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Root, shoot and soil parameters required for process-oriented models of crop growth limited by water or nutrients

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Abstract

A review is given of the prospects for using process-oriented models of water and nutrient uptake in improving 'integrated agriculture'. Government-imposed restrictions on the use of external inputs will increase the likelihood of (temporary) nutrient or water stress in crop production in NW Europe and thus a better understanding is required of shoot-root-soil interactions than presently available. In modelling nutrient and water uptake, three approaches are possible: 1) models-without-roots, based on empirically derived efficiency ratios for uptake of available resources, 2) models evaluating the uptake potential of root systems as actually found in the field and 3) models which also aim at a prediction of root development as influenced by interactions with environmental factors. For the second type of models the major underlying processes are known and research can concentrate on model refinement on the one hand and practical application on the other. The main parameters required for such models are discussed and examples are given of practical applications. For the third type of models quantification of processes known only qualitatively is urgently needed.

Introduction

The tradition of root ecological research in the Netherlands dates back to the beginning of the 20'th Century (Maschhaupt, 1915). Although concepts (Greenwood et al., 1985; Schuurman, 1983; Van Noordwijk and De Willigen, 1987; Wiersum, 1962) as well as methods (Schuurman and Goedewaagen, 1971; Van Noordwijk, 1987) of root research have shown considerable development since then, knowledge of root growth and function is not often applied directly to farm management. Farm operations such as choice of crops and cultivars, type and amount of fertilizer applied at a specific time and place, soil tillage, drainage and irrigation are still largely guided by empirical evidence of yield effects or by management models in which empirically derived water or nutrient uptake efficiencies (output/input ratios) are used. This category of models can be designated as 'models-without-roots'. Research aimed at avoiding nutrient and water limitations to crop production could progress without detailed description of the plant response to such limitations, as long as the environmental effects of excess applications were disregarded. Presently, a much sharper identification of the transition zone between insufficient and surplus is required as environmental problems are not restricted to situations of a real excess, but start within the range of soil nutrient levels required for near-maximum crop production (Neeteson et al., 1989; Van Noordwijk et al., 1990). This is certainly the case when the spatial heterogeneity of agricultural fields is taken into account (Van Noordwijk and Wadman, 1992). Instead of aiming at a complete avoidance of 'stress' conditions, farm management in 'integrated' agricultural systems will be directed at minimizing losses of yield and crop quality while keeping environmental side-effects at acceptable levels. The increasing concern

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for environmental consequences of farm management operations thus requires a more complete understanding of crop performance. Periods with restricted availability of nutrients or water, competition between crop plants and weeds, incomplete elimination of pests and diseases will be difficult to avoid in 'integrated' agricultural systems. If we are to take full advantage of the plasticity of the crop's developmental and physiological processes, improved understanding is needed of plants and crops as self regulatory systems. Until now much effort has been put into the study of single factors, a logical choice as all single factors should be at a nonrestrictive level in order to reach maximum yields. In a multiplicative model, maximum yield is only achieved if all reduction factors (defined to be in the range 0 to 1.0) are 1.0. If final yields of, say, 90% of the maximum are acceptable, a large number of solutions exist (e.g. $1.0 \times 0.95 \times 0.95$, $1.0 \times 0.9 \times 1.0$ or 0.965×0.965) when a multiplicative model with more factors is involved. To optimize crop productions systems operating well below the maximum yield, a more complete understanding of interactions and trade-off's between production factors is required, e.g. between soil tillage, fertilization, soil disinfestation and the use of better rooting genotypes. Key processes of crop growth, root development and functioning, as well as relations with fertility and structure of soils, should be integrated into models of the plant-soil system. Future management systems, based on simplified versions of process-oriented models, will require crop- and site-specific information, either from easily operated monitoring equipment, or from accurate databases. Apart from the need for accurate input data, however, a bottleneck is formed by a lack of sufficiently validated, process-oriented models of uptake processes, based on operationally defined parameters.

In this paper, we will review recent achievements in modelling crop performance aimed at improving decisions on farm operations. The knowledge required, as well as experimental data for parametrization of models of root growth and function, will be discussed. The complexity of the models required in relation to the actual problem to be solved will be dealt with, giving some examples of using knowledge on root systems in recommendations on soil fertility, irrigation, soil tillage and plant breeding.

Crop growth and demand for water and nutrients

Models of shoot growth of different complexity

To describe crop growth and yield formation as influenced by environmental conditions, three types of factors can be distinguished (Rabbinge and De Wit, 1989): *a*) factors determining potential yield (such as light, temperature, and CO_2), *b*) factors limiting growth (such as nutrients and water), *c*) factors reducing growth (such as pests and diseases). The distinction between *a* and *b* is mainly based on the degree to which the factors can be controlled by the farmer. Crop growth models have been developed for, and applied to, widely varying crop types and growing conditions. All models have to take factors of type *a* into account. In a stepwise fashion factors of type *b* and *c* can be added. Models for shoot growth range in complexity from a simple, direct conversion of the amount of light energy intercepted into an amount of biomass, to models including such details as stomatal response and light interception per leaf layer in a closed crop canopy (Goudriaan, 1977; Penning de Vries and Van Laar, 1982; Spitters, 1987, 1990; Spitters et al., 1989b; Van Keulen and Seligman, 1987; Van Wijk and Feddes, 1986; Weir et al., 1984; Williams et al., 1989). As a first estimate, the potential rate of dry matter production of a closed crop canopy in the Netherlands is about 200 kg ha^{-1} day^{-1}. This figure applies to situations with complete interception of photosynthetically active radiation (PAR) and absence of factors of type *b* or *c* that limit or reduce crop growth. By multiplying this daily production rate by the crop-specific duration of the linear growth period, a first estimate of the biomass production potential of crops can be obtained.

Based on knowledge of the development of the light interception capacity from plant emergence to full ground cover, the total biomass production by a crop can be predicted from $\Sigma\ PAR_i \times LUE$ (Monteith, 1977), where PAR_i is the amount of PAR intercepted and LUE is the 'light use efficiency', or biomass per unit PAR intercepted, (g MJ^{-1}). Such a direct conversion of intercepted light to biomass produced is only valid in conditions where LUE does not change. A constant LUE can only be expected if losses by, for instance, respiration processes and conversion costs for structural material and metabolites (such as oils and proteins) do not change substantially during the growing period (Penning de Vries, 1972, 1975; Vertregt and Penning de Vries, 1987). In Figure 1 the conversion steps between assimilation rate and growth rate are represented, as well as first estimates of the various conversion factors. To estimate crop yield on a fresh weight basis two further conversion factors are needed, the harvest index HI (dry weight of harvested product as a fraction of total or aboveground biomass) and the dry matter concentration of the harvested product D_m (dry weight per unit fresh weight). A simple model (Porter, 1984) to predict the yield Y of grain crops (on a fresh weight basis) is thus formed by:

$$Y = \Sigma \, PAR_i \, LUE \, HI/D_m \qquad (1)$$

The period over which PAR_i has to be summed depends on the rate of crop development. Plant development can usually be very well described using the concept of heat units or Growing-Day-Degrees (GDD) above a certain threshold temperature. The duration of four phases in plant development, 1. from sowing to emergence, 2. ground cover development, 3. linear growth period and 4. senescence, appear to be relatively simple functions of GGD for many crops. In addition, the response of phenological development to day length and vernalization should be taken into account, especially in induction of flowering (Kirby, 1987; Robertson, 1983; Spitters, 1987). A model as presented by Equation 1 can be used to analyze causes of observed yield differences between situations, crops or crop cultivars in terms of phenologically or physiologically meaningful and quantified components. Especially for the evaluation of goals set for plant breeding (such as earliness and leaf area duration) these simple models have proved to be useful (Spitters, 1987; Spitters and Schapendonk, 1990; Spitters et al., 1989a). Also, the effects of the attack of crops by those pests and diseases which work predominantly through a reduction in light interception, can be quantified satisfactorily (Rabbinge and Bastiaans, 1989). The validity of the concept in this case depends on otherwise unrestricted growth of the crop. If conditions directly affect LUE, anomalous results can be expected.

More detailed mechanistic models include gas-exchange properties of individual leaves, profiles of light interception in the canopy, corrections for leaf angle distributions and extinction coefficients. In some cases growing conditions will not only be reflected in the level of biomass production, but also in the distribution of biomass over plant organs (Groot, 1987a, 1987b; Van Heemst, 1986) and specific reactions such as the formation of thicker leaves. Such models start from the calculation of the instantaneous rate of photosynthesis at different levels in the canopy, using photosynthesis/light response curves for individual leaves. The assimilated CO_2 is converted into carbohydrates (CH_2O), which can be used for maintenance of the standing biomass and the operation of specific physiological processes (together described as 'maintenance respiration' in Fig. 1) as well as for conversion into new biomass. In Figure 1 a 2:1 ratio between biomass production and 'growth respiration' is assumed. In the SUCROS model (Kropff et al., 1987; Spitters et al., 1989b), maintenance respiration does not only depend on temperature, but also on the protein level in the plant organ considered (more protein leads to more respiration).

Apart from general models, crop-specific models have been developed, which consider specific processes such as vernalization, tiller formation, and intermediate storage of reserve material (starch, sugars) in vegetative plant parts, later to be remobilized and transported to storage organs or seeds (Jones and Kiniry, 1986; Penning de Vries and Van Laar, 1982; Ritchie and Otter, 1985; Van Keulen and Seligman, 1987; Weir et al., 1984). Even if no growth limiting factors such as water or nutrient supply are taken into account in these models, the belowground part of the plant should not be neglected as it forms an important and variable sink for carbohydrates. To evaluate whether or not water and nutrient supply are non-limiting, crop demand for water and nutrients should be quantified.

Relations between shoot growth and root functions

Carbon allocation

The allocation of carbon to the roots can be described as a 'loss' of part of the assimilates from the plant tops. In reality, however, such losses are investments necessary for the uptake of water and nutrients. Based on an apparent conversion efficiency of assimilates to root dry weight and on the specific root length (root length per unit dry weight, m g^{-1}) the carbon allocation to root growth can be converted to a total root length (Van Noordwijk, 1983). Although considerable situation-dependent variation exists in specific root length, we may use the following crop-specific values, which are probably within a factor 2 of the real values found in the field under normal conditions: 10 m g^{-1} for fine tree roots, 50 to 200 m g^{-1} for dicotyledonous crops, 200 m g^{-1} for cereals, and 400 m g^{-1} for fine-rooted grasses (Van Noordwijk and Brouwer, 1991).

Unfavourable soil conditions (hardpans, high levels of Al) may lead to a considerable thickening of

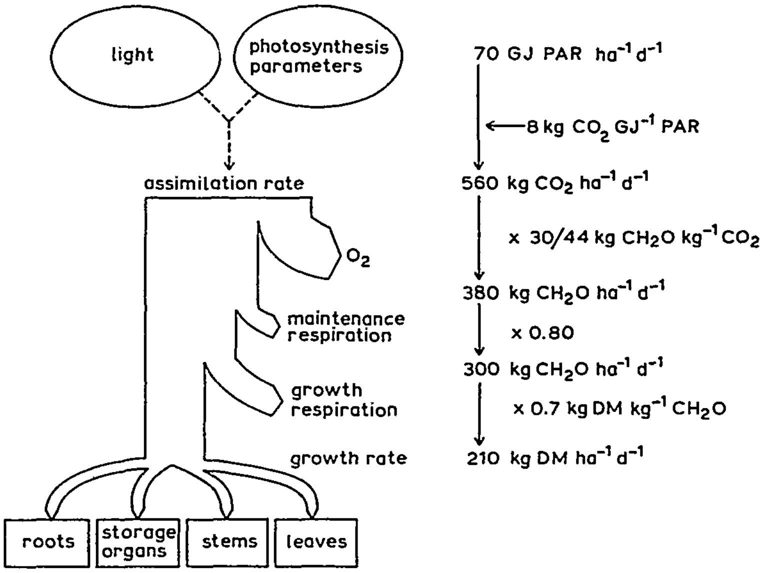

Figure 1. Conversion steps between light and dry matter production (Spitters et al., 1989b).

roots and hence decrease of specific root length. For the same root length, an increase in C-allocation to the root system is needed in such cases. Few experimental data exist on the conversion efficiency of carbohydrates to root biomass. In relatively young plants, a 1:1 ratio of root biomass production and respiration plus exudation was found (Lambers, 1987). According to Veen (1980), growth respiration, root activity (uptake), and maintenance respiration each account for approximately one-third of total root respiration in young maize plants. In older plants maintenance respiration and uptake activity will become relatively more important. When root growth has stopped, a substantial carbon allocation is still required to maintain root tissue and to allow uptake to proceed. When carbon allocation is expressed as a fraction of photosynthesis, it strongly depends on external conditions, as the absolute size of the root system is relatively constant in a range of soil physical and soil chemical conditions where the shoot shows a strong response (Schuurman, 1983). Hamblin et al. (1990) showed that the root dry weight of wheat under limited water and nitrogen supply, under conditions which allow a grain production of 1.5 to 3 Mg ha^{-1}, is similar to the root dry weight found elsewhere, under conditions which allow a grain production of 8 to 10 Mg ha^{-1}. Most carbon allocation data discussed below pertain to plants without obvious water or nutrient stress.

Carbohydrate allocation to the roots is usually a large fraction (about 50%) of the total carbohydrate supply in the plant immediately after germination and subsequently decreases. Several reports (Keith et al., 1986; Van Veen et al., 1991) indicate that for annual crops as much as 20 to 30% of the total carbon fixed in a growing season is translocated belowground. Keith et al. (1986) determined the proportion of assimilates flowing to the roots using pulse labelling with ^{14}C at various stages of wheat growth and concluded that up to harvest time, four times more carbon has been allocated to the belowground system than what remains in root biomass. As the aboveground efficiency of dry matter production (biomass per unit carbohydrates) is often 0.5 to 0.7 (Fig. 1), it is 2 to 3 times as high as the belowground efficiency. A shoot:root ratio of 10 on a dry weight basis at harvest time, which is a commonly found value for cereals on a fertile soil, thus corresponds to a cumulative carbohydrate investment belowground of 20 to 30%.

Some controversy exists on carbohydrate partitioning to roots in later stages of growth. In several models carbohydrate allocation to roots vanishes in the final stages of growth (Groot, 1987a; Spitters et al., 1989b; Van Keulen and Seligman, 1987). Goudriaan (pers. comm.), however measured canopy photosynthesis and root respiration and concluded that at the silking stage maize still used 7.4% of its daily gross photosynthesis in belowground processes. Spitters (1990) recalculated data of Louwerse et al. (1990) and showed that an almost linear relationship exists over the whole season between intercepted radiation, gross photosynthesis, net photosynthesis and aboveground biomass production (Fig. 2). This linearity indicates that constant fractions of gross photosynthesis are used for growth of shoots, for respiration and for allocation to roots. Further uncertainty still exists on the carbohydrate partitioning between roots and rhizosphere biota. The fact that a smaller fraction of available carbohydrates is converted into biomass in roots compared with shoots, is partly due to the production of root cap and mucigel material, for which no aboveground equivalent exists. These carbohydrates as well as the biomass of dying roots are certainly available as an energy source for the rhizosphere foodweb (Smucker, 1984). To what extent soluble carbohydrates are exuded from roots after their initial development is less certain, as root and rhizosphere respiration are hard to distinguish experimentally. Helal and Sauerbeck (1989) concluded from experiments with antimicrobial agents that only 16% of total CO_2 production is respired by the root and the remainder by rhizosphere organisms. Swinnen (1994) concluded from a different method that 75% of the carbon transfered to the root over a three week period after assimilation is respired by the root system. According to Van Veen et al. (1991), higher nitrogen levels in the soil promote the release of organic substances into the soil, even when root growth is unchanged. Also, drought may increase the carbon flow. Maintaining the fungal partner in mycorrhizas and the bacterial partner in root nodules for nitrogen fixation involves considerable extra carbohydrate costs (Lambers, 1987).

We may conclude that for the carbon costs for developing and maintaining a root system under 'normal' agricultural conditions a reasonable set of quantitative hypotheses exists, which can be further explored and tested as part of crop growth models. Insufficient knowledge exists, however, on the regulation of carbohydrate allocation to roots with symbiotic partners and on the response to abiotic and biotic factors in the root environment. More precise knowledge about the effect of both the developmental stage of the plant and of the actual soil conditions on carbon requirement and utilization by roots is required. A link of carbon allocation data to root extension growth and root functioning should be further pursued.

Demand for water

A shortage of water has immediate effects on plant growth. In most crops, internal buffering for water is negligible. The demand for water is directly determined by plant characteristics and meteorological conditions and extensive literature exists on this topic. Water requirement of a crop can be calculated from the Penman equation (Penman, 1948; Van Keulen and Wolf, 1986). If the rate at which water can be extracted from the rooted volume falls below the demand, the plants will react by partly closing the stomata, thus reducing transpiration. Simultaneously, the rate of photosynthesis drops because the higher stomatal resistance impedes the diffusion of CO_2 into the leaf to a similar degree as the diffusion of water vapour out of the leaf. This direct link between water loss and photosynthesis may explain why, at a given air humidity and carbon-dioxide concentration, the Water Utilization Efficiency (WUTE = dry weight production per unit volume of water transpired; elsewhere defined as WUE (Spitters, 1990)) is often constant for different crops and within a crop over a considerable range of degrees of water stress. For the Netherlands, the potential rates of evapotranspiration of approximately 4 L m^{-2} -day^{-1} in the growing season, combined with the above-mentioned rate of dry matter production of 200 kg ha^{-1} day^{-1}, lead to an expected WUTE of 5 g L^{-1}; in various experiments WUTE values of 3 to 7 g L^{-1} were reported (De Wit, 1958), with high efficiencies for crops with a C_4 and lower for those with a C_3 pathway in carbon assimilation. The simplest version of a yield model for situations where only the water supply limits crop growth is:

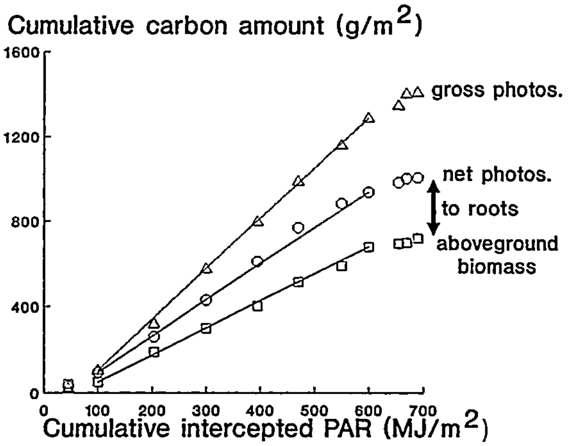

Figure 2. Recalculation by Spitters (1990) of data on maize aboveground biomass production, gross and net photosynthesis of Louwerse et al. (1990).

$$Y = W_U \text{ WUTE HI}/D_m \qquad (2)$$

where W_u (L m^{-2}) is the total amount of water which the plant could possibly extract from the soil during the growing season, which includes water stored in the soil at planting plus inputs from rainfall, irrigation and possibly capillary rise, minus surface evaporation and percolation losses. Conventionally all water retained in the soil between field capacity and the permanent wilting point is considered to be available to the plant, as far as it occurs above the effective rooting depth (see below). Other ways to relate the amount of water extracted W_u to the amount available W_a ($L\ m^{-2}$) are discussed below.

Apart from effects on carbon assimilation and biomass production, a limited water supply may affect phenological development of the crop and may lead to specific responses in critical growth stages (Van Keulen, 1987). Prolonged water shortage may lead to accelerated development of the crop or to early senescence. Also, the carbon allocation to the different plant organs may change. Direct effects of water shortage on root growth are usually negative, but plants usually respond to water shortage by a larger relative carbon allocation to roots. If this continues over a sufficiently long period of time, it may lead to an enhanced root growth in an absolute sense (Husain et al., 1990), but usually only the relative root distribution over soil layers and the shoot/root ratio are modified by drought.

Demand for nutrients

In contrast to the immediate reaction of plants to restricted water supply, shortage of nutrients affects plant growth only after a certain time lag, due to considerable internal buffering. Plants tend to keep the concentration of nitrogen and other nutrients in various organs relatively constant, between a lower threshold and a maximum concentration. Plant performance is affected if the tissue concentration drops below a critical value. In general, this will lead to reduced photosynthesis, modified specific leaf area and reduced leaf area duration. The organ will die if the concentration reaches a lower threshold. The crop demand for nutrients in a given period can be calculated from the change in biomass per organ and the corresponding tissue concentration required. In the previous section, we assumed that aboveground factors determine uptake of nutrients as well as water when the supply is adequate. This approach is not (yet) widely accepted, as models of nutrient uptake have been primarily based on the supply side, i.e. on nutrient concentrations around the root (Barber, 1984; Nye and Tinker, 1977; Rijtema and Kroes, 1991). If crop demand is supposed to determine uptake rates, in fact an efficient feedback or regulation of the uptake rate of an individual root by the nutrient status of the whole plant is assumed to operate. In earlier models, such feedback was largely neglected (Barber, 1984; Nye and Tinker, 1977) and the uptake by a whole root system was described as a simple summation of the possible (maximum) uptake of single roots. In the approach of Van Noordwijk and De Willigen (1979) and De Willigen and Van Noordwijk (1987a, 1991, 1994a,b), a complete regulation of uptake according to demand is assumed and two situations are distinguished: *a.* the sum of the possible current uptake rates of all roots is less than 'crop demand', *b.* the sum exceeds crop demand.

In the first situation, the plant is assumed to maximize its uptake rate, and model calculations are based on zero-sink uptake by individual roots. Usually the physiological uptake efficiency is so high that no detailed knowledge of the parameters of uptake kinetics is needed and only small errors are made when roots are considered to be zero-sinks (De Willigen and Van Noordwijk, 1987a, 1994a,b). In situation *b*, crop demand is assumed to determine the current uptake by the whole root system. In experiments where the growth rate of the plant is modified, e.g. by variation in nitrogen supply, tissue concentrations of other nutrients such as potassium or phosphate in the crop usually remain constant. Total potassium or phosphate uptake by the crop thus depends on nitrogen supply, whereas the size of the root system can be unaffected by the nitrogen supply. Models which relate nutrient uptake only to size of the root system, nutrient supply in the soil and age-dependent physiological uptake parameters, necessarily fail to predict such effects (Seward et al., 1990). Recent plant physiological experiments have suggested several mechanisms for internal regulation of net uptake rates, but also indicate that the regulation may involve a certain time-lag, especially relevant under rapidly changing conditions, and that regulation may be incomplete (Clarkson, 1985; De Willigen and Van Noordwijk, 1987a; Glass, 1989). The assumption of complete and instantaneous regulation thus represents a simplification which may be allowed when longer periods (e.g. weeks) are considered, not when the short-term response (e.g. hours) is predicted. As a simplification, we may define crop demand for nutrients as the current rate of dry matter production multiplied by the nutrient content per unit dry weight typical of well-fed plants at the growth stage considered. In a far-reaching simplification, cumulative crop demand for nitrogen, $N_u(N)$ ($kg\ ha^{-1}$), can be empirically related to the dry weight of the crop, Y_D (Mg

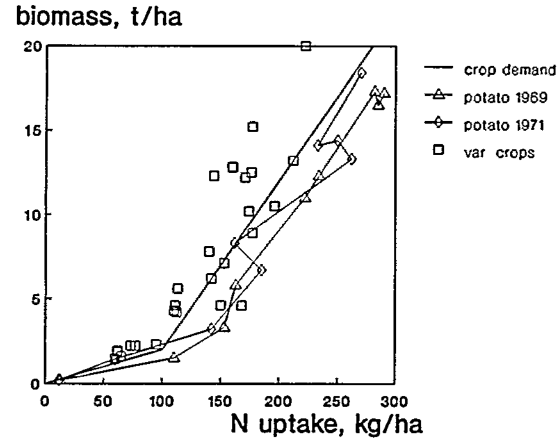

Figure 3. Relation between nitrogen uptake and dry matter production during development of a number of crops when the N supply is non-limiting; the line can be used to define N demand in uptake models; points are derived from experiments with potatoes, sugar beet, cereals, beans, grass and various vegetables (Greenwood et al., 1985; De Willigen and van Noordwijk, 1987a).

ha^{-1}), in the following way (Fig. 3; De Willigen and Van Noordwijk, 1987a):

$$N_u(N) = 50Y_D \text{ for } Y_D < 2\mathrm{Mg\ ha}^{-1} \qquad (3)$$

$$N_u(N) = 80 + 10Y_D \text{ for } Y_D > 2\mathrm{Mg\ ha}^{-1} \qquad (4)$$

As a first approximation this description may be used for a wide variety of crops, including potato, sugar beet, cereals and grass (Greenwood et al., 1985). The transition point roughly corresponds to the transition from the exponential to the linear growth phase. The Specific Leaf Area (SLA) for most crops is in the range of 0.01–0.03 $\mathrm{m}^2\ \mathrm{g}^{-1}$ (Van Keulen and Wolf, 1986). For a crop with two-thirds of its aboveground biomass present as green leaves and an SLA of 0.015 $\mathrm{m}^2\ \mathrm{g}^{-1}$, a biomass of 2 $\mathrm{Mg\ ha}^{-1}$ is equivalent to a leaf area index of 2. According to Equation (3) and (4) a target for N uptake is a N concentration on a dry-matter basis of 5% until the leaf canopy is closed and 1% in all dry matter formed in the linear growth phase. The latter value refers to a crop average; by internal recirculation tissues formed later will have a N concentration higher than 1%. In the classical terminology part of this 'demand' is designated as 'luxury consumption', which means that a certain reduction in internal concentration has no direct effects on crop growth. Thus, we still need to specify a critical value and we have to indicate how seriously dry matter production and partitioning are affected when nutrient uptake falls short of demand. Experiments in which the amount of nutrients added to a rapidly recirculating nutrient solution are controlled as a certain fraction of 'crop demand' (Ingestad and Agren, 1988) may help to clarify these aspects. By integrating an uptake module into a crop growth model, in which rates of photosynthesis per leaf depend on N contents, more refined estimates of nutrient demand as well as of the feedback of insufficient uptake to reduced subsequent dry matter production is possible (Groot and De Willigen, 1991). If the supply of a particular nutrient limits crop growth, the simplest prediction of yield might, by analogy with Equation (1) and (2) be based on:

$$Y = N_u\ \mathrm{NUTE\ HI}/D_m \qquad (5)$$

where N_u is the amount of the particular nutrient taken up from the soil in a growing season and NUTE is the amount of biomass produced per unit nutrient taken up. NUTE is equal to, or (slightly) lower than, the inverse of the minimally required average tissue concentration at final harvest. At maximum production levels, NUTE may be half the maximum value and thus an ascending branch of a quadratic function through the origin can describe the relation between N_u at harvest and total biomass production (Van Noordwijk and Scholten, 1994). Sudden changes in nutrient supply during the growth of the crop may affect HI. As NUTE is approximately constant over a considerable part of the nutrient-limited range, this formula shifts the problem to a prediction of N_u. N_u will be a certain fraction of the available pool of nutrients during the growing season. The overall agronomic nutrient use efficiency (NUSE = harvested product per unit nutrient input, kg kg^{-1}) can be analyzed (Fig. 4) as a product of the 'application efficiency' (NAPE = available amount per unit nutrient input, kg kg^{-1}), the 'uptake efficiency' (NUPE = amount taken up per unit available nutrients, kg kg^{-1}), the 'utilization efficiency' (NUTE = amount of biomass per unit nutrient uptake, kg kg^{-1}) and 'harvest index' (HI = amount of harvested produce per unit biomass, kg kg^{-1}):

$$\mathrm{NUSE} = \mathrm{NAPE} \times \mathrm{NUPE} \times \mathrm{NUTE} \times \mathrm{HI}/D_m \qquad (6)$$

The definition of availability is a key to this approach. De Willigen and Van Noordwijk (1987a) defined the available pool of nutrients as that part of the total amount present in the rooted part of the soil profile which can be taken up within a growing season by a hypothetical crop with an infinitely high uptake capacity and an infinitely high root length density (of negligible volume). Because real plants have a finite root length density, finite transport rates in the soil

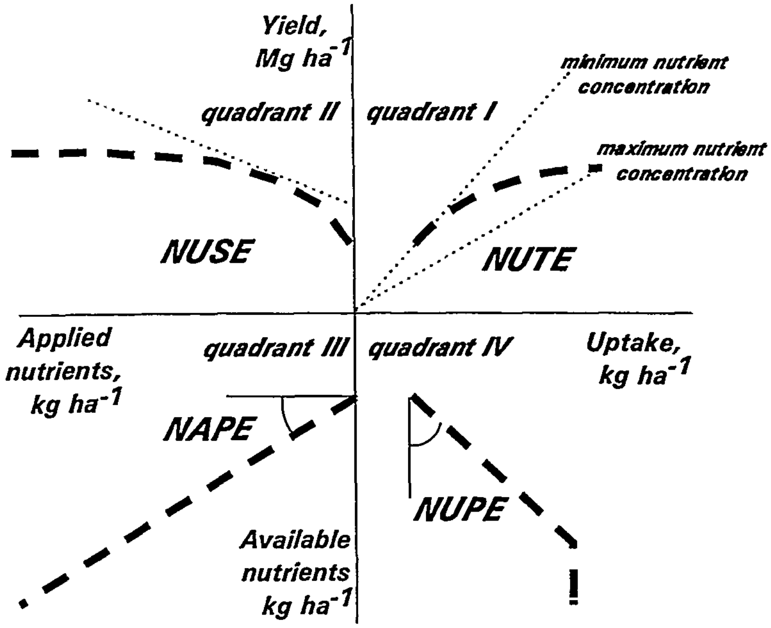

Figure 4. Four-quadrant scheme for analyzing the response of crop yield to fertilizer application in quadrant II (NUSE is 'nutrient use efficiency') on the basis of three components: 'nutrient application efficiency' (NAPE), 'nutrient uptake efficiency' (NUPE) and 'nutrient utilization efficiency' (NUTE). The scheme is an extension of the 3-quadrant presentation of De Wit (1953).

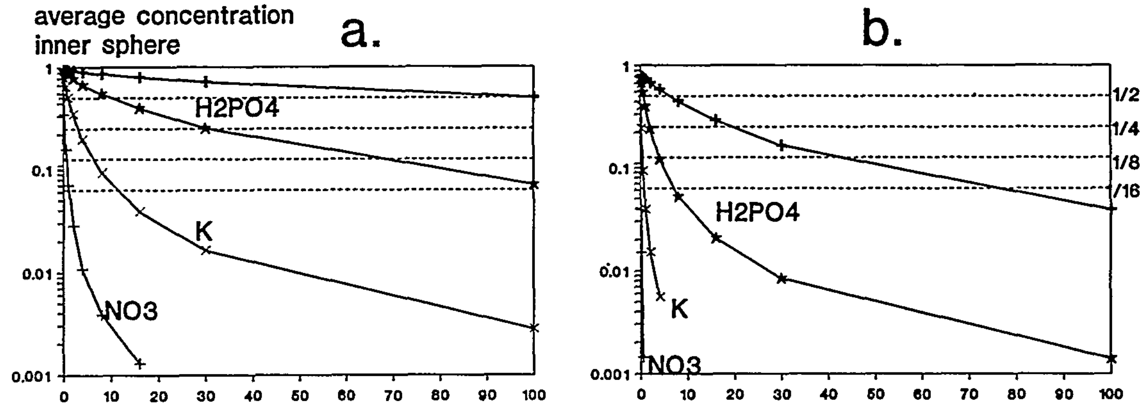

Figure 5. Decrease in concentration in a spherical 'hot spot' of radius R_0 by diffusion into the surrounding soil up to radius R_1, according to Eq. (9); $R_1 = 20$ cm; a. $R_0 = 0.25$ cm, b. $R_0 = 1$ cm.

limit the possible uptake rate of a root system, even if individual roots act as a 0-sink. Real plants can thus only obtain a part of the available amount at the rate required per unit root length; this is indicated as the unrestrictedly available amount. The remainder is restrictedly available, as it can only be taken up at a rate determined by other factors, and may fall short of that required by crop demand, actual uptake rates are in this case determined by transport rates in the soil. Only after an infinitely long time all available resources can be absorbed by a crop of finite root development. The empirical approach to soil fertility has guided farmers in the Netherlands to increase the available amount of all essential nutrients to such a level that the unrestrictedly available amount is sufficiently high to meet crop demand at any stage during the growing season. Only when we understand the factors determining the present situation can we hope to increase the nutrient use efficiencies involved. Increases in overall efficiency NUSE can be mainly expected from increased NAPE and NUPE, as the internal efficiency in the plant, NUTE, is fairly constant and selection for higher NUTE may lead to a change in product quality, e.g. for nitrogen to a lower protein content in cereals (Groot and Spiertz, 1991). The main emphasis in this contribution will be on the uptake efficiency NUPE determined by the degree of synchrony and synlocation of supply and demand (Van Noordwijk and De Willigen, 1986), as influenced both by the mobility of the major nutrients in the soil and by root development in time and space.

Models of root growth and uptake of water and nutrients

Four levels of complexity in root models

In the models of aboveground production discussed in the previous section, we distinguished between relatively simple production models which start with measurable parameters such as the development of light interception and the length of the growing season, and empirical (apparent) constants such as the light use efficiency, water utilization efficiency, or nitrogen utilization efficiency. In more complex mechanistic models, more basic processes are included and the rate of crop development is related to measurable abiotic factors such as temperature. In the simplest models of nutrient and water uptake, roots are not considered at all, but empirically derived values of NUPE are used. This approach can be characterized as 'models-without-roots'. For nitrogen in temperate climates, NUPE is independent of the external nitrogen supply over a considerable range (Van Keulen and Van Heemst, 1982), and within a well-defined range empirically derived constants may be used for calculations on required amounts of N fertilizer. Between years, crops and conditions, however, considerable differences in NUPE occur, which require analysis of underlying mechanisms. Two broad categories of more complex 'models-with-roots' exist: models which take actual root development and distribution for granted and concentrate on a prediction of NUPE, and models which also aim at a prediction of root development in time and space. By subdividing these two categories, four levels of complexity were distinguished in modelling uptake by root systems (De Willigen and Van Noordwijk, 1987a).

A. Models predicting uptake on the basis of observed root development: using measurements of root length density as a function of depth and data on root pattern on root maps as input, interpolating between experimental results.

B. Models using descriptive functions (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 including predictions on root growth in interaction with shoot growth. Usually such models are based on 'functional equilibrium' concepts, and relate 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 including root growth as in *C*, but including 'local response', i.e. relating root growth in any specific layer or zone of the soil to local conditions such as: mechanical resistance as a function of soil water content, aeration status as a function of internal and external aeration, local nutrient concentrations, local pH, hardpans and local aggregate structure to account for rooting pattern.

As in the discussion of aboveground models, the most basic mechanistic model level *D* may scientifically seem desirable, but for practical purposes the simpler models may be satisfactory; they may even be preferable from the point of view of robustness and ease of parameter estimation. Level *D* may have to include a wide range of biotic and abiotic factors modifying root growth. The models presented here are based on the assumption that effects of such factors on crop growth act via effects on water and nutrient uptake. For modelling uptake by whole root systems at level *A* through *D*, a crucial problem is that of distinguishing 'typical' single roots in such a way that integration to simulate uptake by whole root systems is possible. Reasons for differentiating between classes of typical roots are of two types: *a.* the distribution of resources (nutrients and/or water) is heterogeneous and *b.* differences exist between roots due to differences in position, root-soil contact, age, or other characteristics.

Reasons for differentiating between classes of typical roots

Heterogeneity of resources

Heterogeneity of resources can be described by measurement of the 'pattern' of places with relatively rich and relatively poor supply. For a more basic understanding, we should concentrate on the 'processes' explaining the dynamics (rise and fall) of small-scale differences in concentration (Kooistra and Van Noordwijk, 1995). In discussions of patterns in ecology, a useful distinction is made between the 'grain size' (scale) and the 'intensity' of the local differences in the measured quantity (Pielou, 1969). In agricultural soils natural heterogeneity of soils is modified by management, either on purpose or as a side effect of activities such as soil tillage, drainage, irrigation, planting patterns and crop residue management. Often clear hypotheses on scale and intensity of the resulting pattern can be formulated. In the continuum of scales of spatial heterogeneity, an important breakpoint is formed by the size of the root system of an individual plant. To heterogeneity within the reach of its root system, a plant can respond meaningfully; on this scale heterogeneously distributed resources may even be used more efficiently than homogeneously distributed ones. Heterogeneity on a larger scale (nearly) always contributes to a reduced efficiency of using resources (Van Noordwijk and Wadman, 1992).

Several agronomic activities create heterogeneity of resource supply within the reach of a single plant: soil tillage and the plowing-down of crop residues, farmyard or green manure, fertilizer placement, trickle irrigation or fertigation, and agricultural traffic. In such cases, a two-dimensional - and sometimes three-dimensional - subdivision of the root environment is needed for models of nutrient and water uptake. The primary division of the root environment is usually formed by distinguishing horizontal layers. For studying the water balance, such a division is obviously required as inputs (rain, irrigation, capillary rise) and outputs (drainage, evaporation) are nonuniform and usually occur either from the top or from the bottom compartment. The number of layers distinguished depends on the purpose of the model. Often in the upper layers, smaller depth intervals are considered than in deeper layers, as important parameters will change over smaller distances. For mobile nutrients such as nitrate the need for a vertical division of the root environment is a direct consequence of the differences in water balance between layers. For less mobile nutrients, such as phosphate, soil tillage may be the primary determinant of the vertical distribution. In simple models, we may assume that phosphate is homogeneously mixed through the plow layer and that subsoil P supply is negligible. In that case, a single root compartment may be sufficient for the model. In a more detailed analysis of soil tillage effects, however, it becomes apparent that plowing does not lead to homogeneous mixing and a distinct heterogeneity in the horizontal plane, perpendicular to the direction of the tractor, exists in most plow layers. Whether or not heterogeneity of resource supply should be included in the model also depends on the expected persistence of 'hot spots', locations of high resource supply (Van Noordwijk et al., 1993b). Various processes contribute to the evening out of heterogeneity. The most general process is probably formed by diffusion: gradients in concentration lead to diffusion, and in an exponential-decay type of process homogeneity will be approached, if nothing interferes. The time involved in this smoothing out depends on the 'apparent diffusion constant', D^*, the dimensions of the heterogeneity and its intensity. Kooistra and Van Noordwijk (1995) described a simple model of a spherical hot spot of radius R_0 and concentration C_0 inside a larger sphere of radius R_1 and of uniform low concentration C_1. The apparent diffusion constant D^* is equal to $D'/(K_a + \Theta)$, where D' is the 'effective diffusion constant', K_a is the 'apparent adsorption constant' and Θ the volumetric soil water content. Figure 5 shows examples using values of D^* of 1, 0.1 and 0.01–0.001 $cm^2\ day^{-1}$ as roughly representative for nitrate, potassium and phosphate. We may conclude that 'hot spots' in nitrate concentration of a few cm diameter are unlikely to persist in a soil at field capacity for more than a few days. For smaller 'hot spots' it is a matter of hours or less. Horizontal differentiation for nitrate supply is only required under continued heterogeneous supply (e.g. by mineralization from a green manure, plowed down as a band, or from injected slurry). For potassium, evening out of 'hot spots' of 1 cm diameter is a matter of weeks and for phosphate it is a matter of months.

In drier soil, the effective diffusion slows down considerably and heterogeneities will persist longer. The effective diffusion constant D' is derived as the product of the diffusion constant in water D_j, the volumetric water content Θ and the impedance (tortuosity) factor f_l (Nye and Tinker, 1977). So and Nye (1989) found that for a tenfold decrease of D' from its value at field capacity (-100 cm), a sandy loam has to dry out down to a water potential of -2000 cm and a silty clay down to -32000 cm. Such a tenfold decrease in D' renders the diffusion of nitrate in a dry soil similar to that of potassium at field capacity.

Plant roots may reduce heterogeneity by preferential uptake in the 'hot spots'. In a split-root experiment Sonneveld and Voogt (1990) found that differences in nutrient concentration between two sides of the root system were difficult to maintain because of preferential water uptake on the dilute side and preferential nutrient uptake on the concentrated side. Figure 6

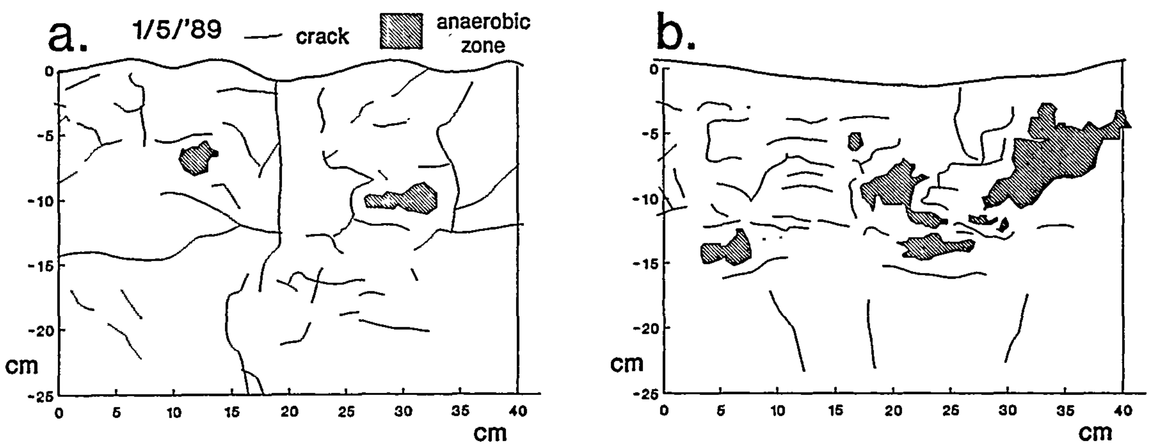

Figure 6. Maps of the plow layer in spring of two plots (a. conventionally tilled, b minimum tillage) of the Dutch programme on soil ecology of arable farming systems (Kooistra et al., 1989); anaerobic (blue) spots and major cracks were mapped on polythene sheets.

shows a simple map of a section of the plow layer in a conventionally tilled and a reduced-tillage soil at the start of the growing season. As diffusion of oxygen in water is 10^4 times slower than that in air, a few mm's of wet soil may form a substantial barrier to oxygen diffusion and anaerobic spots may occur close to large air-filled gaps and cracks. To describe such a plow layer in a clay soil as an environment for root development at least two zones have to be distinguished: solid aggregates of a cylindrical shape with a diameter of approximately 10 cm, extending in the direction of the field operations, and zones which are loosely filled with relatively fine aggregates. The ability of roots to penetrate the relatively dense and wet aggregates depends on the formation of cortical air spaces (aerenchima) to supply the growing root tip with sufficient oxygen (De Willigen and Van Noordwijk, 1989b).

Differences between roots

The simplest description of nutrient uptake starts from the assumption that 'all roots are equal'. In that case a single root in a cylinder of soil can represent a whole root system. In many cases, however, external conditions allow 'some roots to be more equal than others...'. Reasons for differentiating between classes of typical roots are:

1. in different soil layers different average root length densities are found, along with differences in initial water and nutrient contents, as well as their rate of replenishment,
2. root distribution within a soil layer is not homogeneous; individual roots in a single layer will exploit smaller or larger than average volumes of soil and their degree of eccentricity in the volume exploited may differ,
3. roots may differ in their degree of root-soil contact,
4. roots differ in age and thus differ in uptake capacity and physiological activity, especially for nutrients such as calcium (Clarkson, 1985); uptake or exclusion of calcium may modify the dynamics of other nutrients in the rhizosphere,
5. roots may differ in their external pH effect, and thus induce differences in mobility of nutrients such as phosphate,
6. roots may differ in rhizospheric or symbiotic companions and in degree of attack by parasites or herbivores.

Even if we differentiate roots according to only four criteria, in only three classes each, we have to deal with $3^4 = 81$ classes. The first question thus is which complications of soil conditions, root-soil geometry and root physiology are really important. This question can best be answered using single root models considering the complications mentioned one by one, in a sensitivity analysis for model assumptions. Based on De Willigen and Van Noordwijk (1987a), we may expect that root length density and soil water content have a major effect on the dynamics of nutrient depletion and should be taken into account in any prediction of the uptake by single roots. The fact that root distribution in a layer is never regular but random or clustered must be included, especially for nutrients of intermediate mobility, such as potassium, and for water (De Willigen and Van Noordwijk, 1987b; Tardieu, 1988). Incomplete root-soil contact may hamper uptake (De Willigen and Van Noordwijk, 1987a) but variation in

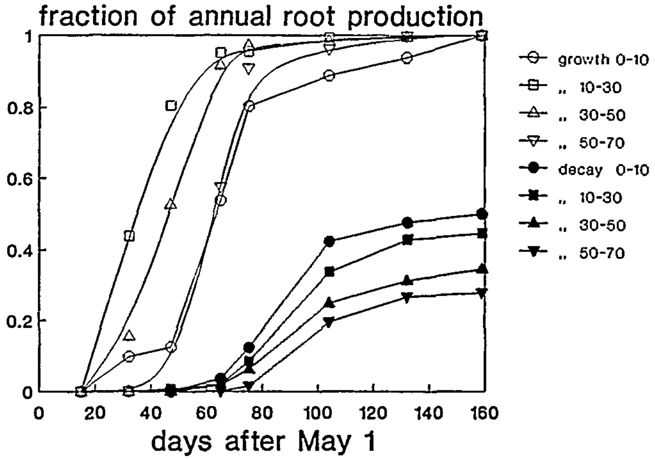

Figure 7. Dynamics of root growth and decay (99) for sugar beet grown at the Lovinkhoeve soil ecology project (Kooistra et al., 1989).

the degree of root-soil contact in the field is largely unknown as yet (Van Noordwijk et al., 1993c) and the tendency of many roots to form root hairs when root-soil contact is incomplete may render this aspect less important as a factor to distinguish between classes of roots. External pH effects of the roots and/or excretion of substances influencing availability or mobility of nutrients can be important for uptake of P and micronutrients; often marked patterns of rhizosphere pH exist along the roots as a function of root age, with the root tips usually being more acid (Römheld and Marschner, 1986) but more alkaline in conifers (Gijsman, 1990). Only in the case of 'proteoid' roots, however, does sufficient information exists to distinguish between alkalizing and acidifying roots as part of the same root system (Dinkelaker et al., 1995). In summary, a differentiation between soil horizons is almost always required, as both soil water content and root length density vary in this way. A classification according to nonhomogeneous root distribution within each layer is desirable, although information on actual patterns is still scarce. A number of modifying factors, such as rhizosphere pH and the possibilities for Ca uptake, can be accounted for by a classification according to root age. To make such a differentiation operational we need reliable methods to predict root development in space and time.

Root length in space and time

Plant-based description

For the measurement of root length in space and time, two approaches can be followed: plant-based and soil-based. In the plant-based approach the growth of roots originating from the seed or other planting material and their branch roots of various orders is monitored. In a descriptive system the length of bare root tips before the first branch roots, the average density of branch roots per unit length of main axis, and the average length of branch roots are determined. For example, Schuurman and De Boer (1970) described the developmental pattern of roots and shoots of oats under favourable conditions. Total root length, which is mainly determined by the finest classes of branch roots, was not accurately determined in much of the older work, as the emphasis was on the development of main axes.

Recently the plant-based approach received a new stimulus from two models for branching patterns, by Diggle (1988) and Pagès et al. (1989). By including information on root orientation (degree of geotropism) as a function of the branching order of the root, predictions of the spatial distribution of roots can be made. The model of Pagès et al. (1989) explicitly considers the influence of soil temperature on root development in each soil layer. Models based on fractal properties have provided a useful framework for evaluating real-world branching patterns (Berntson, 1992). For roots with significant secondary thickening, regularities in the change of root diameters upon branching may be exploited for plant-based descriptions (Van Noordwijk et al., 1994a; Spek and Van Noordwijk, 1994).

Roots are subject to turnover in the soil. With the mini-rhizotron technique, it is possible to estimate root length densities at any time per depth interval, provided that root intensities on the images (cm cm^{-2}) have been calibrated with root length densities (cm cm^{-3}) derived from auger samples. It is also possible to compare images of roots at the same position throughout the growing season and in this way obtain estimates of root appearance and decay (Van Noordwijk, 1987; Fig. 7). As root decay and new root growth may occur simultaneously in a single layer, this technique yields more information than methods based on comparisons of total root length between sampling dates. Van Noordwijk et al. (1994b) reported turnover values during a growing season of about 15%–50% for wheat, depending on the cropping system, and 50% for sugar beet. Swinnen et al. (1995) found slightly higher ^{14}C turnover values: about half the carbon transfer to the roots of wheat had been respired by the end of the season. Box and coworkers (Box and Johnson, 1987; Cheng et al., 1991) developed a similar system to quantify root turnover below a wheat crop and found a turnover of 50% during the growing season. Differences in measured turnover may be primarily related to drying/wetting patterns of the soil. A problem in interpreting mini-rhizotron data is that conditions in the observation plane may differ significantly from conditions elsewhere in the soil. Incomplete contact between the mini-rhizotron wall and the soil may lead to roots creeping over the surface of the mini-rhizotron wall (Van Noordwijk et al., 1985a). Abundance of root hairs on the root images may indicate that such a problem exists. The use of inflatable mini-rhizotrons (Gijsman et al., 1991) may be preferred to reduce this problem. Repacked soils with horizontally placed minirhizotrons also circumvent this incomplete joint between tube wall and soil (Van de Geijn et al., 1994).

Soil based description

The majority of the existing quantitative root data have been obtained by soil sampling. The sampling scheme should be based on the smallest representative soil volume, related to plant density, in order to avoid bias (Van Noordwijk et al., 1985b). Root length per unit volume of soil is obtained by washing roots from known volumes of soil and measuring root length by the line-intersect method. Subsampling with root weight as an intermediate parameter is usually possible because the coefficient of variation in specific root length is smaller than that for amount of roots per unit volume of soil (Van Noordwijk et al., 1985b). In the latter case some attention should be given to the problem of dry weight losses during handling of roots (Van Noordwijk, 1987).

Distribution of roots over various soil layers can be described in different ways, based on a negative exponential distribution or on a relative pattern as derived from crop and soil specific observations. In certain descriptions of the water balance of a soil (see below) only a boundary between "rooted" and "non-rooted" soil is considered, which is moving downwards in time. An alternative approach to measurement of root length is to count the number of intersections between roots and horizontal or vertical planes. Two such methods are the core-break and the root mapping technique (Böhm, 1979). Although these methods are less time-consuming, interpretation of the results is difficult as the calibration factor between number of roots intersected per cm^2, N, and root length density L_{rv} critically depends on root orientation (Van Noordwijk, 1987). Apart from these theoretical calibration factors, often considerable further corrections are required as in this technique fine roots may be overlooked (Van Noordwijk et al., 1995).

Root maps in the horizontal and vertical plane (trench method) not only yield information on average root length density per soil layer, but also allow quantification of the distribution pattern within each layer (Barley, 1970; Diggle, 1983). The frequency distribution of nearest-neighbour distances of random points to the nearest root on such a map indicates the possibilities for transport by diffusion of all soil resources (Rappoldt, 1990; Van Noordwijk, 1987). A major assumption in this approach is that a classification of soil according to the nearest root (i.e. a Dirichlet tessellation) is acceptable. If all roots start to function at the same time, this assumption does not lead to large errors (De Willigen and Van Noordwijk, 1987b). In the model representation, the cumulative frequency distribution of transport distances should be conserved. For any frequency distribution of distances to a spatial point pattern, a frequency distribution of cylinders can be derived which fulfills this criterion (Rappoldt, 1990; Van Noordwijk, 1987; Van Noordwijk et al., 1994a). A partly unresolved problem is the fact that the real three-dimensional distances of points in space to the nearest root are smaller (except for roots growing perpendicular to the mapped plane) than the two-dimensional distances measured on the map. For a random root orientation, the frequency distribution of three-dimensional distances coincides with that for 0.71 times the two-dimensional distances (Van Noordwijk, 1987). For non-random root orientation the problem is unresolved; a serious complication is the fact that a plane represents a biased sample of roots, as roots growing almost perpendicular to the plane are over-represented and roots growing almost parallel to the plane are under-represented. Van Noordwijk et al. (1993 a, d) described how a single conversion factor R_{per} ('root position effectivity ratio') can be defined and measured to convert root length densities in any pattern to equivalent regularly distributed root systems for which standard uptake models exist.

At a more detailed level several recent models of uptake require information on root-soil contact (De Willigen and Van Noordwijk, 1984, 1987a). The thin-section technique used in soil micromorphological characterization allows in situ measurement of root-soil contact if adequate precautions are taken (Altemüller and Haag, 1983). As yet, the technique is too time-consuming for routine applications.

By a combination of techniques we may thus determine values of the basic root parameters listed in Table 1.

Integration

A simple check of plant-based and soil-based descriptions is to determine whether or not data on carbon allocation in the plant and measurements of root length density agree. For a wheat crop in the Netherlands a total aboveground biomass of 19 Mg ha^{-1} may be expected, which represents a grain production of 8.5 Mg ha^{-1} when the harvest index is 0.45. For such a crop, a shoot:root ratio on a dry weight basis in the range of 10 to 15 may be expected at harvest (see above) and thus a total living root biomass of around 1.3–1.9 Mg ha^{-1}. For a specific root length of 200 m g^{-1} this leads to a total root length of 26–38 km m^{-2} or 2.6–3.8 m cm^{-2}. If the average root diameter is 0.2 mm, the Root Area Index A_{ra} will be in the range of 16 to 24 (m^2 m^{-2}). The lower value of this range can be reached by an L_{rv} value of 6 cm cm^{-3} in the top 30 cm, a value of 2 cm cm^{-3} in the next 30 cm and 0.5 cm cm^{-3} in the remaining 40 cm of a 1 m deep profile. Values in this range were found experimentally (Barraclough and Leigh, 1984; Van Noordwijk and Brouwer, 1991). From the model of Pagès et al. (1989) we can relate plant-based and soil-based descriptions of root development, as the model allows the construction of root maps in any plane, given the branching rules of the root system. If actual root maps contain more or less clustering than is to be expected on the basis of the inherent branching rules of the root system, the difference can be attributed to soil heterogeneity.

Models to evaluate uptake capacity, given a certain root development

Water uptake

In conditions where water uptake is the primary limitation to crop growth, a description of water uptake W_u in relation to water availability W_a is needed to apply Equation (2) or more complex variants which distinguish between the effects of drought in various growth stages (Doorenbos and Kassam, 1979). Conventionally W_a, in L m^{-2}, is defined as the integral over a certain depth of the amount of water retained in the soil, per unit soil volume, between field capacity and permanent wilting point. The depth over which available soil water content should be integrated is defined as the "effective rooting depth". A drawback of this method is that no operational definition for measuring "effective rooting depth" exists. By model calibration, however, crop-specific values have been found which can be used for predictions of a regional water balance over a growing season (Feddes et al., 1988). McKeague et al. (1984) defined "effective rooting depth" on the basis of measurements of the volumetric water content as a function of depth during a period of critical water stress (Fig. 8a). Although by this technique model predictions of the water balance can be made to fit, this definition shows that the concept of an effective rooting depth is not valid: a considerable amount of water above this depth is in reality not taken up by the crop, while an equal amount from below this depth is used. To predict the commonly found gradual transition from "complete depletion" to "no depletion", models of water uptake should be based on the actual root distribution and the possible rate of water uptake per unit root length, as determined by soil and plant parameters (Fig. 8b and c).

Several mechanistic models of water uptake exist in which the micro-level of uptake by individual roots is coupled to the macro-level of a root system growing in a soil profile. For the uptake by individual roots, two major resistances to water flow should be taken into account: the physiologically determined entry resistance and the resistance formed by transport through a relatively dry rhizosphere. If thermodynamically free water is available, commonly measured values for the physiological root conductance, L_p, indicate that a considerable root area is required to meet the transpirational demand at an acceptable pressure head of water

Table 1. Parameters of root-soil geometry required for process-oriented uptake models

L_{rv} - Root length density (cm cm^{-3}) as a function of time, depth and - if required - horizontal position,
R_0 - root diameter, including root hairs (unless root hairs are considered separately in the model),
R_{per} - Root position effectivity ratio, accounting for effects of non-regular root distribution (Van Noordwijk et al., 1994a,d),
v_1 - fraction of root perimeter in direct contact with soil.

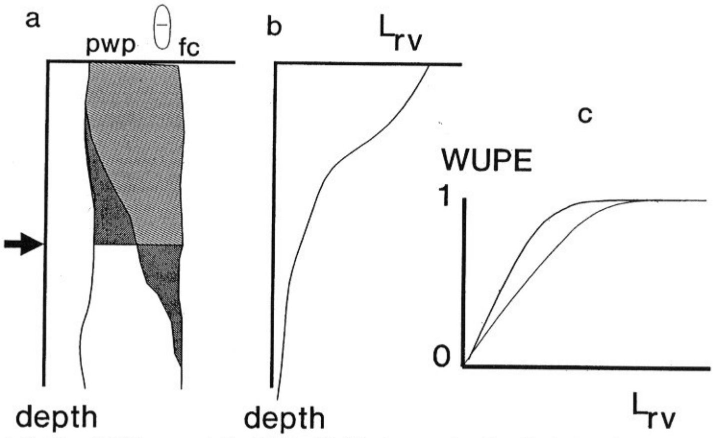

Figure 8. **a.** Illustration of the definition (McKeague et al., 1984) of 'effective rooting depth' (indicated by the arrow) based on a measurement of a profile of soil water content in a dry period: the amount of 'available water' not used at less than the 'effective rooting depth' equals the amount of water utilized from below this depth, as indicated by the two dark shaded polygons of the same surface area. **b.** and **c.** give an alternative approach based on root length density and water uptake efficiency (WUPE) as a function of root length density L_{rv} derived from micro-models, for various parameter combinations; the two curves in **c** refer to different transpiration rates, as the possible soil water extraction decreases with an increase in the required rate.

in the plant (De Willigen and Van Noordwijk, 1987a):

$$A_{ra} = \frac{E}{F_w} = \frac{E}{L_p(P_r - P_p - I)} \tag{7}$$

where

A_{ra} = root area index, root surface area per unit cropped area (m^2 m^{-2}),
E = transpirational demand (L m^{-2} day^{-1}),
F_w = volume flux of water per unit root surface area (L m^{-2} day^{-1}),
L_p = hydraulic conductance of root (L m^{-2} MPa^{-1} day^{-1}),
P_p = pressure head of water in the plant (MPa),
P_r = pressure head of water at the root surface (MPa),
I = a factor (MPa), which depends on the osmotic value of the root environment and the reflection coefficient for solutes (Van Noordwijk, 1990); in non-saline soils, "I" can be neglected for the present purpose, as it is probably less than 0.1 MPa.

If E is 4 L m^{-2} day^{-1}, L_p is in the range 0.5–10 L m^{-2} MPa^{-1} day^{-1}, P_r is 0 and P_p is 0.5 MPa, the root area index A_{ra} has to be in the range of 16 to 0.8. For a leaf area index (LAI) of 2 this means that shoot:root ratios on a surface area basis cannot be more than 0.125–2.5. As the specific root surface area (SRA) is often at least ten times higher than the SLA, this calculation predicts maximum leaf/root ratios on a dry weight basis of 1.25–25; for a leaf weight fraction of 0.6, this corresponds with maximum shoot:root ratios on a dry weight basis of 2–40. The value of L_p is critical in this respect, but literature values cover the range indicated (De Willigen and Van Noordwijk, 1987a). This simple calculation may explain why, even when water is available at a low pressure head in the subsoil, a low root length density is insufficient to use this water at the rate required by transpiration. In certain crops, especially monocots without secondary thickening of roots, the resistance to longitudinal water transport in the root may hamper water uptake from deeper layers (Richards and Passioura, 1989; Wind, 1955). Depending on the soil physical properties, transport through the rhizosphere may constitute a further resistance. As described by De Willigen and Van Noordwijk (1991) the possible flux of water to a sink of radius R_0 in the center of a soil cylinder of radius R_1 can be approximated by a steady-rate approximation in terms of the matric flux potential, Φ, (Raats, 1970), which for our purpose is defined as:

$$\Phi = \int_{\Theta}^{\Theta_{sat}} D_w \, d\Theta = \int_{P}^{P_{sat}} K \, dP \qquad (8)$$

where D_w is the diffusivity of water in cm^2 day^{-1}, Θ is the volumetric water content in mL cm^{-1}, K is the hydraulic conductivity in cm day^{-1} and P is the pressure head in cm water. Θ_{sat} and P_{sat} refer to a water-saturated soil. If Φ^* represents the average value of Φ in the soil cylinder with length H and Φ_{rs} the value of Φ at the root-soil interface defined by $P = P_r$, the flow of water towards the root is given by U_t:

$$U_t = 2\pi \, H \, L_{rv} \frac{\rho^2 - 1}{2G(\rho, 0)} (\Phi_{rs} - \Phi^*) \qquad (9)$$

with

$$\rho = \frac{R_1}{R_0} = 2(\pi L_{rv} D_m^2)^{-0.5} \qquad (10)$$

and

$$G(\rho, 0) = \frac{\rho^2}{8}[-3 + \frac{1}{\rho^2} + \frac{4 \ln\rho}{\rho^2 - 1}] \qquad (11)$$

Flow of water towards the root is only possible if the soil water content at the root surface is lower than the average for the cylinder, and hence Φ^* - Φ_{rs} is positive. In many situations a very small difference in soil water content is sufficient to generate the flow per unit root length required by crop demand. If the demand per unit root length is high, however, transport restrictions in the soil may limit the part of the available water which can be extracted at the required rate. Still largely unresolved, reduced root/soil contact in dry soils may further increase the resistance for water uptake. The formulation given by Herkelrath et al. (1977) for this resistance leads to the prediction that very high root length densities are needed to use practically all available water from a soil layer (Van Noordwijk, 1983). Because of uncertainty about the role of root hairs in maintaining root-soil contact in a drying soil, this concept is usually not included in models of water uptake. Further complications, which are usually neglected, are the observation that the entry resistance for water may increase under drought and upon rewetting may decrease again, but to different degrees for different species (Wiersum and Harmanny, 1983). Based on a combination of (constant) physiological resistance and transport limitations, De Willigen and Van Noordwijk (1991) describe a procedure to predict which pressure head of water in the plant, P_p, is required for a certain root system and in a soil profile of given water content, to meet transpirational demand. The procedure also predicts the distribution of water uptake over various layers (or zones) of soil. To implement such a mechanistic model of water uptake into a crop growth model, the relation between P_p and possible reductions in transpiration due to stomatal closure should be known.

Nutrient uptake

Mechanistic models of nutrient uptake should be linked to adequate descriptions of the water balance per layer (or zone) of soil, because soil water content has a strong effect on the effective diffusion of solutes (see above) and because water transport in the soil leads to mass flow of solutes. To describe nutrient uptake by a root system, first of all we have to know A_t, the maximum possible transport of solutes by mass flow and diffusion towards a unit root length over a given time interval. This flow can be approximated (De Willigen and Van Noordwijk, 1991) from a steady-rate solution to the transport equation as:

$$A_t = 2\pi \, H \, D \, L_{rv} \frac{\rho^2 - 1}{2G(\rho, \nu)} (c^* - c_{rr}) \qquad (12)$$

with

$$\begin{aligned} G(\rho, \nu) = & \frac{1}{2(\nu + 1)} \\ & \{\frac{1 - \rho^2}{2} + \frac{\rho^2(\rho^{2\nu} - 1)}{2\nu} + \frac{\rho^2(\rho^{2\nu} - 1)(\nu + 1)}{2\nu(\rho^{2\nu+4} - 1)} \\ & + \frac{(1 - \rho^{2\nu+4})(\nu + 1)}{(2\nu + 4)(\rho^{2\nu+2} - 1)}\} \end{aligned} \qquad (13)$$

where

$\nu = R_0 \, V / 2 \, D$, dimensionless group based on rate of mass flow,

V = flux of water per unit root surface area (cm day^{-1}),

c^* = the average concentration in the soil cylinder,

c_{rr} = the concentration at the root surface required for uptake; in many cases c_{rr} is approximately zero, and we may assume a 0-sink uptake process.

If we take the limit for ν approaching zero, $G(\rho, \nu)$ in Equation (13) converges to Equation (11) for $G(\rho,0)$. For nutrients with a non-linear adsorption isotherm, such as phosphate, an adequate approximation can be obtained by these equations (De Willigen and van Noordwijk, 1991). For the effects of incomplete root-soil contact a term $F(\nu_1)$ should be added to the G term. De Willigen and Van Noordwijk (1991) also described a sub-model for predicting nutrient uptake by a multiple root system, based on the assumption of complete internal regulation of uptake. A multiple root system is supposed to consist of a number of compartments, each characterized by a root length, a volume of soil, and state values for all parameters affecting potential uptake rate. The compartments are chosen in such a way that each one can be represented by a single characteristic root (see above). For each compartment a bookkeeping system for nutrients and water is maintained and changes in state values other than by uptake, e.g. by exchange of nutrients and water between compartments, are supposed to alternate with uptake, in a sequence of sufficiently small time steps. First of all, the distribution of water uptake over the various compartments is calculated from Equation (9). Subsequently for each time step, nutrient uptake from each compartment is calculated in an iteration cycle. As a first step, current crop demand for nutrients is divided by the total root length to obtain the average required uptake per unit root length. Multiplying this value by the root length in a given compartment yields the required uptake from that compartment. For each time step and for each compartment, the required uptake rate is compared with the potential uptake, based on Equation (12). If for any compartment the potential uptake rate during a time step is less than the required uptake, actual uptake is taken to be equal to the potential uptake and the compartment is assigned to category 1. Compartments where potential uptake exceeds required uptake are assigned to category 2. If there are no roots in category 1, actual uptake in all compartments equals required uptake. Otherwise, crop demand minus the actual uptake from all compartments in category 1 is divided by the total root length of all compartments in category 2 to obtain a new, higher estimate of required uptake per unit root. For all compartments in category 2 the potential uptake is compared with this new required uptake and compartments are again assigned to category 1 or 2, and so on. The iteration cycle ends either when all compartments are in category 1 or when during an iteration cycle all compartments remained in category 2. In the first case, total uptake cannot meet crop demand, in the second case uptake equals demand for that time step. The model implies that all roots in favorable conditions equally compensate as much as possible for roots in conditions less favorable for uptake. A special problem is the modelling of nitrogen uptake in situations where both nitrate and ammonium are present at the root surface (Gijsman and De Willigen, 1991). Physiological knowledge on the degree of feedback between uptake rates for N in these two forms and on uptake preference is still inadequate.

Table 2. Plant parameters for process-oriented uptake models

E – required transpiration rate, as determined by climatic conditions and LAI,
P_{pc} – pressure head of water in the plant at which transpiration starts to become reduced by stomatal closure,
P_{p0} – pressure head of water in the plant at which leaves wilt permanently,
L_p – hydraulic conductance of roots,
C_{rr} – minimum concentration at the root surface required for nutrient uptake; in many cases a value of 0 can be used,
C_{max} – maximum nutrient concentration in plant tissue, determining the setpoint of regulated nutrient uptake,
C_{crit} – critical concentration in the plant where reductions of growth rate start.

Table 3. Soil parameters for process-oriented uptake models

Θ – volumetric water content, described as a function of pressure head H_p,
D_w – water diffusivity, described as a function of Theta or,
K – hydraulic conductivity, described as a function of pressure head H_p,
D_j – diffusion constant of solutes in water,
K_a – adsorption constant or parameters describing concentration-dependent adsorption isotherm,
f_j – impedance factor for diffusion in non-watersaturated soils, described as a function of Θ or H_p,
C_{ij} – initial nutrient concentrations in the various soil compartments.

Required parameters

Plant and soil parameters required for an uptake model as described here, are listed in Tables 2 and 3, respectively.

Models including root growth in interaction with the shoot

Functional equilibrium

With models of the types discussed in the previous sections the consequences of a given root development for uptake can be predicted. If the development of the root system in space and time is known, as well as the aboveground crop demand for water and nutrients, the conditions in which the supply by the soil will (just) fall short of that required to meet crop demand can be calculated. To understand the growth of plants under conditions of restricted supply, however, further knowledge is needed on the feedback from conditions in the shoot to growth and functioning of the roots. Since Brouwer (1963) introduced the concept of a 'functional equilibrium' between shoot and root growth, quantitative hypotheses for such feedback could be formulated. Subsequent physiological research (Brouwer, 1983; Lambers, 1983) suggests that the mechanism of feedback is more complicated than initially formulated by Brouwer. In addition, much more genetically determined variation exists in both the speed and the degree of return to the original shoot/root ratio after disturbance. Kuiper et al. (1990) compared salt-tolerant and salt-sensitive barley cultivars. Survival of salt application by cultivars was strongly related to the capability to rapidly adjust their shoot/root ratio, a process that can be inhibited by added cytokinins. Such experiments suggest a complexity of mechanisms underlying the functional equilibrium response, making a direct incorporation into crop growth models difficult.

Relatively simple versions of incorporating a functional equilibrium response into crop growth models where used initially by Brouwer and De Wit (1969) and subsequently by Spek and Van Oijen (1988). Carbon allocation to root growth is described as a function of N status of root and shoot. Functional equilibrium response of crops certainly has to be included in the model if external disturbance of the shoot:root equilibrium is part of the problem studied, for instance cutting, pruning or grazing of roots or shoots. When root growth stops temporarily, existing root tips may survive and resume growth subsequently. Under prolonged disturbance, existing roots die and new roots may have to start from the base of the stem. Dieback of rootlets and nodules after pruning trees may lead to significant transfer of N to accompanying food crops in the alley cropping system (Kang et al., 1990). Recent biotechnological techniques for modifying root growth should also be interpreted as modifications on the endogenous functional equilibrium response (Van de Geijn et al., 1988).

Local response

Root observations in the field often show evidence of a 'local response', an increased development of branch roots close to local sources of water and/or nutrients. In the field the most striking examples of local response are usually found for local accumulations of P. Experiments with a split-root technique by De Jager (1982) have shown however, that this response is by no means unique for P and that it may occur for any nutrient in short supply in the plant. Local response can only be expected under field conditions if heterogeneities of resource supply persist (see above). Measurements of Goedewaagen (1937; compare De Jager, 1985) showed that increased branching was restricted to roots passing within 10 mm from a P fertilizer granule, thus in the range where slightly increased concentrations may be expected. When sulfur-coated urea is used as a slow-release fertilizer, increased root branching of *Lolium perenne* roots at about 1 mm from the fertilizer granules was found (Van Noordwijk, unpublished). Similar effects were observed for ammonium fertilizer (Kasten and Sommer, 1990). Local response is usually restricted to factors in short supply to the plant as a whole and root branching becomes independent of a local source if the plant becomes well-supplied, with the exception of the response to Ca (De Jager, 1985) and oxygen. Internal transport and redistribution is probably responsible for the normal growth of roots which cannot obtain essential nutrients from their own environment.

For an adequate model description of local response, we thus have to quantify two processes: the rise and fall of heterogeneities in resource supply and the internal distribution of nutrients within the plant. In the model of Spek and Van Oijen (1988), the mechanism which leads to a modified shoot:root ratio under limited N supply is also used to predict the response of a 'split-root' plant to a local supply of nitrogen to part of the root system. The local response to water availability may be easier to describe, by specifying a range of soil water contents with unimpeded root growth, a range where soil gradually becomes too wet for root growth and a range on the dry side where mechanical resistance gradually limits root extension growth (Boone, 1988; Letey, 1985). Growth rules based on these principles may be adequate to predict root distribution in a soil profile which is gradually drying out. The critical values, both on the wet and on the dry side, are species-dependent as both internal aeration and abilities to overcome mechanical impedance show genotypic variation.

Conclusion: choosing the appropriate level of detail

Models which contain parameters for which no independent measuring technique is available, can only be used for an improved 'curve-fitting' exercise ('the survival of the fitter'). Such models can be useful for purposes of interpolation within the range for which model parameters were fitted, but cannot be trusted for extrapolation to new conditions. Model improvement therefore often depends on improvement of measuring techniques. On the other hand, mechanistic models often require values for a large number of parameters which can only be roughly estimated for any specific combination of crop/soil and climate. Although models at level *D*, including dynamic shoot-root equilibrium and local root responses, may seem desirable, at the moment insufficient knowledge exists to formulate them and to determine all relevant parameters by independent measurements. The choice of the appropriate level of detail therefore depends on an a priori estimate of the importance in a specific situation of a large number of possible complicating factors and on the practical feasibility of obtaining the required parameters. Some examples of such choices will be discussed here. Various models on level *A*, evaluating the uptake potential of root systems as actually found under field conditions, are now available. Van Noordwijk et al. (1990) showed that with a model based on a limited number of crop- (average root length density L_{rv} in the plow layer, root diameter, daily phosphorus demand during the period of constant daily uptake, total P-demand) and soil parameters (P adsorption isotherms, Θ and impedance factor f_l) the required P supply of a soil can be estimated in which P is not limiting growth of various crops. If the required P supply is expressed as a single soil parameter, based on the Pw-method as used for arable crops in the Netherlands, calculated requirements per crop are in the same range as values used in the current fertilizer recommendation scheme, which has an empirical basis (Fig. 9). This model might be the basis for future refinements of a fertilizer recommendation scheme, as it suggests how site- and crop-specific deviations from the average values, necessarily used in a general scheme, influence the results.

In this model approach to P nutrition, two important simplifications were made: instead of considering the whole growing season, calculations were confined to a single critical period (in this case the end of the period of linear uptake) and only a single layer of roots (in this case the plow-layer, as soil tillage is the main agent for P transport in arable cropping systems). For a comparable effort in predicting required N supply in the soil, neither of these simplifications is acceptable, as transport of N between layers of the soil profile during the growing season is important. Table 4 shows model predictions of nitrogen uptake efficiency by maize on an acid soil in the humid tropics (De Willigen and Van Noordwijk, 1989a). The nitrogen uptake efficiency found in the field could be adequately predicted on the bases of root densities as a function of time, depth and homogeneity in a horizontal plane as actually observed. The model was subsequently used to evaluate the effects of hypothetic 'deeper' or 'wider' root distribution, at constant total root weight, and of various combinations of timing and placement of fertilizer. Some of these predictions have since been tested and confirmed in new field experiments on fertilizer application in ridges to separate water and nitrogen flow patterns. This procedure shows the value of process-oriented models, which allow exploration of new situations. In both examples, the amount of fertilizer to be added, and/or the level of inherent soil fertility to be maintained, was the primary target of model calculations. Indirectly such models indicate what benefits or detrimental effects can be expected if crop parameters are modified, e.g. by plant breeding. Simple rules for estimating whether or not an increase in root length density can be advantageous were given by Van Noordwijk (1983, 1991). If the possibilities of increasing fertilizer use efficiency by fertilizer placement are to be evaluated, a subdivision within the plow-layer is necessary in the model. If effects of soil tillage or biologically modified structure of the soil are to be evaluated, rooting pattern (maps of profile walls) and possibly root-soil contact (soil thin sections) should be included in the model and in the measuring scheme. Irrigation strategies to obtain non-limited crop growth are relatively easy to formulate, but strategies which optimize the use of water as a scarce resource are more difficult to develop. In that case, the effects on root distribution of periods of water stress early in the season should be predicted (model level *C* or *D*) as well as physiological effects (e.g. on flower initiation, seed set and seed production) at different growth stages. Effects of soil water content in various layers on nutrient uptake should be included, the principles of which were shown for potato by De Willigen and van Noordwijk (1991). For grain crops growing on stored water reserves, restricted water use early in the season may conserve water for the essential

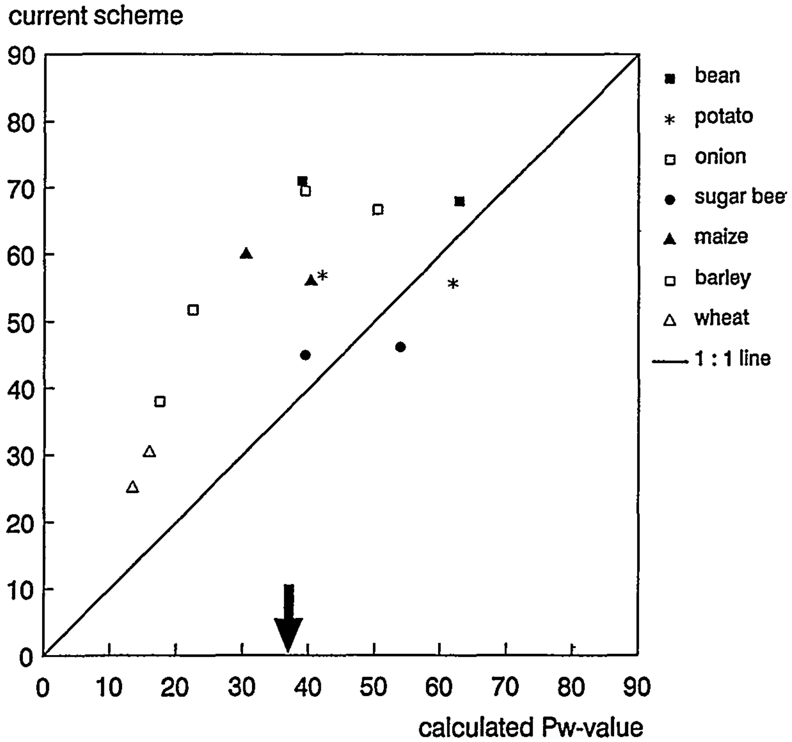

Figure 9. Comparison of model predictions on the P supply required on a wide range of soils for adequate growth of a number of crops, with the point in the current Dutch P recommendation scheme where P fertilization is equal to crop removal of P; P levels of the soil are expressed as the Pw-value, the result of a water extraction of soil with a 1:60 soil:water ratio; for the model only average root length density in the plow layer, maximum P requirement per day and total amount of P required during a growing season are needed as crop parameters (Van Noordwijk et al., 1990).

grain-filling period. Delayed root development in the subsoil, due to mechanical impedance, may in such a case lead to increased yields (Jakobsen and Dexter, 1988; Tardieu, pers. comm.). Selection for high longitudinal resistances to water flow in the root has been partly successful in Australia in a similar situation (Richards and Passioura, 1989).

De Willigen (1991) compared 18 models for winter, wheat growth, N uptake, and soil N dynamics. Most models accounted for vertical distribution of root length density when calculating nitrogen uptake. Root distribution was either directly derived from the data set supplied (model level *A*) or calculated from total root dry matter, specific root length and root radius, assuming an exponential decrease in L_{rv} with depth (model level *B*). All uptake models were demand-driven and, generally speaking, crop uptake could be calculated accurately for a given set of experimental data for different rates of N application. The main problems were encountered in the description of immobilization and mineralization of N in the soil. Groot and Van Keulen (1990) showed that for the situations studied, winter wheat in the Netherlands on silty loam soils, a detailed description of uptake processes is not necessary for accurate predictions of N-uptake, as for the given soil water contents L_{rv} seldom limits N uptake. For this situation a 'model-without-roots' is sufficient to predict the N response of a crop. Potatoes grown at 'economically optimum' fertilizer rates leave much more residual nitrogen in the soil at harvest time than wheat (Neeteson and Zwetsloot, 1989), probably due to a lower root length density and drier conditions in the ridge, and detailed 'models-with-roots' are required to understand this situation (De Willigen and Van Noordwijk, 1991).

At present, models for nutrient and water uptake based on actual root development can be successfully applied to improve the agronomic efficiency of fertilizer and water use. Major questions remain concerning the feedback mechanisms and the integration of uptake activities within a root system, and especially in modelling root development as the outcome of the interaction between plants as self regulatory organisms and their complex environment. Progress will

Table 4. Model predictions of the amount of fertilizer nitrogen in kg ha^{-1} required to obtain a maize dry matter yield of 6.5 Mg ha^{-1} and the predicted apparent recovery of fertilizer nitrogen in this case. Predictions were made for three distributions of the same amount of roots, 'standard', 'deep', and 'wide' and for average climatic conditions in S.E. Nigeria, with a rainfall of about 2400 mm per year. Various combinations of timing and placement of fertilizer were simulated: Br - broadcast, Lo - localization of fertilizer at 20 cm from the plant, Sp - fertilizer applied in three splits, Nsp - application at the start of the growing season. Infiltration of water was supposed to be uniform or non-uniform, e.g. as influenced by growing maize on ridges (De Willigen and Van Noordwijk, 1989a)

Water infiltration	Uniform				Non-uniform	
Fertilizer placement	Br	Br	Lo	Lo	Br	Lo
„ timing	Nsp	Sp	Nsp	Sp	Sp	Sp
N fertilizer requirement (kg ha^{-1})						
Root distribution:						
Standard	300	130	300	95	100	70
Wide	250	90	300	80	90	65
Deep	90	75	90	50	75	45
Percentage N recovery						
Root distribution:						
Standard	16	37	16	51	49	69
Wide	18	49	15	55	49	49
Deep	41	49	41	74	49	82

depend on a balanced combination of simple single-factor experiments, carefully controlled and monitored lysimeter/rhizotron studies (Van de Geijn et al., 1994), measurements in the more complex field situation, and the establishment of databases of key parameters for future specific application at the farm level. Models will serve as a quantitative link between these various steps and may thus help to incorporate root knowledge in the search for 'integrated agriculture'.

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