$\text{(A10.30)} \quad c(r,\psi) = 1 - \frac{t}{\phi\eta} - \frac{\Theta\beta r^2}{4\phi\eta} + u(r,\psi) \; .$$

The concentration at point A (fig. 10.5), where $r = \rho_2$, and $\psi = 0$, is:

$$\text{(A10.31)} \quad c(\rho_2,0) = 1 - \frac{t}{\phi\eta} - \frac{\Theta\beta\rho_2{}^2}{4\phi\eta} + u(\rho_2,0) \; .$$

Now (Gradsteyn and Ryzhik, 1965, page 527, 4.224 7):

$$\int_0^{2\pi} \ln(2\rho_2{}^2 - 2\rho_2{}^2\cos\lambda)d\lambda = 4\pi\ln\rho_2 \; ,$$

so

$$u(\rho_2,0) = u_0 + \frac{\rho^2\Theta\beta}{\phi\eta}\ln\rho_2 - \frac{\rho_2\Theta\beta\rho^2}{2\pi\phi\eta}\sum_{k=0}^{n_R-1}\int_{p(n_R)}^{q(n_R)}\ln(2\rho_2{}^2-\rho_2 r\cos\lambda)d\lambda$$

Subtraction of (A10.31) from (A10.30) and substitution of the expressions for $u(r,\psi)$ and $u(\rho_2,0)$ finally yields the result given in (10.8).

11. EFFECTS OF VARIATION IN ROOT DISTRIBUTION PATTERN ON DEPLETION

11.1 Introduction

One of the main assumptions underlying the discussions in chapters 9 and 10 has been a regular distribution of roots in the soil. A regular distribution allows for an obvious allocation of the soil over the roots, each root being surrounded by a hexagon, or square, which can be approximated by a circle. The uptake by such a root system can be studied by considering a single root. In this chapter the uptake by a root system of arbitrarily distributed parallel roots will be discussed. Of course, in reality roots will not be parallel, though their main orientation will be vertical. With the assumption of parallelism the problem is reduced to two dimensions. In chapter 6 it has been mentioned that three-dimensional distances between roots will be smaller or at most equal to two-dimensional distances. The calculated values for the period of unconstrained uptake, presented here and in chapter 12, therefore give a lower boundary of the possibilities for uptake of a set of non-uniformly distributed non-parallel roots, just as those calculated for a regularly distributed parallel root system would give an upper boundary. Four aspects of the problem at hand will be discussed here: the allocation of the soil over the roots (discussed in section 11.2), the statistical distribution of the region associated with a root (section 11.3), the position of the root in the region (section 11.4), and the shape of the region (section 11.5). Separate and combined effects of these four aspects on the uptake potential of a root system will be treated here.

11.2 Allocation of the soil to the roots

As was mentioned, we will assume parallel roots. The distribution of the soil over the roots then is equivalent to the distribution of a planar area over a given number of points. Ideally the division should be such that it is consistent with the flow pattern generated in the soil by the uptake. With the assumed constant uptake, roots can be regarded as line sinks of equal strength, and existing theory from hydrology (e.g. Bear, 1972) can be used in principle to calculate the boundaries (equivalent to watersheds in hydrology) of the region associated with a root. This, however, is very complicated and time-consuming. Barley (1970) proposed to construct around each root a polygon, consisting of the locus of points in the soil nearer to that root than to any other. This construction - called the Dirichlet tesselation (Green and Sibson 1977) - is also applied in geography (Rhynsburger, 1973) and plant ecology (Mead, 1971) and seems as a first approximation an acceptable way to define the region of influence of each root. The polygons obtained are usually called Thiessen polygons. Green and Sibson (1977) designed a computer program, with which the tesselation can be computed efficiently.

A necessary condition for the Dirichlet tesselation to be concordant with diffusive flow, as generated by root uptake, is that on the boundary of the polygons the condition of vanishing flux is satisfied, which implies that isoconcentration lines, whenever they cross the boundaries, are perpendicular to these boundaries. This was examined in the following way. Carslaw and Jaeger (1959, page 261, eq(5)) present the solution of linear diffusive flow in an infinite region to a line sink of constant strength. In our notation it reads:

$$(11.1) \qquad C = C_i - \frac{A}{4\pi L_{rv} DH} E_1\left\{\frac{R^2}{4DT}\right\},$$

where $E_1(z)$ is defined as:

$$(11.2)\qquad E_1(z) = \int_z^{\infty} \frac{\exp(-u)}{u}\, du.$$

As the governing equation is linear the solution for N roots can be found by superposition:

$$(11.3)\qquad C = C_i - \frac{A}{4\pi L_{rv} DH} \sum_{n=1}^{N} E_1\left\{\frac{R_n^{\,2}}{4DT}\right\},$$

where R_n is the distance from the n-th root. With (11.3) isoconcentration lines can be constructed, which we did for a root system of randomly distributed roots. Also for this distribution the Dirichlet tesselation was constructed, and results are shown in figure 11.1. As can be seen, isoconcentration lines generally cross the boundaries of the polygons perpendicularly, except sometimes near sharp vertices. This has been done for several distributions with similar results, so that it can be concluded that a Dirichlet tesselation gives an acceptable subdivision of the soil around roots, and such a tesselation will be the basis of the discussions presented in this chapter.

The Dirichlet tesselation offers a possibility to characterize the distribution, and provides information concerning size of the area of the polygon and the location of the root in the polygon, so that their influence on uptake potential can be studied.

11.3 Distribution of areas of the Thiessen polygons

Figures 11.2a-d show the tesselation for root maps made in the field in arable soils. The standing crop was winter wheat, and prior to sowing four different types of tillage were performed. When the upper 30 cm are considered, as done here, the roots are found to be clustered rather than randomly distributed (see also section 6.4), as has been tested by various methods mentioned by Diggle (1983).

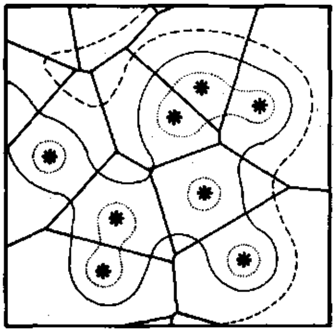


Fig.11.1 Isoconcentration lines and the Dirichlet tesselation, associated with 8 roots. These 8 roots form a subset of 100 randomly distributed roots, all taking up at equal rate.

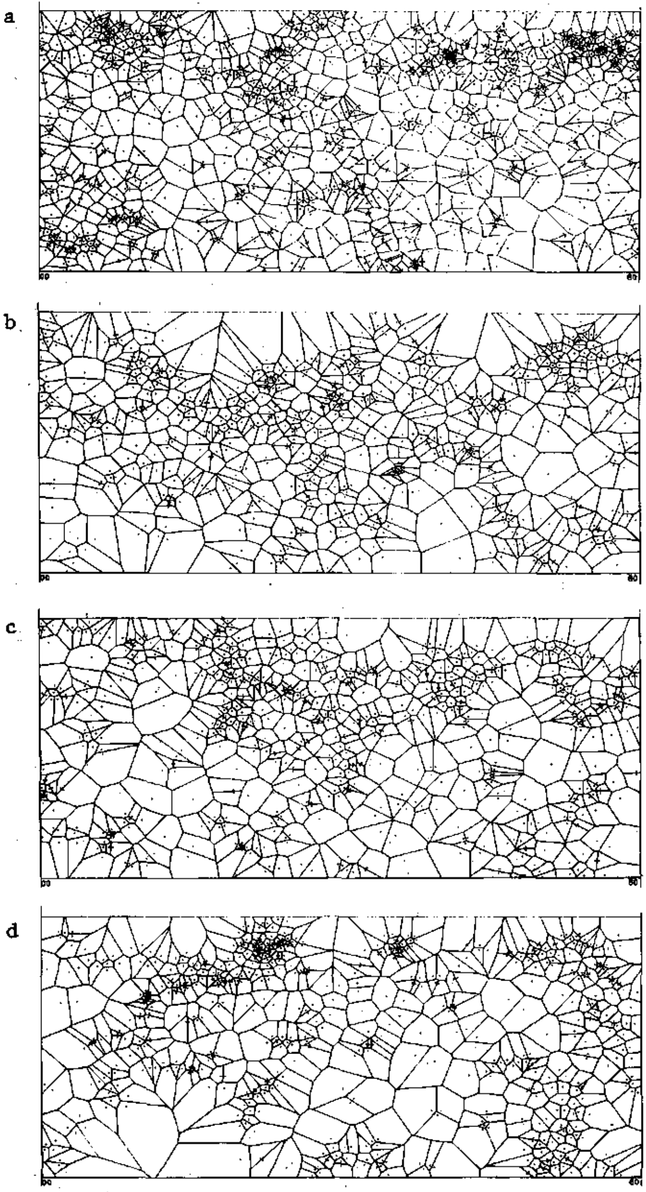


Fig. 11.2 Root maps and corresponding Dirichlet tesselation of the plow layer under wheat crop. The map shows an area with a length of 60 cm, and a width of 30 cm.

a. tillage by normal plow, b. tillage by paraplow, c. tillage by cultivator, d. tillage by rotadigger.

When the soil is homogeneous as far as soil fertility is concerned, an uneven distribution of roots - which may be due to the growing of plants in rows, variation in soil physical properties etc. - has an adverse effect on uptake. To illustrate the disadvantages of an uneven distribution, it was calculated how with the given distribution of areas, the total demand of the crop should be distributed optimally over the roots. As was shown in chapter 9, for a root taking up at a constant rate from a confined area, sooner or later a steady-rate situation will develop, where the rate of decrease of the concentration everywhere in that area will be constant. For a cylindrical geometry, with cylinder radius R_k, the time the root can take up at the required rate can be calculated with an equation like (9.19):

$$(11.4) \qquad t_{c,k} = \frac{\rho_k{}^2-1}{\rho_k{}^2}\,\eta\phi_k - \frac{\Theta\beta}{2}\left\{\frac{1-3\rho_k{}^2}{4} + \frac{\rho_k{}^4\ln\rho_k}{\rho_k{}^2-1}\right\}.$$

For a set of N cylinders, N such equations apply. Optimally all $t_{c,k}$ should be the same, so the individual uptake rate A_k (which is incorporated in the definition of ϕ_k, see table 9.1) of the k-th root, should be chosen so as to fulfill this requirement. The N+1 unknowns, viz., t_c and $\phi_1 \ldots \phi_N$ can be found from the N equations (11.4), and the requirement that total uptake should equal the demand of the crop:

$$(11.5) \qquad \sum_{k=1}^{N} R_k{}^2 A_k = A\sum_{k=1}^{N} R_k{}^2.$$

For the root maps shown, and for a root map constructed by generating random points with the computer, the optimal t_c as a function of the adsorption constant was calculated. The area of the root maps was adjusted so that the average root density was 1 cm/cm³. The Thiessen polygons were approximated by circles of the same area. Uptake and supply parameters chosen were those of potassium (table 9.2), which implies a maximum period of unconstrained uptake of 200 days. Results are displayed in figure 11.3, which shows the optimal T_c as a function of the adsorption constant. As a reference, also T_c for a completely regular distribution is shown. This distribution is the most favourable, but also the random distribution leads at higher adsorption to considerably better results than the measured distribution in the field. The root distribution corresponding to the paraplow treatment results in the lowest and that corresponding to the rotadigger treatment in the highest T_c.

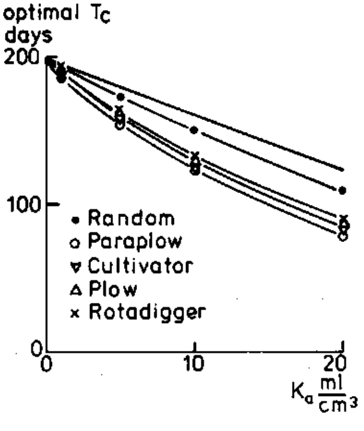


Fig. 11.3. Optimal period of unconstrained uptake as a function of the adsorption constant for a regular distribution (the straight line), a random distribution and the four distributions shown in figure 11.2. Parameters are those for supply and uptake of potassium (table 9.2), the average root density is 1 cm/cm³.

The Dirichlet tesselation was justified on the basis of a calculation involving equal uptake by all roots. The optimal depletion pattern just presented implies unequal uptake. An uptake rate larger than average would make the area allocated to the root in question larger, smaller uptake rates likewise result in smaller areas. A completely correct calculation should be iterative, where tesselation (with weights proportional to uptake rates associated with each root) and optimalization should alternate. The effect on optimal t_c calculated here is a minimum effect, i.e. the result of the iterative procedure would give a lower optimum t_c. Nevertheless the optimal t_c calculated as explained above can still be used to characterize the uptake possibilities of a given distribution and to compare its achievements with those of other distributions. It gives an upper bound of the real period of unconstrained uptake, in chapter 12 a lower bound of t_c will be calculated.

11.4 Eccentric position of the root

The treatment above assumed that the Thiessen polygons could be approximated by circles with the root located in the centre, precisely as Barley (1970) has done. But the position of the root in the region can be expected to have considerable effect on the possibilities for uptake.

In order to analyze the influence of the position of the root, we started from the steady-rate situation in a cylinder, which is an approximation to the polygon, with the root located outside the centre. The position of the root is given by its eccentricity, the distance of the root to the centre of the soil cylinder relative to the radius of the soil cylinder. In appendix A11 a solution for this problem is presented. With this solution the period of unconstrained uptake T_c can be calculated. Figure 11.4 shows T_c in days as a function of the eccentricity, for some values of the adsorption constant. For a mobile nutrient like nitrate, eccentricity of the root has little effect on the potential uptake period, while for a strongly adsorbed nutrient like phosphate, with an adsorption coefficient of 100 or more, the period of unconstrained uptake is seriously affected by the location of the root.

In figure 11.5 the cumulative frequency of the relative distance of the root to the barycentre of its Thiessen polygon of the root distributions of figure 11.2 is given. The relative distance is obtained by dividing the absolute distance between root and barycentre by the radius of a circle with the same area as the polygon. The curves are similar, with the exception of that of the paraplow treatment. About 50% of the roots has an eccentricity of more than 0.5, and about 10% (for the paraplow treatment 20%) an eccentricity of 0.9. The corresponding figures for randomly distributed roots are 30% and 1%, considerably more favourable. Taking into account the

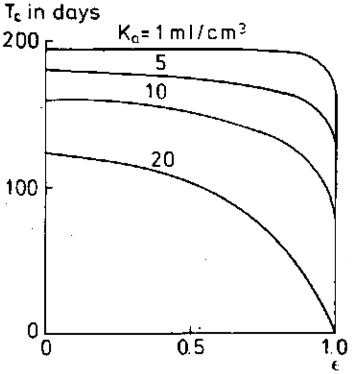


Fig. 11.4 Period of unconstrained uptake as a function of the eccentricity of the position of the root. The eccentricity is the distance of the root to the centre of the soil cylinder, relative to the radius of the soil cylinder. Parameters as in figure 11.3.

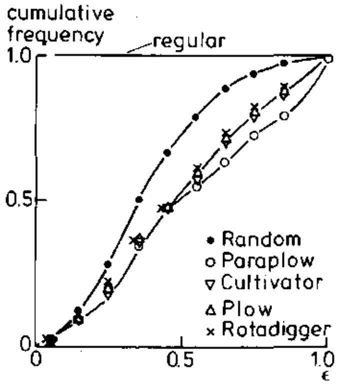


Fig. 11.5 Cumulative frequency of the eccentricity of the root for the distributions of figure 11.2.

position of the root in calculating the optimal T_c renders the effect of the treatments somewhat more pronounced (figure 11.6).

As mentioned in the introduction, Barley (1970) was the first to propose to use a Dirichlet tesselation to distribute a soil area over parallel, non-regularly distributed roots. He then approximated the polygons, generated by the tesselation, by circles of the same area, and calculated the uptake by the root system. According to his calculations effects of root distribution on uptake were small. Baldwin et al. (1972), using an electrical analogue, found much greater effects. This could partly be due to the neglect of the position of the root in Barley's approach as shown above.

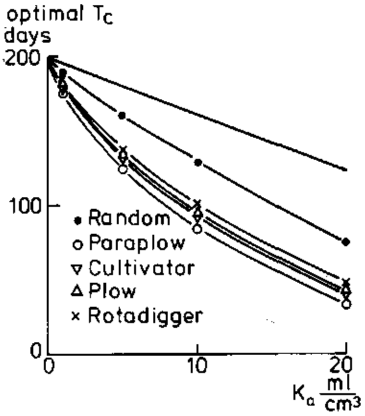


Fig. 11.6 As figure 11.3, but taking the position of the root into account.

11.5 Form of the polygon

Up to now it has been assumed that the polygons constructed could be replaced by equivalent circles. Shape itself will play an important role if it deviates significantly from more regular forms like a square or a hexagon. For the sake of simplicity it was decided to use a rectangle as the basic form for our calculations. Roots were assumed to be distributed such, that the Thiessen polygons were identical rectangles, with the roots located in their centre. It was calculated how t_c depends on χ, the ratio of the short side of the

(A11.9) $\xi=\xi_1$ $$\frac{\partial c}{\partial \xi} = \frac{-\omega}{a_1(\cosh\xi_1 - \cos\psi)} ,$$

where $$\xi_0 = \ln\left|\frac{a_1(x_1-\rho)+a_0+1}{a_1(x_1-\rho)+a_0-1}\right| ,$$

$$\xi_1 = \ln\left|\frac{a_1+a_0+1}{a_1+a_0-1}\right| .$$

Because of symmetry only half the circle is considered, leading to two more boundary conditions:

(A11.11) $\psi=0$ $\quad \frac{\partial c}{\partial \psi} = 0$,

(A11.12) $\psi=\pi$ $\quad \frac{\partial c}{\partial \psi} = 0$.

To solve (A11.7), we apply the Fourier cosine transformation with respect to ψ. This transformation of a function $G(\psi)$ is defined as (Churchill, 1972):

(A11.13) $g_n = \int_0^\pi G(\psi)\cos n\psi d\psi$, with $n=0,1,2,\ldots$

whereas the inverse transformation is given by:

(A11.14) $G(\psi) = \Sigma g_n \cos n\psi$,

where Σ denotes summation of n from 0 to ∞. Applying the transformation (A11.13) to (A11.7), with boundary conditions (A11.11) and (A11.12), yields:

(A11.15) $$-n\hat{c}_n + \frac{d^2\hat{c}_n}{d\xi^2} = \frac{-q}{a_1^2} \int_0^\pi \frac{\cos n\psi}{\cosh\xi - \cos\psi} d\psi .$$

The boundary condition (A11.9) becomes:

(A11.16) $\xi=\xi_1$ $$\frac{d\hat{c}_n}{d\xi} = \frac{-\omega}{a_1} \int_0^\pi \frac{\cos n\psi}{\cosh\xi_1 - \cos\psi} d\psi .$$

For n = 0, the integral on the Rhs of (A11.15) becomes (Gradsteyn & Ryhzik 1965, abbreviated G&R, page 383, 3.661 4):

$$\int_0^\pi \frac{1}{(\cosh\xi - \cos\psi)} d\psi = \frac{\pi\cosh\xi}{\sinh^3\xi} .$$

The solution of (A11.15) with (A11.8) is:

(A11.17) $$\hat{c}_0 = \frac{-\pi q}{2a_1^2}\left\{\coth\xi + a_1^2\rho^2\xi\right\} + B,$$

where use is made of the fact that $\sinh\xi_0 = 1/(a_1\rho)$, and B is an integration constant.
For n=1,2,3,..., the integral at the Rhs of (A11.15) is (G&R page 369, 3.616 7):

(A11.18) $$\int_0^\pi \frac{\cos n\psi d\psi}{(\cosh\xi-\cos\psi)}\, d\psi = \pi\exp(-n\xi)\left\{\frac{\cosh\xi}{\sinh^3(\xi)} + \frac{n}{\sinh^2(\xi)}\right\} = \pi P(\xi) .$$

The solution of (A11.15) now is (Spiegel, 1968, page 105, 18.8):

(A11.19) $$\hat{c}_n = A_1\exp(n\xi) + A_2\exp(-n\xi) +$$

$$\frac{-\pi q\exp(n\xi)}{2na_1^2}\int\exp(-n\xi)P(\xi)d\xi +$$

$$\frac{\pi q\exp(-n\xi)}{2na_1^2}\int\exp(n\xi)P(\xi)d\xi \quad .$$

The first integral on the Rhs of (A11.18) yields eventually

$$\int\exp(-n\xi)P(\xi)d\xi = -\frac{\exp(-2n\xi)}{2\sinh^2(\xi)} ,$$

and the second

$$\int\exp(n\xi)P(\xi)d\xi = \frac{-1}{2\sinh^2\xi} + \frac{n\exp(-\xi)}{\sinh\xi} .$$

After some algebraic manipulations:

(A11.20) $$\hat{c}_n = A_1\exp(n\xi) + A_2\exp(-n\xi) - \frac{\pi q}{a_1^2}\,\frac{\exp(-n\xi)}{\{\exp(2\xi)-1\}} .$$

The constants A_1 and A_2 can be found from the boundary conditions (A11.14) and (A11.15). The integral on the Rhs of (A11.15) can be found with G&R, page 366, 3.6132. (A11.16) becomes:

(A11.21) $$\xi=\xi_1 \qquad \frac{d\hat{c}_n}{d\xi} = \frac{\pi\omega}{a_1}\,\frac{\exp(-n\xi_1)}{\sinh\xi_1} .$$

A1 and A2 can be calculated by substitution of (A11.20) in (A11.21) and (A11.8):

(A11.22) $$A1 = \frac{-\exp(-2n\xi_1)}{n[1-\exp(-2n(\xi_1-\xi_0))]}\left\{\frac{na_1}{2}\,(\exp(-\xi_1)-\exp(-\xi_0))+\frac{a_1}{2}\,(1-\rho^2)\right\} ,$$

$$(A11.23)\quad A2 = \frac{-\exp(-2n(\xi_1-\xi_0))}{n[1-\exp(-2n(\xi_1-\xi_0))]}\left\{\frac{na_1}{2}\,(\exp(-\xi_1)-\exp(-\xi_0))+\frac{a_1}{2}\,(1-\rho^2)\right\} + \frac{\exp(-\xi_0)a_1\rho}{2} + \frac{a_1{}^2\rho^2}{2n}\ .$$

The concentration can now be given as (Churchill, 1972):

$$(A11.24)\quad c = \frac{\hat{c}_0}{\pi} + \frac{2}{\pi}\,\Sigma\,\hat{c}_n \cos n\psi\ .$$

The constant B which is contained in $\hat{c}_0$ (see (A11.17)) can be found in a similar way as was done in appendix A10 (see (A10.16) and (A10.17)). But for our purpose it is sufficient to write the concentration with respect to the minimum concentration which is found at point A in the z-plane or point A' (with coordinates ξ_1 and π) in the ζ-plane. The end of the period of unconstrained uptake can be found as the difference between the initial amount of available nutrient and the amount left, divided by the uptake rate.

12. INTEGRATION OVER A ROOT SYSTEM AND GROWING SEASON

12.1 Introduction

Many crop growth models in the literature largely neglect root growth and functioning, as far as uptake of nutrients is concerned. As long as these models are meant to be used on soils of high fertility, such as found in Western Europe, there is some justification for this neglect, as here even a sparse root system may suffice to take up a nutrient for a sufficiently long period at the required rate. At such a level of nutrient supply, when the main interest is in prediction of aboveground dry matter production, it does not seem worthwhile to speculate about root growth and uptake to a great detail. On the other hand on soils of lower fertility, or where root growth is hampered by whatever limitation, root growth and especially functioning can be the main limiting factor for overall crop growth.

The theory developed in the preceding three chapters can be used as a building stone for a model which accounts for uptake by a (growing) root system over a whole growing season. It has to be extended, however, as the theory presented thus far only deals with the period of unconstrained uptake t_c.

We will assume here that after the period of unconstrained uptake the root will behave as a zero sink, i.e. its uptake rate then equals the rate at which nutrients arrive at the root surface. In our description the plant thus either takes up at the required rate, as long as the soil can maintain a sufficiently high transport rate of the nutrient to the root, or it takes up at the same rate at which the nutrient arrives at its surface. This approach is similar to that suggested by Olsen and Kemper (1968).

We will formulate solutions to the diffusion problem in the period of constrained uptake (i.e.after time t_c), for a regularly distributed root system. Like in chapter 9, first an exact solution for the problem at hand will be derived, from which subsequently simpler equations will be derived.

12.2 Constrained uptake by regularly distributed roots

The mathematical formulation of the problem, the calculation of diffusion of nutrients to a zero sink, is very similar to that treated in section 9.3. Only one of the boundary conditions (at r=1), and the initial condition differ. The partial differential equation (with $\nu = 0$) and the other boundary condition retain the same form as given in (9.11) and (9.12), respectively. The boundary condition replacing (9.13) in the zero sink situation reads:

$$(12.1) \qquad r = 1,\ c = 0\ .$$

If at $t=t_c$ the series part of (9.15) can be neglected, then substitution of (9.19) in (9.15) gives:

$$(12.2) \qquad c = \frac{\omega}{\rho^2-1}\left\{\frac{r^2-1}{2} - \rho^2 \ln r\right\}.$$

Equation (12.2) then is the initial condition which applies here instead of (9.14). The exact solution of (9.11) with (12.1), (9.12) and (12.2) is derived in appendix A12. This solution is rather complicated but it can be approximated by a simple equation obtained by the following reasoning. Assume that the concentration in the zero-sink situation can be approximated by a steady-rate equation similar to (12.2):

$$c = \frac{\omega(t)}{\rho^2-1}\left\{\frac{r^2-1}{2} - \rho^2\ln(r)\right\}, \tag{12.3}$$

where $\omega(t)$ now is the time-dependent rate of uptake, to be calculated later, and t pertains to the time elapsed after t_c. The total available nutrient (in dimensionless units) at any one moment is:

$$s_{tot}(t) = 2\pi\eta\int_1^\rho r\Theta\beta c dr = -2\pi\eta\Theta\beta\omega(t)G(\rho,0), \tag{12.4}$$

where (12.3) has been substituted in (12.4), and $G(\rho,0)$ is defined in (9.19). From (12.4):

$$\frac{ds_{tot}}{dt} = -2\pi\eta\Theta\beta G(\rho,0)d\omega(t)/dt. \tag{12.5}$$

But also

$$\frac{ds_{tot}}{dt} = -2\pi\eta(\partial c/\partial r)_{r=1} = 2\pi\eta\omega(t). \tag{12.6}$$

Thus:

$$d\omega(t)/dt = \frac{-\omega(t)}{\Theta\beta G(\rho,0)}, \tag{12.7}$$

and hence,

$$\omega(t) = \omega(0)\exp\left\{\frac{-t}{\Theta\beta G(\rho,0)}\right\}, \tag{12.8}$$

where $\omega(0)$ equals ω appearing in (12.2) i.e. $\omega(0) = -\rho^2\Theta\beta/(2\eta\phi)$.
In figure 12.1 the uptake calculated with (12.8) is compared with that calculated from the exact solution presented in appendix A12 and it can be seen that the approximation is very good.

A consequence of the assumption that the concentration profile is given by the steady-rate equation (12.3) is, that uptake is proportional to the average concentration in the soil cylinder, for from (12.4):

$$\bar{c} = s_{tot}/(\pi\eta\Theta\beta(\rho^2-1)) = -2\omega(t)G(\rho,0)/((\rho^2-1)), \text{ or}$$

$$\omega(t) = \frac{-(\rho^2-1)\bar{c}}{2G(\rho,0)} \tag{12.9}$$

When the initial concentration is constant, say c_0, condition (12.2) must be replaced by:

$$t = 0,\ c = c_0. \tag{12.10}$$

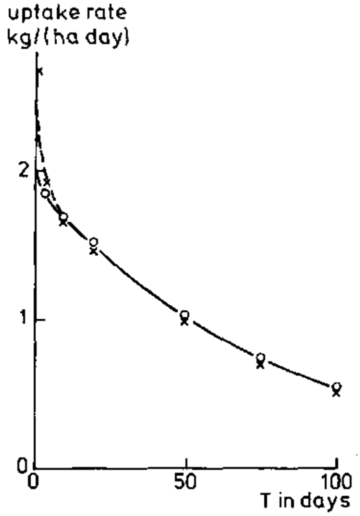


Fig. 12.1 Uptake rate of a root, which behaves as a zero-sink, as a function of time, for a root density of 1 cm/cm^3, and an adsorption constant of 20 ml/cm^3; uptake and supply parameters are those of potassium, i.e. available amount 400 kg/ha, required uptake rate 2 kg/(ha.day). The line gives the uptake rate when the initial concentration is that in the steady-rate situation, i.e. it is calculated with the exact solution. The open points were calculated with the approximation given in (12.8). The points indicated by a cross were calculated with the exact solution for constant initial concentration, corresponding to the average concentration in the steady-rate situation.

When due to a low supply, high adsorption or a high demand the concentration at the root surface drops to zero before a steady-rate profile has been developed, (12.10) also applies, as it can be assumed that the root behaves as a zero-sink from the beginning. For this case also an exact solution can be derived (appendix A12). From figure 12.1 it appears that very soon this solution can also be approximated by a sequence of steady-rate solutions. Uptake can be approximated similarly. This is also shown in figure 12.1.

Summarizing, the concentration of the nutrient in the soil around a root which behaves as a zero-sink can be satisfactorily approximated by a sequence of steady-rate solutions, irrespective of the initial condition. This finding can be used to calculate t_c and uptake after t_c for arbitrarily distributed roots, and uptake of growing root systems.

12.3 Constrained uptake by arbitrarily distributed roots

For an arbitrarily distributed root system consisting of parallel roots, the soil can be allocated to the roots by a Dirichlet tesselation as was shown in chapter 11. There, the "optimum demand distribution" was used to quantify possibilities for uptake by a heterogeneous root system. This optimum distribution implies that roots in a large Dirichlet cell take up nutrients at a higher rate (per unit root length) than roots in a small cell, in such a way that t_c is equal for all roots. Obviously this is an overestimate of the possibilities for roots to adjust their uptake rate: it assumes a difference in uptake rate between roots right from the start, when all roots are still exposed to the same concentration.

Here we will use an assumption which will give a lower bound to the period of unconstrained uptake. When part of a root system is no longer able to fulfill the uptake demand imposed upon it, due to e.g. local depletion, the remaining part of the root system enhances its uptake (De Jager, 1985). When all roots start to take up at an equal rate, after a certain time the root with the smallest area at its disposal can no longer take up at the required rate, the concentration at its surface having reached the limiting (zero) concentration. From this moment on, its uptake follows an exponential course, as was derived in section 12.2 (equation (12.8)). The other roots then have to increase their uptake rate so as to meet the total demand of the plant.

This assumption probably results in an underestimation of uptake potential, as it delays the shift in demand to the time that roots in the smallest cells are confronted with zero concentration. In fact an earlier response is possible on the basis of the different concentrations experienced by the roots in large and small cells. Real uptake potential can be expected to be somewhere between the uptake potential calculated in chapter 11 and that to be calculated with the suppositions explained above. The procedure of this last calculation is as follows.

Consider a population of roots under the unit soil area (section 6.3, fig. 6.3A), or a smaller area if representative. Let the roots be distributed over N classes, according to the area of soil allocated to them, and let there be a total of N_T roots, where the relative frequency of occurrence of roots in class i, is λ_i. The number of roots in class i is therefore:

$$(12.11)\quad n_i = \lambda_i N_T \ .$$

The area of soil allocated to a root is approximated by a circle of the same area. The total demand A_T to be satisfied by the roots is:

$$A_T = A\sum_{i=1}^{N} n_i \pi (R_1^{\,i})^2 \ ,$$

where $R_1^{\,i}$ is the equivalent radius of the soil cylinder in class i, and A is the demand of the plant per cm² of soil surface per day (see table 9.1). The equivalent radii are arranged in ascending order. Initially each root has to take up:

$$\frac{\pi A \Sigma n_i (R_1^{\,i})^2}{N_T} = \pi A \Sigma \lambda_i (R_1^{\,i})^2 \ .$$

Therefore initially the boundary condition at the surface of any and all roots reads:

$$(12.12)\quad 2\pi H D R_0 \frac{\partial C}{\partial R} = \pi A \Sigma \lambda_i (R_1^{\,i})^2 \ ,$$

or in dimensionless units:

$$(12.13)\quad \frac{\partial c}{\partial r} = \frac{\Theta\beta}{2\eta\phi} \Sigma \lambda_i \rho_i^{\,2} = -\omega_0 \ .$$

The roots of class 1 will be the first to exhaust the nutrient supply in the allocated area to such a degree that the concentration at their surface becomes zero. Let this occur at time $t=t_1$, where t_1 can be calculated with (9.19):

$$(12.14)\quad t_1 = \frac{-(\rho_1^{\,2}-1)\Theta\beta}{2\omega_0} - \Theta\beta G(\rho_1,0) = \frac{-(\rho_1^{\,2}-1)\Theta\beta}{2\omega_0} + F_1 \ ,$$

where for convenience the term $-\Theta\beta G(\rho_1,0)$ is denoted by F_1. From this time on roots of this class take up at a rate (see (12.8)):

$$(12.15)\quad 2\pi\eta\left\{\frac{\partial c}{\partial r}\right\}_{r=1} = -2\pi\eta\omega_0\ \exp\{(t-t_1)/F_1\}\ .$$

These roots form a fraction λ_1 of the total number of roots; accordingly, the fractional uptake of class 1 is now:

$$-2\pi\eta\lambda_1\omega_0\ \exp\{(t-t_1)/F_1\}\ .$$

The remaining fraction $1-\lambda_1$ then has to take up the total demand minus the uptake of the roots of class 1. The uptake condition for roots of class 2 to N thus reads:

$$(12.16)\quad \frac{\partial c}{\partial r} = \frac{-\omega_0}{1-\lambda_1} + \frac{\lambda_1}{1-\lambda_1}\,\omega_0\exp\{(t-t_1)/F_1\}\ .$$

Next, at $t=t_2$, when the concentration at the surface of roots of class 2 has dropped to zero, the concentration profile in the soil cylinders of class 2 can be assumed to be given by a steady-rate profile, as was shown in section 12.2:

$$(12.17)\quad c = \frac{\omega_1}{\rho_2{}^2-1}\left\{\frac{r^2-1}{2} - \rho_2{}^2\ln r\right\},$$

where ω_1 now is (see 12.16):

$$(12.18)\quad \omega_1 = \frac{-\omega_0}{1-\lambda_1} + \frac{\lambda_1}{1-\lambda_1}\,\omega_0\exp\{(t_2-t_1)/F_1\}\ .$$

The total amount of nutrient left in the soil around roots of this class at $t=t_2$ is:

$$(12.19)\quad s_2(t_2) = 2\pi\eta\int_1^{\rho_2} r\Theta\beta c\,dr = 2\pi\eta\omega_1F_2\ .$$

Thus the total amount of nutrient taken up by roots of this class is:

$$\pi\eta(\rho_2{}^2-1)\Theta\beta - 2\pi\eta\omega_1F_2\ ,$$

where the first term gives the total amount initially present. But the total amount taken up is also equal to:

$$2\pi\eta\left\{\int^{t_1}-\omega_0dt + \int_{t_1}^{t_2}\left[\frac{-\omega_0}{1-\lambda_1} + \frac{\lambda_1}{1-\lambda_1}\,\omega_0\exp(\frac{t-t_1}{F_1})\right]\right\}\ .$$

Equating the two expressions for total uptake in the period t_2 thus yields:

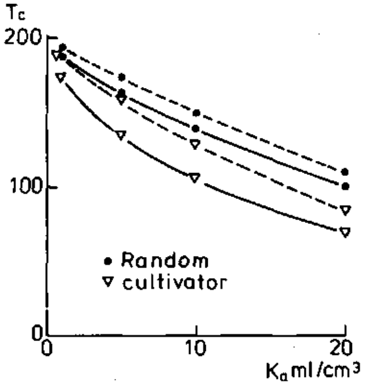


Fig. 12.2 The period of unconstrained uptake as a function of the adsorption constant for two of the root distributions treated in figure 11.3. The interrupted lines give the optimal T_c, the solid lines are calculated with (12.20). Parameters as in figure 12.1.

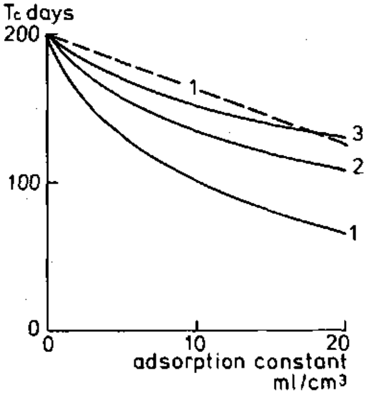


Fig. 12.3 The period of unconstrained uptake for uniform (interrupted line) and nonuniformly distributed roots as a function of the adsorption constant and the root density. The latter is given by the number at the curves. Other parameters as in figure 12.1.

$$-2\omega_0\left\{t_1 + \frac{t_2-t_1}{1-\lambda_1} - \frac{\lambda_1 F_1}{1-\lambda_1}\left[\exp\left(\frac{t_2-t_1}{F_1}\right) - 1\right]\right\} = (\rho_2{}^2-1)\Theta\beta-2\omega_1 F_2 . \tag{12.20}$$

From this equation t_2 can then be calculated. A similar reasoning and procedure can be followed to calculate $t_3, t_4, \ldots . t_N$. The last value, t_N, then gives the period of unconstrained uptake of the whole root system. In figure 12.2 this t_c is given as a function of the adsorption constant for the tillage treatments discussed in chapter 11. The calculations as in chapter 11 pertain to a root density of 1 cm/cm^3. The optimal t_c, as it was calculated in chapter 11, is higher than the t_c calculated in the way explained above, though the difference is not very great. Both can be used to estimate the unconstrained uptake period, the value of which is expected to lie between the value calculated in chapter 11 and that calculated here.

Figure 12.3 compares results for the root distribution of the paraplow treatment for a root density of 1, 2 and 3 cm/cm^3. The detrimental effect of non-uniform root distribution can be counteracted by higher root densities. With a root density of 3 cm/cm^3 and nonuniformly distributed roots, the period of unconstrained uptake is higher than that for a regular root system of root density 1 cm/cm^3 when the adsorption constant is 19 ml/cm^3 or higher.

As far as the uptake by the root system up to a certain time t after t_c is concerned, it can be calculated as the sum of the uptake rates of the N classes, integrated in time and weighted with the relative frequency of occurrence:

$$-2\pi\eta\sum_{i=1}^{N} \lambda_i\omega_{i-1}\int_0^{t'}\exp((t-t_i)/F_i)dt =$$

$$-2\pi\eta\Sigma\ \lambda_i F_i \omega_{i-1}\left\{\exp((t'-t_i)/F_i) - \exp(-t_i/F_i)\right\},$$

where $t' = t - t_c$.

12.4 Uptake by a growing root system

According to Brouwer's concept of functional equilibrium (see chapter 3), which has been verified many times, the shoot/root ratio shifts in favour of the roots when any of the substances (nutrients, water) to be taken up from the soil is in short supply. By increasing its root density, the plant can distribute its demand over more roots, leading to lower required uptake rates per root, while at the same time average transport distances in the soil are decreased. Moreover, by extending the root zone in a vertical direction new areas of soil can be explored, though for some important nutrients (potassium, and notably phosphate) the major part of the potentially available amount often is concentrated in the upper 20-30 cm.

With some of the equations derived in section 12.1 it is possible to estimate the advantages of a growing root system with respect to a non-growing root system with the same time-averaged root density. To do this we assume that the former grows in discontinuous steps with a constant fraction γ_1, only when the required uptake rate cannot be maintained, and that root growth is confined to one soil layer.

Consider N_1 roots belonging to a root system with root density $L_{rv,1}$ cm/cm^3, growing in a soil layer of H cm, which contains initially a potentially available amount of S_1 mg/cm^3. The dimensionless quantities $\phi,\rho,\eta,\Theta\beta$ are defined as usual (table 9.1). When $t=t_1$, where t_1 is given by:

$$(12.21)\quad t_1 = \frac{\rho_1^2-1}{\rho_1^2}\eta\phi_1 + F_1\ ,$$

the root system can no longer satisfy the demand of the plant. The average content of nutrient left in the soil now is

$$(12.22)\quad S_2 = \frac{N_1\pi R_1^2(HS_1-AT_1)}{N_1\pi R_1^2 H} = S_1 - AT_1/H\ ,$$

so that the dimensionless supply/demand parameter now becomes:

$$(12.23)\quad \phi_2 = \frac{DS_2}{AR_0} = \phi_1 - \frac{t_1}{\eta}\ .$$

If the root system is now extended by a fraction γ_1 in the same soil layer, the root density becomes:

$$(12.24)\quad L_{rv,2} = L_{rv,1}(1+\gamma_1)\ ,$$

or dimensionless:

$$(12.25)\quad \rho_2 = \rho_1/(1+\gamma_1)\ .$$

With this extended root system an extra uptake period Δt_2 can be realized:

$$(12.26)\quad \Delta t_2 = \frac{\rho_2{}^2-1}{\rho_2{}^2}\,\eta\phi_2 + F_2 \;.$$

The total period of unconstrained uptake of the extended root system is thus:

$$(12.27)\quad t_2 = t_1 + \Delta t_2 \;.$$

Then at time t_2 again the root system is increased with fraction γ_1 and a new $t_c = t_3$ is realized, and so on. It thus is assumed that the concentration in the soil immediately after the extension of the roots everywhere in the soil cylinder has the same value. This causes an initial overestimation of uptake possibilities, but as long as the timespan between two extensions is not too short (about 10 days when the adsorption constant is 20 ml/cm³, and even shorter for lower adsorption) no serious error is made (see figure 12.1). Some results are shown in figure 12.4, where T_c is given as a function of time-averaged root density for a growing and non-growing root system. An increasing root system can realize a considerably higher T_c than a stagnant system.

The results discussed above imply that the root area duration (RAD defined in chapter 1) is only of limited value as a parameter to characterize the uptake potential of a root system over a season, as a growing and stagnant root system of similar RAD give different possibilities for uptake.

The relative advantage of a growing root system over a stagnant root system with the same average root density involves two aspects:

i) the growing root system constantly explores new soil within the same layer; in our model this is represented by assigning the current average concentration to all roots for every time-step in which root growth occurs. From figure 12.1 it can be derived that this effect is relatively unimportant.

ii) the growing root system has a higher root density and consequently a lower demand per unit root in the critical situation near the final t_c. As discussed before (chapter 9) such a lower demand per unit root allows for more complete exhaustion of available nutrients.

Contrary to the view commonly expressed in the literature, which attributes the advantage of root growth mainly to a constant exploration of new soil, we may conclude that the second aspect probably is dominant, the more so as the buffering is higher, at least when root growth is confined to one layer.

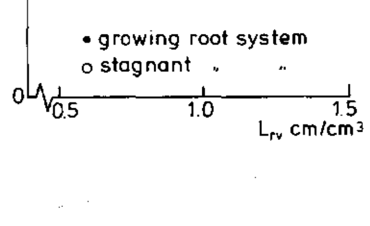


Fig. 12.4 The period of unconstrained uptake as a function of time-average root density, for a growing and a non-growing root system. In the case of the growing root system, the initial root density was 0.5 cm/cm³, the final root density is given by the number at the curve. Adsorption constant 20 ml/cm³. Other parameters as in figure 12.1.

12.5 Dynamic models of root growth and function during the growing season

The main purpose of all theory developed up to this chapter was to allow a functional interpretation of root densities as they occur in cropped fields. The quantification of the uptake potential as a function of root length density can be used as a part of dynamic models of root growth and function during the growing season. In such models, however, dynamic descriptions of root distribution in space and time are required as well. We may define four levels of increasing complexity in modelling root growth:

A. Models using measurements of root length density as a function of depth and data of root pattern on root maps as input, interpolating between experimental data.

B. Models using descriptive curve-fits to root growth in space and time under non-limiting soil conditions, e.g. negative exponential functions to describe root length density as a function of depth.

C. Models based on "functional equilibrium" concepts, relating overall root growth to the internal water- and nutrient status in the plant. Distribution of new roots over various soil depths may follow either approach A or B.

D. Models based on "functional equilibrium" concepts, relating overall root growth to the internal water- and nutrient status in the plant and relating root growth in any specific layer or zone of the soil to local conditions such as: mechanical resistance as a function of moisture content, aeration status as a function of internal and external oxygen supply, local nutrient concentrations, local pH and local aggregate structure to account for "root pattern".

Although models at level D may be the eventual synthesis of knowledge of soil-root systems aimed at, constructing such models now would seem premature. Such a model would contain a large number of interactions which first have to be tested separately. For the time being we will concentrate on models at level A, using measured root length densities as an input, to test whether or not the uptake potential of the root system as a whole can be adequately described by the processes taken into account in our models. In a later stage shoot-root interactions can be included (level C).

In the following two chapters two sets of experimental data will be used as a test of our description of uptake potential: data on N-uptake by maize in a humid tropical climate and data on P-uptake by grasses in a temperate climate.

Appendix A12. Zero-sink uptake condition

The differential equation to be solved is (cf (9.11) without production term and mass flow):

$$\text{(A12.1)}\quad \Theta\beta \frac{\partial c}{\partial t} = \frac{1}{r}\frac{\partial}{\partial r}\, r\, \frac{\partial c}{\partial r}\ ,$$

with boundary conditions:

$$\text{(A12.2)}\quad r = \rho\ ,\qquad \frac{\partial c}{\partial r} = 0\ ,$$

and

$$\text{(A12.3)}\quad r = 1\ ,\qquad c = 0\ .$$

As written in the main text, two initial conditions will be treated:

1. The initial condition is that corresponding to a steady-rate situation, i.e. a particular function of the distance from the root surface.
2. The initial concentration is uniform.

A12.1 Steady-rate initial condition

This initial condition can be concisely formulated as (see (12.2)):

$$\text{(A12.4)}\quad t = 0\ ,\qquad c = \frac{\omega}{\rho^2-1}\left[\frac{r^2-1}{2} - \rho^2 \ln r\right] .$$

For convenience a new dimensionless time τ and concentration u are defined as:
(A12.5) $\tau = t/\Theta\beta$,

$$\text{(A12.6)}\quad u = c - \frac{\omega}{\rho^2-1}\left[\frac{r^2-1}{2} - \rho^2 \ln r\right] .$$

With these new variables (A12.1) to (A12.4) become:

$$\text{(A12.7)}\quad \frac{\partial u}{\partial \tau} = \frac{1}{r}\frac{\partial}{\partial r}\, r\, \frac{\partial u}{\partial r} + \frac{2\omega}{\rho^2-1}\ ,$$

$$\text{(A12.8)}\quad r = \rho\ ,\quad \frac{\partial u}{\partial r} = 0\ ,$$

$$\text{(A12.9)}\quad r = 1\ ,\quad u = 0\ ,$$

$$\text{(A12.10)}\quad \tau = 0\ ,\quad u = 0\ .$$

Applying the Laplace transform with respect to τ, denoted as before as L{-}, with parameter s, transforms (A12.7) with (A12.10) into:

$$\text{(A12.11)}\quad s\hat{u} = \frac{1}{r}\frac{d}{dr}\, r\, \frac{d\hat{u}}{dr} + \frac{2\omega}{s(\rho^2-1)}\ ,$$

where $\hat{u} = L\{u\}$.
The solution of (A12.11) is:

$$\text{(A12.12)}\quad \hat{u} = \frac{2\omega}{s^2(\rho^2-1)} + A_1 I_0(r\sqrt{s}) + A_2 K_0(r\sqrt{s})\ ,$$

where I_0 and K_0 are modified Bessel functions of zero order, and A_1 and A_2 are integration constants. Substitution of (A12.12) into the boundary conditions (A12.8) and (A12.9), respectively, yields:

$$\text{(A12.13)}\quad A_1 I_1(\rho\sqrt{s}) - A_2 K_1(\rho\sqrt{s}) = 0\ ,$$

$$\text{(A12.14)}\quad A_1 I_0(\sqrt{s}) - A_2 K_0(\sqrt{s}) = \frac{-2\omega}{s^2(\rho^2-1)}\ ,$$

from which A_1 and A_2, respectively, can be found as:

$$\text{(A12.15)}\quad A_1 = \frac{-2\omega}{\rho^2-1}\,\frac{K_1(\rho\sqrt{s})}{s^2\{V_{1,0}(1,s)+W_{1,0}(1,s)\}} ,$$

$$\text{(A12.16)}\quad A_2 = \frac{-2\omega}{\rho^2-1}\,\frac{I_1(\rho\sqrt{s})}{s^2\{V_{1,0}(1,s)+W_{1,0}(1,s)\}} ,$$

where

$$V_{n,m}(r,s) = K_n(\rho\sqrt{s})I_m(r\sqrt{s}) ,$$

$$W_{n,m}(r,s) = I_n(\rho\sqrt{s})K_m(r\sqrt{s}) ,$$

so that $\hat{u}$ can be given as:

$$\text{(A12.17)}\quad \hat{u} = \frac{2\omega}{\rho^2-1}\left(\frac{1}{s^2} - \frac{V_{1,0}(r,s)+W_{1,0}(r,s)}{s^2\{V_{1,0}(1,s)+W_{1,0}(1,s)\}}\right) .$$

The inverse transform of the first term within brackets at the Rhs of (A12.17) is:

$$\text{(A12.18)}\quad L^{-1}\{\,1/s^2\,\} = \tau$$

The inverse transform of the second term can be found by applying the complex inversion integral, i.e. the inverse is the sum of the residues of $\hat{u}.\exp(s\tau)$ at the poles of $\hat{u}$. The residue for the double pole at s=0 is found by expansion of the Bessel functions around s=0 (De Willigen and Van Noordwijk, 1978), this yields:

$$\frac{a_1 + a_2 s + O(s^2)}{s^2\{b_1 + b_2 s + O(s^2)\}} ,$$

where

$$a_1 = b_1 = 1/\rho ,$$

$$a_2 = \frac{\rho^2+r^2}{4\rho} + \left(\ln\frac{\rho}{2} - 1\right)\frac{\rho}{2} ,$$

$$b_2 = \frac{\rho^2+1}{4\rho} + \frac{\rho}{2}(\ln\rho - 1) ,$$

and $O(s^2)$ represents terms in s of degree two and higher. The inverse transform corresponding to s=0, can now be derived as (Churchill, 1972):

$$\text{(A12.19)}\quad \lim_{s\to 0}\frac{d}{ds}\,\frac{e^{s\tau}\{a_1 + a_2 s + O(s^2)\}}{b_1 + b_2 s + O(s^2)} = \tau + \frac{a_2-b_2}{b_1} .$$

Next the residues have to be found for which

$$I_0(\sqrt{s})K_1(\rho\sqrt{s}) + K_0(\sqrt{s})I_1(\rho\sqrt{s}) = 0 .$$

By applying the relations between Bessel and modified Bessel functions (cf Abramowitz and Stegun, 1970 (abbreviated A&S), page 375: 9.6.3 and 9.6.4), this expression can be written as:

(A12.20) $Y_0(i\sqrt{s})J_1(i\rho\sqrt{s}) - Y_1(i\rho\sqrt{s})J_0(i\sqrt{s}) = 0$.

The zero's of (A12.20) are all real and simple (A&S page 374). Let the n-th root be denoted by α_n, (A12.20) thus being zero for

$$i\sqrt{s} = \alpha_n \quad \text{or} \quad s = -\alpha_n^2 \ .$$

For convenience we will use α in stead of α_n. The residue for these zero's can be found as (Churchill 1972, page 176 (10)):

(A12.21) $$\left[\frac{e^{s\tau}\{V_{1,0}(r,s)+W_{1,0}(r,s)\}}{s^2 \frac{d}{ds}\{V_{1,0}(1,s)+W_{1,0}(1,s)\}} \right]_{s=-\alpha^2}$$

The sum in the numerator of (A12.21), $V_{1,0}(r,s)+W_{1,0}(r,s)$, can be written, again using A&S 9.6.3 and 9.6.4, as:

$$\pi i/2\{\ Y_1(\rho\alpha)J_0(r\alpha) - J_1(\rho\alpha)Y_0(r\alpha)\ \} \ .$$

After performing the indicated differentiation and using:

$$I_0(\sqrt{s})K_1(\rho\sqrt{s}) + K_0(\sqrt{s})I_1(\rho\sqrt{s}) = 0 \ ,$$

the denominator reads:

$$\frac{\alpha^4}{2i\alpha}\left\{ V_{1,1}(1,i\alpha)-W_{1,1}(1,i\alpha) + \rho\{\ W_{0,0}(1,i\alpha)-V_{0,0}(1,i\alpha)\} \right\} .$$

The last expression can be written as:

$$\frac{\alpha^4}{2i\alpha}\,\frac{\pi}{2}\left\{ Y_1(\alpha)J_1(\rho\alpha) - J_1(\alpha)Y_1(\rho\alpha) + \rho\{J_0(\alpha)Y_0(\rho\alpha) - J_0(\rho\alpha)Y_0(\alpha)\} \right\} .$$

This can be further simplified . Because of (A12.20):

$$Y_1(\rho\alpha) = \frac{Y_0(\alpha)J_1(\rho\alpha)}{J_0(\alpha)} \ ,$$

and therefore:

(A12.22) $$Y_1(\alpha)J_1(\rho\alpha)-J_1(\alpha)Y_1(\rho\alpha) = \frac{J_1(\rho\alpha)}{J_0(\alpha)}\left\{ Y_1(\alpha)J_0(\alpha)-Y_0(\alpha)J_1(\alpha) \right\} .$$

The expression between brackets { } at the Rhs of (A12.22) equals (A&S page 360, 9.1.16) $-2/\pi\alpha$.
Thus:

$$Y_1(\alpha)J_1(\rho\alpha)-J_1(\alpha)Y_1(\rho\alpha) = \frac{-2\ J_1(\rho\alpha)}{\pi\alpha\ J_0(\alpha)} \ .$$

Again because of (A12.20):

$$Y_0(\alpha) = \frac{J_0(\alpha)Y_1(\rho\alpha)}{J_1(\rho\alpha)} ,$$

and so

$$J_0(\alpha)Y_0(\rho\alpha) - J_0(\rho\alpha)Y_0(\alpha) = \frac{2}{\pi\rho\alpha}\,\frac{J_0(\alpha)}{J_1(\rho\alpha)} .$$

The denominator of (A12.21) thus can be given as:

$$\frac{-i\alpha^4}{2\alpha}\left\{\frac{-J_1(\rho\alpha)}{\alpha J_0(\alpha)} + \frac{1}{\alpha}\,\frac{J_0(\alpha)}{J_1(\rho\alpha)}\right\} = \frac{-i\alpha^2}{2}\left\{\frac{J_0{}^2(\alpha) - J_1{}^2(\rho\alpha)}{J_0(\alpha)J_1(\rho\alpha)}\right\} .$$

Consequently (A12.21) eventually reads:

$$\text{(A12.23)}\quad \frac{-\pi\ J_0(\alpha)J_1(\rho\alpha)}{\alpha^2}\ F_0(r,\alpha)\exp(-\alpha^2\tau) ,$$

where $$F_0(r,\alpha) = \frac{Y_1(\rho\alpha)J_0(r\alpha) - Y_0(r\alpha)J_1(\rho\alpha)}{J_0{}^2(\alpha) - J_1{}^2(\rho\alpha)}$$

By combining (A12.18), (A12.19) and (A12.23) and substituting (A12.6), the solution for c is obtained:

$$\text{(A12.24)}\quad c = \frac{2\pi\omega}{\rho^2-1}\,\Sigma\,\frac{J_0(\alpha)J_1(\rho\alpha)}{\alpha^2}\,F_0(r,\alpha)\exp(-\alpha^2\tau) ,$$

where Σ stands for summation from 1 to ∞.
The uptake rate is the flow of nutrient over the root surface area $2\pi\eta$:

$$\text{(A12.25)}\quad 2\pi\eta\left\{\frac{\partial c}{\partial r}\right\}_{r=1} = \frac{-8\pi\eta\omega}{\rho^2-1}\,\Sigma\,\frac{J_1{}^2(\rho\alpha)\exp(-\alpha\tau)}{\alpha^2 J_0{}^2(\alpha)-J_1{}^2(\rho\alpha)} .$$

A12.2 Uniform initial concentration

Instead of (A12.4) now:

$$\text{(A12.26)}\quad t = 0 , \qquad c = c_0 ,$$

applies. Using τ instead of t and applying the Laplace transform with respect to τ, transforms (A12.1) into:

$$\text{(A12.27)}\quad s\hat{c} - c_0 = \frac{1}{r}\frac{d}{dr}\,r\,\frac{d\hat{c}}{dr} .$$

The solution of (A12.27) is:

$$(\mathrm{A12.28})\quad \hat{c} = \frac{c_0}{s} + A_1 I_0(r\sqrt{s}) + A_2 K_0(r\sqrt{s})\ .$$

The integration constants are found from the boundary conditions as :

$$(\mathrm{A12.29})\quad A_1 = -c_0\,\frac{K_1(\rho\sqrt{s})}{s(V_{1,0}(1,s)+W_{1,0}(1,s))}\ ,$$

$$(\mathrm{A12.30})\quad A_2 = \frac{A_1 I_1(\rho\sqrt{s})}{K_1(\rho\sqrt{s})}\ .$$

Substitution of (A12.29) and (A12.30) into (A12.28) yields:

$$(\mathrm{A12.31})\quad \hat{c} = c_0\left(\frac{1}{s} - \frac{V_{1,0}(r,s)+W_{1,0}(r,s)}{s(V_{1,0}(1,s)+W_{1,0}(1,s))}\right)\ .$$

The inverse transform of 1/s is 1. Finding the inverse transform of the second term of the RHS of (A12.31) proceeds similarly as finding the inverse transform of the second term of (A12.17), except that $s=0$, now is a simple pole. The inverse transform corresponding to this pole is found as:

$$a_1/b_1 = 1\ .$$

The solution for c can thus be given as:

$$(\mathrm{A12.32})\quad c = \pi c_0 \Sigma J_0(\alpha) J_1(\rho\alpha) F_0(r,\alpha)\exp(-\alpha^2\tau)\ .$$

The uptake rate is similar to (A12.25):

$$(\mathrm{A12.33})\qquad 2\pi\eta\left\{\frac{\partial c}{\partial r}\right\}_{r=1} = -4\pi\eta c_0 \Sigma\,\frac{J_1{}^2(\rho\alpha)\exp(-\alpha\tau)}{J_0{}^2(\alpha)-J_1{}^2(\rho\alpha)}\ .$$

13. ROOTING DEPTH, SYNCHRONIZATION, SYNLOCALIZATION AND N-USE EFFICIENCY UNDER HUMID TROPICAL CONDITIONS

13.1 Introduction

The traditional upland crop production systems in large parts of the humid tropics rely on a short cropping period followed by a long bush fallow period for soil fertility restoration. This production system is characterized by a low cropping intensity and low crop yields, with little or no input of chemicals. These systems have provided farmers for generations with stable production methods. However, during the last few decades the traditional system is undergoing rapid changes, mainly due to increasing population pressure. This has led to an increase in cropping intensity and a shortening or elimination of the much-needed fallow period, resulting in rapid decline in natural fertility and low yields.

For prolonged or continuous cropping the loss in soil fertility in the cropping phase must be compensated by the use of organic nutrient sources and/or fertilizers. Traditional farmers in many parts of the humid tropics cannot afford costly inputs. So-called modern techniques for fertilization are often characterized by low use efficiencies, except where these are based on knowledge of local soil, climate and crops. For fertilizer recommendations for tropical countries Janssen et al. (1986) use an apparent N-recovery of 20-35% depending on soil type. With such efficiencies, fertilizer use by small farmers is often not economically justifiable. Efforts have to be made therefore to reduce dependence on chemical fertilizers by maximizing recirculation of all available waste materials and by maximizing biological N-fixation and/or to increase efficiency of fertilizer use.

In this chapter we will use a model for nitrogen uptake by maize in the humid tropics to investigate the effects of rooting depth and method of fertilizer application (synchronization and synlocalization) in the N-use efficiency obtained. The model (based on De Willigen, 1985a) will first be tested with experimental data for a location in southeastern Nigeria (Onne). The model is subsequently used to examine the effects of different root distributions, different methods of application of fertilizer and different infiltration patterns of rain water into the profile.

Experiments with N-15 in the humid zone of southeastern Nigeria have indicated that recovery of nitrogen given in three split applications during the growing season of maize and localized near the crop is only about 40% (Van der Heide et al., 1985). Low uptake efficiencies under these conditions may be expected, as there is continuous leaching during the growing season. In this respect the situation resembles that in artificial substrates in modern horticulture discussed in chapter 5. In contrast to this horticultural situation, however, the amount of water leached is not under direct human control. Leaching can only be reduced by increasing surface runoff, with a risk of increased erosion; possibilities may exist, however, to influence the pattern of infiltration, e.g. by ridging or by covering parts of the soil surface with mulch material to create differential infiltration patterns, i.e. zones with increased and zones with reduced infiltration.

By a careful combination of techniques higher N-use efficiencies might thus be obtained. Measurements of root distribution have shown maize to be shallow-rooted in this soil, with soil acidity and/or soil compaction as a limiting factor for deeper rooting (Hairiah and Van Noordwijk, 1986). A description of the climate and of some physical and chemical properties of the soil in Onne is given by Lawson (undated) and Pleysier and Juo (1981), respectively. Van der Heide et al. (1985) provide data on maize growth and N-use efficiencies.

13.2 Model description

Geometry and time resolution

In the model a two-dimensional cross section of the unit soil area is considered for a maize plant in a row. This rectangular region of the soil is described by 55 compartments (five "columns" of 11 layers each). Within each compartment the concentration of nutrients and the root density is assumed to be uniform. The first four layers have a thickness of 5 cm, the next four of 10 cm, and the remaining three of 20 cm, the total length of the column thus comprising 120 cm. Because of the high infiltration rate in the growing season (see below) leading to high rates of vertical transport of nutrients, the lateral transfer of nutrients (which will, for the major part, be due to diffusion) plays only a minor role; it is neglected completely in the model. The five columns together cover half the row distance of 1 meter, each column having a width of 10 cm.

Timestep used in the calculations was 1 day.

Water and solute transport

For the growing period in which rainfall exceeds evapotranspiration, the soil profile is assumed to have a water content of 0.2 ml/cm^3 throughout, corresponding to the water content at field capacity (Arora and Juo, 1982).

The velocity of water flow is calculated as the difference between the average rainfall and evapotranspiration over the various months. Data on precipitation and evapotranspiration are shown in figure 13.1.

Transport of solutes through the soil in the model consists of two components, mass flow and dispersion flow. The former is calculated as the product of the flow rate of water and the local concentration, the latter is proportional to the concentration gradient; the proportionality constant is the product of the velocity of the water flow and a so-called dispersion length. The value of this last parameter was set at 3 cm after Frissel et al.(1970).

Contrary to soils in temperate regions, some soils in the tropics do adsorb anions like nitrate and chloride. Adsorption of nitrate was assumed to be appropriately described by a linear adsorption isotherm, the value of the adsorption constant being 0.3 ml/cm^3, as inferred from data of Pleysier and

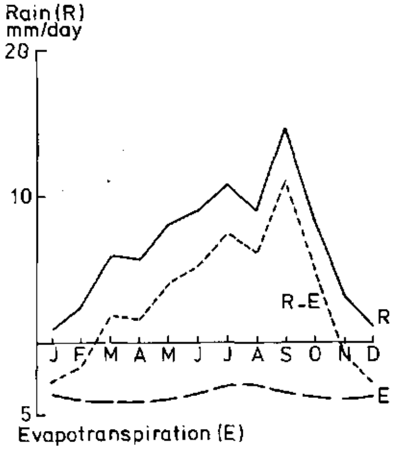


Fig. 13.1 Average precipitation (R), evapotranspiration (E) and net precipitation (R-E) at Onne, Nigeria (Lawson, undated).

Juo (1981).

As to the adsorption of ammonium, the results of Pleysier et al. (1979) were used as the starting point. They present data on the exchange equilibria of various cation pairs of the Onne soil, and calculated selectivity coefficients of Ca/K-, K/Na-, Al/K-, and Al/Ca-exchange. From these data the distribution coefficient, i.e. the ratio of adsorbed ammonium to ammonium in solution, was calculated as a function of bulk density of ammonium and the electrolyte concentration of the soil solution (De Willigen, 1985a). In the computer program a two-way table is introduced containing the results of these calculations.

The concentration of nitrate in the soil solution is calculated from the bulk density of nitrate divided by the sum of the adsorption constant and the water content. The concentration of ammonium in the soil solution is calculated similarly, using the distribution coefficient. The concentration of ammonium in the soil solution cannot exceed that of nitrate, as the latter is assumed to be the only anion present.

N-transformations

All microbial transformations of nitrogen (mineralization, immobilization and nitrification) are assumed to take place in the upper 20 cm of the profile only, which initially contains an amount of 20 kg NO_3 per ha.

Mineralization and immobilization of nitrogen is calculated according to the method of Van Faassen and Smilde (1985), a modification of the model of Jenkinson and Rayner (1977). Plant residues are assumed to consist of two fractions: rapidly decomposable plant material (DPM) and resistant plant material (RPM). Soil organic matter is subdivided into three fractions: microbial biomass, physically (POM) and chemically (COM) stabilized organic matter. All organic material is subject to biodegradation by the biomass. Products of biodegradation are CO_2, biomass, POM and COM. By assigning C/N ratios to each of the fractions of plant residues and soil organic matter, the rate of mineralisation can be calculated. The initial amounts of DPM and RPM were set at 340 and 1370 kg carbon per ha, respectively, corresponding to 3400 kg dry matter per ha of residues of a maize crop. Initial biomass was assumed to be 80 kg carbon per ha.

At the prevailing pH of the soil in Onne (4.5 or lower, Van der Heide et al., 1985) the nitrification rate may be lower than the release of ammonium during decomposition of organic matter. Hence, the assumption usually made in models of the nitrogen cycle in the soil that all mineral nitrogen occurs in the form of nitrate is not valid. Arora and Juo (1982) presented data on the production rate of nitrate in the Onne soil as a function of soil pH. The oxidation of ammonium to nitrite is considered the rate-limiting step in the nitrification process, which implies that no nitrite will accumulate. De Willigen (1985a) described the production rate of nitrate from the growth rate of the population of ammonium-oxidizing bacteria. In figure 13.2 the production of nitrate calculated this way, is shown together with the measured production. In our present model nitrification is described similarly; no variation in soil pH is considered.

Appreciable denitrification at low pH-values is improbable (Alexander, 1977), denitrification therefore is not incorporated in our model.

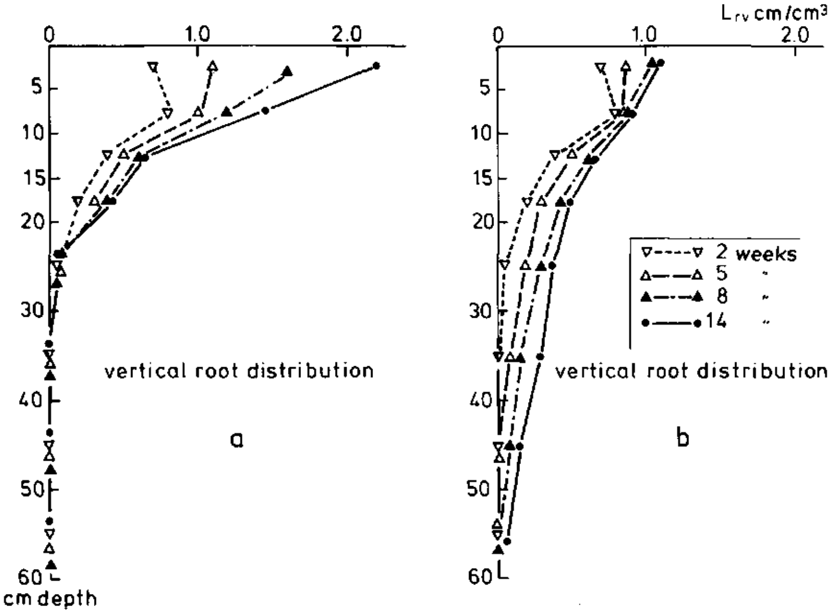


Fig. 13.4a Root length density of maize crop as function of time (weeks after sowing) and depth. Data of Hairiah and Van Noordwijk (1986). b Assumed root length density distribution of the hypothetical deep root system.

found midway between the plant rows, and highest in the immediate vicinity of the plant. From the cumulative frequency distribution curve the average value of root density for which the cumulative frequency is 20% or less can be read. This value then is attributed to soil column 5. The average value found for cumulative frequency between 20 and 40% is attributed to soil column 4, etc. The distribution in the first layer (with depth 5 cm) obtained in this way is given in table 13.1a. The horizontal distribution in deeper layers was derived from the average root densities given in figure 13.4. By assuming that in each layer the ratio between the numbers of roots in the soil columns was identical to that in the top layer, root length density in a soil column at a given depth can be calculated from the average root density at that depth. The roots were assumed to be distributed homogeneously in each layer of each column. The root system constructed in this way will be indicated by the term standard root system.

To study the influence of root distribution, in addistion to the standard system two others were constructed: a deeper root system (indicated by the term "deep" in the following) and a horizontally more extended root system ("wide"), both with total root length equal to the standard root system. The vertical distribution of the deep root system is given in figure 13.4b, its horizontal distribution is identical to that shown in table 13.1a. The assumed horizontal distribution of the wide root system is shown in table 13.1b, its vertical distribution is identical to that given in figure 13.4a. In the model a value for root density for each compartment on each day is found by linear interpolation between the values given in figures 13.4 a and b and table 13.1.

Table 13.1 Horizontal distribution of root length density in cm/cm^3 at 5 cm depth at four times.

a. Distribution based on observations by Hairiah and Van Noordwijk (1986), used for the standard and deep root system.

	Distance from plant row in cm (soil column)				
Time in weeks from sowing	5 (1)	15 (2)	25 (3)	35 (4)	45 (5)
2	3.0	0.4	0.1	0.0	0.0
5	3.5	1.5	0.4	0.1	0.0
8	4.0	2.6	1.2	0.2	0.0
14	4.5	3.7	2.2	0.5	0.1

b. Assumed distribution for the wide root system.

	Distance from plant row in cm (soil column)				
Time in weeks from sowing	5 (1)	15 (2)	25 (3)	35 (4)	45 (5)
2	3.0	0.4	0.1	0.0	0.0
5	3.5	1.0	0.6	0.3	0.1
8	3.5	2.0	1.2	0.8	0.5
14	3.5	2.5	2.2	1.8	1.0

N-uptake

Uptake of nitrogen by the root system is calculated in an iterative way. First (step 1) the nitrogen demand calculated with (13.3) is divided by the total root length to obtain the required uptake per unit root length. Multiplying this by the root length in a compartment yields the required uptake from each compartment. From (9.32) the average concentration (C_0) in the soil cylinder around a root can be calculated, when the concentration at the surface of the root is zero. This concentration is a function of uptake rate and root density. If the average concentration in a compartment exceeds C_0, uptake from this compartment equals the required uptake. If the average concentration is less than C_0, the roots in the cell behave as zero-sinks, their uptake can be calculated as explained in chapter 12. For convenience these compartments will be indicated as compartments of category 1. The total uptake by the root system is the sum of the uptake rates of the individual compartments. If the uptake in each compartment can proceed at the required rate, total uptake equals nitrogen demand and no iteration is required. If it is less than the nitrogen demand, it is investigated if uptake from those compartments where the concentration was sufficiently high to fulfil the original required uptake (for that particular compartment) can be raised to increase total uptake, possibly up to the nitrogen demand.

This is achieved in the following way. In step 2, first the difference between demand and total uptake, as calculated in step 1, is divided by the total root length of those compartments (category 2), that were able to satisfy the required uptake rate of step 1. This yields an additional uptake rate. The required uptake rate for compartments of category 2, in step 2, now equals the required uptake rate of step 1, augmented with the additional uptake rate. With this uptake rate for each compartment of category 2 C_0 is calculated, and it is examined if the compartment can satisfy the required uptake. If not, roots in such compartments behave as zero-sinks. If all compartments of category 2 can satisfy the required uptake of step 2, total uptake equals demand and the iteration ends. If none of the compartments of category 2 can satisfy the required uptake of step 2, i.e. in all compartments of category 1 and 2 zero-sink uptake occurs, the iteration also ends. If only a part of the compartments of category can satisfy the required uptake of step 2, iteration proceeds to step 3, etc.

This calculation procedure implies that roots in favourable conditions will compensate as much as possible for roots in less favourable conditions. It is thus assumed that information about the necessary behaviour, as far as uptake is concerned, is instantaneously available throughout the complete root system.

13.3 Model results

Dry matter yield and nitrogen recovery under standard conditions

Model calculations for a situation resembling actual experiments in Onne were compared with actual results of N-uptake of the crop as a function of N-fertilization. Maize was grown in a nitrogen fertilizer trial with five treatments: 0, 45, 90, 135 and 180 kg/ha. Row width was 100 cm, plant spacing in the row 25 cm. Nitrogen was given in the form of ammonium nitrate in three split applications and placed about 20 cm from the plant. In our model all fertilizer was added to column 2. As no information was available on the mineral nitrogen content of the soil at the start of the growing season, this parameter was used for roughly calibrating the N-uptake without fertilizer addition; an initial amount of 20 kg/ha seems reasonable.

Figure 13.5 shows the measured and calculated time course of dry matter production of maize, for a fertilization rate of 90 kg/ha (only in this treatment the time course of dry matter has been determined). A reasonable fit appears between calculations and measurements.

As shown in figure 13.6, the model also describes final nitrogen uptake as

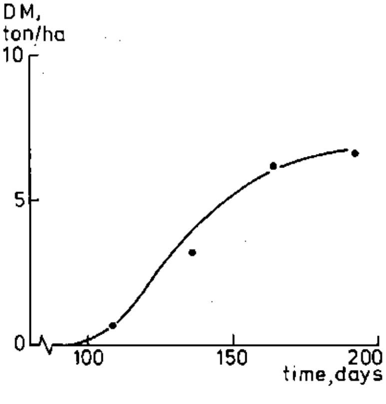


Fig. 13.5 Time course of dry matter production of a maize crop in Onne, as calculated (line) and as measured, at an N-fertilization rate of 90 kg/ha Data of Van der Heide (pers.comm.).

a function of application rate in the experiment reasonably well, although the efficiency of nitrogen use is overestimated. Uptake without fertilizer use is slightly underestimated (calculated 37 kg/ha, measured 41 kg/ha), uptake at intermediate fertilizer application levels is overestimated.

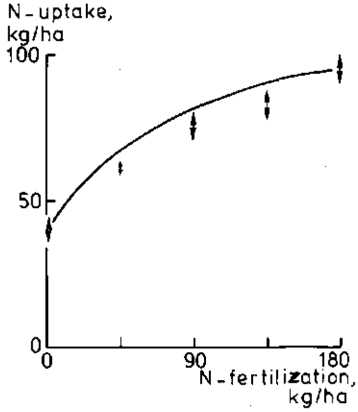


Fig 13.6 Nitrogen uptake as a function of N-fertilization in experiments at Onne; calculated uptake (line) is compared with experimental results, the vertical lines indicate the range of the experimental results. Data of Van der Heide (pers. comm.).

Different root distributions

The model was subsequently used for examination of the effects of root distribution, under various conditions of localization and time-distribution of the nitrogen fertilizer, and for a large range of fertilization rates. Table 13.2 summarizes the results. It gives the amount of fertilizer required to achieve a nitrogen uptake of 85 kg/ha, which corresponds to a yield of 6.5 ton/ha, or about 90% of the potential yield, and the recovery of the fertilizer nitrogen.

According to the calculations crops with a deep root system need much less nitrogen fertilizer to realize a yield of 6.5 ton/ha than crops with either of the other two root systems. The wide system usually gives somewhat better results than the standard root system, except where fertilizer is placed and given as a basal dressing.

Uptake without N-fertilization for both the wide and the deep root system

Table 13.2 Required application rate of fertilizer nitrogen in kg/ha to obtain a yield of 6.5 ton/ha of dry matter (90% of potential yield), and between brackets percentage recovery of fertilizer nitrogen. Br = broadcast, Lo = localization of fertilizer at 20 cm from plant, Sp = fertilizer applied in three splits, Nsp = application at start of growing season.

	Treatment					
	Uniform infiltration				Non-uniform infiltration	
root system	Br Nsp	Br Sp	Lo Nsp	Lo Sp	Br Sp	Lo Sp
standard	300(16%)	130(37%)	300(16%)	95(51%)	100(48%)	70(69%)
deep	90(41%)	75(49%)	90(41%)	50(74%)	75(49%)	45(82%)
wide	250(18%)	90(49%)	300(15%)	80(55%)	90(49%)	65(49%)

was higher than that for the standard root system, viz., 41, 48 and 37 kg/ha, respectively. The wide root system occupies the whole topsoil faster than the standard root system and thus utilizes mineralized nitrogen in column 5 more efficiently; the deep root system recovers nitrogen leached to deeper soil layers in the initial growth period.

Synchronization

Under climatic conditions with a continuous surplus of rain during the growing season, synchronization of fertilizer supply to crop demand is very important; comparison of columns 1 and 2 of table 13.2 shows that if all N would be given at sowing, much more nitrogen would have to be applied to obtain a yield of 6.5 ton/ha than when given in three equal splits. By further increasing the number of splits improvement of recovery would be possible; labour costs of such spoon-feeding would have to be evaluated as well as the benefits.

Synlocalization

The data in column 3 and 4 of table 13.2 show that localization of fertilizer is only beneficial if it is combined with split application. As might be expected, the N-recovery of the wide root system improves when N is broadcast. Localization closer to the plant, in the first instead of in the second column, would give higher recoveries, but osmotic problems of high salt concentrations close to the seed may limit applicability of such localization.

Nonuniform infiltration.

If it would be possible to reduce infiltration in the immediate vicinity of the plant, for instance by ridging and/or by covering the soil surface with a mulch of plastic or banana leaves, one would expect that higher recoveries could be obtained. To calculate the effect of a modified pattern of infiltration, the average infiltration rate was multiplied by a factor of 0.33, 0.67, 1.0, 1.33 and 1.67 respectively for the five soil columns. As the last two columns of table 13.2 show, a considerable improvement of recovery might be obtained in that way, especially when fertilizer is localized. Localization of the fertilizer within 10 cm of the plant in this case would give even better results.

13.4 Discussion

As shown in figure 13.6 the relation between amount of N applied and amount taken up by the crop is curvilinear. If different amounts of nitrogen are applied in a constant number of splits, such a curvilinear response may be expected for conditions of high precipitation surplus, because of the small buffering capacity which protects only a small absolute amount of N against leaching.

Calculated apparent N-recoveries as shown in table 13.2 give an indication of the possibilities for improving N-efficiency in practice. To obtain the same production the amount of N required varies between 45 and 300 kg/ha, with efficiencies of 82% and 16%. The experimental techniques chosen, split application and localization (column 4 in table 13.2), obviously are much better than broadcast application as a basal dressing (column 1). Further improvement may be possible, however.

Manipulation of rooting depth would have a positive effect on N-recovery with current fertilization techniques. Cultivar selection for tolerance to acid soil conditions may be the safest way to achieve a deeper root development as increasing soil pH by liming would lead to increased N-mobility and leaching (De Willigen, 1985a). Selection for a more rapid colonization of the whole top layer by a more laterally developed root system would only be effective for broadcast fertilizer application. If the N-source consists of decomposing (Leguminous) cover crops, localization would not be possible to the same extent as with fertilizer N.

Manipulating the pattern of infiltration, in combination with localization of the N-source near the plant, would be effective. Split application of fertilizer N might not be required if leaching through the zone near the plant could be reduced. Practical ways of achieving such a heterogeneous infiltration will now be investigated in new field experiments.

A question that arises when the infiltration pattern is considered, is how homogeneous the actual pattern in the field is. Heterogeneity of infiltration is much more important for solutes than for water itself; the whole topsoil will be water-saturated after heavy rainfall, regardless of the infiltration pattern. Infiltration in practice will be influenced by local relief, topsoil structure as well as by characteristics of the plant canopy. Stem-flow, especially for plants such as maize where the leaves may lead a water film onto the stem during rain, may concentrate water around the plant; drip-tips of leaves may have an umbrella-effect, increasing infiltration between the plants. Localization of fertilizer at 20 cm from the stem might prove to be the best practice in that situation. Remarkably little research appears to have been done on such aspects of crop canopies.

Mixed cropping of maize and cassava under the conditions of Onne leads to an increased efficiency of N-use, at least partly because of the deeper root development of cassava (Hairiah and Van Noordwijk, 1986). Cassava thus utilizes nitrogen leached from the root zone of maize. Alley-cropping (Kang et al., 1985) with certain tree species may have a similar positive effect on N-use efficiency of cropping systems, although selection of trees with suitable root systems requires local research on each soil type. Our analysis shows that detailed information on root length distribution of crops is important for understanding nitrogen use efficiencies in the highly dynamic situation in the humid tropics. In climates where during the growing season leaching losses are negligible, details of root length distribution are less important. There, even a sparse root system can take up all nitrogen (nitrate) at the required rate, at least when the soil is not too dry. This was shown in chapter 9, figure 9.3.

The model presented here belongs to models of category A, mentioned in section 12.5. Total root length and root length distribution are not generated by the model, but are introduced as forcing functions. Including a flexible shoot: root response in the model, where the plant may respond with accelerated root development to internal N-shortage, may be possible now that the evaluation of the effects of measured root distributions on N-uptake is possible with reasonable success (model categories C and D). The degree of the response of dry matter partitioning over root and shoot to changing N-supply for the maize cultivar used is not known as yet. By theoretically modifying such parameters, the scope for selection on root characteristics in plant breeding programmes could then be further specified. The three root distributions used in this chapter are possible with the same root length, i.e. with the same investment of carbohydrates. Costs and benefits of investing in greater or smaller production of carbohydrates for root growth can only be evaluated in models of category C or D.

14. P-UPTAKE BY GRASSES IN RELATION TO ROOT LENGTH DENSITY

14.1 Introduction

Theory presented in chapter 9 predicts that, in the range of root length densities, L_{rv}, of 1 - 5 cm/cm^3, more roots lead to improved capacity for P-uptake of the root system. This prediction is in agreement with field data (Kuchenbuch and Barber, 1987), as well as data from pot experiments (figure 4 in Van Noordwijk and De Willigen, 1986). In this chapter experimental results on P-uptake and root length density of grasses will be discussed to test this prediction more precisely, at model level A as discussed in section 12.5. This means that measured values of L_{rv} and root diameters will be used as well as soil chemical and soil physical measurements on the soils used in the experiment. Tests of model predictions will be based on total uptake by the root system or on uptake per unit root length. We are especially interested in the transition points where P-supply is just a limiting factor for dry matter production.

Two types of experiment will be discussed: experiments where variation in L_{rv} on the same soil is obtained by using different genotypes (section 14.3) and experiments where variation in L_{rv} in the P-containing zone is obtained by using different soil profiles (section 14.4). In section 14.2 the expected relation between root length density and P-uptake will be calculated for each soil. The zero-sink description of P-transport to the root, given in section 12.2, will be used for estimating constrained uptake capacity of roots in the initial growing period. The transition point to unconstrained uptake, where supply becomes equal to demand, can be predicted, if P-demand under the conditions used can be estimated.

14.2 Model calculations

P-supply by the soils used

For the model calculations we need parameters of the adsorption isotherms for the soils used in the experiments. Five soils (a - e) were used, mostly taken from old P-fertilization experiments; only for soil d, used in experiment 3, P-fertilization one month before the experiment was used to obtain variation in P-status. Adsorption isotherms of the soils were determined (figure A14.1A in the appendix); they appeared to be well described by a two-term Langmuir equation (eq. 7.1); parameters of the adsorption isotherms are listed in table A14.1. For a given P_w the corresponding bulk density of adsorbed phosphate (C_a) can with reasonable success be calculated from the adsorption isotherm (De Willigen and Van Noordwijk 1978, figure 15.3); in figure A14.1B, C_a calculated from P_w and the parameters of the adsorption isotherm is compared with measured C_a for the same soil sample. Agreement is again satisfactory: the desorption process during a P_w extraction can be reasonably well calculated from adsorption isotherms. The strongest deviation was found for the newly fertilized soil, d. In the experiments fixed water tables were maintained; volumetric water contents as a function of depth were determined in experiment 2 and 3. Figure 9.18 shows the importance of the water content of the soil for mobility of P.

Zero-sink P-uptake

The main emphasis in the preceding chapters was on calculations of unconstrained uptake in the linear phase of crop growth; in chapter 12 a zero-sink

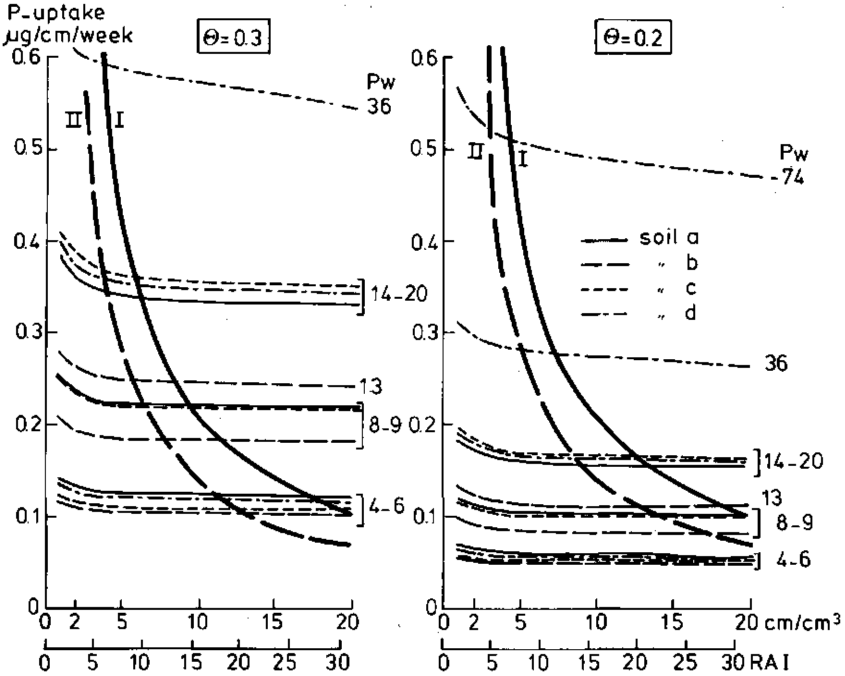


Fig. 14.1 Model calculations on zero-sink P-uptake per unit root length per week as a function of root length density L_{rv}, for soils a-d at P_w-values used in experiments 1-3, for two values of volumetric water content, Θ (v/v) (left and right); lines I and II indicate demand per unit root length for a P-containing zone of 20 cm, for a dry matter production of 200 kg/(ha day), and 3 and 2 $^0/_{00}$ P, respectively; mass flow equivalent to 1 cm/day; other parameters as in table 9.1.

description was added to cover the period of constrained uptake after T_c. The zero-sink solution can be used to predict P-uptake in the initial phase as well. For the high root length densities of grasses in top soil the limiting concentration for adequate P-uptake, C_{lim}, may be negligible (compare section 3.4). It has not been possible to derive approximations to the solution for nonlinear adsorption based on that for linear adsorption. So a solution was sought by numerical methods. A numerical simulation model, similar to that presented by De Willigen and Van Noordwijk (1978), was used for calculating possible P-uptake per unit root length per week for regularly distributed roots behaving as zero-sinks; mass flow was taken into account; the effects of water contents on P-diffusion were described as in section 9.3.3.

Figure 14.1 shows results for four soils at the various P-levels used in the experiments. Zero-sink P-uptake capacity per unit root length during a period of one week only shows a slight decrease with increasing L_{rv} values up to 20 cm/cm³. This decrease is mainly due to the reduction of mass flow per unit root length with increasing root length density L_{rv}. Lines I and II in figure 14.1 indicate P-uptake per unit root length required to satisfy crop demand at 3 and $2^0/_{00}$ P respectively for a dry matter production of 200 kg/(ha day), as a function of L_{rv} for a 20 cm P-containing zone. Figures 14.1A and B show that a difference in average water content of a soil layer (from Θ = 0.3 to Θ = 0.2) results in a considerable decrease of P-uptake capacity per unit

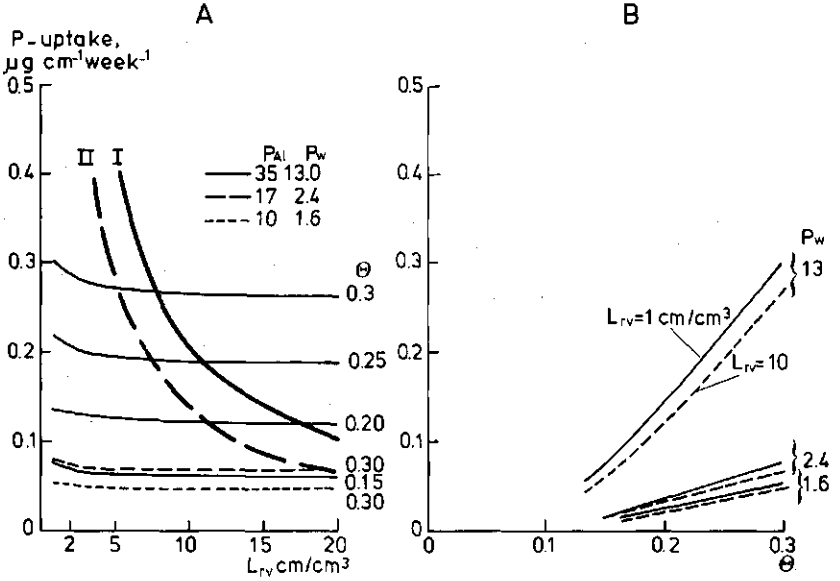


Fig. 14.2 Calculated P-uptake per unit root length as a function of water content, Θ, for soil e at three P-levels; **A.** shows calculated results as a function of L_{rv}, **B.** shows the same results as a function of Θ.

root length (a reduction by about 53%). As can be seen from figure 14.2B for soil e, for a given P_w possible P-uptake per unit root length is an approximately linear function of Θ in the range 0.15 - 0.3.

Various combinations of L_{rv}, P_w *and* Θ *can give the same* uptake rate. For example, figure 14.1A shows that on soils a, c and d the required P-uptake according to line I can be met by a root system with L_{rv} = 6 cm/cm³ for a P_w value of 14 to 20, by a root system with L_{rv} = 10 cm/cm³ for a P_w-value of 8 to 9 and by a root system with L_{rv} = 18 cm/cm³ for P_w-values of 4 to 6. If root length densities increase in time, we may predict how long it will take before grassland on a soil with a low P-status reaches P-uptake rate necessary for the potential rate of dry matter production (compare figure 1.7). In figure 14.1B we can see that in drier soil conditions the respective required L_{rv} values become 12, 20 and >>20 cm/cm³. In figure 14.2A we can see that on soil e at P_w = 13 uptake requirements can be met at L_{rv} = 8 cm/cm³ for Θ = 0.3, at L_{rv} = 11 cm/cm³ for Θ = 0.25, and at L_{rv} = 17 cm/cm³ for Θ = 0.2. Possible uptake at P_w = 13 and Θ = 0.15 is approximately equal to that at P_w = 2.4 or 1.6 at Θ = 0.3. We conclude that knowledge of Θ and L_{rv} is at least as important as knowledge of P_w to predict possible P-uptake.

14.3 Differences in root development of two clones of Lolium perenne: effects on P-uptake

14.3.1 Introduction

Two clones of Lolium perenne were chosen for research, which show a considerable difference in root weight and shoot/root ratio on a dry weight basis, with approximately equal dry matter production when well-nourished (Baan Hofman and Ennik, 1980). Differences in root dry weight increased with successive cuts of grass. The clones, 39 and 40, differ in competitive ability against other Lolium clones, but in monoculture grass yields are slightly higher for clone 40 with lower root weight and lower competitive ability. Baan Hofman and Ennik (1982) showed clone 39 to win belowground competition with couchgrass (Elytrigia) while clone 40 and other clones with a lower root density are replaced by couchgrass. In pot-experiments in monoculture where N-supply is varied, differences in root development between the two clones do not lead to differences in shoot production at suboptimal N-supply (Ennik and Baan Hofman, 1983).

We decided to compare the P-response of these two clones in a series of pot experiments, to obtain data on combinations of root length density and P-status of the soil which just allow a sufficient P-uptake. Dry matter production and P-content of the two clones were measured under a wide range of P-supply conditions to test wether any differences in P-demand might influence the results. P uptake per unit root length for the two clones was compared as well, to check for possible effects through influences on rhizosphere pH or other complicating processes. Only if the clones do not differ in these respects, differences in root development can be held directly responsible for differences in required P-supply.

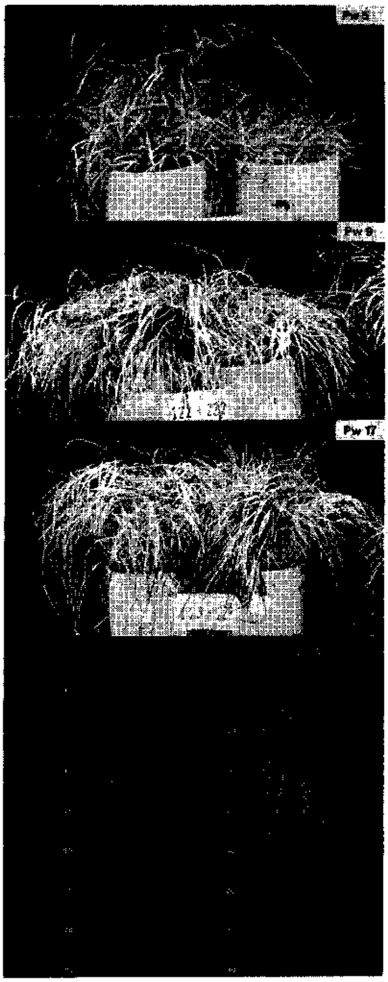


Fig. 14.3 Shoot growth of clone 39 (left) and clone 40 (right) on soils with three P-levels (experiment 2); metal rings which reduced the amount of grass overhanging the edge of the pot, have been removed for taking the photograph; the root systems shown were obtained at a P_w value of 9.

In the experiments we tried to maintain environmental conditions as close to those assumed in our model as possible: water supply was non-limiting by maintaining a fixed water table at about 50 cm depth, an extended linear growth phase was obtained by placing all tubes with grass in a dense spacing to simulate a close crop canopy and by gradually lifting a metal ring around each pot to prevent grass leaves from shading neighbouring pots. Three experiments will be discussed here; details of research methods and results are described in appendix A14.

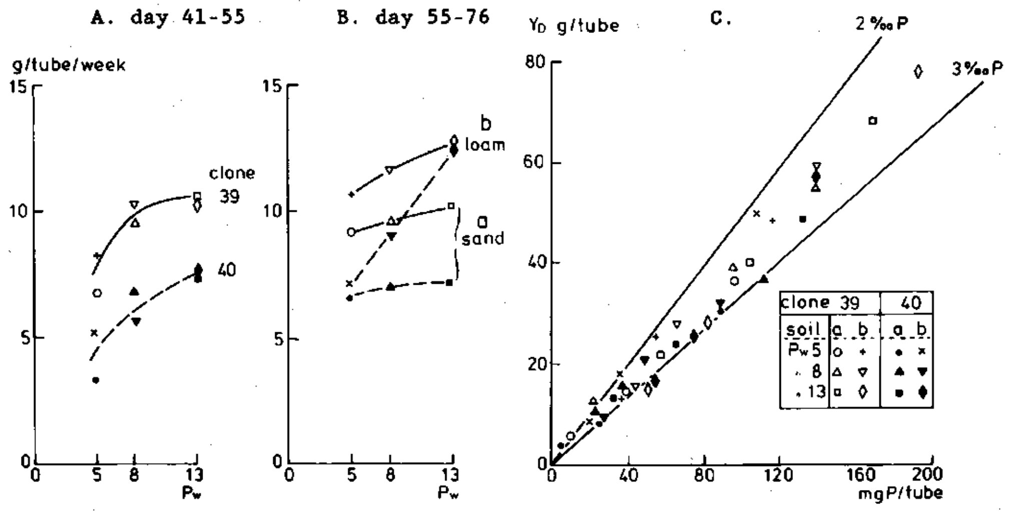
14.3.2 Growth pattern of the clones

As shown in figure 14.3, the expectation that clone 39 with the higher root length density required a lower P_w-value of the soil to reach its maximum growth rate than clone 40, with less roots, was confirmed. On more detailed analysis, however, other differences than root development may have influenced the results: the two clones differ in morphology and growth pattern above- as well as belowground. Clone 39 developed faster from planted single shoots and produced longer leaves and side-shoots but formed a less dense turf of grass. Final number of shoots per plant was lower than for clone 40.

Initial root development was faster in clone 39 as well. The difference in rooting depth shown in figure 14.3 remained evident throughout the experiments. Clone 40 made more fine branch roots in the topsoil than clone 39. The maximal difference in L_{rv} was a factor 1.5. Clone 40 had a slightly higher specific root length (m/g) and a slightly smaller root diameter; relative differences between the clones in root dry weight were larger than differences in root length.

14.3.3 Response to P-levels on two soils (experiment 1)

Figure 14.4 shows results for dry matter production in experiment 1 where the two clones were grown on two soils. From the three sampling dates growth


A. day 41-55

B. day 55-76

C.

Fig. 14.4A. and B. Response in dry matter production to P_w value of the two clones on two soil types in two growing periods; C. Relation between P-uptake and dry matter production (experiment 1).

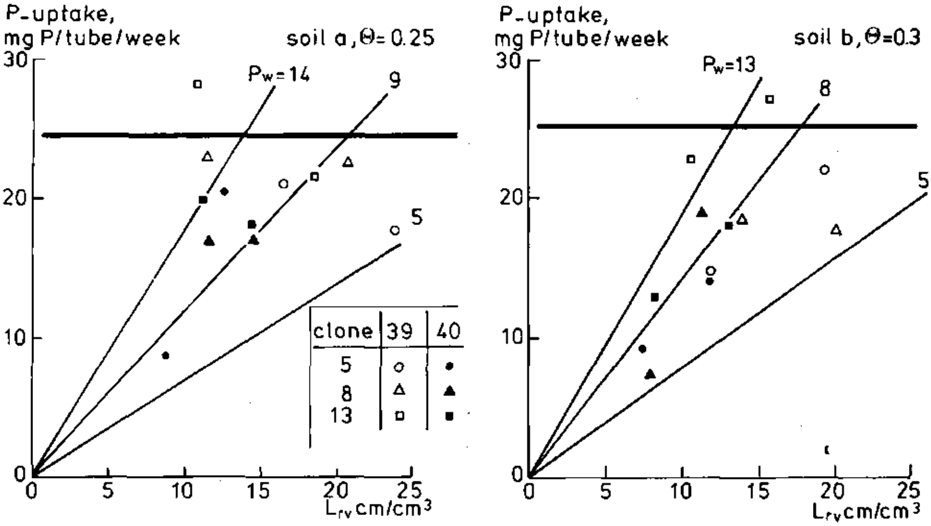


Fig. 14.5 Relation between P-uptake and root length density L_{rv} in experiment 1 on soil a and b (left and right); lines through the origin indicate model calculations for zero-sink uptake (figure 14.1); the horizontal line indicates P-requirement as evident in this experiment.

rates can be calculated for two periods. In the first period of two weeks (figure 14.4A), both clones showed a comparable response to P_w of the soil, but maximum growth rate of clone 39 was considerably higher than that of clone 40; growth on soil b (loam) was only slightly better than on soil a (sand). In the second period (three weeks), production levels on the loam were higher than on the sand; P-response was more pronounced on the loam as well, especially for clone 40. Dry matter production at a P_w value of 13 for clone 40 was approximately equal to that for clone 39; at a P_w value of 9 the clones differed clearly on the loam soil.

The indicated production for grass + stubble of 12 g/week per tube corresponds with 280 kg/(ha day), if allowance is made for grass 2 cm overhanging the edge of the pot (estimated canopy diameter 28 cm). As stubble weights were only 10% of this value, growth rates in our experiment were high when compared with calculated potential dry matter production rates for grassland in the Netherlands. As figure 14.4C shows, the two clones did not differ in P-content; the majority of measurements was between 2 and 3 $^0/_{00}$ P. Maximum dry matter production was found at a P-content of 2.5$^0/_{00}$.

In figure 14.5 measured P-uptake per tube in the two growing periods is shown as well as the average L_{rv} in that period, for both soils. Calculated uptake capacity by a zero-sink is also shown; the almost constant P-uptake per unit root in figure 14.1 is now reflected as almost straight lines through the origin. As no detailed information on water content was available for this experiment, comparison between observations and calculations is difficult.

Although measured points are in the same range as calculated values, measured P-uptake per unit root length is higher than the predicted value, especially on the poorest soils. The difference in L_{rv} between the two clones can be seen, as open symbols (clone 39) are found in the upper right corner of the graphs. Higher L_{rv}-values for clone 39 compared with clone 40 correspond with higher P-uptake per tube, at approximately constant P-uptake per unit root length. The solid line in figure 14.5 indicates P-requirement for a dry matter production of 10 g/week per tube and 2.5$^0/_{00}$ P. Clone 39, with its higher L_{rv} approaches this line at lower P_w than clone 40.

14.3.4 P-uptake per unit root length and mycorrhiza development (experiment 2)

In a subsequent experiment on a different soil with similar P_w-values, time course of P-uptake was followed in three in stead of two growing periods and attention was given to water content of the soil. Mycorrhiza development was measured as well, as it may influence P-uptake per unit root length.

As figure 14.6a shows, initial growth again differed between clones and between soil P-levels in experiment 2. At higher P_w values dry matter production was approximately linear in time. At low P_w, initial growth was slow, but later on the rate of dry matter production approached that at higher P_w. Figure 14.6c shows the P-content of the grass: at low P_w it increased to a value of 2$^0/_{00}$ between the second and third harvest, at P_w = 17 the P-content of the grass was around 3$^0/_{00}$ throughout. The two clones showed the same P-contents at all P_w-values.

The increase in plant P-levels at low P_w occurred during a period of stagnating dry matter production and increase in root length density in the P-containing zone. In the same period mycorrhizal associations developed. In figure 14.7 measured P-uptake per unit root length is shown; in the same figure calculated uptake by a zero-sink of the same radius as that of the roots is shown for two water contents: Θ = 0.25 and Θ = 0.2, the average water content in the P-containing zone at the start and end of the experiment, respectively. In the first period P-uptake per unit root length was obviously influenced by the P_w-value of the soil. At a P_w-value of 17, P-uptake per unit root length decreased substantially with time (figure 14.7A), from a value close to the uptake potential for a zero-sink to a much lower value. This decrease probably reflects regulation of P-uptake: P-uptake per unit root length was lower than possible, given the external supply. At a P_w-value of 5,

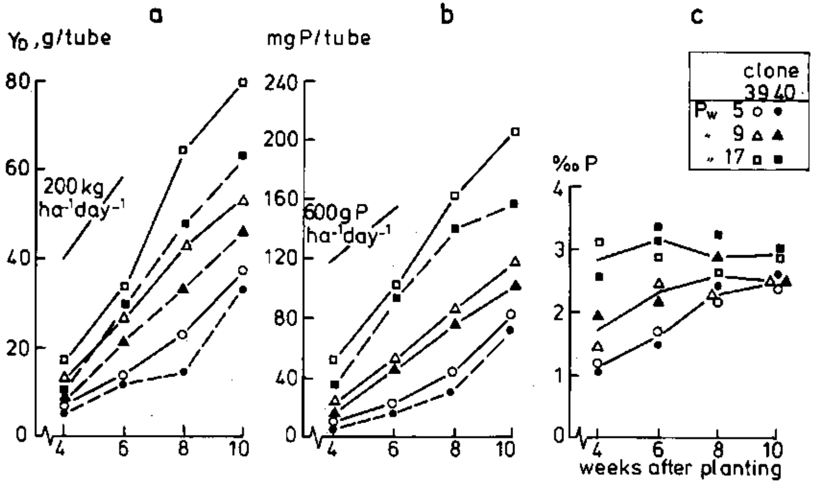


Fig. 14.6 Dry matter production (a), P-uptake (b) and P-content (c) of grass of the two clones in experiment 2.

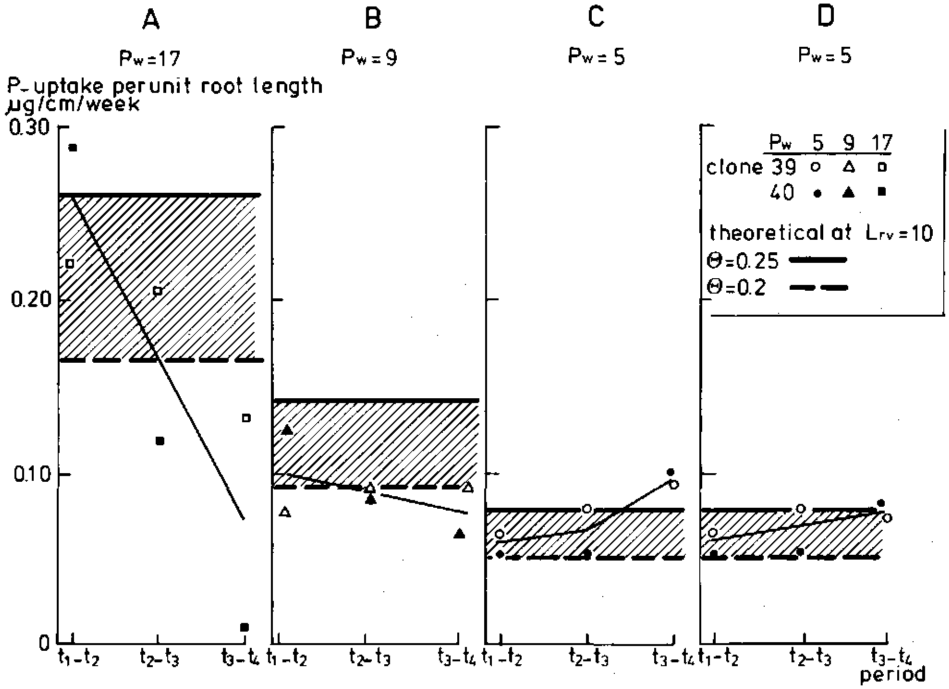


Fig. 14.7 A-C P-uptake per unit root length in experiment 2 at three P_w-values; in D. measured P-uptake is divided by length of roots + mycorrhizal hyphae; the solid lines indicate uptake capacity by a zero-sink at two values of Θ; theoretical values are given for L_{rv} = 10 cm/cm³, but do not depend strongly on L_{rv}.

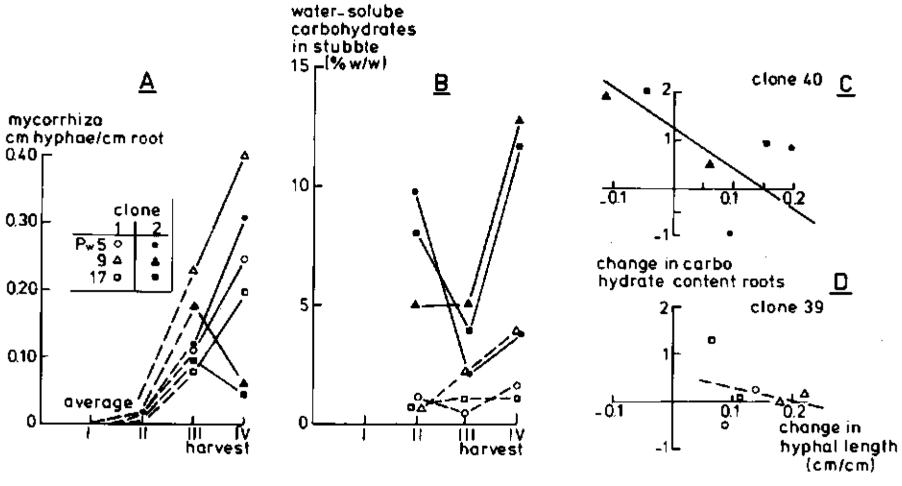


Fig. 14.8 Development of mycorrhiza (A) and water soluble carbohydrate levels in stubble (B) in experiment 2; C and D. Change in soluble carbohydrate levels between sampling periods, in relation to change in mycorrhiza.

P-uptake per unit root length apparently increased with time (figure 14.7C) and exceeded the predicted uptake potential by a zero sink at this P_w-value. However, P-uptake per unit root + mycorrhiza length was fairly constant (figure 14.7D). Again, between the two clones no consistent difference in P-uptake per unit root length was found.

Development of mycorrhiza mainly occurred in the second phase of the experiment, as shown in figure 14.8A. Clone 40 developed less mycorrhiza than clone 39, except at the lowest P_w. As the fungal partner in the mycorrhizal association depends on the plant for its carbohydrate supply, data on soluble carbohydrate levels in the plant may be compared with those on mycorrhiza development. Soluble carbohydrate levels were higher for clone 40 than for 39, in both stubble (figure 14.8B) and grass. As figure 14.8C shows for clone 40 an increase in soluble carbohydrate levels coincided with a decreasing or constant mycorrhizal level (hyphal length per unit root length); for clone 39 soluble carbohydrate levels remained at a low value while mycorrhiza developed (figure 14.8D). We conclude that differences in mycorrhizal development between the two clones were not related to either P or soluble carbohydrate content.

14.3.5 Response to a wide range of P_w-values and to mowing (experiment 3)

In experiment 3 the two clones were grown on a wider range of P_w-values in order to investigate whether in the initial growth period and in the recovery phase after a cut of grass a further P-response would occur than observed at

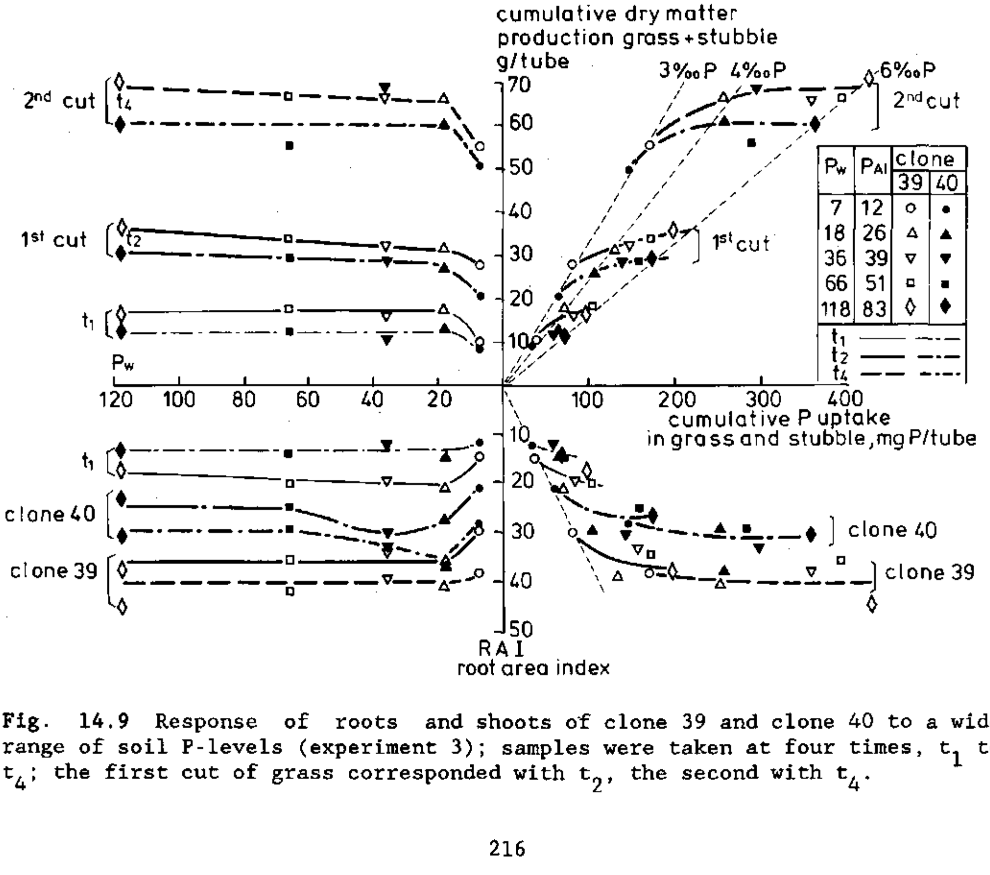


Fig. 14.9 Response of roots and shoots of clone 39 and clone 40 to a wide range of soil P-levels (experiment 3); samples were taken at four times, t_1 to t_4; the first cut of grass corresponded with t_2, the second with t_4.

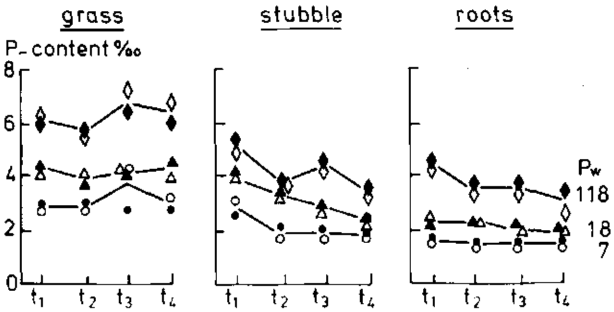


Fig. 14.10 P-content of grass, stubble and roots of the two clones in experiment 3, at three selected P_w values (experiment 3, t_1 - t_4); symbols as in figure 14.9.

the comparatively low soil P status in experiments 1 and 2. Also, a comparison could be made of the degree of morphological response of the two clones to high external P-supply which theoretically allows them to grow at higher shoot/root ratios.

Figure 14.9 shows the response of the two clones to a wide range of soil P-levels. Only between P_w-values of 7 and 18 an increase in dry matter production was found (Quadrant II). Clone 39 again developed faster than clone 40, irrespective of external P-level. After the first sampling, growth rates were roughly the same for both clones at higher P_w. At the second sampling, when grass was cut in all remaining containers, a positive but weak response of growth to P_w-value between P_w 7 and 18 was found for clone 39 and a more pronounced response for clone 40. Between the first and second cut of grass all treatments showed an approximately equal dry matter production.

The difference between the clones in initial growth was not related to P-uptake: at a very high P_w-value dry matter production of clone 40 was still considerably slower than that of clone 39, despite high P-concentrations. Quadrant I in figure 14.9 shows that the P-content of grass + stubble varied between $3^{0}/_{00}$ and $6^{0}/_{00}$; only a weak growth response was seen above $3^{0}/_{00}$ P and no growth response was found above $4^{0}/_{00}$ P in the first interval; the clones again did not differ in P-content for any part of the plant. For both clones P-contents of grass were higher than those of stubble and root (figure 14.10).

Quadrant III in figure 14.9 indicates that the root area index was not much influenced by soil P-status. For clone 40 a weak optimum around a P_w value of 18 was found from the second sampling onwards; root area index, RAI, was around 30. For clone 39 RAI increased to 40 between P_w values of 7 and 18 and remained unaffected up till a P_w value of 118. Root growth stopped at the first cut of grass (second sampling); between the third and fourth sampling some new root growth occurred. As quadrant IV shows, P uptake continued after the first cut (second sampling), without appreciable new root growth. P-uptake per unit root surface area increased, but much less than proportional, with increasing P_w of the soil. P-uptake per unit root surface area, in the period up till the first cut was approximately equal for the two clones at the lowest P_w value, as evident from the slope of the line connecting observation points to the origin in quadrant IV.

14.3.6 Discussion

The experiments were primarily done to test quantitative predictions of P-uptake per unit root length. Experimental conditions were chosen to agree with model assumptions: a homogeneous root distribution in the rooted zone was possible and soil water content was approximately constant. Model calculations were based on the assumption that roots behave as a zero-sink, that the whole root length participates in P-uptake and that physico-chemical transport is adequately described.

In figure 14.7 a satisfactory agreement was obtained between measured P-uptake per unit root and calculated uptake capacity by a zero-sink. This agreement suggests that our basic assumptions probably are reasonable: if only a small part of the observed root length would be active in P-uptake, measured P-up- take per unit root length should deviate greatly from predicted values. If only part of the total root length would participate in uptake, a considerable extra uptake by this active part has to be postulated, in excess of the uptake by an equivalent zero-sink. This is not likely for our experiment.

A further test of theoretical predictions, especially the interactions of P-uptake and water content of the soil, will be given in section 14.4 on the basis of experiments 4 and 5, where P-distribution over the profile was varied and several combinations of L_{rv}, P-status and Θ were obtained.

Figure 14.7A shows that, when P-supply to the roots exceeded P-demand (as evident from adequate P-contents), uptake per unit root length rapidly decreased to a value much below that for a zero-sink. Thus a basic assumption for the period of unconstrained uptake is confirmed. Efficient regulation of P-uptake is not only a logical necessity, as discussed in chapter 3, it can actually be demonstrated: at higher P_w-values P-uptake per unit root eventually was lower than at low P_w (figure 14.7).

The difference in P-response of the two clones observed, especially in the initial growth phase, could be directly related to differences in root length development, as P-contents did not differ among the clones and P-uptake per unit root length was the same. This conclusion is important for defining selection criteria for plant breeding for conditions of low P-supply. Rapid development of a high root length density obviously is important, while there is no scope for selection on classical "physiological" parameters such as K_m or I_{max} (chapter 3): external concentrations cannot be lower than zero; uptake per unit root length can only be increased by changing the chemical environment around the root or by changing the geometry by root hairs. Experiment 2 showed that after a sufficiently long phase of root + mycorrhiza development, even a P_w-value of 5 is enough for P-requirement of grass at the growth rate found at high external P-supply. We conclude that mycorrhizal hyphae contribute to P-uptake in a similar was as an increase in L_{rv}. The experiment was not continued sufficiently long to observe depletion of soil P, as is evident in figure 1.7.

Interesting differences between the two clones were found in regulation of both root growth and mycorrhizal development. Clone 40 shows a lower root length and root weight at high external P-supply when compared with intermediate P-levels, while clone 39 does not show such a decrease. Clone 39 may be said to show "luxury root development", in excess of its requirement in fertile soil. As will be discussed in section 14.5 the decrease in root development at higher P-supply shown by clone 40 is much less than theoretically possible as well. Under ample nutrient and water supply in the experiments of Baan Hofman and Ennik (1982), clone 40 showed a slightly higher shoot + stubble production than clone 39. Thus, clone 39 seems to be better adapted to growth under low P-supply, while clone 40 is slightly better adapted to growth under high nutrient supply. Clone 40 maintains higher soluble carbohydrate levels in the stubble and may thus be more resistant to frequent cutting: it represents a "meadow-type" of grass, while clone 39 represents a "hay-type". The conclusion that mycorrhizal development differs between the two clones and that differences are not related to carbohydrate or P-levels in the plant is interesting from a physiological point of view. In an elegant split-root experiment Menge et al. (1978) demonstrated that internal conditions in the plant, and not external conditions in the soil determine mycorrhizal development. We may now speculate on a more specific regulation than possible by carbohydrate or P-level. Apparent differences between genotypes in control over mycorrhizal development may be interesting for plant breeding for conditions where mycorrhiza may matter: at the lower edge of the soil fertility range found in agriculture world-wide.

14.4 P-distribution over the profile

14.4.1 Introduction

In the past most of the grassland in the Netherlands was used as permanent pasture, in which phosphate (in the absence of soil tillage) accumulates near the soil surface. Soil sampling for P-fertilization recommendations consequently could be confined to the 0-5 cm layer. Including deeper soil layers yielded no further information in the past. After recent modifications in the use of grassland, P has often been mixed through a ploughlayer of roughly 20 cm depth (Ehlert, 1985). The question of the relative availability of P at this depth is thus of practical relevance. Lower root length densities in the zones below the 0-5 cm layer suggest that the uptake capacity for available soil P from deeper layers will be less and consequently that the interpretation of chemical soil analysis for fertilizer recommendations has to be adapted if deeper soil layers are sampled. From section 14.2 we may expect, however, that differences in soil water content Θ between the top 5 cm and deeper layers may, at least partly, compensate for differences in root length density, L_{rv}. The outcome of the two effects, lower L_{rv}, but higher Θ was tested in experiments where P-distribution over the profile was varied, at equal total P-content of the soil.

Two experiments will be discussed, in which four distributions of P over the top 20 cm were compared. These profiles were chosen to obtain direct evidence whether a sample of 0-5 or 0-20 forms the safest basis for a soil test for a fertilizer recommendation scheme. The profiles were:

1. an undisturbed profile with P rich soil in the top 5 cm only,
2. an inverted profile with P rich soil in the 15-20 cm layer,
3. a homogenized profile with the same amount of P-rich soil mixed through the 0-20 cm layer, and
4. a homogenized-rich variant, with P-rich soil in 0-20 cm depth.

On grassland it is conventional to measure the P-status with the P_{Al}-value, (section 7.2.2). Profile 1 and 4 had the same P_{Al} value in a 0 - 5 cm sample (35), while for profile 3 and 2 values of 17 and 10 were found, respectively. A P_{Al} determination of a sample of the zone 0 - 20 cm gives the same outcome for profiles 1, 2 and 3 (17) and a much higher value for profile 4 (35). In view of the nonlinear adsorption isotherms it is remarkable that linear averages of the P_{Al} values of two soil samples describe the P_{Al} value of a mixed sample; as can be derived from table A14.1 this is not true for the P_w-value.

In experiments 4 and 5 a Lolium perenne mixture (BG3: 50% hay- and 50% meadow type) was used as in grassland practice.

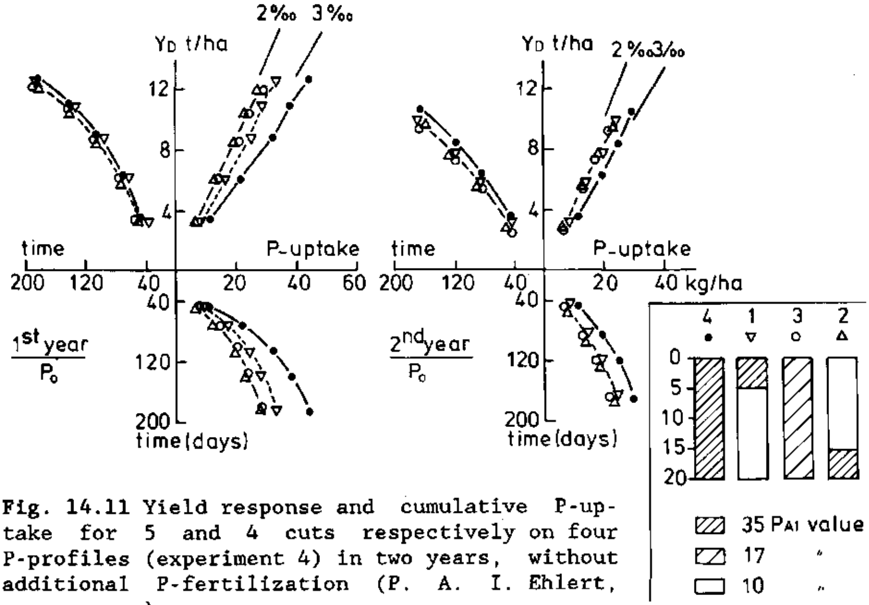


Fig. 14.11 Yield response and cumulative P-uptake for 5 and 4 cuts respectively on four P-profiles (experiment 4) in two years, without additional P-fertilization (P. A. I. Ehlert, pers. comm.).

14.4.2 Experiment 4

As shown in figure 14.11 for two experimental years, growth response and P-uptake mainly differed between profile 4 (homogenized rich) and the three others. For the three profiles with equal average P-content in the top 20 cm, the undisturbed P-distribution allowed faster initial growth, but total P-uptake and dry matter production over all cuts of grass was remarkably similar in both years. The experiment thus allows the conclusion that when variation exists in the P-distribution over the top 20 cm, a sampling depth of 20 cm gives more information on the P-supply to grassland than a sampling depth of 5 cm, as the difference between profiles (1, 2, 3) versus 4 is much larger than that between profiles (1, 4) versus 3 and 2, respectively.

A quantitative explanation of the approximately equal P-uptake from profiles 1 and 2, which form the extremes in relative P-distribution, should be based either on a morphological response (extra root development in the zone 15-20 cm of profile 2) or a functional response (extra P-uptake per cm root in the P-rich zone on profile 2). Figure 14.12A shows root development during this experiment, averaged over all treatments. An attempt was made at four sampling occasions to separate living root mass from dead material using the TTC technique (tetrazolium chloride; Goedewaagen, 1954). Root area index for living roots in spring (16/4) was about 3, at the first cut of grass (3/6) appr. 15. Figure 14.12 B and C compares root length density in the P-containing zone on the undisturbed and the inverted profiles, 1 and 2 respectively. In both situations some local stimulation of root growth is evident: in the 0-5 cm zone root length density is higher on the undisturbed than on the inverted profile; for the zone 15-20 cm depth the reverse is true. On the undisturbed profile, L_{rv} in the P-containing zone is roughly 40, on the inverted profile appr. 13. A similar difference is found for the roots coloured in the TTC test. Apparently, P-uptake per unit root length has been higher by a factor of around 3, on the inverted than on the undisturbed profile.

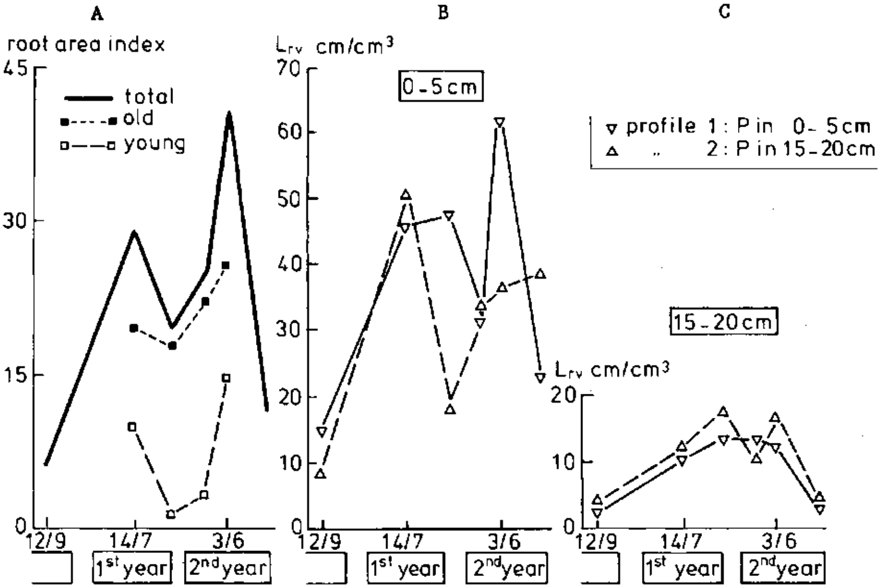


Fig. 14.12 Root development in experiment 4; **A.** shows the root area index (averaged over 4 profiles) as measured at 6 dates during the 2.5 years of the experiment; total root surface area is divided over "old" and "young" based on a TTC-colour reaction (Goedewaagen, 1954); **B** and **C** show a comparison of L_{rv} in the P-containing 5 cm on profile 1 and 2, 0-5 and 15-20 cm respectively.

As an explanation for the higher P uptake per unit root length in the P-containing zone when this zone is at 15-20 instead of 0-5 cm depth, interactions between P-mobility and soil water are likely. As shown in figure 14.5, a difference in average Θ between the two layers of at least 0.1 (v/v) is required to explain the observed differences in P-uptake per unit root length. As the topsoil may dry out more frequently than deeper layers of the soil, such a difference may in fact occur. In experiment 4 the depth of the soil water table was about 1 m; water conditions in the profile depended directly on weather conditions. A follow-up experiment was designed in which water content of the soil could be better controlled and measured.

14.4.3 Experiment 5

In experiment 5 the same four soil profiles were used as in experiment 4; two soil water tables were maintained, two P-fertilization and two N-fertilization levels were used. Matric potential of the layers 0-5 and 15-20 cm was measured with tensiometers. At the end of the experiment the water retention curve was determined. The experiment was performed at two levels of nitrogen fertilization, primarily to test whether or not the conclusion about similar P-uptake from profiles 1 and 2, holds under a wide range of growth rates. When the water table was kept at -80 cm, the topsoil dried out before the first cut of grass and several times later. In the zone at 15-20 cm depth soil water only decreased before the first cut of grass, but later and less severe than in the layer 0-5 cm depth (figure 14.13). For the tubes kept at a water table of -40 cm, no decrease of soil matric potential below equilibrium values was found during the experiment. From the water retention curve of the profile 2, L_{rv} in the P-containing zone is only one-third of that on profile 1, but differences in water content may compensate for this difference. Total estimated P-uptake on both profiles is equivalent to around 0.3 kg/(ha day), allowing a dry matter production of appr. 150 kg/(ha day) at the P-content of appr. $2^0/_{00}$ found. Between the first and second cut actual rate of dry matter production was higher than this value, between second and fourth cut it was slightly lower. Despite several uncertainties about model assumptions, model calculations give satisfactory agreement with experiments. A further discussion of indices of soil fertility, based on our model description for the period of unconstrained uptake, will be given in chapter 15. Some extensions of the theory can be given now.

14.5 Optimal root length density for P-uptake

At least for the soils used in these experiments, with rather high adsorption constants compared with the five soils used in chapter 7 to 9, we may conclude that the range of root length densities for which more roots lead to increased capacity for P-uptake, extends up to 20 cm/cm³. Figure 14.16 shows that if zero-sink uptake would continue for a long period, e.g. when the required uptake rate is never met, uptake rate per unit root length would only gradually be reduced. Cumulative uptake per cm root at L_{rv} = 20 cm/cm³ would after 100 days still be 90% of that at L_{rv} = 5 cm/cm³; total uptake by the root system would thus be a factor 3.6 higher. Figure 14.16C shows that at L_{rv} = 20 cm/cm³ the concentration at the edge of the soil cylinder would still be half the original value in this stage. Uptake capacity by the root is determined by the slope of the concentration profile near the root, which remains remarkably constant.

To the theory about the period of unconstrained uptake presented in chapter 8 to 10, we have added a description for the final stage (after T_c) in chapter 12 and a description for the initial stage, before the period of unconstrained

Table 14.1 Estimated P-uptake for zero-sink uptake in four layers of two soil profiles, for water content and root length density as found in experiment 4 and 5; P-uptake per unit root length as given in figure 14.2.

		Undisturbed profile 1				Inverted profile 2			
Depth cm	Θ v/v	P_{Al}	L_{rv} cm/cm³	P-upt. µg/(cm week)	P-upt. µg/(zone week)	P_{Al}	L_{rv} cm/cm³	P-upt. µg/(cm week)	P-upt. µg/(zone week)
wet period									
0- 5	0.25	35	45	0.25	56	10	40	0.02	4
5-10	0.28	10	20	0.03	3	10	20	0.03	3
10-15	0.32	10	15	0.04	3	10	15	0.04	3
15-20	0.35	10	10	0.05	2.5	35	15	0.32	24
total µg/(week cm²)					65				34
dry period									
0- 5	0.15	35	45	0.06	13.3	10	40	0.012	2.3
5-10	0.18	10	20	0.018	1.8	10	20	0.018	1.8
10-15	0.22	10	15	0.028	2.1	10	15	0.028	2.1
15-20	0.25	10	10	0.035	1.8	35	15	0.188	14.1
total µg/(week cm²)					19.0				20.3

uptake, in this chapter. During the establishment phase of a crop, we may expect the P-uptake rate per unit root length to be virtually constant, up to the point of interception of the demand and the supply lines in figure 14.1. The point of interception determines the start of the period of unconstrained uptake.

From figure 14.16 it can be concluded that, even when considered over extended periods, a plant is hardly confronted with diminishing returns of P-uptake when investing dry matter in a higher root length density. Under conditions of limiting P-supply, the adagium "the more roots, the better shoot growth" (compare chapter 2) is valid up till high L_{rv} values. As investing dry matter in extra root growth possibly reduces shoot growth, we may define a maximum shoot/root ratio for a given external P-supply from a comparison of P-supply and P-demand. Total P-supply by the soil-root system equals P-uptake rate per unit root length x total length of the root system. P-demand by the plant equals dry weight of root and shoot multiplied with the respective P-concentrations required in root and shoot. Hence the maximum shoot/root ratio is:

$$(14.1) \qquad \frac{Y_{D,s}}{Y_{D,r}} = \frac{U_r \, L_r/Y_{D,r} - M_r}{M_s} \, ,$$

where:

$Y_{D,r}$ and $Y_{D,s}$ are root and shoot dry weight respectively [g],

M_r and M_s are minimally required P-contents of root and shoot [mg/g],

$L_r/Y_{D,r}$ is the specific root length [m/g],

U_r is the total P-uptake capacity over a certain period of time, per unit root length [mg/m].

The main problem now is to choose the time-span for which U_r has to be calculated; in the following we choose a period of 1 week. Figure 14.17 shows the resulting maximum shoot/root ratio as a function of P_w for soil d (experiment 3); the other parameters were chosen in the range found for the experiments with the two clones. In the same graph observed shoot/root ratios for the two clones are shown: for clone 39 they hardly increased with higher P-supply, for clone 40 they are still far below the theoretical maximum at high P-supply. Further reduction of root growth would be possible, as long as the supply of water (or other nutrients) will not become limiting (compare chapter 4).

If $(U_r L_r/Y_{D,r} - M_r)$ equals 0, no shoot growth is possible. In this case uptake by the root is just enough to obtain its required P-supply, without any transport of P to the shoot. Conditions of P-status and water content of the soil which do not allow a higher uptake U_r form an absolute lower boundary to plant growth. Increasing the specific root length and reducing the P-requirement of root tissue, which is more important than that of shoot tissue according to (14.1), are the only options for the plant to survive at this lower boundary. As mycorrhizal hyphae show a much higher specific length (m/g) than roots, their importance at low P-supply follows, even under conditions where extra root growth would not be possible for the plant. If U_r is calculated over an extended period, the lower boundary shifts to a lower P-supply. For the plant this means that it takes a longer time before any interest on the amount of P (e.g. from seeds) invested in root growth will be available for shoot growth. Further aspects of "optimal" root systems will be discussed in chapter 16.

With these equations it will be investigated whether depth of rooted nutrient-rich layer (H), buffering of the soil (K_a) and root length density L_{rv} (related to ρ) should be considered when developing a sampling method and constructing a soil fertility index.

The term $G(\rho,\nu)$ indicates how the amount of nutrients left in the soil at the end of the period of unconstrained uptake depends on L_{rv}. In equation (15.1) we can see that the total amount remaining in the soil at T_c is almost proportional to the adsorption constant K_a. When a soil becomes drier (Θ decreases), the amount of nutrients remaining in the soil at T_c increases. In figure 15.2 a summary is given for N, K and P of the amount remaining in the soil at T_c, as a function of L_{rv} and other parameters.

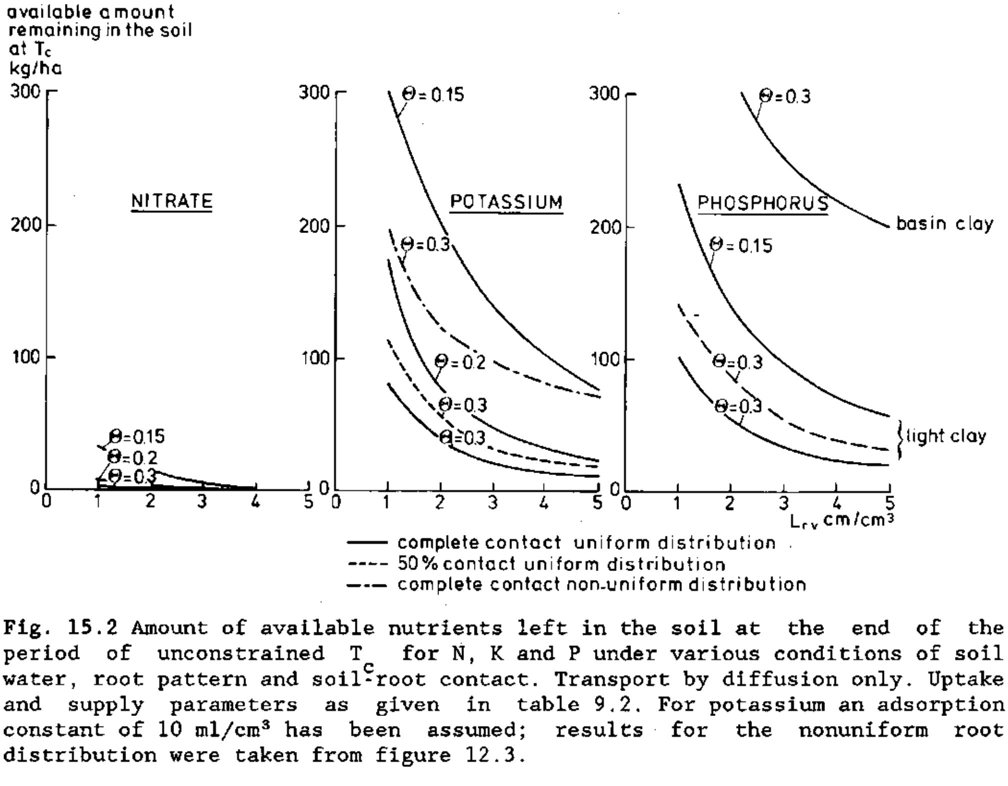


Fig. 15.2 Amount of available nutrients left in the soil at the end of the period of unconstrained T_c for N, K and P under various conditions of soil water, root pattern and soil-root contact. Transport by diffusion only. Uptake and supply parameters as given in table 9.2. For potassium an adsorption constant of 10 ml/cm³ has been assumed; results for the nonuniform root distribution were taken from figure 12.3.

15.2.2 Nitrogen

As shown in figure 15.2, in a moist soil small root length densities are sufficient for the almost complete depletion of nitrate. Under dry soil conditions ($\Theta < 0.2$) high root length densities are required and even then, relative depletion may be less than 1.0. In such a situation improved water supply will be more effective than increasing the N-supply by fertilization.

Soil analysis methods for fertilization schemes should aim at extracting the complete pool of available nitrogen, to predict actual uptake capacity by the crop. As low values of L_{rv} in moist soils are sufficient to utilize almost all available nitrogen in a soil layer, sampling depth has to be chosen according to the depth reached by the deepest roots during the growing season. The major practical problem is that the available pool of nitrogen cannot yet be recognized at the start of the growing season. Losses from and gains by the mineral N pool in the soil cannot yet be predicted accurately. Recently some successes were achieved with the N_{min}-method (Neeteson and Smilde, 1983) which extracts all available N in early spring. This amount is apparently also correlated with the amount of nitrogen which will be mineralized in the subsequent growing season.

In section 9.3.1.2 it was concluded that, in the absence of leaching during the growing season, all nutrients mobilized during the growing season can be added to the available pool at the start of the growing season, when plant demand is constant in time. The time course of mineralization thus seems to be of less interest than the total amount mineralized during the growing season as a whole. This may explain the relative success of the nitrogen model of Greenwood et al. (1985), in which a constant daily mineralization is assumed. Although daily fluctuations in mineralization under influence of weather conditions probably are considerable, the total amount of N mineralized in the course of a growing season may be largely related to the overall organic matter balance of the soil. Hence the position in the crop rotation may be more important than the soil type and year effects. However, the crop is largely dependent on mineralization of organic N, then the time course of mineralization can be important, as the N supply often will be insufficient in early spring and may be excessive in later phases of the crop. Especially on soils rich in organic matter, denitrification after heavy rainfall in spring and summer may deplete all mineral N present. Subsequent mineralization is then vital for the plant, as the internal storage capacity of the plant is limited.

15.2.3 Potassium

Soil extraction technique

Figures 9.8 and 15.2 show that for root length densities above 1 cm/cm^3, in moist soils only a small amount of available K cannot be taken up by the crop during the growing season at the required rate, for the standard value of crop requirement assumed sof ar. For a crop such as potato actual requirement can be considerably more: a critical K-content of 3% instead of 1% as assumed in table 9.2, leads to a required uptake rate A three times higher and to an amount of K remaining in the soil at T_c which is three times higher as well, according to (15.1).

In the plough-layer, which stores the largest amount of potassium, root length densities above 1 cm/cm^3 are commonly found for agricultural crops (table 6.2). Poor root development, drier conditions of the topsoil, very low degrees of soil-root contact or clustered root distributions may significantly affect fractional depletion potential (figure 15.2).

Soil analysis methods should thus aim at measuring a considerable part, depending on K_a, Θ, A, L_{rv} and root distribution, of the pool of available potassium in the soil. In the Netherlands, as mentioned in chapter 7, the index for soil potassium status, the K-value, is derived from K-HCl (the amount extracted by 0.1 N HCl and 0.4 N oxalic acid), which essentially gives the available amount of potassium per unit soil weight. Potassium is much less bound by organic matter than by clay (Grimme et al., 1971). For sandy and peaty soils where the major part of the cation exchange capacity can be attributed to organic matter, K-HCl (expressed per unit volume of soil) will also give the unconstrained available amount. The correction for organic matter content of the soil, which is applied in the calculation of the K-value from K-HCl, takes the bulk density of the soil into account, which on these soils is directly related to organic matter content.

For clay soils, K-HCl is corrected for clay content - the higher the clay content the lower K-HCl is rated - probably because of the higher buffer capacity at higher clay content, which diminishes the unrestrained available amount, as (15.1) shows. Another correction is made for soil pH: the higher the pH the lower the K-value; this again may be viewed as an effect of pH on buffer capacity, as adsorption is higher at higher pH-values (Nemeth, 1975).

If the K-adsorption isotherm is approximately linear (as shown in figure 7.1), it is possible to propose an extraction method with water with which the soil potassium status can be assessed. As will be shown, this method allows the same interpretation on various soils as far as unconstrained uptake capacity is concerned. The reasoning is as follows.

The amount of potassium ($K(V_w)$ in mg/1000 cm³) extracted at a volume ratio V_w of water to soil equals:

$$(15.4) \quad K(V_w) = 1000\ V_w\ C = (1000\ V_w\ S) / (K_a + V_w) \qquad [\text{mg K} / 1000\ \text{cm}^3].$$

When comparing two soils at the same $K(V_w)$-value we can find a value of V_w for which T_c for a given root system is independent of K_a. From (15.2):

$$(15.5) \quad T_c = f_2\ S - f_3\ (K_a + \Theta)\ G(\rho,\nu) \ ,$$

where

$$f_2 = H/A \ ,$$

$$f_3 = R_0^2 / D \ .$$

The term $(K_a + \Theta)$ is approximately equal to K_a. If two soils X and Y with adsorption constant $K_a(X)$ and $K_a(Y)$, respectively, have the same $K(V_w)$ value, then from (15.5):

$$(15.6) \quad S(X) = S(Y)\ \{K_a(X) + V_w\} / \{K_a(Y) + V_w\}.$$

For the unconstrained uptake capacity of the two soils to be the same, T_c should be the same, $T_c(X) = T_c(Y)$; substituting (15.5) and (15.6):

$$(15.7) \quad f_2\ [S(Y)\ \{K_a(X) + V_w\} / \{K_a(Y) + V_w\}] - f_3\ K_a(X)\ G(\rho,\nu)$$
$$= f_2\ S(Y) - f_3\ K_a(Y)\ G(\rho,\nu) \ .$$

Solving for V_w we obtain

$$(15.8) \quad V_w = \{f_2\ S(Y) - f_3\ K_a(Y)\ G(\rho,\nu)\} / \{f_3\ G(\rho,\nu)\}$$

and hence:

$$(15.9) \quad V_w = T_c / \{f_3\ G(\rho,\nu)\} \ .$$

From this equation we see that the volume ratio V_w for which soils X and Y will allow a similar unconstrained uptake when compared at the same $K(V_w)$-value, will serve this function for other soils as well, as V_w does not depend on K_a or on the ratio of $K_a(X)$ and $K_a(Y)$. The optimal choice of V_w directly depends on T_c and $G(\rho,\nu)$.

We conclude that in the case of linear adsorption for every T_c and root area index a unique choice of V_w is possible for which the interpretation of $K(V_w)$ can be independent of soil type. Higher root length densities lead to smaller values of ρ and also of $G(\rho,\nu)$, so higher volume ratios V_w of water to soil will be required to make the interpretation of $K_w(V_w)$ independent of K_a.

Sampling depth

The aspect of choosing a correct sampling depth for potassium has been considered by Prummel (1978). In arable land, the depth of the K-rich layer is mainly determined by ploughing depth. The depth of the plough layer varies from soil to soil, however, and the question was raised whether or not the K-fertilization recommendation should be corrected for ploughing depth. The total size of the available pool, at a given concentration of K in the soil clearly depends on ploughing depth. If potassium fertilizers are applied before ploughing, a constant amount of potassium is mixed through a larger volume of soil as ploughing depth increases, and this will result in a smaller increase of the K-concentration. The question is whether K-fertilizer can then be extracted by the crop with the same efficiency.

In a deeper plough layer we may expect a lower average L_{rv} value. Hence relative depletion of the available pool per unit volume of soil will be lower the greater the ploughing depth. The overall effect of ploughing depth on expected K-uptake can be predicted from a modification of (15.2):

$$(15.10) \quad T_c = T_{c,max} - \frac{K_a + \Theta}{D} R_0^2 \, G(\rho,\nu)$$

$$= \frac{100 \, N_a + H \, S_i}{A} - \frac{K_a + \Theta}{D} R_0^2 \, G(\rho,\nu) \quad ,$$

where N_a is the amount added to the available pool by the amount of fertilizer applied [kg/ha]. The factor 100 converts the dimension of N_a [kg/ha] into that of S_i [mg/cm³].

The second term in this equation is indirectly dependent on H, if we assume total root length per unit cropped area (or root area index) to be constant. Figure 15.3 shows some results of calculations, using this assumption and a high value for K-demand, corresponding to measurements by Prummel. The effect of ploughing depth on calculated T_c is positive for higher values of the K-value and negative for soils poor in K. For every value of the root area

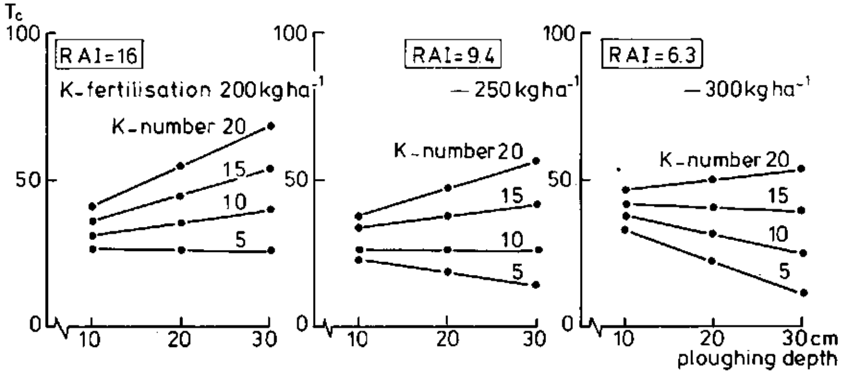


Fig. 15.3 Predicted interaction between ploughing depth H, soil fertility of the ploughlayer and length of the unrestricted uptake period T_c for potassium, assuming a constant Root Area Index (RAI), with L_{rv} homogeneously distributed over the plough layer; an adsorption constant K_a of 15 was assumed; a K concentration of the crop was taken as 3.3%, to make calculations applicable to the potato experiment of Prummel (1978); other parameters as in table 9.2.

index a K-level of the soil exists where T_c is independent of H. From (15.6) we see that in this case the second term, the amount of K remaining in the soil, should be (approximately) equal to - H S_i / A. Only in the special case that T_c = 100 N_a / A can T_c be independent of H. The K remaining in the soil at T_c is in this case equal to the initial available amount (before fertilization); hence fertilization equals crop uptake. The value of S_i for which this apparent equilibrium situation is attained depends on the root area index.

Prummel (1978) performed an experiment on the K-response of potatoes at three ploughing depths (12, 18 and 24 cm). To obtain a clear K-response he chose a soil low in potassium; the experiment (conducted on a sandy soil with a deep water-table) showed that for shallow ploughing depths maximum production levels were lower but the interpretation of the K-value in a fertilization scheme was hardly different from that for a deep ploughing layer. Our theory indicates that Prummel's conclusion may not be extrapolated to soils richer in K. For K-levels of the soil which are higher or lower than the ones used in the experiment of Prummel, correction for ploughing depth may improve the interpretation of K-values for fertilizer recommendations. The relative distribution of roots over plough layers of various depths and the water content of various soil layers would have to be taken into account to before more precise predictions of possible K-uptake can be made.

15.2.4 Phosphate

T_c as a function of L_{rv} and P_w-value

In chapter 9 results of calculations on the relation between root density L_{rv} and period of unconstrained uptake T_c were shown for different soils, where comparisons were based on a constant size of the available pool. In figures 9.15 and 9.16 considerable effects of soil type on the relation between L_{rv} and T_c were thus obtained. Fertilizer recommendation schemes for arable crops in the Netherlands are currently based on the P_w-value, which is determined by measuring the soil-P-concentration 24 hours after mixing pre-moistened dry soil with water in a volume ratio of 1:60 (Van der Paauw et al., 1971). As discussed by De Willigen and Van Noordwijk (1978) and in section 14.2, the result of a P_w measurement can be adequately predicted from the parameters of the adsorption isotherm and knowledge of the total amount of available phosphate (figure 15.4b). Figure 15.4a indicates the fraction of total available phosphate which is extracted from the soil in a P_w-measurement. This fraction varies with soil type and depends on soil P-status, because the adsorption isotherms vary with soils and are nonlinear. Fractional depletion of available P by a P_w-determination can be compared with fractional depletion by crop root systems over a growing season, as will be discussed now. Figure 15.5 shows calculated T_c values for regularly distributed roots, with complete soil-root contact in a moist soil, as a function of L_{rv} for five soils at three P_w-values. Calculations were made as indicated in section 9.3.2., taking into account the limiting concentration, as discussed in section 3.1, using a value for the root absorbing power α of 0.17 m/day. Figure 15.5 shows that under certain conditions the five soil types will allow a similar T_c when compared at the same P_w.

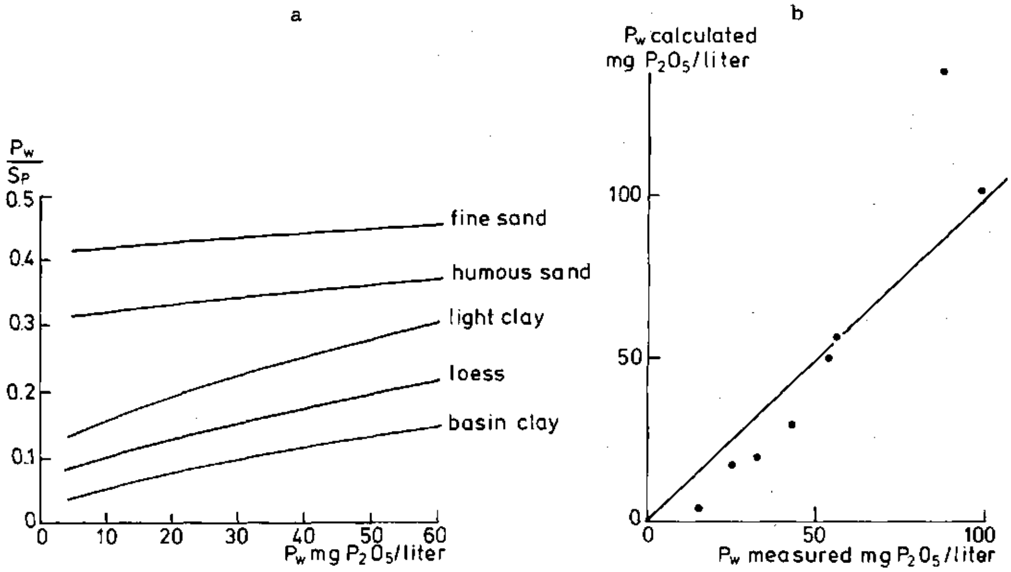


Fig. 15.4a Fraction of total available phosphate, S_P, measured by P_w, as a function of P_w for five soil types; parameters of the adsorption isotherms are given in table 7.1; b relation between calculated and measured P_w, on the five soils (De Willigen and Van Noordwijk, 1978).

Soil extraction technique

As figure 15.5 shows the succes of the P_w-value appears to depend on the root density in the P-containing zone or the required P-uptake per unit root. For a root density of 1 cm/cm^3 for instance T_c is about the same for all soils at P_w-values of 30 and 50. But for higher root densities the calculated values of T_c differ considerably. Apparently the relative success of the P_w-value as an index of plant available soil P depends on the root density in the P-containing zone or the required P-uptake per unit root.

The P_w-value as defined by Van der Paauw et al. (1971) is one of an infinitely large number of compromises between a measurement of P-concentration of the soil solution and total available amount. As described by De Willigen and Van Noordwijk (1978), the amount of P extracted – $P(V_w)$ – can be calculated from the adsorption isotherm of a soil and the total amount of available P for any volume ratio of water to soil during the extraction. For higher (or lower) volume ratios of water to soil than the 60:1 ratio used by Van der Paauw et al. (1971), a larger or a smaller amount of soil P will be extracted, but not for all soils in the same way.

As shown in section 15.2.3, for a linearly adsorbed nutrient an ideal volume ratio of water to soil V_w exists for each combination of desired T_c and root area index, for which the interpretation of a water extraction of the soil is independent of soil type. For nonlinear adsorption isotherms no ideal V_w in this sense exists, but an optimum V_w can be found for which the amount of P extracted accounts for the variation among soils, as reflected in unconstrained uptake capacity, in the best way. As shown in figure 15.6 (De Willigen and Van Noordwijk, 1978), for increasing values of L_{rv} higher optimal values of V_w are found. The higher L_{rv} (or the lower the P-requirement per unit root) the higher is the relative depletion potential of the root system

For plants growing in soil, probably fewer possibilities exist to increase porosity by selection and maintain the penetration ability of the roots and we have to accept that root porosity of most crops is not sufficient to meet the oxygen demand of the roots by the internal pathway only. External aeration thus is critical. Recently Boone (1986) formulated a quantitative approach of the range in which soil water content Θ may vary to avoid aeration problems on the wet side, and critical values of penetration resistance for root growth on the dry side (when extra roots are needed to meet the plant's demand for nutrients and water). The range of Θ in which unhindered plant growth is possible can in this way be quantified if external aeration requirements of the crop (a function of root-air contact and air-filled porosity) and soil physical data on the relation between penetration resistance and Θ, and between oxygen diffusion and Θ are known. Estimates by Boone (1986) show that in some of the sandy soils studied the acceptable range of Θ in the present soil physical condition of the soil is very narrow. Effective drainage and frequent irrigation are the only way to maintain un-impeded crop growth in that case. For soils of better structure the range can be wider and less regulation of soil water content is necessary. The quantification of simultaneous internal and external oxygen transport in chapter 8 may help in applying Boone's approach in agricultural practice.

16.3 Optimal root morphology

In figure 9.20 a comparison was made between the relative depletion capacity of roots of various diameters; when compared on a volume or weight basis, the smaller the root diameter, the higher the depletion capacity is. Fine roots thus are the most effective per unit carbohydrate invested; minimum root diameter may be determined by the requirement of having at least five cell layers (epidermis, cortex, endodermis, xylem, phloem) (McCully and Canny, 1985). As discussed in 14.5 mycorrhizal hyphae may be more efficient in P-uptake per unit carbohydrate invested in the root system.

Larger root diameters are required when internal rather than external aeration is important, as discussed in 16.2, and when transport functions of roots are considered. Xylem diameter is important in determining longitudinal resistance to water movement. If roots become branched the transport rates through the main axes gradually increase; for Monocotyledonae, which do not have the possibility of secondary thickening, xylem diameters may become a limiting step in water transport in this case (Newman, 1974). Wind (1955) discussed the possibility that in grass roots internal resistance against water-flow limits the possibility of using available water more than 50 cm below the surface. The resistance to water transport from deeper layers by capillary rise would be less than that for transport through the root. In the normal pattern of root growth in cereals, nodal roots take over when the transport capacity of the seminal root system becomes limiting. Plumbing aspects of the architecture of root system were considered by Fowkes and Landsberg (1981).

The diameter of individual xylem cells has to be a compromise between high transport rates in good conditions (according to Hagen-Poiseuille's law conductivity is proportional to the fourth power of the radius of a channel) and the risk of cavitation (becoming air-filled) in dry conditions (Tyree et al., 1986).

16.4 Optimal root length density

By definition, for uptake of all available soil moisture infinitely high root length densities are required. As figure 15.7 shows, the plant is dealing with strongly diminishing returns of extra water uptake when investing in further root growth in a zone containing roots already. Based on these diminishing returns, an optimum root length density can be defined for which the marginal water yield just equals the cost to the plant. The costs for the plant of making new roots consist first of all of the dry weight per unit root length/surface area (figure 6.2). To this dry weight the amount of carbohydrates respired during root growth and root maintenance has to be added. The amount of carbohydrate required per unit root length/surface area can be transferred to an amount of water required for transpiration, if we may assume the transpiration ratio (photosynthate produced per unit transpirational water loss; De Wit, 1958) to be constant. For a dry matter production of 200 kg/(ha day) and a transpiration rate of 4 mm, a transpiration ratio of 5 mg/cm^3 can de derived. A specific root length of 200 m/g is a typical value for fine roots. For growth plus maintenance respiration roughly a similar amount of carbohydrate is required as found in the root dry weight (Lambers, 1987). Combining these figures we see that for every cm^3 of water transpired the plant can make circa 50 cm of roots. Hence a marginal root water efficiency of 0.02 cm^3 water per cm root length can be used as a first estimate. In figure 15.8 this marginal efficiency was used to estimate the optimum root length density for water uptake from the amount of available soil water left in the soil when the soil-root contact resistance prevents further uptake at the required rate, as a function of L_{rv}, for different soils at two values of internal water potential. At this value of L_{rv} all extra photosynthesis possible by extra water uptake is invested in root growth. If a certain shoot/root ratio has to be maintained a higher marginal efficiency value has to be used. From the graph we conclude that depending on soil type and internal moisture tension in the plant a root length density L_{rv} of 2 - 6 cm/cm^3 is the optimum; for lower values of transpiration rate than used in figure 15.8 (1 cm/day = 0.5 cm in a 12 hour light period), the optimim would be found at lower values of L_{rv}. In this calculation we consider one drying cycle only; if soil moisture is replenished frequently higher L_{rv} values than indicated may still be acceptable for the C-economy of the plant.

Jordan and Miller (1980) reviewed root research on Sorghum cultivars, in the context of selection for drought avoidance. They concluded that a root length density L_{rv} larger than 2 cm/cm^3 below 50 cm depth would allow water extraction to meet high evaporative demands, until the soil dried to approximately -0.3 MPa. Whether or not such root development can be obtained without reducing grain yield potential remains to be demonstrated, according to Jordan and Miller. From the calculations presented above, we may expect that such root development may still increase the yield in conditions of limited water supply, by better utilization of available water. On the other hand, in well-watered situations probably higher yields can be obtained with cultivars investing less carbon in their root system.

For nutrient uptake similar calculations are not possible as the relation between nutrient uptake and photosynthesis is not as clear as that between transpiration and photosynthesis. The quantification of possible shoot/root ratios in terms of the nutrient economy of the plant, given in 14.5, gives equivalent results, however. Cultivars or species with an extensive root development (low shoot/root ratio) may give higher yields under poor conditions, while cultivars with less roots may have a higher yield potential, which can only be obtained under a continuously high nutrient supply.

In chapter 2 we stated that although the "functional equilibrium" theory of Brouwer is in line with a large number of observations on plant response to external conditions, in actual regulation of root and shoot growth other factors than internal carbohydrate, nutrient and water supply may play a role. In chapters 4 and 14 we found some situations where root development under favourable conditions of nutrient and water supply was higher than actually required for adequate uptake. In chapter 4 we concluded that tomato in pots without physical obstructions to root development formed a root system of about twice the surface area required for uptake of water and nutrients; for cucumber the largest root surface area still allowed the highest fruit production in a period of high transpirational demand. The two clones of *Lolium perenne* tested, differed in responsiveness of shoot/root ratio to external conditions, but the morphological response of both clones to situations of high nutrient and water supply is much less than possible (figure 14.17). In grassland the required root morphology for a genotype to survive competition between species and/or cultivars demands a much higher root length density than necessary for utilization of available resources by the combined crop canopy (Baan Hofman and Ennik, 1982).

Kuiper (pers. comm.) described differences among *Plantago* species and among Barley cultivars in responsiveness to drought and high salt concentration. Genotypes which respond quickly to a change in water availability with a change in allocation of dry matter over root and shoot, probably perform better in environments where a small decrease in water availability is the start of a longer dry period; in environments where droughts never last, a less responsive, more conservative behaviour of the plant may give higher aboveground production. In this sense we may expect that different genotypes are required for "high input, well regulated" environmental conditions then for "low input, variable" conditions.

For phosphate, better utilization of available resources by better root systems with or without mycorrhizan, does not replace the need to fertilize to maintain soil fertility in the long run. By reference to figure 1.1 we can state that the "apparent equilibrium point" where fertilization equals crop uptake can be shifted to the left by obtaining better root systems. Wether such a lower current soil fertility level will lead to lower losses to the environment and thus to higher nutrient use efficiency at the farming system level, depends on a number of climatic and soil physical and chemical factors. In chapter 13 possibilities were explored for obtaining higher nitrogen recoveries by a combination of different fertilization technique and different root distribution; the calculations suggested considerable scope for improvement of farming practice. In chapter 5, for the rockwool culture situation with a transport rate for all nutrients similar to that found only for nitrogen in normal soils, high nutrient use efficiencies were found to be possible with small root systems, if a sophisticated regulation of the content of the nutrient solution provides the required synchronization of nutrient supply to demand. Theoretically, optimal root systems can be defined for each set of environmental conditions. In a number of situations a closer approach to this optimum by plant breeding and/or management of soil structure may lead to a higher nutrient use efficiency of both the crop and the farming system.

ROOTS, PLANT PRODUCTION AND NUTRIENT USE EFFICIENCY

SUMMARY

In this thesis a theoretical framework is formulated for an evaluation of the role of roots in plant production and in the nutrient use efficiency of crops. Such a framework is required for a quantitative theory of soil fertility, which can be developed in addition to the present, largely empirical, approach. Adjustment of nutrient supply to the nutrient demand by the crop in quantity, timing and place may lead to increased nutrient use efficiency. Quantification of the depletion of "available" water and nutrients by root systems is the central question in this thesis.

As a basic concept we use the "functional equilibrium" between root and shoot growth. Leaf and root surface area, as interfaces with the above- and belowground environment of the plant, respectively, have to fulfill basic needs for the plant by uptake from the environment. Growth of root and shoot is mutually regulated by the success of the complementary organ. As the relation between leaf area index, LAI, and interception of light and CO_2 has been successfully quantified in crop ecology, we attempt a similar quantification of the relation between root area index, RAI, (and/or root length density) and nutrient and water uptake.

Transport by diffusion and mass flow of available water and nutrients to the root surface often limits uptake rates by the crop. Formulating and solving this transport problem in mathematical models forms an important part of this thesis. The outline of the models is presented in chapter 1. A basic concept of our models, which contrasts with the majority of models published so far, is that of internal regulation by the plant of nutrient uptake: as long as the supply is adequate, nutrient uptake by the root system as a whole matches with plant demand. As a consequence, in larger root systems individual roots can take up water and nutrients at a lower rate. During the linear growth phase of the crop, nutrient uptake patterns often show a "constant daily uptake" phase.

The various assumptions used in our model are discussed in the initial chapters. Chapter 2 considers the evidence for the functional equilibrium concept in contrast with older concepts such as the morphogenetic equilibrium between root and shoot growth. In chapter 3 physiological aspects of water and nutrient uptake by roots are considered and the physiological assumptions of our model are described and discussed. The assumption of internal regulation of nutrient uptake according to the requirements of the plant as a whole, is acceptable as a generalization for N, P and K. The external concentration which allows nutrient uptake at the required rate is negligibly small for N and K; for P it is negligibly small at higher root length densities. For water uptake, a constant hydraulic conductivity of roots is assumed. Differences in uptake capabilities among age categories of roots are assumed to be negligible.

Under conditions of a continuous and optimum supply of water and nutrients to the root surface the uptake capacity of the roots per unit surface area will determine the total root surface area required for maximum plant growth. This situation, which may occur in modern horticulture on artificial substrates, is analysed in chapter 4. Physiological limits to the shoot/root ratio appear to be determined by the entry resistance for water into roots and not by possibilities for nutrient uptake. Tomato and cucumber differ in a number of the parameters of the water balance and hence in minimally required root surface area.

Chapter 5 considers the synchronization requirements for nutrition in modern horticulture with a very small buffering capacity of the root environment. It is concluded from a simple theory that the present combination of small root systems and low nutrient use efficiencies in horticulture is not

a necessity; the low buffering capacity of such a system, however, makes a sophisticated regulation of external nutrient supply necessary in order to obtain reasonable nutrient use efficiencies.

In chapter 6 the geometry of the soil - root system is considered and literature on root length densities and root area index in the field for various crops is reviewed. The main geometrical situations to be considered in subsequent chapters for solving the general transport equation are described. The simple cylindrical geometry usually assumed in models of nutrient uptake by roots - a regularly distributed parallel root system in complete contact with soil - may serve as a theoretical reference situation; in practice considerable variation occurs in root distribution and soil - root contact.

Chapter 7 describes mobility and availability of water and nutrients in the soil and formulates the general transport equation to be solved. Availability of water and nutrients is defined by reference to a hypothetical root system of infinitely high root length density. The uptake capacity of a root system of finite density and given distribution is a fraction of the total available pool. The uptake capacity of a root system consists of two parts: an "unconstrained" part, and a "constrained" part. In the unconstrained part the plant can take up at the required rate; in the constrained part the rate of transport towards the root limits the uptake rate. In chapters 9 to 11 we concentrate on the unconstrained uptake period, in chapter 12 and 14 the constrained uptake after and before the period of unconstrained uptake is discussed.

In chapter 8 aeration requirements of roots in soil are formulated for various degrees of soil - root contact and for various degrees of air-filled root porosity, allowing longitudinal transport of oxygen inside the root. The percentage of air-filled pores in the root is an important parameter for root growth in soils of inadequate external aeration.

In chapter 9 diffusion and mass flow of nutrients in a simple, cylindrical soil - root geometry is considered during the unconstrained uptake period. The general transport equation can be solved analytically for constant daily uptake in the case of linearly adsorbed nutrients. The constant uptake leads to a concentration profile in the soil which approaches to a steady-rate profile, in which the decrease in concentration is independent of both time and distance to the root. The adsorption constant of a nutrient in the soil largely determines which root length density is required to effectively deplete available nutrient resources in the soil. The steady-rate solution is used to derive simple approximations for the more complex problems in the case of non-linearly adsorbed nutrients and for water transport. Water content of the soil has a considerable effect on nutrient uptake capacity of a root system, because of its influence on the diffusion coefficient of nutrients in soil. When potential uptake rates of roots of various diameters are compared, root length and root surface area form a better basis for comparison than root volume.

In chapter 10 the effects of variation in soil-root contact on transport of water and nutrients to the root are considered in the steady-rate situation. The higher the adsorption constant, the motre severe are the consequences of incomplete soil-root contact.

In chapter 11 effects of variation in root distribution pattern are described. Root distribution patterns in the field, which usually differ from regular or random patterns, may have significant effects on the average root length density required to meet a certain demand of the crop, especially for homogeneously distributed nutrients with a high adsorption constant in the soil. The uptake potential of a heterogeneous root system is analysed for an "optimum" distribution of total demand over all roots present.

When the nutrient demand by the crop cannot be met by the soil - root system, subsequent uptake by the root can be described as a zero-sink process. In chapter 12 a solution to the diffusion equation for zero-sink uptake is derived and used to calculate uptake capacity of root systems in the period of constrained uptake, when uptake is lower than the demand of the crop. The solution can be approximated fairly well by a sequence of steady-rate solutions. Time-dependent uptake now becomes proportional to the average nutrient concentration in the soil. The approximation is used to calculate a minimum of the uptake potential of non-regularly distributed roots; this minimum does not differ much from the maximum uptake potential calculated in chapter 11. Depletion by a non-growing root system is compared with that of a growing root system, with the same time-averaged root density (root area duration); the growing root system has a higher uptake capacity.

In chapters 13 and 14 two applications of the general model are discussed in relation to experimental results on N-uptake by crops in the humid tropics (chapter 13) and on the P-uptake by grass (chapter 14). Model calculations on the nitrogen balance for conditions of continuous leaching during the growing season in the humid tropics showed a reasonable agreement between N-uptake, as predicted on the basis of observed root distribution, and actually measured uptake. Practical possibilities for increasing nutrient use efficiency by better synchronization and synlocalization of nutrient supply in relation to nutrient demand by the crop are discussed.

Experiments on the P-uptake by grasses showed that, when P is a growth-limiting factor, P-uptake per unit root length, averaged over the whole root system, agrees with predicted values for zero-sink uptake on the same soil at the same moisture content; at higher P-supply, uptake per unit root length is lower than that by a zero-sink. A comparison of two clones of *Lolium perenne* which differ in root development at approximately equal shoot production, showed that faster root development leads to higher P-uptake at equal P-uptake per unit root length; thus a lower P-status of the soil may be sufficient. In a comparison of P-uptake by grasses from four different profiles, the importance of moisture content for P-uptake is discussed: from a P-rich layer at 15-20 cm depth, the same P-uptake was possible as from a P-rich layer at 0-5 cm depth, as differences in water regime between these layers compensated for a threefold difference in root length density.

In chapter 15 indices of soil fertility are discussed; the question is raised to which extent our present theory may explain observations of the relative depletion of soil water and nutrient reserves by various crops at normal values of the root area index for these crops. The possibilities and limitations of indices, which allow an interpretation of possible uptake independent of soil type, are discussed. For any given value of demand per unit root length, such indices can be constructed for P and K, but they will have little validity for other demand values.

Optimization of the root system is considered in chapter 16; optimization is required as aeration and uptake of water and nutrients are affected in opposite directions by variation in degree of soil/root contact and as internal oxygen transport in roots and uptake put opposite demands on root diameter. The amount of extra water which becomes available by having more roots has to be balanced by the carbon costs of making and maintaining more roots.

In a number of situations better root systems, obtained by plant breeding and/or manipulation of the root environment may lead to higher nutrient use efficiencies of both the crop and the farming system.

WORTELS, PLANTENGROEI EN EFFICIENT NUTRIEENTGEBRUIK

SAMENVATTING

Dit proefschrift behandelt de rol die de beworteling van gewassen speelt bij gewasgroei en bij de efficiëntie van nutriëntgebruik, als bijdrage aan een kwantitatieve theorie over bodemvruchtbaarheid. Afstemming van het nutriëntenaanbod op de behoefte van het gewas qua hoeveelheid, tijd en plaats kan leiden tot efficiënter meststoffengebruik; hiervoor is kwantificering van de benutting door wortelstelsels van het "beschikbare" aanbod van water en meststoffen noodzakelijk.

Als uitgangspunt is gekozen voor de theorie over het "functioneel evenwicht" tussen wortel- en spruitgroei. Groei van wortel en spruit wordt volgens deze theorie bepaald door het succes waarmee het complementaire orgaan de benodigde grondstoffen uit het milieu kan opnemen, via het blad- en het worteloppervlak. In dit proefschrift trachten we de relatie tussen totaal worteloppervlak (en/of wortellengte) en opnamemogelijkheden voor water en nutriënten te kwantificeren.

In veel gevallen beperkt de snelheid waarmee transport naar de wortel via diffusie en massastroming mogelijk is de opnamemogelijkheden van het gewas. Wiskundige beschrijving en oplossing van dit transportprobleem is een belangrijk onderdeel van dit proefschrift, zoals wordt geschetst in hoofdstuk 1. In tegenstelling tot de thans gangbare modelbeschrijvingen gaan wij uit van een volledige interne regulatie van de opnamesnelheid door de plant: zolang het aanbod toereikend is veronderstellen we dat de behoefte van het gewas de opname bepaalt. Een consequentie van deze aanname is dat individuele wortels in een uitgebreider wortelstelsel een lagere opnamesnelheid vertonen. Tijdens de lineare groeifase van het gewas is er vaak een aanzienlijke periode waarin de dagelijkse nutriëntenbehoefte van het gewas constant is.

De diverse aannames in ons model worden besproken in de eerste hoofdstukken. In hoofdstuk 2 wordt het functioneel evenwicht tussen spruit en wortel besproken en geplaatst tegenover oudere concepten zoals het morfogenetisch evenwicht tussen spruit- wortel. In hoofdstuk 3 worden fysiologische aspecten van water- en nutriëntenopname door wortels en de door ons gehanteerde aannames daarover beschreven. Interne regulatie van de opnamesnelheden door de plant is aanvaardbaar als algemene beschrijving van N-, P- en K-opname. De concentratie aan de wortelwand die nodig is om de vereiste opnamesnelheden te handhaven is verwaarloosbaar klein voor N en K; voor P is deze concentratie verwaarloosbaar bij grotere worteldichtheden. We nemen aan dat de watergeleidbaarheid van wortels constant is. Verschillen in fysiologische opnamemogelijkheden tussen wortels van verschillende leeftijd worden verwaarloosbaar geacht.

Bij voortdurend optimaal aanbod van water en nutriënten zullen de maximale opnamesnelheden bepalend zijn voor de vereiste omvang van het wortelstelsel. Deze situatie, die in de moderne tuinbouw bij substraatteelt voorkomt, wordt geanalyseerd in hoofdstuk 4. Fysiologische grenzen aan de spruit/wortel verhouding blijken bepaald te worden door de intreeweerstand voor water in de wortel en niet door mogelijkheden tot nutriëntenopname. Tomaat en komkommer verschillen in een aantal parameters van de waterbalans en daarmee in het minimaal vereiste worteloppervlak.

In de praktijk van de substraatteelt in de tuinbouw, met een geringe buffercapaciteit van het wortelmilieu, is een goede synchronisatie van nutrientenaanbod en de behoefte van het gewas noodzakelijk (hoofdstuk 5). De huidige combinatie van een geringe wortelomvang en een geringe efficiëntie van het meststofverbruik berust niet op een oorzakelijk verband: bij een verfijnd regelsysteem voor de nutriëntentoediening kan ook bij een geringe wortelomvang een redelijke efficiëntie worden bereikt.

In hoofdstuk 6 wordt de geometrie van het bodem-wortel-systeem besproken en worden literatuurwaarden vermeld van wortellengtedichtheid, totaal worteloppervlak in het veld en specifieke wortellengte. De diverse geometrische situaties worden beschreven waarvoor in latere hoofdstukken de transportvergelijkingen worden opgelost. De simpele cylindergeometrie die doorgaans wordt gebruikt in modelbeschrijvingen van nutriëntenopname, overeenkomende met regelmatig verdeelde, parallele wortels in volledig contact met de grond, kan dienen als theoretisch uitgangspunt; in de praktijk komt echter aanzienlijke variatie voor in wortelverdeling en de mate van contact tussen wortel en grond.

In hoofdstuk 7 worden mobiliteit en beschikbaarheid van water en nutriënten in de bodem besproken en wordt de algemene transportvergelijking gepresenteerd. Beschikbaarheid van water en nutriënten wordt gedefinieerd op basis van een hypothetisch wortelstelsel met oneindig grote bewortelingsdichtheid. De opnamecapaciteit van een wortelstelsel met eindige bewortelingsdichtheid en gegeven wortelverdeling is een deel van de totale beschikbare voorraad. Een deel van de totale opnamecapaciteit van een wortelstelsel kan met de vereiste snelheid door het gewas worden opgenomen, het "niet-beperkt beschikbare" deel; bij een ander deel beperkt de aanvoersnelheid de opnamemogelijkheden. In de hoofdstukken 9 tot en met 11 wordt de periode van niet-beperkte opname besproken, in de hoofdstukken 12 en 14 de periode van beperkte opname na en voor de periode van niet-beperkte opname.

In hoofdstuk 8 worden de eisen geformuleerd die aan de externe zuurstofconcentratie gesteld moeten worden voor een goede zuurstofvoorziening van het wortelstelsel, bij variatie in de mate van contact tussen wortel en grond en bij variatie in luchtgevulde porositeit van de wortels. Het percentage luchtgevulde poriën in de wortel is belangrijk voor het longitudinaal zuurstoftransport in de wortel en daarmee voor de wortelgroei in gronden met onvoldoende externe aëratie.

In hoofdstuk 9 worden diffusie en massastroming van nutriënten in een simpele, cylindrische geometrie besproken tijdens de periode van niet-beperkte opname. De algemene transportvergelijking kan analytisch opgelost worden bij constante dagelijkse opname voor lineair geadsorbeerde nutriënten. De constante dagelijkse opname leidt tot een concentratieprofiel dat nadert tot een "constante snelheid" ("steady rate") profiel, waarin de concentratiedaling in de cylinder grond voor alle plaatsen gelijk is en constant is in de tijd. De adsorptieconstante voor een nutriënt in de grond bepaalt grotendeels welke bewortelingsdichtheid nodig is voor een effectieve benutting van de beschikbare voorraad in de grond. De constante-snelheids-oplossing kan gebruikt worden voor simpele benaderende berekeningen voor de complexere problemen bij niet-lineair geadsorbeerde nutriënten en bij watertransport. Het vochtgehalte van de grond heeft een aanzienlijke invloed op de opnamemogelijkheden voor nutriënten, doordat het de diffusiecoëfficiënt beïnvloedt. Bij een beoordeling van de opnamemogelijkheden door wortels van verschillende diameter blijken wortellengte en worteloppervlak beide een betere vergelijkingsbasis te geven dan wortelvolume.

In hoofdstuk 10 wordt de invloed beschreven van de mate van contact tussen wortel en grond op de opnamemogelijkheden voor water en nutriënten bij transport met constante snelheid. De gevolgen van onvolledig contact tussen wortel en grond zijn des te groter, naarmate de adsorptieconstante hoger is.

In hoofdstuk 11 wordt het effect besproken van variatie in het verspreidingspatroon van wortels. Verspreidingspatronen in het veld, die veelal afwijken van regelmatige of toevallige patronen, kunnen een aanzienlijke invloed hebben op de worteldichtheid die nodig is om aan een bepaalde gewasbehoefte te voldoen, vooral voor homogeen verdeelde nutriënten met een hoge adsorptieconstante in de grond. De opnamemogelijkheden voor niet-regelmatig verdeelde wortels wordt geanalyseerd bij een "optimale" verdeling van de opnamebehoefte over de aanwezige wortels.

Als aan de opnamebehoefte van een gewas niet meer voldaan kan worden door het bodem-wortel-systeem, kan de dan nog mogelijke opname worden beschreven als "nul-put" - proces ("zero-sink") aangezien de concentratie aan de wortelwand nagenoeg op nul gehouden wordt door de wortel. In hoofdstuk 12 wordt een oplossing afgeleid voor de diffusievergelijking voor een nul-put; deze oplossing wordt gebruikt voor het berekenen van opnamemogelijkheden in de periode van beperkte opname. De oplossing kan met redelijk succes worden benaderd met een opeenvolging van constante-snelheid profielen. De opname is nu tijdsafhankelijk en evenredig met de gemiddelde concentratie in de grond. De benaderende oplossing wordt gebruikt voor een berekening van een ondergrens aan de opnamemogelijkheden van niet-regelmatig verdeelde wortels; de op deze wijze berekende ondergrens verschilt weinig van de in hoofdstuk 11 berekende bovengrens. Opnamemogelijkheden van een groeiend wortelstelsel blijken groter dan die van een constant wortelstelsel van dezelfde over de tijd gemiddelde worteldichtheid.

In de hoofdstukken 13 en 14 worden twee toepassingen van het algemene model besproken in verband met proefresultaten over stikstofopname door gewassen in de humide tropen (hoofdstuk 13) en fosfaatopname door grassen (hoofdstuk 14). Modelberekeningen over de stikstofopname op grond van gemeten wortelverdeling en bodemeigenschappen, bij voortdurende uitspoeling van stikstof ten gevolge van een neerslagoverschot tijdens het groeiseizoen in de natte tropen, bleken redelijk in overeenstemming te zijn met de in proeven gemeten opname. Door een betere afstemming van het stikstofaanbod qua tijd en plaats (synchronisatie en synlocalisatie) aan de behoefte van het gewas en de beworteling, moet het in de praktijk mogelijk zijn de efficiëntie van meststofverbruik aanzienlijk groter te maken.

Proeven over de fosfaatopname van grassen toonden aan dat, in het geval dat het fosfaataanbod aan de wortel limiterend is, de fosfaatopname per eenheid wortellengte overeenkomt met voorspelde waarden voor een nul-put bij dezelfde fosfaattoestand en vochtgehalte van de grond; bij hoger P-aanbod is de feitelijke opname lager dan de maximaal mogelijke. Een vergelijking van twee klonen Engels raaigras (Lolium perenne) die verschillen in wortelontwikkeling bij nagenoeg gelijke bovengrondse produktie, toonde dat een snellere wortelontwikkeling tot verhoogde P-opname leidde (bij nagenoeg constante P-opname per eenheid wortellengte) en daarmee tot een lagere eis aan de fosfaattoestand van de grond. Mogelijkheden tot fosfaatopname door grasland bij vier typen profielopbouw bleken samen te hangen met het vochtgehalte: uit een fosfaatrijke laag op 15-20 cm diepte kan evenveel fosfaat worden opgenomen als uit een fosfaatrijke laag op 0-5 cm doordat verschillen in vochthuishouding tussen deze lagen een drievoudig verschil in worteldichtheid kunnen compenseren.

In hoofdstuk 15 worden indices voor bodemvruchtbaarheid besproken; nagegaan wordt in hoeverre met de thans beschikbare theorie verschillen tussen gewassen in de mate van benutting van de beschikbare voorraad water en nutriënten begrepen kunnen worden bij de voor die gewassen normale wortelontwikkeling. De mogelijkheden voor en beperkingen van indices voor bodemvruchtbaarheid die dezelfde betekenis hebben voor de mogelijke opname, onafhankelijk van de grondsoort, worden aangegeven. Voor elke gegeven waarde van de opnamebehoefte per eenheid wortellengte blijkt het mogelijk zo'n index te ontwikkelen voor fosfaat en kalium, maar deze indices zullen weinig waarde hebben voor andere opnamebehoeftes.

Optimalisering van het wortelstelsel wordt besproken in hoofdstuk 16; compromissen zijn nodig aangezien zuurstofvoorziening en opnamemogelijkheden voor water en nutriënten tegengestelde eisen stellen aan de wortel. Tegenover de extra hoeveelheid water die het gewas op kan nemen bij grotere worteldichtheid staan de koolhydraatkosten van het aanmaken en onderhouden van meer wortels. In een aantal gevallen zal een betere beworteling, verkregen door plantenveredeling en beïnvloeding van het wortelmilieu, kunnen leiden tot een efficiënter meststoffenverbruik door het gewas en door landbouwsystemen in bredere zin.

LIST OF SYMBOLS USED IN THE MAIN TEXT

I symbol, II first page and equation where symbol is used, III name, IV dimension.

I	II		III	IV
A_{ra}	38	(3.4)	root area index	
$A_{r,n}$	48	(4.1)	required minimum root surface per plant for nutrient uptake	m^2
A_i	48	(4.1)	atomic weight constituent i	g/mol
$A_{r,w}$	48	(4.2)	required root surface per plant for water uptake	m^2
A_r	74	(6.1)	root surface area	m^2
A_{rp}	74	(6.1)	root surface area per plant	m^2
A_1,A_2	96	(7.1)	parameters Langmuir adsorption equation	mg/cm^3
A	120	(9.3)	nutrient uptake rate	kg/(ha.day) $mg/(cm^2.day)$
A_T	186	(12.11)	total demand	kg/(ha.day)
B_1,B_2	96	(7.1)	parameters Langmuir adsorption equation	ml/mg
C_i	11		initial concentration of nutrient	mg/ml
C_{lim}	11		limiting concentration	μmol/l
C_{min}	36		minimum concentration (compensation point)	μmol/l
C_0	39		concentration at root surface	mol/l
C_s	63		concentration nutrient in solution	mol/l
C_u	63		uptake concentration	mol/l
$C_s(h)$	69		highest C_s	mol/l
$C_s(\ell)$	69		lowest C_s	mol/l
$C_s(d)$	69		desired C_s	mol/l
C_n	70	(5.5)	concentration of the replenishment nutrient in solution	mol/l
C	96	(7.1)	concentration substance in fluid	mg/cm^3
C_a	96	(7.1)	bulk density adsorbed nutrient	mg/cm^3
C_ℓ	102	(7.18)	concentration O_2 in liquid phase	mg/cm^3

C_A	107	(8.5)	concentration O_2 in atmosphere	mg/cm^3
C_{so}	107	(8.6)	concentration O_2 in soil atmosphere	mg/cm^3
D_2	82	(6.16)	two-dimensional distance	cm
D_3	83	(6.18)	three-dimensional distance	cm
D	99	(7.5)	diffusion coefficient	cm^2/day
D_w	100	(7.11)	soil water diffusivity	cm^2/day
$D_{w,s}$	100	(7.12)	soil water diffusivity at saturation	cm^2/day
D^*	101	(7.16)	effective diffusion coefficient	cm^2/day
D_ℓ	103	(7.21)	diffusion coefficient O_2 in liquid phase	cm^2/day
D_Z	107	(8.3)	diffusion coefficient O_2 root in longitudinal direction	cm^2/day
D_R	107	(8.3)	diffusion coefficient O_2 root in radial direction	cm^2/day
D_s	107	(8.7)	diffusion coefficient O_2 in soil	cm^2/day
D_0	136	(9.46)	diffusion coefficient of nutrient in free water	cm^2/day
$D_{w,i}$	147	(9.69)	initial water diffusivity	cm^2/day
$\bar{D}_w$	147	(9.69)	average water diffusivity	cm^2/day
E	31	(3.4)	transpiration rate	ml/(cm^2.day)
E_p	48	(4.2)	transpiration rate per plant	l/hr, cm^3/day
E_1	172	(11.1)	exponential integral	
F_w	38	(3.1)	volume flux of water	cm^3/(cm^2.day)
F_{s*}	38	(3.2)	active solute flow across membrane	mol/(cm^2.day)
F_{max}	48	(4.1)	maximum uptake rate	mol/(m^2.day)
F_r	74	(6.2)	root fresh weight	g
$\vec{F}$	99	(7.2)	flux of substance	mg/(cm^2.day)
$\vec{F}_C$	99	(7.3)	convective flux	mg/(cm^2.day)
$\vec{F}_D$	99	(7.3)	diffusive flux	mg/(cm^2.day)
F_R	109	(8.17)	radial flow O_2 into root	mg/day
F_Z	110	(8.19)	vertical flow O_2 into root	mg/day

$G(\rho,0)$	125	(9.19)	function	
$G(\rho,\nu)$	130	(9.29)	function	
$H_{p,p}$	39		pressure head of water in plant	MPa
$H_{p,s}$	39		pressure head of soil water	MPa
H_p	100	(7.8)	pressure head of water	cm^3/cm^2
H	120	(9.3)	root length	cm
I_{max}	11		maximum uptake rate	mol/(cm.s)
I_0, I_1	109	(8.13)	modified Bessel functions of the first kind	
J_o, J_i	124	(9.15)	Bessel functions	
K_m	26		Michaelis-Menten parameter	mol/cm^3
K_a	36		adsorption constant	ml/cm^3
K_w	99	(7.7)	hydraulic conductivity	$day.cm^3/mg$
K_H	100	(7.8)	hydraulic conductivity	cm/day
$K_{a,0}$	152	(9.52)	adsorption constant at the surface of the root	ml/cm^3
$K(V_w)$	234	(15.4)	amount of potassium extracted from soil by water, V_w ratio water/soil	mg/dm^3
L_{rv}	23		root length / unit soil volume	cm/cm^3
L_p	38	(3.2)	hydraulic conductance of root	$cm^3/(cm^2.bar.s)$
L_r	74	(6.1)	root length	cm
L_{rp}	77	(6.7)	root length / plant	cm
L_{ra}	77	(6.7)	root length / unit soil area	cm/cm^2
$L_r(e)$	80	(6.9a)	root intensity at end of season	cm/cm^2
$L_n(e)$	80	(6.9a)	cumulative new root length	cm/cm^2
$L_t(e)$	80	(6.9a)	cumulative total root length	cm/cm^3
$L_d(e)$	80	(6.9a)	cumulative length of decayed roots	cm/cm^3
L	107	(8.6)	conductance of root wall for oxygen	cm/day

M_v, M_g	48	(4.1)	required composition of vegetative (v) and generative (g) dry matter	g/g
$M_{d,r}$	74	(6.2)	dry matter content of roots	g/cm^3
M_ℓ	99	(7.7)	volumic mass of soil solution	mg/cm^3
M_w	99		volumic mass of water	mg/cm^3
M_{so}	136		bulk density of soil	g/cm^3
M_r	225	(14.1)	required composition of root dry matter	mg/g
M_s	225	(14.1)	required composition of shoot dry matter	mg/g
N_s	3		available nutrient supply by soil	kg/ha
N_a	3		addition to available pool by fertilization	kg/ha
N_{a*}	3		applied amount of nutrients in fertilizer or manure	kg/ha
N_u	3		nutrient uptake by the crop	kg/ha
$N_{e,p}$	3		pool of potential nutrient losses	kg/ha
N_p	48	(4.1)	plant density	./ha
N_ℓ	69	(5.1)	leached amount of nutrients	kg/ha
N_x,N_y,N_z	81	(6.10)	number of roots on 3 perpendicular planes	$./cm^2$
N_m	81	(6.10)	$N_m = 1/3\ (N_x+N_y+N_z)$	$./cm^2$
N_T	186	(12.11)	total amount of roots	
N_{pl}	200	(13.1)	amount of nitrogen in the crop	kg/ha
N_c	200	(13.1)	nitrogen content of the shoot	
$N_{c,o}$	201	(13.3)	optimum nitrogen content	
P_T	99	(7.7)	total soil water potential	$mg/(cm.day^2)$
P_m	99	(7.7)	matric potential	$mg/(cm.day^2)$
P_g	99	(7.7)	gravitational potential	$mg/(cm.day^2)$
Q_ν	133	(9.34)	unconstrained uptake capacity	mg/cm^3, kg/ha
RAD	6		Root area duration	
RAI	6		Root area index = A_{ra}	
R_g	38	(3.2)	gas constant	$cm^3.MPa/(K.mol)$

R_0	39		root radius	cm
R_1	39		radius soil cilinder	cm
$\bar{R}_0$	74	(6.3)	average root radius	cm
$\tilde{R}_0$	74	(6.4)	quadratic average root radius	cm
R	103	(7.21)	radial coordinate	cm
R_2	160	(10.7)	aggregate radius	cm
R_n	173	(11.3)	distance from nth root	cm
R_c	201	(13.3)	time constant	days
S_r	74	(6.2)	specific weight of non-airfilled root tissue	g/cm^3
S	98	(7.2)	bulk density of gas, solute or water in soil	mg/cm^3
S_i	125	(9.17)	initial available amount of nutrient	mg/cm^3
T_k	38	(3.2)	temperature	K
T	98	(7.2)	time	day
$T_{c,max}$	125	(9.17)	maximum period of unconstrained uptake	day
$T^*_{c,max}$	134	(9.38a)	,, ,, ,, ,, ,, ,with production	day
T_c	138	(9.45)	period of unconstrained uptake	day
U_a	77	(6.6)	unit soil area	cm^2/plant
U	98	(7.2)	production/consumption of O_2, nutrient or water	$mg/(cm^3.day)$
U^*	101	(7.16)	effective production/consumption rate	$mg/(cm^3day)$
$U(Z)$	106	(8.1)	volumetric respiration rate of the root	$mg/(cm^3day)$
U_0	107	(8.2)	constant respiration rate main part root	$mg/(cm^3day)$
U_s	107	(8.7a)	respiration rate soil	$mg/(cm^3day)$
U_r	225	(14.1)	uptake capacity per unit root length	mg/m
$V_{r,n}$	48		required root volume for nutrient uptake	cm^3
V_s	71		volume of nutrient solution per plant	cm^3
V_r	74	(6.1)	root volume	cm^3
$\vec{V}$	99	(7.4)	flux of fluid	cm/day

$\vec{V}^*$	101	(7.16)	effective flux of water	cm/day
V	120	(9.5)	flux of water	cm/day
V_w	234	(15.4)	volume ratio of water to soil used for extraction of nutrient	
W_a	69	(5.1)	input of water	m^3/ha
W_u	69	(5.1)	uptake of water	m^3/ha
W_ℓ	69	(5.1)	leaching of water	m^3/ha
Y_D	3		total yield of dry matter	kg/ha
Y_H	3		harvestable yield of matter	kg/ha
$Y_{H,M}$	3		maximum harvestable yield of dry mater	kg/ha
$Y_{D,v}$	48	(4.1)	production rate vegetative dry weight	kg/(ha.day)
$Y_{D,g}$	48	(4.1)	production rate generative dry weight	kg/(ha.day)
$Y_{D,r}$	74	(6.2)	root dry weight	kg/ha
Y_p	200	(13.1)	aboveground crop dry matter	kg/ha
Y_0, Y_1	124	(9.15)	modified Bessel functions	
Z_r	77	(6.8)	depth (length) root zone	cm
Z	99	(7.7)	depth below plain of reference	cm
Z_{max}	108		maximum length root	cm
Z_ℓ	107	(8.7a)	thickness aerobic layer in soil	cm

a_0, a_1	231	(15.1)	parameters Θ-f_ℓ relation
a_n	81	(6.10)	standardized anisotropy factor
b_w	100	(7.12)	parameter D_w-Θ equation
b	111	(8.25)	parameter D_s-ϵ_s relation
c_n	70	(5.5)	C_u/C_n
$c_{s,t}$	71	(5.6)	C_s/C_n
c	108	(8.9)	dimensionless concentration oxygen in root
c_s	108	(8.12)	dimensionless concentration oxygen in soil

$\hat{c}_{so}$	109	(8.15)	Fourier transform of c_{so}	
c	122	(9.11)	dimensionless nutrient concentration	
$\bar{c}$	127	(9.24)	dimensionless average concentration nutrient	
c^*	133	(9.35)	dimensionless nutrient concentration in case of production	
d	82	(6.16)	distance to nearest root	cm
d_w	105		thickness waterfilm on root	cm
f_B	106		fraction of root perimeter not in contact with soil air	
$f_{d,\nu}$	131	(9.32)	fractional depletion of nutrient	
$f^*_{d,0}$	134	(9.40)	fractional depletion with production	
f_ℓ	140	(9.46)	impedance factor	
g	99	(7.7)	gravitational acceleration	cm/day^2
k_g	102	(7.19)	Henry's constant for oxygen	
ℓ_n	70	(5.3)	leaching fraction of nutrients	
ℓ_w	70	(5.4)	leaching fraction of water	
ℓ_r	81	(6.14)	ratio between N_x and N_z	
m_r	131	(9.31)	contribution of massflow to plant demand	
n_R	160	(10.6)	number of roots per aggregate	
p	107	(8.2b)	ration respiration rate root tip to respiration rate in main part	
p_a	143	(9.51)	parameter in K_a-R relation	ml/cm^{3-q}
q	143	(9.51)	parameter in K_a-R relation	
r_ℓ	79	(6.9a)	root length replacement ratio	
r	108	(8.9)	dimensionless radial coordinate	
s_{tot}	184	(12.4)	total available nutrient	
s	122		dimensionless available amount	

t_ℓ	79	(6.9b)	root length turnover	
t	122		dimensionless time	
t_c	122		dimensionless period of unconstrained uptake	
$t_{c,max}$	122		maximum dimensionless period of unconstrained uptake	
t^*_c	134	(9.37)	same as t_c and $t_{c,max}$	
$t^*_{c,max}$	134	(9.38)	but with production	
u	108	(8.9)	dimensionless respiration rate	
u_0	109	(8.13)	dimensionless respiration rate of main part root	
$\hat{u}$	109	(8.16)	Fourier transformation of u	
w	146	(9.64)	matrix flux potential	
w_ℓ	149	(9.73)	limiting matrix flux potential	
z	108	(8.9)	dimensionless vertical coordinate	
z_ℓ	108		dimensionless thickness of the aerobic soil layer	
z_{max}	110	(8.24)	dimensionless maximum root length	

α	28		root absorbing power	m/day
β	122	(8.13)	dimensionless buffercapacity	
γ	109	(8.13)	dimensionless length of root tip	
γ_1	189	(12.24)	dimensionless growth rate of the root system	
Δ	146	(9.60)	dimensionless diffusivity	
ΔH_p	38	(3.2)	difference in pressure head between plant and root environment	MPa
ΔZ	107	(8.2a)	length root tip	cm
δ	147	(9.68)	small number	
ϵ_r	102	(6.2)	air-filled porosity of the root	
ϵ_s	102	(7.18)	gass-filled porosity of the soil	
ϵ_{r*}	106	(8.1)	effective porosity of the root	
ϵ	176		eccentricity of location of root	

η	122		dimensionless root length	
Θ	100	(7.10)	water content	ml/cm^3
Θ_s	100	(7.12)	saturated water content	ml/cm^3
$\Theta(H_{p,p})$	242		water content corresponding to limiting pressure head in plant	
θ	122	(9.60)	scaled water content	
κ	108	(8.9)	auxillary parameter, containing the ratio of longitudinal and radial diffusion coefficients of oxygen in the root.	
Λ	83	(6.18)	number of root tips per unit root length	
λ_r	81	(6.11)	correction factor	
λ	108	(8.12)	dimensionless conductance	
ν	122	(9.11)	dimensionless flux of water	
π_0	38	(3.2)	osmotic value nutrient solution	MPa
ρ	122	(9.12)	dimensionless radius of soil cilinder	
ρ_2	160	(10.8)	dimensionless radius of aggregate	
σ_r	38	(3.2)	reflection coefficient	
υ	122	(9.11)	dimensionless production rate	
υ_o	133	(9.36)	constant dimensionless production rate	
ϕ	122	(9.16)	dimensionless supply/demand parameter	
ϕ_w	146	(9.67)	dimensionless supply/demand parameter of water	
χ	178		shape factor	
ψ_{root}	38	(3.1)	water potential at root surface	MPa
ψ	155	(10.1)	polar coordinate	
ψ_1	86	(10.1)	contact angle root/soil	
Ω	38	(3.1)	resistance	MPa.day/cm
ω	122	(9.13)	dimensionless uptake rate	
$\vec{\nabla}$	98	(7.2)	gradient operator	
$\nabla.$	120	(9.4)	divergence operator	

REFERENCES

Abdul-Jabbar A S, D G Lugg, T W Sammis and L W Gay, 1984. A Field study of plant resistance to water flow in alfalfa. Agron J 76: 765-768.

Aboulroos S A and N E Nielsen, 1979. Effects of phosphorus placement in varying, confined volumes of soil on fineness and density of barley roots and the mean rate of nutrient uptake per root unit. Acta agric Scand 29: 331-336.

Abramowitz M and I Stegun, 1970. Handbook of mathematical functions. New York, Dover Publications 1046 pp.

Addiscott T M, 1982. Computer assessment of the N status during winter and early spring of soil growing winter wheat. In: T Batey, K Vlassak and L M J Verstraeten (eds), Assessment of the nitrogen status of the soils. University Press Leuven, Belgium, pp. 15-26.

Alberda Th, 1948. The influence of some external factors on growth and phosphate uptake of maize plants of different salt conditions. PhD thesis, University of Groningen, 59 pp.

Alblas J, 1984. Resultaten van diep losmaken van zavelgronden in Zuid-West Nederland 1978-1982. Proefst Akkerbouw Groenteteelt Vollegrond, Lelystad.

Alexander M, 1977. Introduction to soil microbiology, second ed. New York etc., Wiley and Sons, 467 pp.

Allison J C S, 1963. Use of the day-degree summation technique for specifying flowering times of maize varieties at different localities in Southern Africa. Rhod J Agric Res 1: 22-28

Allmaras R R, W W Nelson and W B Voorhees, 1975. Soybean and corn rooting in southwestern Minnesota: II. Root distributions and related water inflow. Soil Sci Soc Am Proc 39: 771-777.

Alston A M, 1980. Response of wheat to deep placement of nitrogen and phosphorus fertilizers on a soil high in phosphorus in the surface layer. Aust J Agric Res 31: 13-24.

Altemüller H J and Th Haag, 1983. Microskopische Untersuchungen an Maiswurzeln im ungestörten Bodenverband. Kali-Briefe (Büntehof) 16(6): 349-363.

Anderson W P and J C Collins, 1969. The exudation from excised maize roots bathed in sulphate media. J Exp Bot 20: 72-80.

Andrews R E and E I Newman, 1969. Resistance to water flow in soil and plant III. Evidence from experiments with wheat. New Phytol 68: 1051-1058.

Armstrong W and Wright E J, 1976. Radial oxygen loss from roots: the theoretical basis for the manipulation of flux data obtained by the cylindrical platinum electrode technique. Physiol Plant 35: 21-26.

Armstrong W, 1979. Aeration in higher plants. Adv Bot Res 7: 225-332.

Armstrong W and P M Beckett, 1985. Root aeration in unsaturated soil: a multi-shelled mathematical model of oxygen diffusion and distribution with and without sectoral wet-soil blocking of the diffusion path. New Phytol 100: 293-311.

Arora Y and Juo A S R, 1982. Leaching of fertilizer ions in a kaolinitic Ultisol in the high rainfall tropics: leaching of nitrate in filed plots under cropping and bare fallow. Soil Sci Soc Am J 46: 1212-1218.

Arya L M, G R Blake and D A Farrell, 1975. A field study of soil water depletion patterns of growing soybean root. III. Rooting characteristics and root extraction of soil water. Soil Sci Soc Am Proc 39: 437-444.

Atkinson D and S A Wilson, 1979. The soil-root interface and its significance for fruit tree roots of different ages. In: J L Harley and R Scott Russell (eds) The soil root interface. London, Academic Press, pp. 259-272.

Baan Hofman T and G C Ennik, 1980. Investigation into plant characters affecting the competitive ability of perennial ryegrass (Lolium perenne L.). Neth J Agric Sci 28: 97-109.

Baan Hofman T and G C Ennik, 1982. The effect of root mass of perennial ryegrass (Lolium perenne L.) on the competitive ability with respect to couchgrass (Elytrigia repens (L.) Desv.). Neth J Agric Sci 30: 275-283.

Bakker J W, F R Boone and P Boekel, 1984. Gasdiffusie coefficienten van een aantal Nederlandse gronden. Agric Univ Wageningen Vakgr Grondbewerking, intern report 20 pp.

Baldwin J P, P B Tinker and P H Nye , 1972. Uptake of solutes by multiple root systems from soil. II. The theoretical effects of rooting density and pattern on uptake of nutrients from soil. Plant Soil 36: 693-708.

Barber S A, 1962. A diffusion and massflow concept of soil nutrient availability. Soil Sci 93: 39-48.

Barber S A, 1978. Growth and nutrient uptake of soybean roots under field conditions. Agron J 70: 457-461.

Barber S A, 1984. Soil nutrient bioavailability: a mechanistic approach. New York, John Wiley, 398 pp.

Barley K P, 1970. The configuration of the root system in relation to nutrient uptake. Adv Agron 22: 159-201.

Barraclough P B and P B Tinker, 1981. The determination of ionic diffusion coefficients in field soils. I. Diffusion coefficients in sieved soils in relation to water content and bulk density. J Soil Sci 32: 225-236.

Barraclough P B and R A Leigh, 1984. The growth and activity of winter wheat roots in the field: the effect of sowing date and soil type on root growth of high-yielding crops. J Agric Sci Camb 103: 59-74.

Barraclough P B, 1987. Root growth of winterwheat under P deficiency conditions and modelling of P and K uptake. Rothamsted Exp Stn for 1986, Pt 1: 151-152.

Bear J, 1972, Dynamics of fluids in porous media. New York, American Elsevier Publ Comp, 764 pp.

Bergman W and P Neubert, 1976. Pflanzendiagnose und Pflanzenanalyse. Jena Fischer, 711 pp.

Beringer H, 1985. Adequacy of soil testing for predicting fertilizer requirements. Plant Soil 83: 21-37.

Bird R B, W E Stewart and E N Lightfoot, 1960. Transport phenomena. New York, John Wiley and Sons, 780 pp.

Boekel P, 1962. Betekenis van organische stof voor de vocht- en luchthuishouding van zandgronden. Landbkd.Tijdschr 74: 128-135.

Boekel P, 1963. Soil structure and plant growth. Neth J Agric Sci. 11: 120-127.

Boekel P, 1974. De betekenis van de ontwatering voor de bodemstructuur op zavel- en lichte kleigronden en de financiële consequenties daarvan. Bedrijfsontwikkeling 5: 875-880.

Boekel P, 1982. Soil structure in modern agriculture. Proc. 9th Conf. Intern. Soil Tillage Research Organisation, Osiyek, Yugoslavia , pp. 402-408

Böhm W, 1979. Methods of studying root systems. Berlin, Springer-Verlag, 188 pp.

Bolt G H and M G M Bruggenwert, 1979. Composition of the soil. In: G H Bolt and M G M Bruggenwert (eds) Soil Chemistry A. Basic Elements: 1-11, Amsterdam, Elsevier 1976, 281 pp.

Boonstra A E H R, 1934. Physiologisch onderzoek ten dienste van de plantenveredeling. PhD Thesis, University of Utrecht. 99 pp.

Boonstra A E H R, 1955. Het begrip "wortelwaarde", In: De plantenwortel in de landbouw, Staatsuitgeverij, Den Haag ,pp. 107-118.

Boone F R and B W Veen, 1982. The influence of mechanical resistance and phosphate supply on morphology and function of maize roots. Neth J Agric Sci 30: 179-192.

Boone F R, 1986. Towards soil compaction limits for crop growth. Neth J Agric Sci 34: 349-360.

Borkert C M and S A Barber, 1983. Effect of supplying P to a portion of the soybean root system on root growth and P uptake kinetics. J Plant Nutr 6:

896-910.

Borkert C M and S A Barber, 1985. Soybean shoot and root growth and phosphorus concentration as affected by phosphorus placement. Soil Sci Soc Am J 49: 152-155.

Bray R H, 1954. A nutrient mobility concept of soil plant relationships. Soil Sci 78: 9-22.

Breeze V G, A Wild, M J Hopper and L H P Jones, 1984. The uptake of phosphate by plants from flowing nutrient solution. II. Growth of Lolium perenne L. at constant phosphate concentrations. J Exp Bot 35: 1210-1221.

Brewster J L and P B Tinker, 1972. Nutrient flow rates into roots. Soils Fert 35: 355-359.

Briggs L J and H L Shantz, 1921. The relative wilting coefficient for different plants. Bot Gaz (Chicago) 53: 229-235

Brouwer G and M Van Noordwijk, 1978. Het met zoutzuur vrijspoelen van wortels uit steenwol en het effect daarvan op het wortelgewicht. (With a summary; Separation of roots from rockwool by means of washing with HCL and the effect thereof on root weight). Inst Bodemvruchtbaarheid, Rapp. 4-78. 11 pp.

Brouwer R, 1954. The regulating influence of transpiration and suction tension on the water and salt uptake by the roots of intact Vicia faba plants. Acta Bot Neerl 3: 264-312.

Brouwer R, 1963. Some aspects of the equilibrium between overground and underground plant parts. Jaarb. IBS, Wageningen, pp. 31-39.

Brouwer R, 1983. Functional equilibrium: sense or nonsense? Neth J Agric Sci 31: 335-348.

Brouwer R and L K Wiersum, 1977. Root aeration and crop growth, In: U S Gupta (ed.), Crop physiology vol II. New Delhi, Oxford Univ. Press and IBH Publ. comp., pp. 157-201.

Brown D A and H D Scott, 1984. Dependence of crop growth and yield on root development and activity. ASA Special Publication Number 49 Roots, nutrient and water influx, and plant growth. American Society of Agronomy, Madison.

Brown E A, C E Caviness and D A Brown, 1985. Response of selected soybean cultivars to soil moisture deficit. Agron J 77: 274-278.

Brown K F and P V Biscoe, 1985. Fibrous root growth and water use of sugar beet. J Agric Sci Camb 105: 679-691.

Broyer T C and D R Hoagland, 1943. Metabolic activities of roots and their bearing on the relation of upward movements of salts and water in plants. Am J Bot 30: 261-273.

Buckingham E, 1904. Contributions to our knowledge of the aeration of soils. U S Bur Soils Bull 25.

Burch J G, 1979. Soil and plant resistance to water absorbtion bij plant root systems. Aust J Agric Res 30: 279-292.

CAD, 1984. Adviesbasis voor bemesting van landbouwgronden. Consul. Bodemaangelegenheden in de Landbouw, Wageningen.

Cannell R Q, D G Christian and F K G Henderson, 1986. A study of mole drainage with simplified cultivation for autumn-sown crops on a clay soil. 4. A comparison of direct drilling and mouldboard ploughing on drained and undrained land on root and shoot growth, nutrient uptake and yield. Soil Tillage Res 7: 251-272.

Caradus J R and R W Snaydon, 1986. Plant factors influencing phosphorus uptake by white clover from solution culture. Plant Soil 93: 153-163.

Carslaw H S and J C Jaeger, 1959. Conduction of heat in solids, second ed. Oxford, Clarendon, 510 pp.

Cerda A and J P N L Roorda van Eysinga, 1981. Tomato plant growth as affected by horizontally unequal osmotic concentrations in rockwool. Neth J Agric Sci 29: 189-197.

Chaudhary T N and K S Sandu, 1983. Soil physical environment and root growth. Adv Soil Sci, New Delhi. pp. 1-43.

Churchill R V, 1972. Operational mathematics, third ed. Tokyo etc, McGraw-

Hill-Kogakusha, 481 pp.

Churchill R V, J W Brown, and R F Verhey, 1974. Complex variables and applications, third ed. Tokyo etc., McGraw-Hill-Kogakusha, 332 pp.

Clapp C E, T C Newman, G C Marten and W E Larson, 1984. Effects of municipal wastewater effluent and cutting management on root growth of perennial forage grasses. Agron J 76: 642-647.

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

Clarkson D T, 1985. Factors affecting mineral nutrient acquisition by plants. Ann Rev Plant Phys 36: 77-115.

Corey A T and A Klute, 1985. Application of the potential concept to soil water equilibrium and transport. Soil Sci Am J 49: 3-11.

Cowan I R, 1986. Economics of carbon fixation in higher plants. In Givnish Th J (ed.), On the economy of plant form and function. Cambridge, Cambridge Univ Press, pp. 133-170.

Cram W J, 1973. Internal factors regulating nitrate and chloride influx in plant cells. J Exp Bot 24: 328-341.

Crawford R M M, 1982. Physiological responses to flooding. In O L Lange, P S Nobel, C B Osmond and H Ziegler (eds.), Physiological plant ecology. II. Water relations and carbon assimilation. Encyclop. Plant Physiology 12B. Berlin, Springer, pp 453-478.

Cumbus I P, 1985. Development of wheat roots under zinc deficiency. Plant Soil 83: 313-316.

Dalton F N, P A C Raats and W R Gardner, 1975. Simultaneous uptake of water and solutes by plant roots. Agron J 67: 334-339.

Dalton F N and W R Gardner, 1978. Temperature dependence of water uptake by plant roots. Agron J 70: 404-406.

De Boer A H, 1985. Xylem/symplast ion exchange: mechanism and function in salt tolerance and growth. PhD Thesis, University of Groningen, 112 pp.

De Haan F A M, 1965. The interaction of certain inorganic anions with clays and soils. Wageningen, Pudoc, Agric Res Rep 655, 167 pp.

De Jager A, 1985. Response of plants to a localized nutrient supply. PhD Thesis, University of Utrecht, 137 pp.

De Willigen P, 1981. Mathematical analysis of diffusion and mass-flow of solutes to a root assuming constant uptake. Inst Bodemvruchtbaarheid, Rapp 6-81, 56 pp.

De Willigen P, 1985a. Modelling of transport, transformation and uptake of nitrogen in an Ultisol for high rainfall conditions. In: B T Kang and J van der Heide (eds.), Nitrogen management in farming systems in humid and subhumid tropics. Inst Bodemvruchtbaarheid and International Institute of Tropical Agriculture, Haren/ Ibadan, pp. 73-86.

De Willigen P, 1985b. Nitrogen supply by the soil in the growing season. In: H Lambers, J J Neeteson and I Stulen (eds.), Fundamental ecological and agricultural aspects of nitrogen metabolism in higher plants. Martinus Nijhoff, Dordrecht, pp. 417-432.

De Willigen P and M Van Noordwijk, 1978. Berekeningen over fosfaatopname door een gewas in afhankelijkheid van bewortelingsdichtheid en de fosfaatrijkdom van de grond. (With a summary: Calculations on P-uptake by crops in relation to rooting density and P-status of the soil). Inst. Bodemvruchtbaarheid. Rapp. 19-78, 63 pp.

De Willigen P and M van Noordwijk, 1984. Mathematical models on diffusion of oxygen to and within plant roots, with special emphasis on effects of soil-root contact. I. Derivation of the models. II. Applications. Plant Soil 77: 215-231, 233-241.

De Wit C T, 1953. A physical theory of fertilizer placement. PhD Thesis University of Wageningen. 71 pp.

De Wit C T, 1958. Transpiration and crop yields. Versl Landbouwkd Onderz

64.6, 88 pp.

De Wit C T, 1965. Photosynthesis of leaf canopies. Agr Res Rep 663, Pudoc, Wageningen. 57 pp.

De Wit C T, 1968. Plant production. Misc. Papers Landb. Hogesch. Wageningen 1968 No. 3, pp. 25-50.

De Wit C T and van Keulen H, 1972. Simulation of transport processes in soils. Simulation Monographs. Pudoc, Wageningen.

De Wit C T, 1978. Simulation of assimilation, respiration and transpiration of crops. Simulation monograph. Wageningen, Pudoc.

De Wit C T, H H Van Laar and H Van Keulen, 1979. Physiological potential of crop production. In: Plant breeding perspectives, Wageningen, Pudoc, pp. 47-82.

Deane-Drummond C E, 1986. A substrate cycling model for nitrate uptake by Pisum sativum seedlings: a key to sensitivity of response of net flux to substrate and effectors? In: H Lambers, J J Neeteson and I Stulen (eds.), Fundamental, ecological and agricultural aspects of nitrogen metabolism in higher plants. Dordrecht, Martinus Nijhoff, pp. 47-51.

Diggle P J, 1983. Statistical analysis of spatial point patterns. London etc., Academic Press, 148 pp.

Dijkshoorn W, D J Lathwell and C T De Wit, 1968. Temporal changes in carboxylate content of rye grass with stepwise change in nutrition. Plant Soil 29: 369-390.

Doorenbos J and A H Kassam, 1979. Yield response to water. Irrigation and drainage paper 33. FAO, Rome, 193 pp.

Drew M C, 1983. Plant injury and adaptation to oxygen deficiency in the root environment: a review. Plant Soil 75: 179-199.

Drew M C and J M Lynch, 1980. Soil anaerobiosis, microorganisms and root function. Annu Rev Phytopathol 18: 37-66.

Drew M C and L R Saker, 1980. Direct drilling and ploughing: their effects on the distribution of extractable phosphorus and potassium, and of roots in the upper horizons of two clay soils under winter and spring barley. J Agric Sci Camb 94: 411-423.

Drew M C and A Fourcy, 1986. Radial movement of cations across aerenchymatous roots of Zea mays measured by electron probe X-ray microanalysis. J Exp Bot 37: 823-831.

Drew M C and L R Saker, 1986. Ion transport to the xylem in aerenchymatous roots of Zea mays L. J Exp Bot 37: 22-33.

Drew M C, 1987. Function of root tissues in nutrient and water transport. In: P J Gregory, J V Lake and D A Rose (eds.), Root development and function. Cambridge, Cambridge University Press, pp. 71-101.

Dunlop J, 1974. A model of ion translocation by roots which allows for regulation by physical influences. In: R L Bieleski, A R Ferguson and M M Cresswell (eds.), Mechanisms of regulation of plant growth. R Soc N Z Bull 12: 133-138.

Dyer B, 1894. On the analytical determination of available "mineral" plant food in soils, J Chem Soc Trans 65: 115-167.

Ehlers W, B K Kosla, U Köpke, R Stulpnägel, W Böhm, K Bäumer, 1980. Tillage effects on root development, water uptake and growth of oats. Soil Tillage Res 1: 29-34

Ehlers W, U Köpke, F Hesse and Böhm, 1983. Penetration resistance and root growth of oats in tilled and untilled loess soil. Soil Tillage Res 3: 261-275.

Ehlert P A I, 1985. Betekenis van de fosfaat en kalitoestand van de onder de zode gelegen bodemlagen foor de fosfaat- en kalivoorziening van grasland. 1. Proefplekkenonderzoek op zandgrond. (With a summary: Phosphorus and potassium supply to the sward as affected by the phosphorus and potassium status of soil layers below the sod. 1. Survey of grassland on sandy soils). Inst Bodemvruchtbaarheid, Rapp. 11-85, 32 pp.

El Bassam N, 1983. Bedeutung der Wurzelforschung fur die Pflanzenzuchtung, insbesondere zur Identifikation von low-input Sorten. In: Wurzelokologie und ihre Nutzanwendung, Bundesanstalt Gumpenstein, Irdning, pp. 491-500.

Ennik G C and T Baan Hofman, 1983. Variation in the root mass of ryegrass types and its ecological consequences. Neth J Agric Sci 31: 325-334.

Epstein E, 1972. Mineral nutrition of plants: principles and perspectives. New York, John Wiley, 412 pp.

Evans G C, 1972. The quantitative analysis of plant growth. Oxford, Blackwell, 734 pp.

Faiz S M A and P E Weatherley, 1978. Further investigation into the location and magnitude of the hydraulic resistances in the soil:plant system. New Phytol 81: 19-28.

Feddes R A, 1986. Modelling and simulation in hydrologic systems related to agricultural development: state of the art. Proc Wat Man Agric Development, Greece.

Ferrari Th J, 1965. Naar een bodemvruchtbaarheid in dimensies. IB Gedenkboek 1890-1965, Haren, Inst v Bodemvruchtbaarheid, pp. 3-29.

Findenegg G R, M L van Beusichem and W G Keltjens, 1986. Proton balance of plants: physiological, agronomical and ecological implications. Neth J Agric Sci 34: 371-379.

Fiscus E L, 1975. The interaction between osmotic- and pressure induced water flow in plant roots. Plant Physiol 55: 917-922.

Fiscus E L, 1977a. Effects of coupled solute and water flow in plant roots with special reference to Brouwer's experiment. J Exp Bot 28: 71-77.

Fiscus E L, 1977b. Determination of hydraulic and osmotic properties of soybean root systems. Plant Physiol 59: 1013-1020.

Fiscus E L and P J Kramer, 1975. General model for osmotic and pressure-induced flow in plant roots. Proc Nat Acad Sci USA 72: 3114-3118.

Floris J and M van Noordwijk, 1984. Improved methods for the extraction of soil samples for root research. Plant Soil 77: 369-372.

Follett R F, R R Allmaras and G A Reichman, 1974. Distribution of corn roots in sandy soil with a declining water table. Agron J 66: 288-292.

Fowkes N D and J J Landsberg, 1981. Optimal root systems in terms of water uptake and movement. In: D A Rose and D A Charles-Edwards (eds.), Mathematics and plant physiology. London, Academic Press, pp 109-125.

Frissel M J, P Poelstra and P Reiniger, 1970. Chromatographic transport through soils. III. A simulation model for the evaluation of the apparent diffusion coefficient in undisturbed soils with tritiated water, Plant Soil 33: 161.

Frissel M J (ed.), 1977. Cycling of mineral nutrients in agricultural ecosystems. Agro-ecosystenms 4: 1-354.

Garay A F and W W Wilhelm, 1983. Root system characteristics of two soybean isolines undergoing water stress conditions. Agron J 75: 973-977.

Gardner W R, 1964. Relation of root distribution to water uptake and availability. Agron J 56: 41-45.

Garwood E A and T E Williams, 1967. Growth, water use and nutrient uptake from the subsoil by grass swards. J Agric Sci Camb 69: 125-130.

Garwood E A and J Sinclair, 1979. Use of water by six grass species. 2. Root distribution and use of soil water. J Agric Sci Camb 93: 25-35.

Geddes R D, H D Scott and L R Oliver, 1979. Growth and water use by common cocklebur (Xanthium pensylvanicum) and soybeans (Glycine max) under field conditions. Weed Sci 27: 206-212.

Gilbert M A and A D Robson, 1984. The effect of sulfur on the root characteristics of subterranean clover and annual ryegrass. Plant Soil 77: 377-380.

Givnish Th J (ed.), 1986. On the economy of plant form and function. Cambridge, Cambridge University Press, 717 pp.

Glass A D M, 1975. The regulation of potassium absorption in barley roots.

Plant Physiol 56: 377-380.

Glass A D M, 1983. Regulation of ion transport. Ann Rev Plant Physiol 34: 311-326.

Glass A D M and M Y Siddiqi, 1984. The control of nutrient uptake rates in relation to the inorganic composition of plants. In: P B Tinker and A Läuchli (eds), Advances in plant nutrition vol 1, New York, Praeger, pp 103-147.

Goedewaagen M A J, 1932. De groei van het wortelstelsel der planten bij gelijke en ongelijke vruchtbaarheid van boven- en ondergrond. Versl Landbouwkd Onderz 38A: 179-199.

Goedewaagen M A J, 1937. The relative weight of shoot and root of different crops and its agricultural significance in relation to the amounts of phosphate added to the soil. Soil Sci 44: 185-202.

Goedewaagen M A J, 1942. Het wortelstelsel der landbouwgewassen. 's Gravenhage, Alg. Landsdrukkerij, 173 pp.

Goedewaagen M A J, 1954. Beoordeling van de vitaliteit van het wortelstelsel. Landbouwkd. Tijdschr 66: 553-5.

Goedewaagen M A J, 1955. De oecologie van het wortelstelsel der gewassen. In: De plantenwortel in de landbouw, Den Haag, Staatsuitgeverij, pp. 31-68.

Grable A R, 1966. Soil aeration and plant growth. Adv Agron 18: 58-101.

Gradsteyn I S and I M Ryzhik, 1965. Table of integrals, series, and products. New York etc., Academic Press, 1086 pp.

Greacen E L, P Ponsana and K P Barley, 1976. Resistance to water flow in the roots of cereals. In: O L Lange, L Kappen and E D Schulze (eds.), Water and plant life, problems and modern approaches. Berlin, Springer, pp. 86-100.

Greacen E L, 1977. Mechanisms and models of water transfer. In: J S Russell and E L Greacen (eds.), Soil factors in crop production in a semi-arid environment. St. Lucia, Univ. of Greenland Press, pp. 163-197.

Green P J and R Sibson, 1977. Computing Dirichlet tessellations in the plane. Computer J 21: 168-173.

Greenland D J, 1979. The physics and chemistry of the soil-root interface. In: J L Harley and R Scott Russel (eds.), The Soil-root Interface. London, Academic Press, pp. 83-98.

Greenwood D J, 1967. Studies on the transport of oxygen through the stems and roots of vegetable seedlings. New Phytol 66: 337-347.

Greenwood D J, 1969. Effect of oxygen distribution in the soil on plant growth. In: W J Whittington (ed.), Root Growth. Londen, Butterworths, pp 202-223.

Greenwood D J, J J Neeteson and A Draycott, 1985. Response of potatoes to N fertilizer: quantitative relations for components of growth. Plant soil 85: 163-183.

Gregory P J, M Mc Gowan, P V Biscoe and B Hunter, 1978. Water relations of winter wheat. 1. Growth of the root system. J Agric Sci Camb 91: 91-102.

Gregory P J, 1979. A periscope method for observing root growth and distribution in field soil. J Exp Bot 30: 205-214.

Grimme H, K Nemeth and L C von Braunschweig, 1971. Beziehungen zwischen dem Verhalten des Kaliums im Boden und der Kaliumernahrung der Pflanze. Landw Forsch Sonderh 26: 4-30.

Grimme H, 1974. Potassium release in relation to crop production. Proc. 10th Congr. Int. Potash Inst. Bern, pp. 131-136.

Grimes D W, R J Miller and P L Wiley, 1975. Cotton and corn development in two field soils of different strenght characteristics. Agron J 67: 519-523.

Grimes D W, W R Sheesley, and P L Wiley, 1978. Alfalfa root development and shoot regrowth in compact soil of wheel traffic patterns. Agron J 70: 955-958.

Hackett C, 1973. A growth analysis of the young sorghum root system. Aust J Sci 26: 1211-1214.

Hagan R H, Y Vaadia, M B Russell, D W Henderson and G W Burton, 1959. Soil-plant-water interrelations. Adv Agron XI: 77-118.

Hainsworth J M and L A G Aylmore, 1986. Water extraction by single plant roots. Soil Sci Soc Am J 50: 841-848.

Hairiah K and M Van Noordwijk, 1986. Root studies on a tropical ultisol in relation to nitrogen management, report of field work at IITA's high rainfall substation at Onne (Port Harcourt, Nigeria) in 1985 Inst. Bodemvruchtbaarheid, Rapp. 7-86, 116 pp.

Herkelrath W N, E E Miller and W R Gardner, 1977. Water uptake by plants. II. The root contact model. Soil Sci Soc Am Proc 41: 1039-1043.

Hewitt J S and A R Dexter, 1984. The behaviour of roots encountering cracks in soil. II. Development of a predictive model. Plant Soil 79: 11-28.

Hillel D, C van Beek and H Talpaz, 1975. A microscopic-scale model of soil water uptake and salt movement to plant roots. Soil Sci 120: 385-399.

Hillel D, 1980. Application of soil physics. New York etc., Academic Press, 385 pp.

Hissink D J, 1920. Bijdragen tot de kennis van de adsorptieverschijnselen in de bodem. VI. De methode ter bepaling van de adsorptief gebonden basen in de bodem en de beteekenis van deze basen voor de processen, die zich in de bodem afspelen. Versl. van Landbouwkd Onderz der Rijkslandbouwproefstations 24: 144-250.

Holford I C R and G E C Mattingly, 1975. A model for the behaviour of labile phosphate in soil. Plant Soil 44: 219-229.

Holford I C R and G E C Mattingley, 1976. Phosphate adsorption and plant availability of phosphate. Plant Soil 44: 377-389.

Hooper W D and H B Ash (translators), 1935. Marcus Porcius Cato On agriculture. London, Heinemann. 543 pp.

House C R and N Findlay, 1966. Analysis of transient changes in fluid exudation from isolated maize roots. J Exp Bot 17: 627-640.

Huck M G and H M Taylor, 1982. The rhizotron as a tool for root research. Adv Agron 35: 1-35.

Hunt R, 1982. Plant growth curves, the functional approach to plant growth analysis. London, Edward Arnold, 248 pp.

Itoh S and S Barber, 1983. Phosphorus uptake by six plant species as related to root hairs. Agron J 75: 457-461.

Janssen B H, F C T Guiking, D van der Eyk, E M A Smaling, J Wolf and H van Reuler, 1987. A system for quantitative evaluation of the fertility of tropical soils (QUEFTS). Submitted for publication in Geoderma.

Jenkinson D S and J H Rayner, 1977. The turnover of organic matter in some of the Rothamsted classical experiments. Soil Sci 123: 298- 305.

Jensen C R, R J Luxmoore, S D Gundy and L H Stolzy, 1969. Root air space measurements by a pycnometer method. Agron J 61: 474-475.

Jones H, A D Tomos, R A Leigh and R G Wyn Jones, 1983. Water-relation parameters of epidermal and cortical cells in the primary root of Triticum aestivum L. Planta 158: 230-236.

Jordan W R and F R Miller, 1980. In: N C Turner and P J Kramer (eds) Adaptation of plants to water and high temperature stress. New York, Wiley (Interscience). pp 383-399.

Jungk A, 1974. Phosphate uptake characteristics of intact root systems in nutrient solution as affected by plant species, age and P supply. Proc Int Colloq Plant Anal Fert Probl 1: 185-196.

Jungk A and S A Barber, 1974. Phosphate uptake rate of corn roots as related to the proportion of the roots exposed to phosphate. Agron J 66: 554-557.

Kamke E, 1943. Differentialgleichungen, Lösungsmethoden und losungen. Leipzig, Becker and Erler, 642 pp.

Kang B T, H Grime and T L Lawson, 1985. Alley cropping sequentially cropped maize and cowpea with Leucaena on a sandy soil in Southern Nigeria. Plant Soil 85: 267-277.

Keltjens W G, 1981. Absorption and transport of nutrient cations and anions in maize roots. Plant Soil 63: 39-46.

Kimball B A, 1983. Canopy gas exchange: gas exchange with soil. In H M Taylor, W R Jordan and T R Sinclair (eds.), Limitations to efficient water use in crop production. Wisconsin, Am Soc of Agron, pp 215-225.

Kirkham D and W L Powers, 1972. Advanced Soil Physics. New York etc. Wiley-Interscience, 534 pp.

Klepper B, H M Taylor, M G Huck and E L Fiscus, 1973. Water relations and growth of cotton in drying soil. Agron J 65: 307-310.

Klute A and D B Peters, 1968. Water uptake and root growth. in: W J Whittington (ed), Root Growth: proc fifth Easter school in agric sc, Univ of Nottingham, 1968, London, Butterworths, pp 105-133.

Köpke U, 1979. Ein Vergleich von Feldmethoden zur Bestimmung des Wurzelwachstums landwirtschaftlicher Kulturpflanzen. PhD Thesis, University of Göttingen.

Konings H, 1983. Formation of gas spaces (Aerenchyma) in seedling roots of Zea mays under aerated and non-aerated conditions. In: W Böhm, L Kutschera und E Lichtenegger (eds.) Wurzelokologie und ihre Nutzanwendung. Int. Symp. Gumpenstein 1982, Irdning, pp. 761-765.

Kristensen K J and E R Lemon, 1964. Soil aeration and plant root relations. III. Physical aspects of oxygen diffusion in the liquid phase of the soil. Agron J 56: 195-301.

Kuchenbuch R and S A Barber, 1987. Yearly variation of root distribution with depth in relation to nutrient uptake and corn yield. Comm Soil Sci Plant Nutr, (in press).

Kuilman L W, 1948. Rijst: grond en bemesting, anorganische voeding van het gewas, Omo mentek. In: C J Van Hall and C van de Koppel (eds) De landbouw in de Indische archipel. 's Gravenhage Van Hoeve, IIA, pp. 53-63.

Kuiper D, 1984. Genetic differentiation and phenotypic plasticity in Plantago species. PhD thesis University of Groningen. 126 pp.

Kuiper P J C, 1963. Water uptake of higher plants as affected by root temperature. Meded Landbouwhogesch Wageningen 64: 1-11.

Kutschera L and E Lichtenegger, 1982. Wurzelatlas Mitteleuropäischer Grünlandpflanzen. Band 1: Monocotyledonae. Stuttgart,Gustav Fischer. 516 pp.

Lal R, 1984. Soil erosion from tropical arable lands and its control. Adv Agron 37: 183-248.

Lambers H, 1983. "The functional equilibrium", nibbling on the edges of a paradigm. Neth J Agric Sc 31: 305-311.

Lambers H, 1987. Growth, respiration, exudation and symbiotic associations; the fate of carbohydrates translocated to the roots. In: P J Gregory, J V Lake and D A Rose (eds.), Root development and function. Cambridge, Cambridge University Press, pp 125-145.

Lamont B L, 1983. Strategies for maximizing nutrient uptake in two mediterranean ecosystems of low nutrient status. In: F J Kruger, D T Mitchell and J U M Jarvis (eds.), Mediterranean type ecosystems. Berlin, Springer, pp. 246-273.

Lang A R G and F M Melhuish, 1970. Lengths and diameters of plant roots in non-random populations by analysis of plane surfaces. Biometrics 26: 421-431.

Lawlor D W, 1973. Growth and water absorption of wheat with parts of the roots at different watere potentials. New Phytol 72: 297-305.

Leclercq J and J C Verbrugge, 1984. Approche the'orique de l' interaction me'canique entre une racine et le sol. Bull Rech Agron Gembloux 19: 37-50.

Lemon E R and C L Wiegand, 1962. Soil aeration and plant root relationts. II. Root respiration. Agron J 54: 171-175.

Logsdon S D, J C Parker and R B Reneau, 1987. Root growth as influenced by aggregate size. Plant Soil 99: 267-275.

Loneragan J F and C J Asher, 1967. Response of plants to phosphate concentration in solution culture. II. Rate of phosphate absorption and its relation to growth. Soil Sci 103: 311- 318.

Loneragan J F, 1978. The interface in relation to root function and growth. In: J L Harley and R. Scott Russell, The soil-root interface, London, Academic Press, pp. 351-367.

Lopez-Hernandez D and C P Burnham, 1974. The effect of pH on phosphate-adsorption. J Soil Sci 25: 207-217.

Lupton F G H, R H Oliver, F B Ellis, B T Barnes, K R Howse, P J Welbank and P J Taylor, 1974. Root and shoot growth of semidwarf and taller winterwheats. Ann. Appl. Biol. 77: 129-144.

Luxmoore R J, L H Stolzy and J Letey, 1970. Oxygen diffusion in the soil-plant system: I. A model. J Agron 62: 317-322.

Mackay A D and S A Barber, 1984. Soil temperature effects on root growth and phosphorus uptake by corn. Soil Sci Soc Am J 48: 818-823

Marriot F H C, 1972. Buffon's problem for non-random distribution. Biometrics 28: 621-624.

Marschner H, 1974. Mechanisms of regulation of mineral nutrition in higher plants. In: R L Bieleski, A R Ferguson and M M Cresswell (eds.), Mechanisms of regulation of plant growth. R Soc N Z, Bull 12: 99-109.

McCully M E and M J Canny, 1985. Localisation of translocated 14C in roots and root exudates of fieldgrown maize. Physiol Plant 65: 380-392.

McKeague J A, R G Eilers, A J Thomasson, M J Reeve, J Bouma, R B Grossman, J C Favrot, M Renger and O Strebel, 1984. Tentative assessment of soil survey approaches to the characterisation and interpretation of air-water properties of soils. Geoderma 34: 69-100.

Mead R, 1971. Models for interplant competition in irregularly spaced populations. In: G P Patil et al. (eds.), Penn State University Press, Statistical Ecology, vol. 2, pp. 13-30.

Melsted S W and T R Peck, 1973. The principles of soil testing. In: L M Walsh and J D Beaton, Soil testing and Plant analysis, rev. ed., Madison, Soil Sci Soc Am. pp. 13-23.

Mengel D B and S A Barber, 1974. Development and distribution of the corn root system under field conditions. Agron J 66: 341-344.

Mengel K and E A Kirkby, 1978. Principles of plant nutrition. Intern. Potash Institute, Worblaufen-Bern, 593 pp.

Menge J A, D Steirle, D J Bagy Araj, E L V Jonhnson and T R Leonard, 1978. Phosphorus concentrations in plants responsible for inhibition of mycorrhizal infection. New phytol 80: 575-578.

Merrill S D and S L Rawlins, 1979. Distibution and growth of sorghum roots in response to irrigation frequency. Agron J 71: 738-745

Michel B E, 1977. A model relating root permeability to flux and potentials. Plant Physiol 60: 259-264.

Miller D M, 1985. Studies of root function in Zea mays. IV. Effects of applied pressure on the hydraulic conductivity and volume flow through the excised root. Plant Physiol 77: 168-174.

Minderhoud J W, 1960. Grasgroei en grondwaterstand. PhD Thesis, University of Wageningen, 199 pp.

Misra R K, A R Dexter and A M Alston, 1986. Maximum axial and radial growth pressures of plant roots. Plant Soil 95: 315-326.

Monteith J L, 1981. Does light limit crop production? in: C B Johnson (ed) Physiological proceses limiting plant productivity. London, Butterworths pp 23-38.

Moorby H and P H Nye, 1984. The effect of temperature variation over the root system on root extension and phosphate uptake by rape. Plant Soil 78: 283-293.

Morizet J and M Mingeau, 1976. Influence des facteurs du milieu sur l'absorption hydrique. Etude effectuée sur tomate décapitée en exsudation. Ann Agron 27: 183-205, 333-342.

Mulder E G, 1949. Onderzoekingen over de stikstofvoeding van landbouwgewassen. I. Proeven met kalkammonsalpeter op grasland (Investigations on the nitrogen nutrition of agricultural crops. I. experiments with ammonium nitrate limestone on grassland). Versl Landbouwkd Onderz 55.7.

Neeteson J J and K W Smilde, 1983. Correlative methods of estimating the optimum nitrogen fertilizer rate of sugar beet as based on soil mineral nitrogen at the end of the winter period. In Proceedings of symposium "Nitrogen and Sugar-beet": 409-421. International Institute for Sugar-beet Research, Brussels.

Nederpel W N C, 1975. Onderzoek naar bemestende waarde van een te versnipperen tomategewas (Investigation of mineral content of tomato crop residues) Proefstation Tuinbouw onder Glas, Naaldwijk, report 637.

Nemeth K, 1975. The effect of K fertilization and K removal by ryegrass in pot experiments on the K concentration of the soil solution of various soils. Plant Soil 42: 97-107.

Newman E I, 1973. Permeability to water of the roots of five herbaceous species. New Phytol 72: 547-555.

Newman E I, 1974. Root and soil water relations. In: E W Carson (ed) The plant root and its environment. Charlotteville, University Press of Virginia pp 363-440.

Newman E I, 1976a. Water movement through root systems. Phil Trans R Soc Lond B 273: 463-478.

Newman E I, 1976b. Interaction between osmotic and pressure induced water flow in plant roots. Plant Physiol 57: 738-739.

Newman E I and A Watson, 1977. Microbial abundance in the rhizosphere: a computer model. Plant Soil 48: 17-56.

Nielsen N E and S A Barber, 1978. Differences among genotypes of corn in the kinetics of P uptake. Agron J 70: 695-698.

Niranjan Rao D and D S Mikkelsen, 1977. Effects of acetic, propionic ,and butyric acids on rice seedling growth and nutrition. Plant Soil 47: 323-334.

Nye P H and P B Tinker, 1977. Solute movement in the soil-root system. Studies in ecology vol 4. Oxford, Blackwell Scientific Publications, 342 pp.

Ogston, 1958. Trans. Faraday Soc 54: 1754-1757.

Olsen S R and W D Kemper, 1968. Movement of nutrients to plant roots. Adv Agron 20: 91-151.

Olsen S R and F E Khasawneh, 1980. Use and limitations of physical-chemical criteria for assessing the status of phosphorus in soils. In: F E Khasawneh, E C Sample and E J Kamprath (eds.), The role of phosphorus in agriculture. Madison, Am Soc Agron : pp. 361-404.

Pandey R K, W A T Herrera, A N Villegas and J W Pendleton, 1984. Drought response of grain legumes under irrigation gradient: 111. Plant growth. Agron J 76:557-560.

Passioura J B, 1972. The effect of root geometry on the yield of wheat growing on stored water. Austr J Agric Res 23: 745-752.

Passioura J B, 1983. Roots and drought resistance. Agric Water Manage 7: 265-280.

Passioura J B, 1984. Hydraulic resistance of plants. I. Constant or variable. Aust J Plant Physiol 11: 333-339.

Passioura J B, 1985. Roots and water economy of wheat. In: W Day and R K Atkin, Wheat growth and modelling. NATO ASI series. series A: Life Sciences, vol. 86: 185-198

Passioura J B and Rana Munns, 1984. Hydraulic resistance of plants. II. Effects of rooting medium and time of day , in barley and lupin. Aust J Plant Physiol 11: 341-350.

Pearson C J and B C Jacobs, 1985. Root distribution in space and time in

Trifolium subterraneum. Aust J Agric Res 36: 601-614.

Pielou E C, 1969. An introduction to mathematical ecology. New York, Wiley, 286 pp.

Pitman M G, 1976. Ion uptake by plant roots. In: U Lüttge and M G Pitman (eds.), Encyclop Pl Physiol 2B Transport in plants. Berlin, Springer, pp. 95-128.

Pleysier J L, A S R Juo and A J Herbillon, 1979. Ion exchange equilibria involving aluminum in a kaolinitic Ultisol. Soil Sci Soc Am J 43: 875-880.

Pleysier J L and A S R Juo, 1981. Leaching of fertiliser ions in an Ultisol from the high rainfall tropics: Leaching through undisturbed soil columns. Soil Sci Soc Am J 45: 745-760.

Pommer G, 1983. Haben alte sorten mehr Wurzeln als neue Zuchtsorten In: In: W Böhm, L Kutschera und E Lichtenegger (eds.) Wurzelökologie und ihre Nutzanwendung. Int. Symp. Gumpenstein 1982, Irdning, pp 483-490.

Powell C L, 1974. Effect of P fertilizer on root morphology and P uptake of Carex coriacea. Plant Soil 41: 661-667.

Powell C L, 1977. Effect of phosphate fertiliser and plant on phosphate inflow into ryegrass roots in soil. Plant Soil 47: 383-393.

Proffitt A P B, P R Berliner and D M Oosterhuis, 1985. A comparative study of root distribution and water extraction efficiency by wheat grown under high and low-frequency irrigation. Agron J 77: 655-662.

Prummel J, 1957. De betekenis van de bouwvoordikte voor de interpretatie van de analyseresultaten van het chemisch grondonderzoek. Landbouwkd Tijdschr 69: 703-712.

Prummel J, 1975. Effect of soil structure on phosphate nutrition of crop plants. Neth J Agric Sci 23: 62-68.

Prummel J, 1978. De kalibehoefte van aardappelen op zand- en dalgrond in afhankelijkheid van de bouwvoordikte. (With a summary: Potassium requirements of potatoes on sandy soils as affected by the thickness of the arable layer) Inst. Bodemvruchtbaarheid Rapp. 18-78, 13 pp.

Raadsma S, 1974. Current drainage practices in flat areas of humid regions in Europe. In: J van Schilfgaarde (ed.), Drainage for agriculture. Am Soc Agro Publ. no 17, Madison, pp. 115-143.

Raats P A C, 1970. Steady infiltration from line sources and furrows. Soil Sci Amer Proc 34: 709-714.

Raats P A C, 1980. The supply of water and nutrients in soilless culture. Proc. fifth intern. congr. on soilless culture, Wageningen, 1980. pp. 53-62.

Raper C D and S A Barber, 1970. Rooting systems of soybeans. I. Differences in root morphology among varities. Agron J 62: 581-584.

Reid J B, O Hashim and J N Gallacher, 1984. Relations between available and extractable soil water and evapotranspiration from a bean crop. Agric Water Management 9: 193-209.

Reid J B and M J Goss, 1981. Effect of living roots of different plant species on the aggregate stability of two arable soils. Soil Sci 32: 521-541.

Rhynsburger D, 1973. Analytic delineation of Thiessen polygons. Geographical analysis 5: 133-144.

Rijtema P E, 1969. Soil moisture forecasting. Nota 513, ICW Wageningen, 18 pp.

Riley D and S A Barber, 1971. Ammonium and nitrate fertilization and phosphorus uptake. Soil Sci Soc Am Proc 35: 301-306.

Römer W, 1985. Einfluss von Spross- und Wurzelwachstum auf die Phosphataufnahme bei Getreidepflanzen. Die Bodenkultur 36: 203-211.

Robertson W K, L C Hammond, J T Johnson and K J Boote, 1980. Effects of plant-water stress on root distribution of corn,soybean and peanuts in sandy soil. Agron J 72: 548-550.

Robinson D and H I Rorison, 1985. A quantitative analysis of the relationships between root distribution and nitrogen uptake from soil by two grass species. J Soil Sci 36: 71-85.

Robinson D, 1986. Limits to nutrient inflow rates in roots and root systems. Physiol Plant 68: 551-559.

Rowse H R, 1974. The effect of irrigation on the length, weight, and diameter of lettuce roots. Plant Soil 40: 381-391.

Russell E W, 1973. Soil conditions and plant growth, 10th ed. London, Longman, 849 pp.

Ruyssen M A, 1982. The development and significance of Vesicular-Arbuscular Mycorrhizas as influenced by agricultural practices. PhD Thesis University of Wageningen, 111 pp.

Sanders J L and D A Brown, 1978. A new fiber optic technique for measuring root growth of soybeans under field conditions. Agron J 70: 1073-1076.

Schenk M K and S A Barber, 1979. Phosphate uptake by corn as affected by soil characteristics and root morphology. Soil Sci Soc Am J 43: 881-883.

Schenk M K and S A Barber, 1980. Potassium and phosphorus uptake by corn genotypes grown in the field as influenced by root characteristics. Plant Soil 54: 65-76.

Schothorst C J and D Hettinga, 1983. Grondverbetering: alternatief voor beregening van grasland op lichte zandgrond? Bedrijfsontwikkeling 14: 115-122.

Schulze B, 1911. Wurzelatlas; Darstellung natürlicher Wurzelbilder der Halmfruchte in verschiedenen Stadien der Entwicklung. Paul Parey, Berlin.

Schuurman J J, 1971. Effect of supplemental fertilization of oats with restricted root development. Z Acker- Pflanzenbau 133: 315-320.

Schuurman, J J, 1983. Effect of soil conditions on morphology and physiology of roots and shoots of annual plants. A generalized vision, In: Wurzelökologie und ihre Nutzanwendung. International symposium Gumpenstein, 1982. Bundesanstalt Gumpenstein, Irdning, pp.343-354.

Schuurman J J and M A J Goedewaagen, 1971. Methods for the examination of root systems and roots, second ed. Wageningen, Pudoc, 86 pp.

Schuurman J J, J T N Venekamp and R J de Glopper, 1977. Het producerend vermogen van verschillende zavel-op-zand profielen bij vier grondwaterstanden. Cultuurtechnisch Tijdschz 17: 17-31.

Scott H D and L R Oliver, 1976. Field competition between Tall Morningglory and Soybean. II. Development and distribution of root systems. Weed Sci 24: 454-460.

Scott Russell R, 1977. Plant root systems, their function and interaction with the soil. London, McGraw-Hill, 298 pp.

Scott Russell R, 1981. Root growth in relation to maximizing yields. Proc 16th Colloq Intern Potash Inst, Warsaw. Bern, IPI pp 31-47.

Shierlaw J and Alston A M, 1984. Effect of soil compaction on root growth and uptake of phosphorus. Plant Soil 77: 15-28.

Shone M G T and A V Flood, 1983. Effects of periods of localized water stress on subsequent nutrient uptake by barley roots and their adaptation by osmotic adjustment. New Phytol 94: 561-572.

Sibma L, 1968. Growth of closed green crop surfaces in the Netherlands. Neth J Agric Sci 16: 211-216.

Sieben W H, 1974. Invloed van de ontwateringstoestand op stikstofhuishouding en opbrengst (The effect of drainage conditions of the soil on nitrogen supply and yield). Landbouwkd Tijdschr 76: 785-801.

Silberbush M and S A Barber, 1984. Phosphorus and potassium uptake of field-grown soybean cultivars predicted by a simulation model. Soil Sci Soc Am J 48: 592-596.

Simpson R J, H Lambers and M J Dalling, 1982. Translocation of nitrogen in a vegetative wheat plant (Triticum aestivum). Physiol Plant 56: 11-17.

Singh J S, W K Lauenroth, H W Hunt and D M Swift, 1984. Bias and random errors in estimates of net root production: a simulation approach. Ecology 65: 1760-1764.

Sivakumar M V K, H M Taylor and R H Shaw, 1977. Top and root relations of field-grown soybeans. Agronomy 69: 470-473.

Sjollema B, 1904. Het onderzoek naar het gehalte aan opneembare stoffen in den bodem. Landbkd Tijdschr 9: 330-334.

Sluijsmans C M J, 1965. Bemestingsonderzoek in de landbouw, Inst. Bodemvruchtbaarheid, Gedenkboek 1890-1965, pp. 93-121.

Soileau J M, 1973. Activity of seedling roots as measured by strontium uptake. Agron J 65: 625-628.

Sonneveld C and A Van der Wees, 1980. Voedingsoplossingen voor de teelt van tomaten in steenwol, fifth ed. Proefst Tuinbouw onder Glas, Naaldwijk, 42 pp.

Sonneveld C and W Voogt, 1985. Growth and cation absorption of some fruit-vegetable crops grown on rockwool as affected by different cation ratios in the nutrient solution. J Plant Nutr 8: 585-602.

Spiegel M R, 1968. Mathematical handbook of formulas and tables. New York etc, McGraw-Hill, 271 pp.

Stankov N Z and T P Ladonia, 1976. A new method for studying the morphology of plant root systems . Dokl Vses Ordena Lenina Akad Skh Nauk Im. V. I. Lenina, 6: 17-18.

Steiner A A, 1967. Growth curves of tomato plants. Plant Soil 26: 189-192.

Steiner A A, 1984. The universal nutrient solution. Proc ISOSC Congr, Lunteren, pp. 633-649.

Steinhardt R, R R Van der Ploeg and W Ehlers, 1982. Comparing forms and solutions of the single root soil water extraction model. Soil Tillage Res 2: 347-357.

Steiner A A, 1985. The history of mineral plant nutrition till about 1860 as source of the origin of soilless culture methods. Soilless Culture 1: 7-24.

Steudle E and W D Jeschke, 1983. Water transport in barley roots. Planta 158: 23.

Stevenson M R and K J Fisher, 1975. Effect of container size and peat source on growth and yield of the tomato. N Z J Exp Agric 3: 157-160.

Stroosnijder L, 1976. Infiltratie en herverdeling van water in grond. Wageningen, Pudoc, 213 pp.

Taylor H M and B Klepper, 1971. Water uptake by cotton roots during an irrigation cycle . Aust J Biol Sci 24: 853-859.

Taylor H M and B Klepper, 1974. Water relations of cotton. I. Root growth and water use related to top growth and soil water content. Agron J 66: 584- 588.

Taylor H M and W Böhm, 1976. Use of acrylic plastic as rhizotron windows. Agron J 68: 693-694.

Temple-Smith M G and R C Menary, 1977. Growth and phosphate absorption in lettuce and cabbage plants in dilute solution culture. Aust J Plant Physiol 4: 505-513.

Throughton A, 1981. Length of life of grass roots. Grass Forage Sci 36: 117-120.

Tinker P B, 1976. Transport of water to plant roots in soil. Phil Trans R Soc Lond B 273: 445-461.

Troughton A and W J Whittington, 1968. The significance of genetic variation in root systems. In: W J Whittington (ed.), Root growth. London, Butterworth, pp. 296-314.

Tucker M und C von Seelhorst, 1898. Der Einfluss welchen der Wassergehalt und der Reichtum des Bodens auf die Ausbildung der Wurzeln und der oberirdischen Organe der Haferpflanze ausüben. J Landwirtsch 46: 52-63.

Tyree M T, E L Fiscus, S D Wullschleger and M A Dixon, 1986. Detection of xylem cavitation in corn under field conditions. Plant Physiol 82: 597-599.

Van Burg P F J, 1968. Nitrogen fertilizing of grassland in spring. Neth

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