Roots as Sinks and Sources of Nutrients and Carbon in Agricultural Systems

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INTRODUCTION

Roots are a special category of "soil biota," being part of organisms that live in two very different types of environment, aboveground and belowground. As they belong to the organisms that form the main target of all agricultural interventions and are directly involved in the efficiency with which nutrients and water are used for crop production, root knowledge should be "at the root" of any discussion on sustainable agriculture. Yet, little direct attention is given to roots, possibly because of a lack of (1) clear concepts on what to look for and (2) easy (be it quick and dirty) methods to observe the relevant properties in actual root systems. The need for maximizing resource use efficiency and minimizing environmental pollution has given a new drive for root ecological research. Within the soil, roots are the main sinks for nutrients during the life of the crop, but may also play a role in immobilizing nutrients during the initial stages of their decomposition; subsequently, they will form a source of nutrients for soil organisms and future plants. The efficiency of roots as sinks for nutrients, both during and after their life, partly determines the conflict between environmental and production aims of agriculture.

For a long time the prevailing concept was "the more extensive the root system, the higher crop production." We now know that this is not true across the full range of agricultural production conditions; maximum plant production can be obtained with relatively small root systems if the daily water and nutrient requirements are met by technical means as in intensive horticultural production systems (Van Noordwijk and De Willigen, 1987). Roots are, however, directly involved in the efficiency of plants to use available water and

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nutrient reserves in the soil and therefore in reducing negative side effects of agricultural production by leaching and losses to the atmosphere. As a first estimate, we may still expect that "the more extensive the root system, the higher may be the nutrient and water use efficiency" (Van Noordwijk and De Willigen, 1991). The possibility of obtaining greater resource use efficiency can only be realized if total supply of nutrients and water is regulated according to the crop demands and the attainable resource use efficiency. On a field scale, both resource supply and possible crop production show spatial variability. Inadequate techniques for dealing with this variation may reduce the resource use efficiency well below what is possible in the normally small experimental units considered for research (Van Noordwijk and Wadman, 1992).

Figure 1 shows a scheme of N flows in an arable crop of the temperate zone on the Northern Hemisphere, starting the calendar in spring. If the long-term organic matter balance is secured, system outputs (harvested products, leaching, and gaseous losses) must be balanced by inputs. In the northern temperate zone the main crop growing season normally has a rainfall deficit, and leaching (beyond the crop root zone) is mostly confined to autumn and winter. Denitrification may occur in summer, but in early autumn conditions are especially conducive for this process as relatively high temperatures are

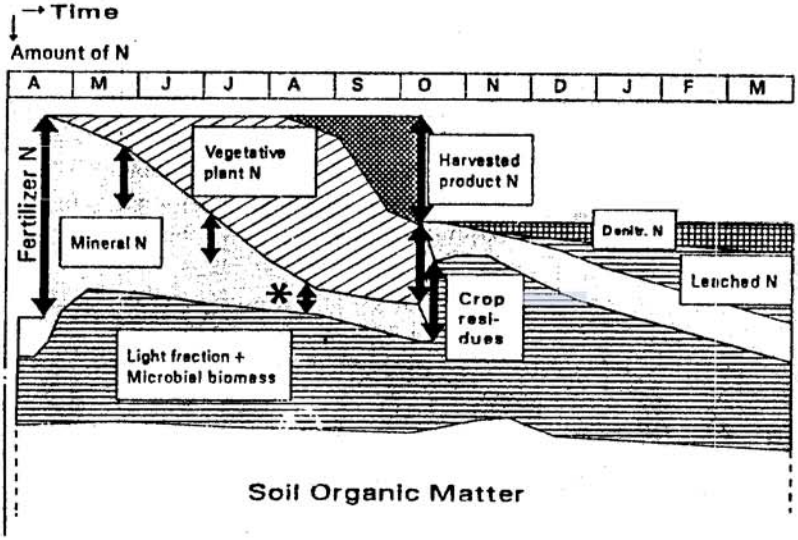

Figure 1 Scheme of N flows in an arable crop of the temperate zone on the Northern Hemisphere, starting in spring (April). The inputs as mineral fertilizer are partitioned over harvested products, crop residues, and soil mineral N at harvest time; losses to the environment by denitrification and leaching mainly occur during autumn and winter. The dynamics of the light fraction plus microbial biomass and its separation from the rest of soil organic matter are subject to debate and uncertainty. The arrows and asterisk indicate $N_{res}(N)$, the amount of mineral N needed to maintain sufficiently rapid diffusive transport toward the root system.

combined with wet soil conditions and ample availability of organic substrates. Rates of net N mineralization are less than required by crop demand during the growing season, but continue after the uptake period. Fertilizer requirements for avoidance of any N shortage in the crop have to allow for the weather-induced variability in crop demand and in rates of net N mineralization and also for the spatial variability within a field treated as a single management unit. Possibilities for "response farming" (i.e., tactical decision making during the growing season based on past and predicted weather conditions) are limited, however, as late fertilizer applications may not reach the roots under dry conditions. The arrows indicate that mineral N cannot be fully depleted, as a certain average concentration is needed to maintain diffusion gradients toward the root system, depending on soil water content, root length density, and current uptake demand (see below). The quantity corresponding with this concentration is termed N_{res} for nutrients in general and $N_{res}(N)$ for mineral nitrogen. $N_{res}(N)$ is normally larger in the first phase of the growing season than later on, but most of this mineral N has to be present as it will be taken up anyway; $N_{res}(N)$ minus forthcoming N demand tends to be largest at the end of the uptake period (De Willigen and Van Noordwijk, 1987). The $N_{res}(N)$ at the end of the growing season (see asterisk) together with late mineralization, thus determines the minimum pool size from which N losses in winter occur. N fertilizer application from organic plus inorganic sources can be restricted to crop uptake plus this quantity $N_{res}(N)$ minus soil available N, but any further restriction will lead to yield loss. N_{res} can be reduced by better root development. Manipulation of the light fraction plus microbial biomass pool to reduce net N mineralization after the uptake period can be an independent means of reducing N losses, for example, by adding residues with a high C:N ratio.

The relevance of various root parameters for predicting uptake efficiency depends not only on the resource studied but also on the complexity of the agricultural system. In intensive horticulture with nearly complete technical control over nutrient and water supply, fairly small root systems may allow very high crop productions in a situation where resource use efficiency ranges from very low to very high, depending on the technical perfection of the often soilless (hydroponic) production system (Van Noordwijk, 1990). In field crops grown as a monoculture, the technical possibilities are far lower for ensuring a supply of water and nutrients where and when needed by the crop, and it is difficult to achieve maximum crop production rates at high efficiency. The soil has to act as a buffer, temporarily storing these resources. Root systems are important in obtaining these resources as and when available and needed. Adjustment of supply and demand in both time and space (synchrony and synlocation) become critical factors. Critical values of root length density (root length per unit volume of soil) needed to obtain a specified water or nutrient use efficiency can be estimated from existing models. Normally, the rate-limiting step is formed by the transport from the soil matrix to the root surface and therefore by the geometry of the root-soil system and the required transport distances. In mixed cropping systems (including grasslands), the belowground interactions between the various plant species add a level of complexity to the system. On the one hand, mixed cropping systems allow complementarity in use of the space and thus of the stored resources, hence, improving overall resource efficiency. On the other hand, it means that root length densities that would be sufficient for efficient resource use in a monoculture may not be sufficient in a competitive situation. The plant mixtures found in agroforestry systems increase the complexity by another dimension, as the perennial and annual components have separate time frames on which to evaluate the interactions.

The soil water balance, as affected by climate, irrigation, and drainage, has a major influence on the required root functions in uptake. As the main crop growing season normally has a rainfall deficit in the northern temperate zone, dry soil conditions hamper diffusive transport and thus increase the root length density required for uptake. A lack of synchrony between N mineralization and N demand, which would lead to a build up of mineral N in the topsoil, is not a real problem under these conditions, as the main leaching risk occurs after the growing season. The main problem for effective use of organic N pools in the temperate zone is that mineralization is too slow in spring. In the humid tropics, by contrast, with a net rainfall surplus during most of the growing season, any accumulation of mineral N will be leached rapidly from the topsoil to deeper layers. Under such conditions synchrony of N mineralization and N demand is essential for obtaining high N use efficiencies and reducing leaching (Van Noordwijk and De Willigen, 1991; Myers et al., 1994).

Roots are a poorly quantified source of carbon in the soil ecosystem, and widely different estimates are available in the literature, at least partly due to uncertainties and biases caused by the methods used. Fine root residues of annual crops at harvest time tend to be low in nutrient content, as annual crops generally remobilize nutrients toward the end of their growth cycle, redistributing them to the seeds or vegetative storage tissue. For perennial crops with a less pronounced phenology, root decay may be a continuous process during the growing season. During their decomposition by microorganisms, roots may form a temporary sink of N. Little is known on the timing of net N mineralization from root residues and its role in the synchrony between net N mineralization and demand by the following crop.

The following root functions will be discussed here:

- Roots as sinks of nutrients (especially N and P) during the growing season, with emphasis on the N_{res} term
- Roots as sources of carbon and hence as sinks and sources of nutrients (mainly N) after their death

Concepts and methods will be briefly reviewed and data will be given that were obtained as part of the Dutch Programme on Soil Ecology of Arable Farming Systems in which a conventional (CONV) and an "integrated" system (INT; reduced use of fertilizer, pesticides and soil tillage) were compared (Brussaard et al., 1988; Kooistra et al., 1989; Lebbink et al., 1994).

MODELS AND METHODS FOR ROOTS AS NUTRIENTS SINKS

A wide array of mathematical models has been developed to integrate the soil chemical, soil physical, and plant physiological processes involved in uptake (Barber, 1984; De Willigen and Van Noordwijk, 1987; Nye and Tinker, 1977). The models can be used for extrapolating to other soil and climate (rainfall) conditions. Major uncertainties remain in the biological interactions in the rhizosphere. The efficiency of a root system in taking up nutrients (or water) from a layer of soil depends on the root length density (including mycorrhizal hyphae), root radius, soil water content, and effective diffusion coefficient for the nutrient (or water).

Model for Simple Root-Soil Geometry

De Willigen and Van Noordwijk (1987, 1991) derived, with simplified assumptions on root-soil geometry, an equation for N_{rcs} as a function of root length density L_{rv}. This relation can be used to predict uptake efficiency from a single homogeneous layer or can be incorporated into dynamic uptake models from layered soils.

$$N_{rcs} = \frac{A(K_a + \theta)D_m^2 G(\rho, v)}{4H(a_1\theta + a_0)\theta D_0} \qquad (1)$$

with the dimensionless root parameter ρ defined as:

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

and the dimensionless function G defined as:

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

where A = daily nutrient demand (kg ha^{-1} d^{-1}),
K_a = apparent adsorption constant (ml cm^{-3}),
θ = soil water content (ml cm^{-3}),
a_1 and a_0 = parameters describing decrease of effective diffusion coefficient with decreasing θ,
H = depth of soil zone considered (cm),
D_0 = diffusion coefficient of nutrient in free water (cm^2 d^{-1}), and
D_m = root diameter used for model (cm).

The function G depends on ρ and v, a dimensionless group based on the transpiration rate (incorporating the effects of mass flow); the version given here is for v equal to zero (compare De Willigen and Van Noordwijk, 1987).

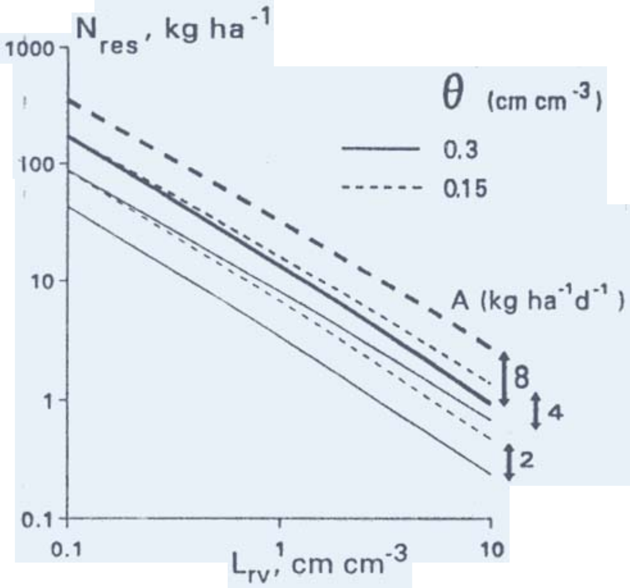

Figure 2 The amount of mineral, N_{res}(N), in the soil (at two water contents θ), required to maintain crop demand A, as function of root length density L_{rv}. (From De Willigen, P. and Van Noordwijk, M., 1987. Doctoral thesis, Agricultural University, Wageningen.)

Figure 2 shows N_{res}(N) as function L_{rv}, A, and θ for a standard parameter set for NO_3 uptake (De Willigen and Van Noordwijk, 1987). N_{res}(N) becomes less than 10 kg ha^{-1} for L_{rv} values in the range 0.4 to 3 cm cm^{-3} (lower values for wetter soil and lower daily N demands). In view of the normal crop root length densities, we may thus expect that N_{res}(N) in the topsoil can be small, except for high demands A on relatively dry soils (De Willigen and Van Noordwijk, 1987). Some of the simplifying assumptions, especially on the uniformity of root diameters and on the effects of root distribution pattern, can now be avoided by incorporating real-world complications into our scheme (Table 1).

Heterogeneity in Root Diameter

If root systems of different diameters are compared at equal root length densities (length · diameter^0), the larger the diameter, the smaller is N_{res} and thus the more efficient the uptake can be. If the comparison is made at equal surface area (length · diameter^1 · π), N_{res} decreases with decreasing root diameter (De Willigen and Van Noordwijk, 1987). If the comparison is made at equal root volume (length · diameter^2 · π/4), or weight, the advantage of the smaller root diameters is even more pronounced. The most stable result (that means: a parameter least sensitive to changes in root diameter) is obtained

Table 1 Steps in Describing Root-Soil Geometry for Uptake Models

1. Choose relevant sampling zones, based on depth, distance to crop rows, and expected synlocation of roots and resources; measure the root length density, $L_{rv}(i,s)$, for each stratum i at sample time s close to the expected maximum root development.
2. Effective root length density for a root system with a known frequency distribution of root diameters (incl. hyphae):

$$L_{rv} = \frac{\sum_{i=1}^{n} L_{rv,i}\sqrt{D_i}}{\sqrt{D_m}} \tag{5}$$

   where D_m = diameter used for model calculations and D_i and $L_{rv,i}$ = root diameter and root length density of n diameter classes.
3. Extrapolation from sampling time s to any time t is based on:

$$L_{rv}(i,t) = L_{rv}(i,s)\frac{R_p(i,t)}{R_p(i,s)} \tag{6}$$

   where $R_p(i,t)$ = relative root presence at zone i at time t on minirhizotron images.

$$R_p(i,t) = R_g(i,t) - R_d(i,t) \tag{7}$$

   where $R_g(i,t)$ = root growth in zone i till time t relative to year production and $R_d(i,t)$ = root decay in zone i till time t relative to year production.
4. Measure effectiveness of the root distribution via the R_{per} method (Van Noordwijk et al., 1993a,b) and derive the effective root length L_{rv} · time t at zone i:

$$L_{rv}^*(i,t) = R_{per}(i,t)L_{rv}(i,t) \tag{8}$$

   where R_{per} = root position effectivity ratio, accounting for nonregular root distribution and incomplete root-soil contact.

for a comparison on equal length · diameter$^{0.5}$. $N_{res}(P)$ can be translated into the required P availability in the soil as indicated by the (water-extractable) P_w index. The more efficient the root system, the lower the required P level of the soil. Figure 3 shows that the required P_w is least sensitive to variations in root diameter if root systems different in diameter are compared on the basis of equal root length · diameter$^{0.5}$. Calculations were made with the P model of Van Noordwijk et al. (1990) and were based on P adsorption isotherms and crop parameters for the growth of the velvet bean *Mucuna* on an Ultisol in Lampung, Indonesia (Hairiah et al., 1995).

With the root-root (length · diameter$^{0.5}$) index, calculation results are approximately independent of root diameter over more than one order of magnitude. We thus have a method to add hyphal length of mycorrhizal fungi (which are about a factor 25 smaller in diameter than the finest roots, based on a root diameter of 200 μm and a hyphal diameter of 8 μm) to the crop root length. Roughly one fifth (or $25^{0.5}$) of the hyphal length can be added to the

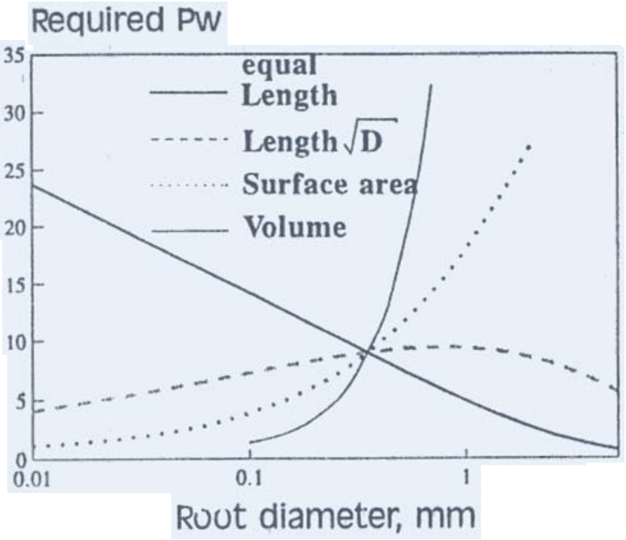

Figure 3 Required P availability in the soil — indicated by the (water extractable) P_w index — when root systems of different diameter are compared on the basis of equal root length, root surface area, root volume, or sum of root length · diameter$^{0.5}$. The P model of Van Noordwijk et al. (1990) was applied to *Mucuna* growth on an Ultisol in Lampung (Hairiah et al., 1994) for these calculations.

root length density. If only "infection percentage" data are available for the mycorrhiza, we have to assume a reasonable length of hyphae per unit infected root length (a value between 10 and 100 seems reasonable, say 50) (Sanderson, personal communication, 1992). We thus obtain an increased root length density by a factor 1 + (0.5) · %inf/5. For a normal infection percentage of 15%, this means that the effective root length density is 2.5 times the length of roots alone. There is an obvious lack of reliable data and relevant methods to quantify the hyphal length per unit infected root length, and this is clearly a priority area for research if process-based models for P uptake are desired. A similar but simpler method can be used to obtain a weighted average root diameter for a branched root system with diversity of root diameters (step 2 in Table 1).

Nonregular Root Distribution

With the "root position effectivity ratio" R_{per} the uptake efficiency for any actually observed root distribution pattern can be related to that for a theoretical, regular pattern. In an approximate manner, the effects of incomplete root-soil contact can also be incorporated (Van Noordwijk et al., 1993a,b). R_{per} is defined as a reduction factor on the measured root length density and accounts for the lower uptake efficiency of real-world root distributions, when compared with the theoretical, regular pattern assumed by most existing uptake models (based on a cylinder geometry of the root-soil system), including the model used to derive Equation 1. For random root distributions, R_{per} is approximately 0.5 (that means root length density X/2 in a regular pattern has the same N_{res} as a random pattern at density X); the figures shown by Van Noordwijk et al. (1993a) are based on a different definition of R_{per}, later corrected by Van Noordwijk et al., (1993b). For clustered root distribution, as may be expected in structured soils, where roots grow mainly along cracks, R_{per} values in the range 0.05 to 0.4 can be expected. R_{per} tends to decrease with higher absolute root length densities.

Dynamics of Root Growth and Decay

Due to the considerable spatial variability of root length density, estimates of L_{rv} normally have a fairly wide confidence interval. If root growth and decay are estimated from a time series of destructive sampling, the results tend to have an unacceptably large uncertainty. If sequential nondestructive observations can be made on the same roots (e.g., those located next to a minirhizotron) and the resulting images are analyzed for changes relative to the root length present, a much smaller sampling error can be obtained. The cost of this, however, is a potential bias, as the observation method may influence root behavior, especially where gaps occur along the observation surface (Van Noordwijk et al., 1985). Details are given by Van Noordwijk et al. (1994a), who presented results of an analysis of sugar beet and winter wheat root turnover based on images obtained with inflatable minirhizotrons (Gijsman et al., 1991; Volkmar, 1993). Step 3 in Table 1 shows how the effective root length density at any time *t* can be estimated from minirhizotron data plus a single destructive sampling.

Effective Root Length Density as Function of Time and Depth

Combining these elements (Table 1), we can derive an effective root length density L_{rv}* as a function of time and depth from

$$L_{rv}*(i,T) = R_{per}(i,T) \cdot \frac{\int_{t=0}^{T} (G_{i,t} - D_{i,t})dt}{\int_{t=0}^{s} (G_{i,t} - D_{i,t})dt} \cdot \frac{\sum_{j=0}^{n} L_{rv}(i,s,j)\sqrt{D_j}}{\sqrt{D_m}} \qquad (4)$$

where L_{rv}*(i,T) = effective root length density (cm cm^{-3}) in layer i at time T,
L_{rv}(i,s) = measured root length density in layer i at time of sampling s,
R_{per}(i,T) = root position effectivity ratio (procedure defined in Van Noordwijk et al., 1993b),
G(i,t) = observed root growth along minirhizotrons as a function of time in zone i,

$D(i,t)$ = observed root decay along minirhizotrons as a function of time in zone i,
D_m = root diameter used for model calculations, and
D_j = root diameter for diameter class j and observed root length density $L_{rv}(j)$.

METHODS FOR ROOTS AS SOURCE OF CARBON

Roots are a source of four forms of carbon: CO_2 from root respiration, soluble (exudates) C compounds, insoluble (mucigel, sloughed off root cap cells, etc.) C compounds released into the rhizosphere (during or after the life of the root), and structural root tissue after root death. Root-derived carbon forms the basis of a separate "energy channel" for the belowground food web (Moore et al., 1988; De Ruiter et al., 1994). It differs from other organic inputs, such as aboveground crop residues and organic manures, not only in quantity and chemical quality, but also in timing and spatial distribution. The position of roots in the soil, partly in the soil matrix and partly in larger aggregates or cracks, differs from the spatial distribution of other organic inputs, which occur in clusters and clumps, to a greater or lesser degree depending on the soil tillage operations used. Relatively stable organic matter-soil linkages are formed in the maize rhizosphere by mucigels from plant and bacterial origin (Watt et al., 1993). ^{14}C pulse labeling techniques have been used to measure the three types of belowground C output from plants (Swinnen, 1994). Integration over the whole growing season is needed to give a reliable estimate. Many previous studies concentrated on young plants only, and this overestimates exudation losses when extrapolated to the whole season.

Maximum standing stocks of fine root biomass are 0.5 to 2.5 Mg ha^{-1} of dry weight for most annual crops and 1.5 to 5 Mg ha^{-1} for pastures and grassland. The values for forests are normally in the same range for fine roots; the perennial woody main root system differs probably more between species and forest types than the fine roots. Data on standing root biomass in forests and under agricultural land use in the tropics are scarce. No belowground equivalent of the aboveground estimation procedure based on diameters at breast height (DBH) is available yet. However, application of fractal branching models holds a promise for new developments in this field (Van Noordwijk et al., 1994b). With methods for quantifying the maximum standing stocks reasonably well established, the annual turnover of the fine roots is the main source of uncertainty.

The C input from structural root tissue consists of root residues at harvest time and turnover of structural root material during the growing season. Structural root residues, especially if they have a low N concentration where plants experience some N stress at the final growth stages, may immobilize N after harvest time and thus reduce N losses by leaching. Estimates of annual turnover (relative to the maximum standing stock) vary from 1 to 10 yr^{-1}. Measurements of root turnover in the past decades have suffered from a lack of adequate methods. The widely used peak-and-trough method (Anderson and Ingram, 1993) is unsuitable in tropical pastures without pronounced seasonality. Despite impressive amounts of samples analyzed, no reliable estimates of turnover could be derived from this method for pastures in the Amazon (Castilla, personal communication). The best current method is based on sequential analysis of images taken in minirhizotrons as described above.

Litter Pots for Studying Root Decay

Decay of root tissue is a gradual process that starts during the life of the root. Root decomposition after crop harvest can be studied by incorporating known amounts of roots (at a natural root length density), sieved or handpicked from soil, into sieved (root-free) soil, which is repacked to a natural soil bulk density and placed back into the field. Ceramic pots can be used as they allow water content in the pot to follow that of the surrounding soil. Pots are recovered at regular times. The remaining intact root mass is collected on a sieve and dried for weighing and chemical analysis (Van Noordwijk et al., 1994a). Caution is needed in interpreting the results of such studies, however, as the immediate root environment, including root-soil contact, has been modified. A comparison with decay along minirhizotron tubes (in a nonnatural but constant environment) is needed.

RESULTS

Root Length Density at Maximum Root Development

Figure 4 shows the distribution of root length density with depth at approximately maximum root development for winter wheat and sugar beet at the Lovinkhoeve experimental farm, The Netherlands. Root distribution differs distinctly from the normal exponential decrease of L_{rv} with depth (which would lead to a straight line on the logarithmic scale used). A sandy layer at around 30 to 35 cm depth restricts root development, but below that zone root length density is fairly uniform up to about 80 cm depth. In sugar beet significant differences in L_{rv} between three sampling positions (one in the crop row and two positions between the rows) persisted until a depth of 50 cm. Winter wheat root length densities were higher than those of sugar beet, throughout the profile. L_{rv} in the INT treatment was slightly higher than that in the CONV treatment.

Root Distribution Patterns

For sugar beet and winter wheat average values of R_{per} obtained for the plough layer are 0.18 and 0.15, respectively (Figure 5). This suggests that a sixfold overestimate of the effective root length density is used if roots are

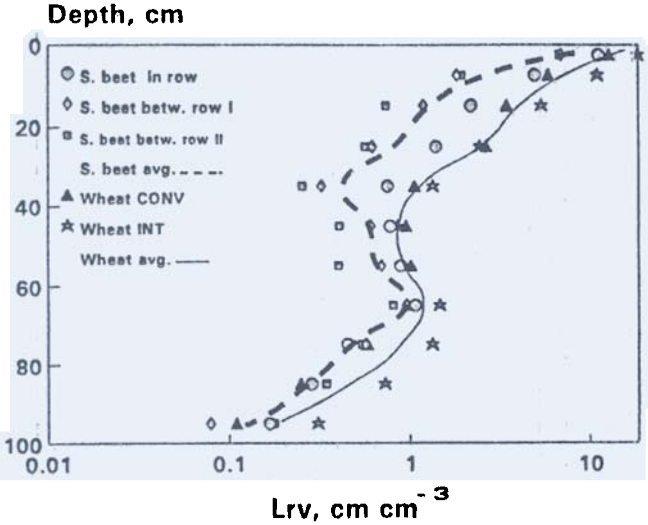

Figure 4 Root length density L_{rv} of winter wheat (late June 1990) and sugar beet (early September 1989) on the Lovinkhoeve experimental farm for the "conventional" (*CONV*) and "integrated" (*INT*) treatment. For sugar beet, two sample positions (I and II) were distinguished between the crop rows.

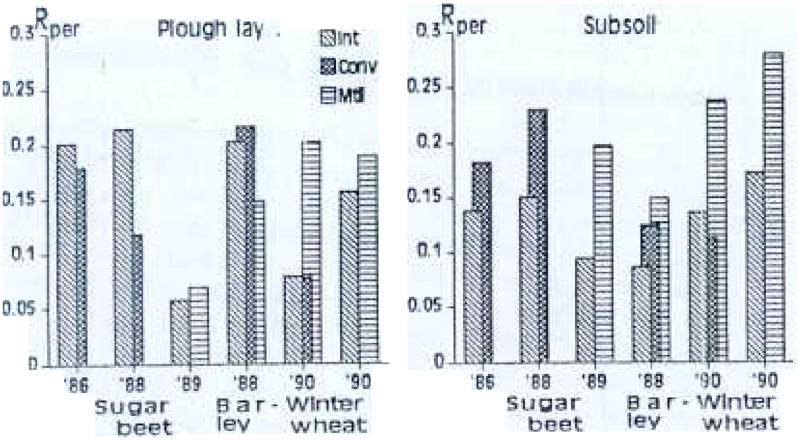

Figure 5 Root position effectivity ratio, R_{per}, for sugar beet, spring barley, and winter wheat on the Lovinkhoeve experimental farm; observations were made on *CONV*, *INT*, and a reduced-tillage treatment (Mtil). Differences between crops and/or cropping systems were not statistically significant (the standard error of differences, S.E.D., for a comparison of crops is 0.03, for crop-system interactions 0.034).

assumed to be regularly distributed. Although no statistically significant differences between crops or cropping systems were found, the absolute value shows that root patterns deserve serious attention.

Dynamics of Root Growth and Decay

For winter wheat and sugar beet grown in "conventional" and "integrated" arable cropping systems in The Netherlands, logistic-curve fits to growth and decay functions were given by Van Noordwijk et al. (1994a). The two crops showed a clearly different pattern, consistent over years of observation and largely independent of crop management regime. In winter wheat only little decay of roots was noticed during grain filling and ripening, and at harvest time 85 and 68% (in 1986 and 1990, respectively) of the structural root production remained as intact roots in the soil in both management systems. In sugar beet a more rapid and gradual root turnover was observed and the harvest residue of intact fine roots was on average 47% of cumulative root production. Figure 6 shows how absolute root length density can be estimated from the relative pattern observed on minirhizotrons and one destructive sampling (compare Table 1). The different depths and sample positions showed a fairly small variation in the growth curves, but a scatter in the root decay curves. Root decay was generally faster in the upper soil horizons (Van Noordwijk et al., 1994a).

Total Structural Root Production

Cumulative root production of winter wheat was about 1700 kg ha^{-1} for CONV and 1960 kg ha^{-1} for INT crop management (Van Noordwijk et al., 1994a); in 1990 the difference between the two management systems was statistically significant. For sugar beet total fine root production was estimated at 1150 kg ha^{-1} in 1987 and 1989, with a significantly lower amount on the field on which minimum tillage was introduced in 1986. Due to the higher turnover and smaller standing stock of sugar beet roots, the difference in total production of structural root material between winter wheat and sugar beet was much smaller than one would expect from single-point sampling.

Roots Decay After Crop Harvest

Winter wheat root decay was studied with litter pots after crop harvest and in the following growing season (Figure 7). Initially, the N concentration in remaining roots increased while dry weight decreased. A slight net immobilization of minerals of N and P during autumn appeared in CONV but not in INT. During the next growing season the N concentration of remaining root debris was approximately constant and thus net mineralization was proportional to loss of root weight in an exponential decay with a half-life of 600°C days (daily temperature sum). This N release pattern during the next growing

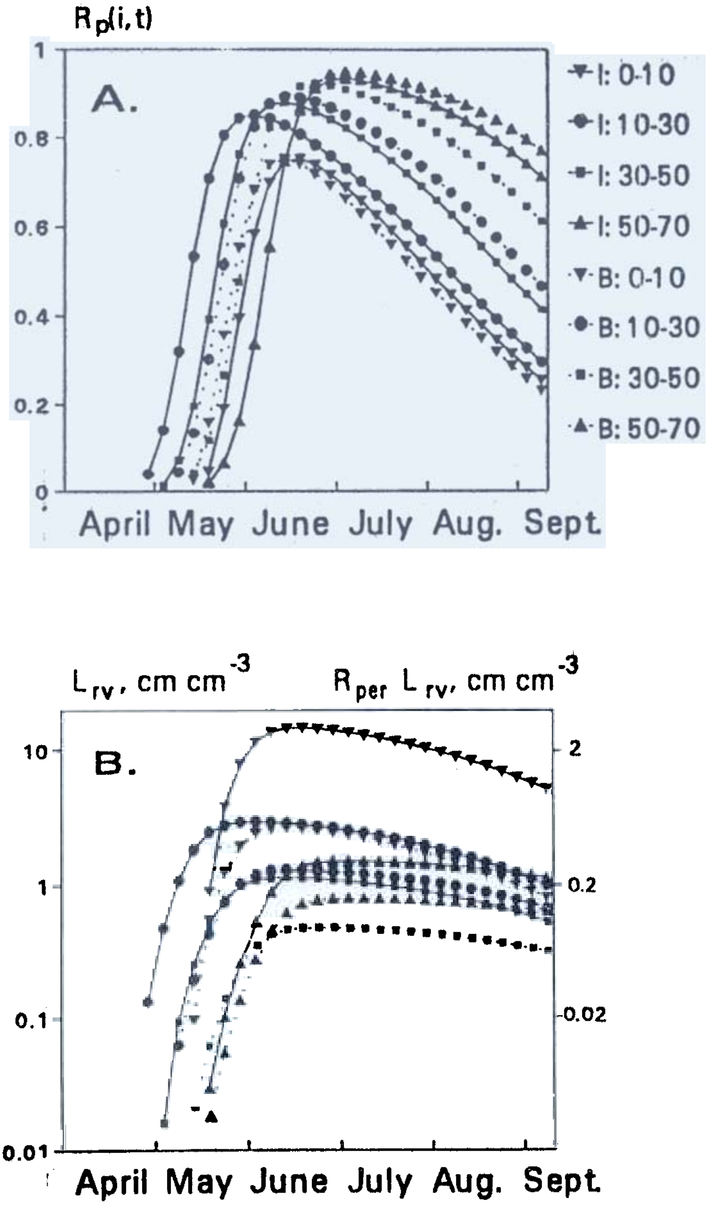

Figure 6 A. Relative root length as function of time, depth, and sample position (*I* = in row, *B* = between rows), as obtained from actual root length density observed in minirhizotrons divided by the cumulative year production, for sugar beet on INT in 1989. B. Estimated absolute root length density, on the basis of the relative pattern and one destructive sampling (log scale); the righthand Y scale estimates the effective root length density, based on an average root position effectivity ratio for sugar beet of 0.2.

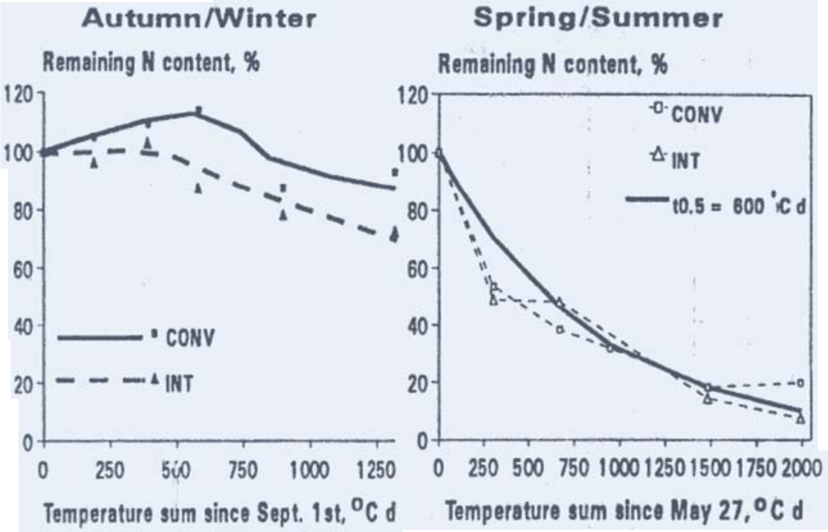

Figure 7 Remaining N content (concentration · dry weight, relative to the initial content) of decaying winter wheat roots in a litter pot decomposition study starting at harvest time (*left*) and one starting in May, with root residues collected in early spring.

period and the slight immobilization in CONV contribute to the synchrony between N demand and supply. Comparison of root decay along minirhizotrons and in the litter pots showed a strong effect of soil depth on root decay in the minirhizotrons (Van Noordwijk et al., 1994a).

DISCUSSION

The combined data show that for both sugar beet and winter wheat the effective root length density in the topsoil, allowing for a R_{per} of around 0.2, has been more than 0.2 cm cm^{-3} throughout the later part of the growing season. As the soil at the Lovinkhoeve rarely dries out below a Θ of 0.2 ml cm^{-3} (De Vos et al., 1994) and crop demand for N at the end of the uptake period will not have exceeded 2 kg ha^{-1} d^{-1}, we may conclude that N_{res} for mineral nitrogen probably has been in the range of 10 to 30 kg ha^{-1} at the most critical point in time (compare Figure 1). In the wheat field both the higher root length density and the presence of mycorhiza will have led to N_{res}(N) values of less than 10 kg ha^{-1}. We may thus tentatively conclude that root development of the nonmycorrhizal sugar beet is on the low side for efficient N uptake, at least if our correction for root distribution via R_{pcr} is correct, while winter wheat has sufficient roots. The application of the R_{pcr} correction assumes that there is no spatial correlation between roots and locally rich N patches; if such a correlation is positive, our conclusions are too pessimistic on the possible uptake efficiency.

A major source of uncertainty in this calculation is the criterion used for distinguishing live from dead roots in the minirhizotron observations. Recent developments of a vitality test based on root electrical properties (Meijboom and Brouwer, personal communication) may resolve this issue in the near future.

In the absence of spatial variability (Van Noordwijk and Wadman, 1992), the minimum N residue at the end of the uptake period can thus be less than 30 kg ha^{-1}. To actually achieve this aim, however, a careful adjustment of the amount of N supplied to expected crop demand is necessary, and this implies that between-year variation in crop performance has to be taken into account. In the integrated system, adjustment may be even more difficult to achieve as organic inputs are used and the predictability of N mineralization is not yet very good. Fortunately, in this system a certain yield depression below the theoretically possible yields is accepted, and thus the crop has considerable uptake capacity for above-average mineralization rates. In the conventional system, near-maximum yields are the goal and low N residues are difficult to obtain, despite the reliance on mineral N fertilizer instead of organic inputs.

An increase in soil mineral N content between the end of the uptake period and late autumn, when the N leaching season starts (De Vos et al., 1994), is to be expected due to late N mineralization. The initial N immobilization in decaying wheat root residues can have a small moderating effect on late N mineralization, but the total effect is probably less than 10 kg ha^{-1} (Van Noordwijk et al., 1994a). Sugar beets are harvested so late that these effects will be small in that crop. Late N mineralization in sugar beet will greatly affect crop quality (higher amino acid content of the beets), but not necessarily increase N leaching, as the crop still has uptake capacity. The major limitations in achieving a high N uptake efficiency and low N losses by leaching thus are formed by post-harvest residue management, spatial variability in the field, and between-year variability in N demand, with root development in a secondary role, although the sugar beet data are in the critical range. For P the root length density of sugar beet observed here requires available P levels to be maintained, which is critical from an environmental point of view (Van Noordwijk et al., 1990).

Although it is a big step, we may try to extrapolate this conclusion to other conditions. Although the processes of the N balance and root growth and activity are the same in temperate zones and in the tropics, the rate at which they occur can be very different. The same crop root development and nutrient demand as in the Lovinkhoeve example would in the high-rainfall tropics lead to serious N loss during the growing season, unless the time pattern of N mineralization and N demand were closely similar and/or a considerable part of the mineral N stayed in the NH_4^+ form (higher K_a) instead of NO_3^- (De Willigen and Van Noordwijk, 1987). On the acid soils, which are typical of the humid tropics, nitrification rates can be fairly slow, but root development is normally shallow, so N leaching losses during the growing season are still to be expected. Deep rooted (tree) components of mixed cropping systems can then act as a "safety-net," intercepting N on its way to deeper layers (Van Noordwijk and De Willigen, 1991). As a first step to a mechanistic approach to nutrient competition between different species in a mixture, we expect the competitive strength of each species to be (inversely) related to its N_{res} value.

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