ROOT FUNCTIONS IN AGRICULTURAL SYSTEMS

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ABSTRACT

Root research in agricultural systems is aimed at increasing the efficiency of using external inputs. Nutrient uptake efficiency is defined as the ratio between uptake during a growing season and the size of the available pool in the soil. Part of the available pool is "unrestrictedly available", i.e. it can be taken up at the rate required for maximum crop growth; the remaining part is "restrictedly available" and its rate of transport to the root determines the uptake rate possible and hence crop growth. Root characteristics determine for a given soil-nutrient combination which part of the available pool is unrestrictedly available and how fast the restrictedly available pool can be depleted. A mathematical formulation of these effects is now available.

Nutrient uptake problems in agricultural systems can be classified according to the adsorption of the nutrient in the root medium considered and the intensity of leaching. For nutrients of low mobility a high root length density is the main requirement, for nutrients of high mobility, especially when leaching is severe, a great rooting depth is required to obtain a high efficiency of nutrient uptake.

INTRODUCTION

An understanding of root functions in agricultural systems is essential when interventions, such as modifications of the root environment or selection of genotypes with desirable root characteristics are contemplated. In the last century the concept of a "morphogenetic equilibrium" between root and shoot growth was formulated, stating that any environmental obstruction to the full realization of the root's growth potential will restrict shoot growth. This concept can be simplified to "the more roots, the better shoot growth". Various types of empirical evidence have since led to the refutation of this concept and its replacement by the concept of a "functional equilibrium" between root and shoot growth of a plant in response to the above- and belowground environment (Van Noordwijk and De Willigen, 1987). By tailoring water and nutrient supply in the root environment to the plant's needs, comparatively small root systems can sustain the high shoot production rates obtained in modern horticultural and agricultural systems. Consequently, the question which factors are critical to root functions in agricultural systems can only be discussed meaningfully in relation to the existing water and nutrient supply.

Maximizing aboveground production is no longer the only or even primary aim of interventions in agricultural systems, as the environmental and energy crises of the last decades have shown. Efficient use of external inputs in combination with reasonable yields is now set as a new aim for agricultural production, integrating economic and environmental criteria. In this context the following aspects deserve attention:

- efficient use of available water and nutrients, to reduce the need for fertilizer and irrigation and reducing losses to the environment,
- low vulnerability to belowground competition from weeds, to reduce the need for herbicides,
- low vulnerability to soil-borne pathogens, to reduce the need for pesticides,
- high ability to penetrate dense soils and tolerate poor aeration, to reduce the need for soil tillage and drainage,
- tolerance to acid soil conditions, to reduce the need for liming.

To maintain reasonable yield levels, carbohydrate use by the root system should not become excessive. Considerable progress in our understanding of each of these aspects has been made, but here we will concentrate on the primary function of roots in nutrient and water uptake. After a summary of available theory on benefits (extra possibilities for uptake) per unit cost (root length), critical root characteristics for various agricultural systems will be discussed.

NUTRIENT USE EFFICIENCY AND AVAILABILITY

Efficiency is usually defined as the ratio between output and input. The boundaries of the system have to be specified first. Here we define *nutrient uptake efficiency* (NUPE) as the ratio of nutrient uptake and the amount of available nutrients in the root zone, both expressed as kg/ha. Nutrient uptake efficiency together with *nutrient application efficiency* (increase in available amount per unit fertilizer applied, NAPE) and *nutrient utilization efficiency* (dry matter production per unit nutrient uptake, NUTE) determine the overall *nutrient use efficiency* of a soil/plant system (dry matter production per unit nutrient applied as fertilizer, NUSE). Efficiency at this level is a component of, but not equal to, nutrient use efficiency at the agro-ecosystem and human ecosystem levels (Van Noordwijk and De Willigen, 1986). The concept of nutrient uptake efficiency we use depends on a definition of "available" nutrient sources. For water a similar set of definitions can be made.

For both water and nutrients we define "availability" by reference to a hypothetical situation with an infinitely dense root system (of negligible volume) (De Willigen and Van Noordwijk, 1987a). In such a situation no trans-

port resistance in the soil would exist and all nutrients in the soil solution and those in desorbable fractions of the soil matrix could be taken up. Root systems of finite density and possibly with additional transport resistances due to non-regular root distribution or incomplete root/soil contact will be able to take up only a part of the "available" pool. If transport limitations exist, the period to be considered has to be specified. In sufficiently rich soils part of the available pool can be taken up at the rate required by the crop at its maximum growth rate (as influenced by other environmental factors); this part we call the "unrestrictedly available" pool. The remaining part of the available pool, the "restrictedly available" amount, can be taken up by a root system of finite density at a rate which is governed by the transport characteristics of the nutrient in the soil considered. The transport rate declines exponentially, as it is proportional with the amount remaining in the soil. Consequently, uptake of all available nutrients takes an infinitely long period of time, and within a normal growing period only part of the restrictedly available pool can be taken up. The size and distribution of a root system determine the boundary conditions for the transport problems considered and thus determine which part of the total available pool can be called "unrestrictedly available" and which part of the "restrictedly available" pool can be taken up during a growing season. Modifications of the chemical environment (pH, redox potential, chelating agents, ligands, etc.) can lead to changes in the available amount. Water availability can be defined similarly, on the basis of transport resistance in the soil and a minimum acceptable plant water potential; plants with finitely dense root systems can take up only part of this water at a rate governed by transpirational demand (the unrestrictedly available amount). By tolerating more negative plant water potentials plants can increase the size of the "available" pool.

In the largely empirical approach to soil fertility problems of the past century, for a large number of crop and soil combinations the inherent soil fertility plus fertilizer levels have been determined at which the unrestrictedly available pool is large enough to meet crop demand over the whole growing season, so no nutrient limitation exists. As the unrestricted availability of part of the available pool critically depends on root factors, the first aim of quantitative root ecology in this stage is to gain an understanding of the empirically found levels on the basis of transport theory. At least in a number of cases fertility levels required for adequate crop growth can then be lowered through a more efficient use of the available pool (Van Noordwijk and De Willigen, 1986).

UNRESTRICTEDLY AVAILABLE RESOURCES

To calculate which part of the available pool of nutrients and water is unrestrictedly available as a function of root parameters, we use a transport model. Transport by diffusion and mass flow is described in a way similar to models by Nye and Tinker (1977) and Barber (1984). Apart from the simple geometry of a soil cylinder around one typical root, analytical descriptions were developed for non-homogeneous root distributions and incomplete root-soil contact (De Willigen and Van Noordwijk, 1987a and b). Methods for measuring root patterns were described by Van Noordwijk (1987). As a boundary condition at the root surface we assume a constant daily uptake per unit root surface, largely independent of the external concentration. This assumption reflects recent plant physiological concepts of internal regulation of nutrient uptake by the plant according to current demand (Clarkson, 1985). A schematic presentation of nutrient demand and root length for an "average" crop life cycle (Figure 1) shows a nearly constant daily demand per unit root length, following a high demand in the initial phase.
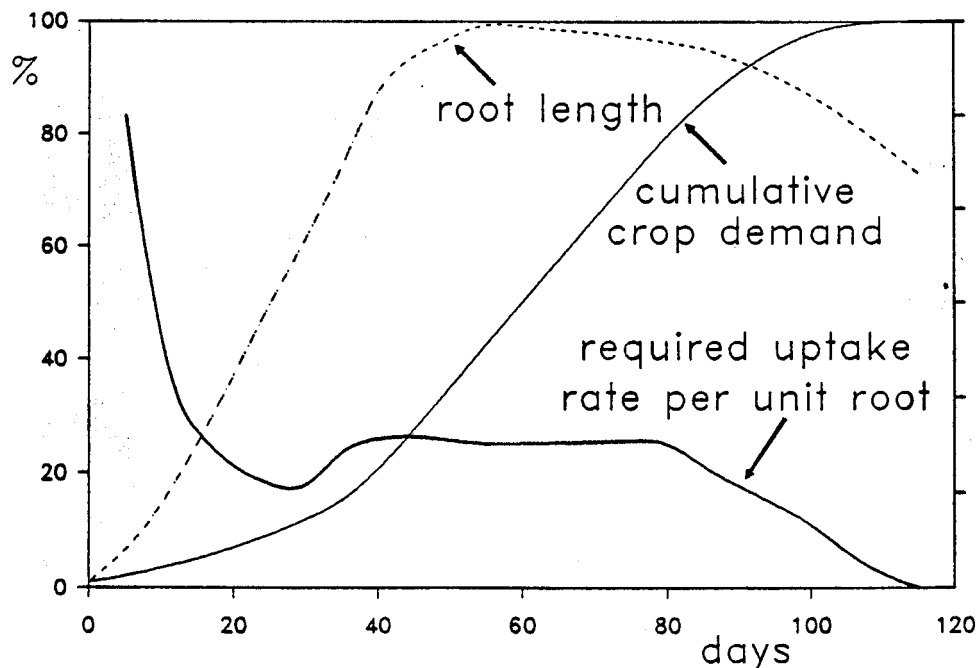

Fig. 1. Nutrient demand (uptake without restrictions in supply), root length and nutrient demand per unit root length for an "average" crop life cycle (schematic).

Constant daily demand per unit root length leads to a *steady rate* solution of the transport equations (Van Noordwijk and De Willigen, 1979). Transport to the root surface can proceed at the required rate until the steady-rate profile is obtained with the physiologically determined limiting concentration of

C_{lim} at the root surface. The amount of available nutrients left in the soil at this point in time is restrictedly available; initial amount minus restrictedly available amount is unrestrictedly available. Equation 1 (De Willigen and Van Noordwijk, 1987a) shows how this amount depends on the various parameters considered:

$$Q_\nu = S_i - \frac{(\Upsilon_{D,v} M_v + \Upsilon_{D,g} M_g)(K_a+\Theta)}{H(a_1\Theta + a_0)\Theta D_0} R_o^{\ 2} G(\rho,\nu) - \pi(K_a+\Theta) C_{lim}(\rho^2-1) \quad [1]$$

where

Q_ν	= unrestrictedly available concentration of nutrients,	mg/cm³
S_i	= initially available concentration of nutrients,	mg/cm³
$\Upsilon_{D,v}$ en $\Upsilon_{D,g}$	= daily growth rate of vegetative and generative dry matter,	g/(cm² day)
M_v en M_g	= nutrient concentration required in vegetative and generative dry matter,	mg/g
K_a	= adsorption constant	ml/cm³
Θ	= volumetric water content,	ml/cm³
H	= depth of nutrient-rich, rooted zone,	cm
D_0	= diffusion constant,	cm²/day
a_1 en a_0	= parameters of relation between Θ and D	ml/cm³ & [ ]
C_{lim}	= concentration physiologically limiting rate of uptake	mg/cm³
R_o	= radius of root,	cm
ρ	= dimensionless radius of soil cylinder, $(R_o\sqrt{\pi L_{rv}})^{-1}$	[ ]
L_{rv}	= root length density	[cm/cm³]
ν	= dimensionless water flux $=-E/(4\pi H D L_{rv})$	[ ]
E	= transpiration rate	cm/day
$G(\rho,\nu)$	= dimensionless function of ρ and ν, defined as	

$$G(\rho,\nu) = \frac{1}{2(\nu+1)}\left\{\frac{1-\rho^2}{2} + \frac{\rho^2(\rho^{2\nu}-1)}{2\nu} + \frac{\rho^2(\rho^{2\nu}-1)(\nu+1)}{2\nu(\rho^{2\nu+2}-1)} + \frac{(1-\rho^{2\nu+4})(\nu+1)}{(2\nu+4)(\rho^{2\nu+2}-1)}\right\} \quad [2]$$

For incomplete root-soil contact a function $F(\psi)$ can be added to the G-function, where 100 ψ equals the percentage root-soil contact, provided the contribution of mass flow to transport is negligible.

Root length density L_{rv} determines ρ which in a strongly non-linear way determines the value of $G(\rho,\nu)$. On the right-hand side in equation [1] the first term indicates the total available amount, the second the amount required to ensure transport to the root at the required rate, and the third

the amount left due to the physiologically limiting concentration C_{lim}. In Table 1 this amount is estimated. From literature values it follows that it is negligible in most agricultural situations, except for phosphate on strongly P-adsorbing soils. The physiological uptake processes are so efficient that they scarcely deserve detailed attention in ecophysiological research, with the possible exception of tolerance to low root temperatures.

TABLE 1

Critical external nutrient concentration C_{lim} as found in physiological literature and the consequent amount of available nutrients (concentration times (adsorption constant plus θ) times volume) left in the soil (at a water content $\theta = 0.25$ v/v) (De Willigen and Van Noordwijk, 1987a).

C_{lim}, critical external nutrient concentration [μmol/l]	Adsorption constant [ml/cm^3]	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

The equation shows that a high nutrient demand, a high adsorption constant of the nutrient in the soil and low soil water contents lead to large amounts of available nutrients which are restrictedly available. Figure 2 shows the amount of available nutrients in the soil which cannot be taken up at the required rate as a function of root length density in the plough layer. Calculations are presented for parameters considered to be standard values for nitrate, potassium and phosphate; considerable variation exists in soil parameters such as K_a and Θ and in crop demand. For N, K and P under "standard" condions, the benefits of extra unrestricted uptake for higher root length densities can be read off the graphs. In the range of root length densities commonly found in most agricultural crops in the top 20 cm of soil, 1-5 cm/cm^3, an increase in root development will provide the crop with a considerable amount of unrestrictedly available potassium and phosphate, but no nitrate, unless the soil is dry. In the absence of competition from weeds or intercrops, improved root development may decrease the soil fertility level required for adequate crop growth for potassium and phosphate, but not for nitrogen.

As a consequence of our assumption of complete internal regulation of uptake, root growth not only leads to exploration of new soil but also to a decrease of the required uptake rate per unit root length for all roots. In fact, in our analysis the latter aspect is dominant. Dynamics of root growth and decay are therefore mainly important insofar as they determine the existing live root length at any point in time and especially at the moment that required uptake exceeds possible transport to the root.
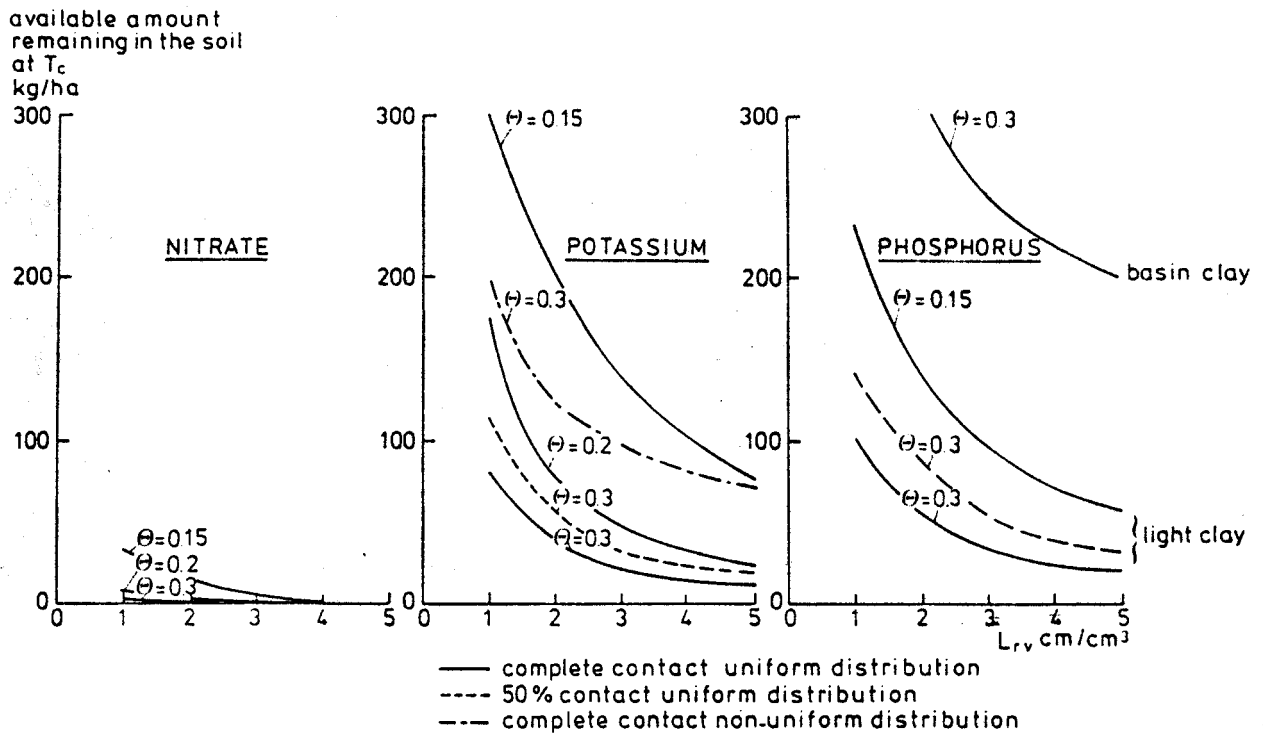
available amount
remaining in the soil
at T_c
kg/ha

Fig. 2. Amount of available nutrients left in the soil when possible uptake rates fall below the rate required for maximum crop growth (in the linear phase), as a function of root length density L_{rv} (De Willigen and Van Noordwijk, 1987a).

For water uptake we evaluated the amount of water left in the soil at the point in time that the transpirational demand can no longer be met, according to the theory of decreasing root-soil contact under drying conditions (Figure 3). An optimum root length density can be derived, as both the benefit of extra water taken up and the cost of root growth and maintenance can be expressed in amounts of carbohydrates, given the crop's transpiration ratio. Figure 3 shows estimated break-even points for root length density if roots deplete a certain soil layer only once in their lifetime (Van Noordwijk, 1983).

RESTRICTEDLY AVAILABLE RESOURCES

In the life cycle of an annual crop nutrient limitations to growth may occur in two periods, as shown by fertilizer response in Figure 4: in the initial growth period (when demand per unit root length is usually high, compare figure 1) and later when the soil around the roots becomes (locally) depleted. Between these periods of constrained uptake, nutrient uptake may allow maximum growth rates to be obtained even on relatively poor soils.
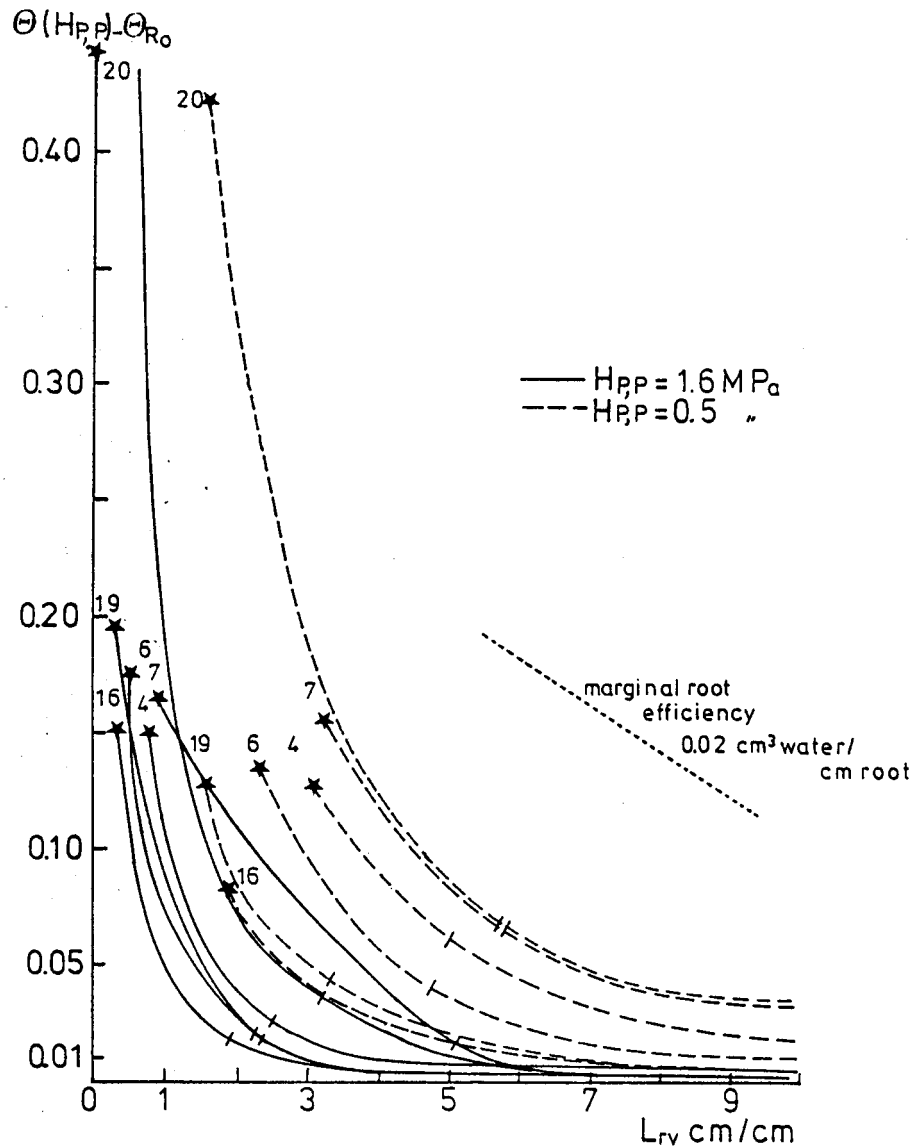
Fig. 3. Volumetric water content of the soil considered to be available to the plant (i.e. released at more than the minimum plant water potential acceptable, -1.6 and -0.5 MPa in this example), but which cannot be taken up at the required transpiration rate due to limiting soil-root interface resistance, as a function of root length density L_{rv} (cm/cm^3). Calculations are shown for six soil types; at the indicated points the slope of each line corresponds to the estimated marginal root efficiency, where every extra cm of root length yields 0.02 cm^3 of water (Van Noordwijk, 1983).

As the limiting concentrations for net uptake are virtually zero (at least when root temperature is not too low), we may assume that if supply to the root is lower than the required uptake rate, roots will behave as zero-sinks, taking up all nutrients as they arrive at the root surface by diffusion and mass flow. The zero-sink solution maximizes possibilities for nutrient uptake by the roots, except for chemical effects on nutrient availability. Uptake by a zero-sink after a usually brief transition period becomes proportional to the average concentration in the soil. For strongly adsorbed nutrients such as phosphate this means that the uptake rate shows only a gradual decline with

time. If root length density increases while total transpirational demand remains constant, the relative importance of mass flow for nutrient supply to the root decreases. Figure 5 shows calculated P-uptake by a zero-sink and P-demand per unit root length, as a function of L_{rv}. We expect that a plant, while increasing its root length, will be nutrient-limited in aboveground growth until the supply and demand lines intersect. If root density continues to increase beyond this point, we expect uptake to follow the demand line rather than the supply line. In soils rich in nutrients or under conditions favouring transport (e.g. wet soil) the point of intersection occurs at lower root length densities.
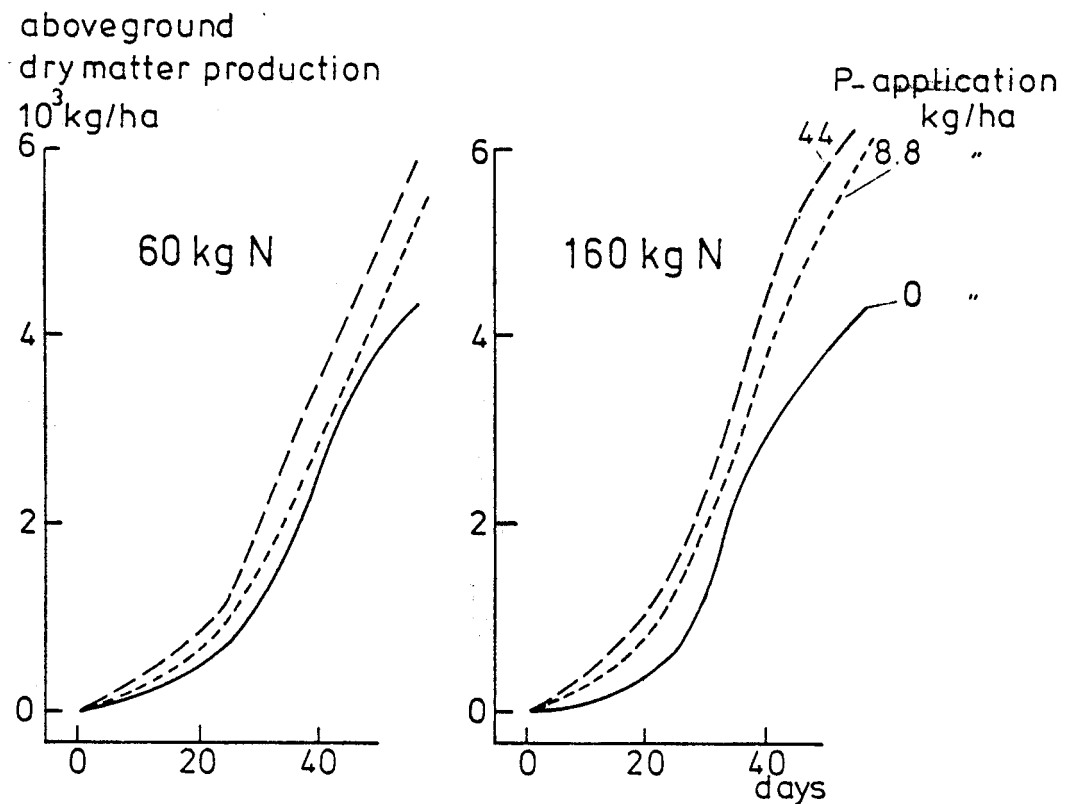

Fig. 4. Dry matter production of grassland in 50 days following P-fertilization at two N-levels; P-application has a positive effect on growth in the initial 20 and the last 10 days, but not in the 20 days in between (De Willigen and Van Noordwijk, 1987a, after data of Mulder, 1949).

Figure 6 shows a test of the model concerned, analysing P-uptake by *Lolium perenne* on soils of different P-status during an extended period of near-linear growth. Measured uptake is close to independently calculated uptake by a zero-sink, except for the later stages on the rich soil when uptake per unit root length decreases. On the poorest soil, P-uptake per unit root length became higher than that calculated for a zero-sink, probably due to mycorrhiza development. The rather rough procedure we used for measuring hyphal length led to an approximately constant uptake per unit length of roots plus hyphae. Rapid initial root development is important to shorten the initial period of

nutrient stress on relatively poor soil and thus to decrease the need for application of "starter" fertilizer. Low temperatures usually slow down root growth, and the physiologically determined C_{min} value may under cold conditions be considerably higher than that used in Table 1.
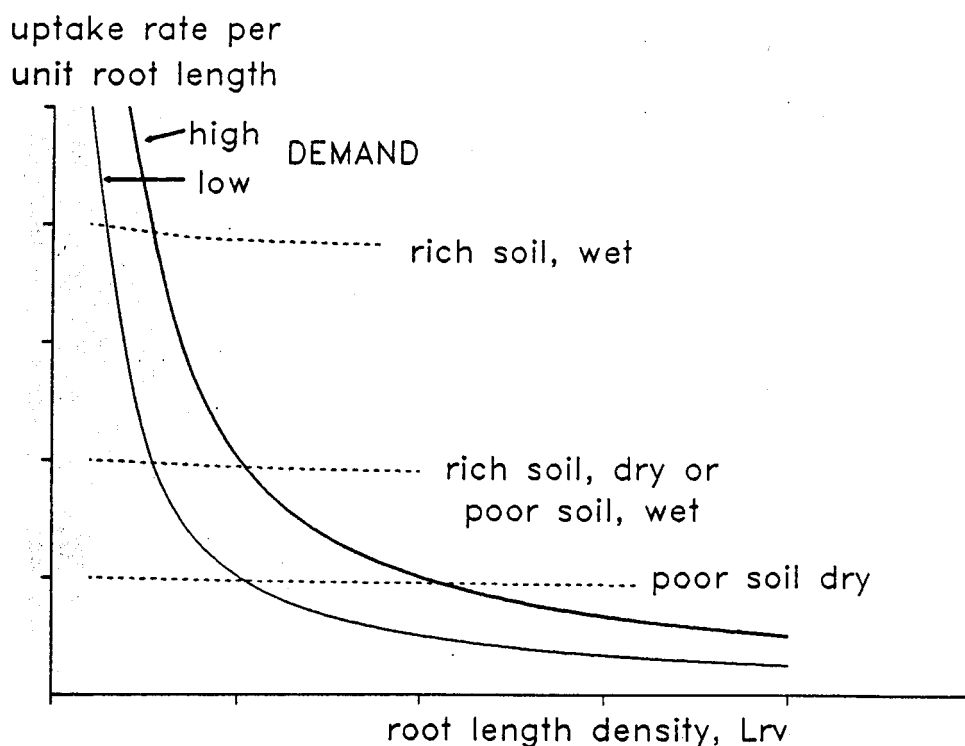

Fig. 5. Schematic presentation of required uptake per unit root length to meet crop demand and supply - under different soil conditions - of phosphate to a root behaving as a zero-sink, as a function of root length density.

NUTRIENT RECOVERY UNDER LEACHING CONDITIONS

While root length density in the nutrient-rich zone is especially important for nutrients with high adsorption constants, rooting depth is especially important for mobile resources where enrichment of the subsoil is common. As root length density usually decreases with increasing depth, only relatively mobile nutrients can be taken up from the subsoil in appreciable amounts. The adsorption constant of a nutrient in a soil layer determines its retardation with respect to water flow $(K_a + \theta)$, if we follow the simplest description of leaching. Leaching intensity can be described by the total input of water (W_i) during the growing season minus total water uptake (W_u), divided by the amount of water stored in the root zone (V_w). In this way we obtain a minimum estimate of leaching: under uneven input conditions or with bypass flow (heterogeneous infiltration), leaching losses may be higher. Nutrient uptake efficiency in highly dynamic systems, where leaching is likely, depends on rooting depth, the time at which the final rooting depth is reached and on the degree of syn-

chronization of the nutrient supply (from mineral fertilizer and/or minerali-
zation of organic nutrient sources) with crop demand.. Simple leaching models
and the consequences for rooting depth are discussed by Van Noordwijk (1989);
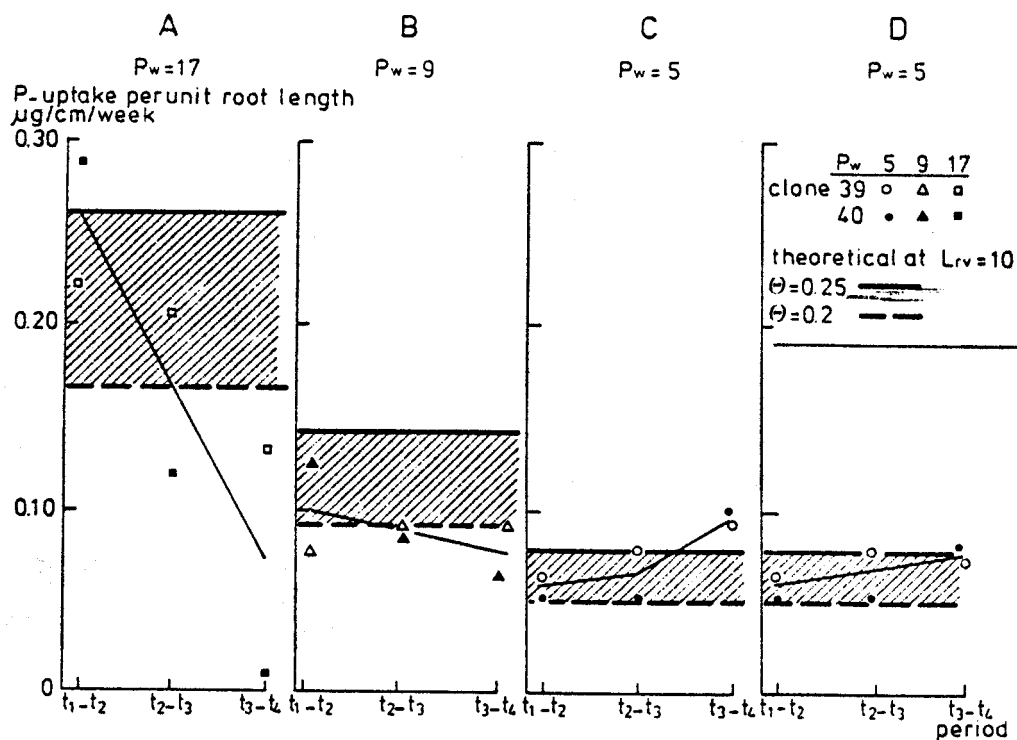a specific, more detailed example is given by De Willigen (1989).

Fig. 6. Measured P-uptake rate per unit root length in experiments with two
clones of *Lolium perenne* at three soil P levels; the shaded area represents
the calculated uptake by a zero-sink at current soil water content, based on
44 hour P-adsorption isotherms; for the lowest P-level measured P-uptake per
unit length of roots + VAM-hyphae is shown as well (De Willigen and Van
Noordwijk, 1987a).

In Figure 7 a schematic classification is given of nutrient uptake problems
in agricultural systems: high leaching intensities lead to low uptake effi-
ciencies, especially for poorly adsorbed nutrients; high adsorption constants
lead to low uptake efficiencies, especially in dry soils. If input of water
during the growing season equals transpiration, leaching intensity as defined
above is zero and the soil will remain moist. Without any replenishment leach-
ing intensity may become -1 if the soil dries out completely. Situations where
high uptake efficiencies are possible occur between these extremes. In the two
shaded areas different aspects of root systems are important for improved nu-
trient uptake efficiency: in the upper left-hand corner rooting depth and the
degree of synchronization of supply and demand, in the lower right-hand corner
root length density, root hairs and mycorrhiza and the degree of synlocaliza-
tion of roots and the nutrient source. In the final section we will use this

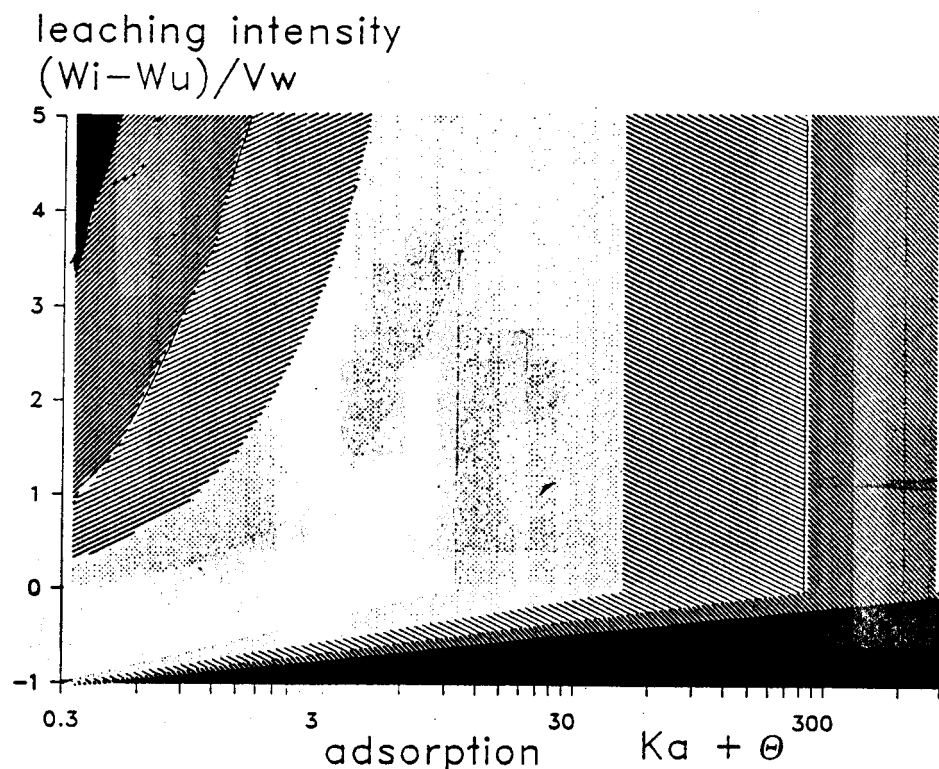figure for discussing root research in some agricultural systems.

Fig. 7. Schematic classification of nutrient uptake problems in agricultural systems, based on adsorption of the nutrient concerned and leaching intensity. Increasing intensity of shading indicates increasing restrictions on nutrient uptake efficiency by leaching (upper left-hand corner) or low mobility (lower right-hand corner). Rooting depth and synchronization of supply and demand are important aspects in the upper left-hand corner, root length density and synlocalization in the lower right-hand corner.

CRITICAL ROOT CHARACTERISTICS IN VARIOUS AGRICULTURAL SYSTEMS

P-supply on temperate grasslands, often soils with high P-adsorption constants (heavy clays or sandy soils rich in iron) constitutes a typical example of the lower right-hand part of figure 6. Calculations show that in such soils root length densities of at least up to 45 cm/cm^3 still lead to increased possibilities of P-uptake. Soil water content is a dominant factor through its effect on the effective diffusion constant. Because the topsoil dries out more readily than deeper layers, phosphate-rich soil at a depth of 15-20 cm may be as effective in supplying P to grass in dry periods as that in the 0-5 cm depth, despite the fact that root length densities in the P-rich zone are only one- third as high (De Willigen and Van Noordwijk, 1987a). Because of the poor mobility of P, synlocalization is important. In the recently developed technique of injecting cattle slurry into the soil in injection slits 50 cm apart, the distance between the slits limits P-use efficiency of injected slurry. Grass root systems are at most 15 cm wide at a depth of 20 cm, so grass between the slits does not benefit from the P-source.

The value of $(W_i - W_u)/V_w$ is between 0 and -1 in temperate arable crops during the growing season and we move from the typical situation for N to that for K and P if we move to the right in the lower part of the graph. Typical values of K_a are 0, 10 and 100 à 1000, respectively. Root length densities in the plough layer can explain part of the differences among crops in the P-status of the soil they require for good growth, not their N-requirements. For positive values of $(W_i - W_u)/V_w$ rooting depth becomes important as it determines V_w and hence leaching intensity. A larger rooting depth increases the chances of intercepting leached N, e.g. by "catch crops" in a crop rotation.

In the humid tropics where intense leaching during the growing season occurs, rooting depth is of primary importance to N-use efficiency. The deeper root development of cassava underneath intercropped maize can explain the favourable effect of such intercropping on N-uptake efficiency (Hairiah and Van Noordwijk, 1986). Permanent "safetynets" under the cropping system provided by deep-rooted alley trees are especially important in the case of highly mobile nutrients. A shift to the right in the graph by keeping nitrogen in the more strongly adsorbed ammonium rather than the nitrate form by maintaining a low soil pH helps to reduce leaching losses (De Willigen, 1985). Maintaining soil organic matter levels in the topsoil is important as the cation exchange capacity in such (low-activity clay or sandy) soils largely depends on soil organic matter. To obtain deep rooting in these soils roots have to be able to tolerate low soil pH and ensuing problems of high Al levels and have to be able to penetrate dense soil layers. In a study in SE Nigeria it was found that channels in the subsoil, formed earlier by tree roots when the cropped field was still a forest, provided a major pathway for roots of crops to explore the subsoil (Hairiah and Van Noordwijk, 1986). A thin coating of decaying root organic matter on the crop roots growing in the old tree root channels may help to overcome Al-toxicity problems.

At the extreme end of the agricultural intensification scale modern glasshouse horticulture on soilless systems is found. These inert media do not adsorb any nutrients, so all nutrients behave like nitrate in the humid tropics. As considerable amounts of water percolate through the root environment and high nutrient concentrations are maintained in solution, nutrient uptake efficiencies are often low. As all nutrients are mobile, relatively small root systems are adequate (root:shoot ratios of 1:20 on a dry weight basis or 1:2 on a surface area basis for tomato) and resistance to water uptake probably determines the root surface area necessary for maximum growth (De Willigen and Van Noordwijk, 1987a). A simple model of the nutrient and water balance of such systems shows that nutrient uptake efficiency depends critically on the degree of synchronization of supply and demand and on the buffer capacity of

the system (i.e. volume of nutrient solution per plant). In the wet root environments that are used, aeration of roots by means of-internal air channels in the cortex is important; differences among crops and cultivars in their ability to increase air-filled root porosity explain their relative success in wet media (Van Noordwijk and Brouwer, 1988).

To improve nutrient uptake efficiencies in various agricultural systems different root characteristics can be of primary importance. In view of the new biotechnological techniques for modifying plant genotypes the question which root characteristics are desirable and which agronomic or environmental benefits could be obtained by modifying roots becomes more urgent (O'Toole and Bland, 1987). A finer tuning of soil tillage and water management to actual crop demands has to be based on an evaluation of both root development and the conditions influencing nutrient and water uptake efficiency (Boone, 1988). By developing quantitative root ecology along the lines indicated here, with emphasis on transport processes in and around the root, we hope to help avoid unrealistic expectations and to find useful applications.

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