INFLUENCE OF THE SPATIAL DISTRIBUTION OF NITRATE ON THE UPTAKE OF N BY PLANTS: A REVIEW AND A MODEL FOR ROOTING DEPTH

I. G. BURNS

(*National Vegetable Research Station, Wellesbourne, Warwick CV35 9EF*)

Summary

Published literature is re-examined in an attempt to understand the influence of the spatial distribution of soil nitrate on N uptake in order to devise a simple method for estimating the depth to which nitrate must be leached before it becomes unavailable to the crop. The evidence suggests that most crops can continue normal growth with less than 15% of their roots exposed to nitrate.

A simple model of nitrate uptake is constructed in which nitrate is assumed to be totally available above a set depth and totally unavailable below it. This effective rooting depth is assumed to coincide with the depth at which uptake per unit length of root declines to half of the maximum rate. Estimates of effective rooting depth have been made from root distribution data for various vegetable crops grown at Wellesbourne and cereal crops at Rothamsted. The results were found to fit a simple regression equation which can be used to calculate effective rooting depths at any stage of growth from the dry weight and population density of the crop and the mean cross-sectional area of its roots. This equation is used in the succeeding papers to estimate the effects of leaching on the N fertilizer needs of crops.

Introduction

THE need to develop better ways of forecasting N fertilizer requirements of crops is of high priority in British Agriculture (Cooke, 1979). Although much of the variability in N response can be attributed to the influence of rainfall on the redistribution of nitrate in the profile (Harmsen and Kolenbrander, 1965), present fertilizer recommendations take little account of it (MAFF, 1973). A simple *practical* method is therefore required to enable the effects of nitrate leaching to be estimated so that the N fertilizer needs of individual crops can be assessed more accurately.

The solutions to two basic problems must be supplied in order to estimate the losses of nitrate from the root zone. First, we need to know how much rainfall is required to displace nitrate from different soils, and second, the depth to which it must be leached before it becomes unavailable to the crop. In recent years, a number of mathematical models for estimating the vertical redistribution of nitrate in soils have been devised (Bresler and Hanks, 1969; Frissel *et al.*, 1970; Warrick *et al.*, 1971; Dutt *et al.*, 1972; Ferrari and Cuperus, 1973; Burns, 1974, 1975, 1976; Frissel and Reiniger, 1974; Addiscott, 1977), which provide various solutions to the first of these problems. The purpose of this paper is to review the literature on the second aspect, the relation between nitrate

uptake and depth, with a view to devising a simple method of estimating at what depth nitrate becomes unavailable to a crop.

Review of the literature

Dependence of uptake on solution concentration

Epstein and Hagen (1952) showed that the rate of ion uptake from stirred solution may be described by a hyperbolic relationship analogous to the Michaelis-Menten equation of enzyme kinetics:

$$I = U/L = \frac{I_{max} \cdot C_a}{K_m + C_a} \tag{1}$$

where I and U are the rates of nutrient inflow (μmol cm^{-1}s^{-1}) and uptake (μmol s^{-1}) respectively, L is the length of root exposed to nutrient (cm), C_a is the nutrient concentration at the root surface (μmol l^{-1}), I_{max} is the maximum value of I, and K_m is constant.

The size of C_a is governed by the rate of nutrient transfer to the root surface, but in well-stirred solution its value approximates to the concentration in the bulk of solution (see Nye and Tinker, 1977, p. 112). I_{max} and, to a lesser extent, K_m tend to be governed by plant factors such as their demand for nutrients and the permeability of their roots (Lycklama, 1963; Jungk, 1974). The general validity of Equation 1 has been confirmed for a wide range of anions and cations (Epstein, 1972), although some deviations are often evident both at very high concentrations, possibly due to additional uptake mechanisms (Epstein and Rains, 1965), and at very low concentrations, because of the inability of the roots to recover nutrients below a limiting level (Claassen and Barber, 1974).

According to Equation 1, I approaches I_{max} asymptotically, with $I/I_{max} = 0.5$ when $C_a = K_m$, and $I/I_{max} > 0.9$ when $C_a = 10\ K_m$. K_m is generally very small so I approaches I_{max} at low concentrations. Many studies have indicated that near-maximal rates of nitrate uptake or of dry matter production occur at concentrations between 80 and 200 μmol l^{-1} (van den Honert and Hooymans, 1955; Lycklama, 1963; Alberda, 1965; Reisenauer, 1969; Lastuvka and Minar, 1970; Warncke and Barber, 1974), but it is evident that depletion of the solution and inefficient stirring during uptake influenced these results. Clement et al. (1974) overcame these problems by designing a flowing-culture system in which bulk concentrations were automatically adjusted at frequent intervals during uptake and localized depletion zones were avoided by rapid circulation of solution. Their results showed that near-normal growth occurred at much lower concentrations, with less than 10 per cent increase in dry matter production when the treatment solutions changed from 14 to 14000 μmol l^{-1} (Clement et al., 1978).

Support for this view is obtained from depletion studies in which plants were allowed to decrease the concentration of nitrate in stirred solution until no more was absorbed. Edwards and Barber (1976a), and Frota and Tucker (1978) showed that the rate of depletion remained approximately constant until the concentration of nitrate in the medium fell below 20–30 μmol l^{-1}, irrespective of the age of the plant. Similar values have been

quoted by Asher and Edwards (1978), although the results of Olsen (1950) suggest that uptake may remain independent of nitrate concentration until it falls to 3 μmol l^{-1} in vigorously stirred solutions. Thus it appears that nitrate uptake by plant roots is not impeded by lowering the concentration at their root surfaces until it reaches 20 μmol l^{-1} or less.

Dependence of uptake on transport processes in the soil

Uptake of nutrients from the soil can be limited by their slow rate of transport to the roots (Watanabe *et al.*, 1960). Nutrients move through the soil by mass flow (*i.e.* convective flow) and diffusion. When the nutrient concentration is high, sufficient quantities can be carried by mass flow to replace those absorbed by the plant and, in extreme circumstances, accumulations may even occur around the roots (Barber, 1962; Lavy and Barber, 1964). More often the concentrations are lower, or the evaporative demand is too small, and the rate of uptake exceeds that of mass flow. The resulting fall in concentration at the root surfaces causes nutrients to diffuse down the concentration gradients creating widening depletion zones in the soil around the roots (Bhat and Nye, 1973).

The soil water content has a critical effect on the absorption of nutrients by plants, because it affects both the concentration in the soil solution and the rate of transport to the roots (Nye and Tinker, 1977, p. 156). Both diffusive and convective fluxes normally decrease as the soil dries. The reduction in diffusive flux originates from a decline in the proportion of water in the system and an associated increase in tortuosity (Porter *et al.*, 1960); the decrease in mass flow is caused by the rapid decline in transpiration which occurs when the water content falls. Because these effects more than compensate for any increase in ionic flux resulting from a greater concentration in the soil solution, there is a net decline in uptake as the soil dries out (Place and Barber, 1964; Dunham and Nye, 1974, 1976).

The pattern of nutrient uptake from the soil may also be complicated by competition between neighbouring roots. The extent of competition depends on the mobility of the nutrient and the root density. Mobile ions such as nitrate can move up to 0.5 or 1.0 cm d^{-1}, whereas the average distance between roots can be as small as 0.2 cm (Barley, 1970). Thus considerable competition between roots is inevitable, especially in the topsoil under well-established closely-spaced crops. This may result in a rapid depletion of these areas of soil and a change in the uptake characteristics of these roots.

Various attempts have been made to model the transfer of nutrients to roots in an effort to understand the interacting effects of soil solution concentration, water content and root density on uptake (see Gardner, 1965; Olsen and Kemper, 1968; Nye and Tinker, 1977). In the following treatment the approach of Baldwin *et al.* (1973) has been adapted to determine the minimum concentration of nitrate necessary to maintain uptake at about the maximum rate for a range of soil, crop and weather conditions. This approach is analogous to that outlined by both Gardner

(1965) and Olsen and Kemper (1968) but is more flexible, because it has been extended to enable higher root densities to be considered.

The procedure involved the derivation of steady state solutions of the mass balance equation which allow the average concentration of nitrate in the soil to be calculated from its concentration at the root surface at any instant in time. When nitrate is transported to the roots by both diffusion and mass flow, Equation (viii) of Baldwin, et al. (1973) applies:

$$\bar{C}_l = \frac{\alpha C_a}{v} + \left(1 - \frac{\alpha}{v}\right)\left(\frac{2C_a}{2 - \frac{av}{D_l\gamma\theta}}\right)\left[\frac{\left(\frac{x}{a}\right)^{2 - (av/D_l\gamma\theta)} - 1}{\left(\frac{x}{a}\right)^2 - 1}\right] \tag{2}$$

Where $\bar{C}_l$ is the mean solution concentration (μmol l^{-1}), C_a is the concentration at the root surface (μmol l^{-1}), a is the root radius (cm), v is the water flux at the root surface (cm s^{-1}), D_l is the diffusion coefficient of nitrate in free solution (cm^2 s^{-1}), θ is the water content of the soil (cm^3 cm^{-3}), γ is an impedance factor and $x = 1/\sqrt{\pi L_v}$, where L_v is the root density (cm^{-2}). α is the root absorbing power (cm s^{-1}) and is defined as:

$$\alpha = \frac{I}{2\pi a C_a}$$

Substituting for x and α in Equation 2 and rearranging gives:

$$\bar{C}_l = \frac{I}{2\pi av} + \frac{C_a - (I/2\pi av)}{1 - (av/2D_l\gamma\theta)}\left[\frac{(\pi a^2 L_v)^{av/2D_l\gamma\theta} - \pi a^2 L_v}{1 - \pi a^2 L_v}\right] \tag{3}$$

Similarly, from their Equation (iii), when nitrate is transported to the roots solely by diffusion (*i.e.* where $v = 0$)

$$\bar{C}_l = C_a - \frac{I}{4\pi D_l\gamma\theta}\left[1 + \left(\frac{1}{1 - \pi a^2 L_v}\right)\ln(\pi a^2 L_v)\right] \tag{4}$$

If $I \simeq I_{max}$, Equations 3 and 4 define the minimum concentrations of nitrate in the soil solution needed to maintain a near-maximal uptake rate for any crop assuming θ and v are constant.

Values for $\bar{C}_l$ have been calculated for typical soil conditions and the results converted into soil nitrate -N concentrations (mg kg^{-1} in dry soil) assuming a bulk density of 1.5 g cm^{-3}. The object of these calculations was to estimate critical solution concentrations during the period immediately following the leaching of nitrate, so the inflow rate was assumed to be equivalent to the maximum influx rate of 10^{-11} mol cm^{-2} s^{-1} (estimated by Barley, 1970) and values of θ were chosen to span the wetter range of values commonly observed for most soils. The calculations were made for two water fluxes: zero (where nitrate is supplied to the roots by diffusion alone), and 5×10^{-6} cm s^{-1} (the water flux for a typical crop transpiring at 0.3 cm d^{-1} when only *ca* 20 per cent of the root system is absorbing water). C_a was assumed to correspond to 20 μmol l^{-1} which represents a typical average value for the lowest concentration in well-stirred solution

culture experiments at which maximum inflow occurred (see previous section), and D_l was assumed to be 1.85×10^{-5} cm^2 s^{-1} (the value given by Porter *et al.* (1960) for chloride, an ion of similar size to nitrate). Values of L_v and a were chosen to span the root densities and root radii normally measured in the field; γ was assumed to approximate to the water content of the soil (Baldwin, 1975).

The results (given in Table 1) show that maximum inflow can still be maintained when the average nitrate content of the soil is relatively low. Differences in water flux had relatively little effect over the range tested, suggesting that the resistance to diffusive flux may be less than to convective flow. The largest nitrate -N concentration is required for low densities of the finest roots in soils with lower water contents. The values range from 1 to 12 mg kg^{-1} (or from 300 to 6400 μmol l^{-1} in soil solution) and are equivalent to nitrate -N contents of between *ca* 3 and 36 kg ha^{-1} respectively in a 20 cm depth of soil. Since nitrate is not buffered (adsorbed) in most soils, these quantities represent only a few days supply for rapidly growing crops. Thus these results support the views of Edwards and Barber (1976*a*) who tentatively suggested that N uptake only becomes concentration dependant when the nitrate content of the soil is almost depleted, and that roots can be considered as either absorbing at a rate close to I_{max} or not absorbing at all.

Equations 2 and 3 assume that there are no changes in θ or v. In practice, changes in both parameters are likely to occur, so the predicted concentrations are likely to be underestimated. Tentative estimates of the minimum concentrations at which growth is not significantly different from optimum, which range from *ca* 20 or 25 mg N kg^{-1} for various glasshouse

TABLE 1

Minimum soil nitrate concentrations required to maintain inflow at the maximum rate. The figures were calculated from the equations of Baldwin, Nye and Tinker (1973) using parameter values given in the text

Root radius (cm)	Root density cm^{-2}	Average soil nitrate -N concentrations (mg kg^{-1}) at zero water flux			Average soil nitrate -N concentrations (mg kg^{-1}) at a water flux of 5×10^{-6} cm s^{-1}		
		$\theta = 0.2$	$\theta = 0.3$	$\theta = 0.4$	$\theta = 0.2$	$\theta = 0.3$	$\theta = 0.4$
0.010	20.0	5.2	3.5	2.7	4.8	3.4	2.6
	5.0	6.9	4.7	3.5	6.3	4.5	3.4
	1.0	9.0	6.0	4.5	7.9	5.7	4.4
	0.1	11.9	7.9	6.0	10.1	7.4	5.7
0.015	20.0	4.2	2.8	2.2	3.9	2.7	2.1
	5.0	5.9	4.0	3.0	5.2	3.8	2.9
	1.0	7.9	5.3	4.0	6.8	5.0	3.9
	0.1	10.8	7.3	5.5	8.8	6.6	5.2
0.035	20.0	2.3	1.6	1.2	2.0	1.5	1.2
	5.0	3.9	2.6	2.0	3.2	2.4	1.9
	1.0	5.8	3.9	3.0	4.4	3.5	2.8
	0.1	8.7	5.8	4.4	5.9	4.9	4.0

and field crops (Winsor, 1969; Fageria and Wilcox, 1977; Doll *et al.*, 1971), would appear to confirm this. Nevertheless these results further emphasise the ability of many crops to continue normal uptake and growth at relatively low nitrate concentrations in the soil.

Dependence of uptake on plant factors

Changes in plant demand for nutrients are usually linked with changes in internal concentration and often result from alterations in the supply of nutrients to the plant. Decreases in internal concentration tend to increase the concentration gradient across the root boundary and increase the size of I_{max}, enabling more nutrients to be absorbed at a given external concentration. Thus when an adequate nutrient supply is re-established to deficient plants, inflow rates are increased in relation to the initial degree of deficiency (Hoagland and Broyer, 1936; Bouma, 1967*a*, *b*; Cram, 1973; Jungk and Barber, 1974; Edwards and Barber, 1976*b*). Measurements of nitrate inflow rate by Jackson *et al.* (1972) suggest that this physiological compensation can be complete within a few hours and is maintained either until the nitrate supply is restricted, or until the plants cease to be nitrate deficient.

Similar increases in inflow rate also occur when the proportion of roots having access to nitrate is reduced (Gile and Carrero, 1917). Such changes may be envisaged when nitrate is leached into the lower regions of the root zone, or when its availability in the surface regions is severely restricted as the soil dries out. The resulting increase in demand on the roots in the nitrate-rich region enables inflow to be increased above the maximum rate observed when all of the roots have access to nitrate. Depending on the rate of growth, up to three-fold increases in I_{max} have been observed where the proportion of roots exposed to nitrate was decreased in split root experiments (Drew *et al.*, 1973; Drew and Saker, 1975; Drew, 1975; Edwards and Barber, 1976*b*), and even larger increases have been observed in other experiments with phosphate under more extreme conditions (Drew and Saker, 1978).

However, there appears to be an absolute limit to the extent to which inflow can be increased to meet demand (Collander, 1959), so this mechanism alone is unlikely to be sufficient to maintain uptake at a completely unchanged rate when there are substantial reductions in the proportion of roots exposed. Temperature, pH and oxygen content of the growth medium (Hoagland and Broyer, 1936; van den Honert and Hooymans, 1955; Hopkins, 1956; Lycklama, 1963), the average age of the roots (Brouwer, 1954; Grasmanis and Barley, 1969; Mengel and Barber, 1974; Barber, 1974) and the water stress of the plant (Dunham and Nye, 1974, 1976) are among many of the factors thought to influence the maximum permeability of roots, but in most experiments it is not clear whether these affect root permeability directly or whether they influence inflow through their effect on plant growth and nutrient demand.

When nitrate is restricted to a small proportion of the roots, plants also compensate by increasing lateral root development and growth in the nitrate-rich zone, often at the expense of the other roots (Drew *et al.*, 1973). Similar effects have been observed in fertilizer placement studies

where root proliferation occurs in the fertiliser band (Wiersum, 1958). Morphological adaptation of this kind will often take a week or more to complete, even under ideal conditions, and the relative growth rate of the shoots may be depressed in the intervening period if physiological compensation is insufficient (Drew and Saker, 1975).

Proportion of roots required to meet plant demand

The first serious attempt to determine the minimum amount of root required to meet the plant demand for N was made by Gile and Carrero (1917) who measured nitrate uptake and growth of maize and rice plants over 21 and 40 days respectively in split root experiments. They found that both uptake and growth declined with each decrease in the proportion of roots exposed to nitrate, despite significant physiological and morphological compensation by the roots. The decreases in uptake were examined by de Wit (1953), who showed that the empirical relation

$$\frac{U_r}{U_b} = \left(\frac{X_r}{X_b}\right)^{0.44} \tag{5}$$

fitted both this and a wide range of other data for both N and P fertilizer. U_r is the uptake when nitrate is available to a fraction X_r/X_b of the roots and U_b is the uptake when all of the roots are exposed; the value of the exponent was obtained by fitting. It follows from Equation 1 and 5 that:

$$\frac{I_{rmax}}{I_{bmax}} = \left(\frac{X_r}{X_b}\right)^{-0.56} \tag{6}$$

where I_{rmax} and I_{bmax} are the corresponding values of I_{max} for the two situations. Calculated values of U_r/U_b and I_{rmax}/I_{bmax} for the range of X_r/X_b examined by de Wit are given in Table 2 to illustrate the interrelationship between relative inflow and uptake rates. These data suggest that despite a

TABLE 2

Changes in relative uptake (U) and inflow (I) rates for different fractions of roots (X_r/X_b) exposed to nitrate calculated by equations (5) and (6)

$\dfrac{X_r}{X_b}$	$\dfrac{U_r}{U_b}$	$\dfrac{I_{rmax}}{I_{bmax}}$
0.1	0.363	3.63
0.2	0.493	2.46
0.3	0.589	1.96
0.4	0.668	1.67
0.5	0.737	1.47
0.6	0.799	1.33
0.7	0.855	1.22
0.8	0.906	1.13
0.9	0.955	1.06
1.0	1.000	1.00

considerable ability of the roots to compensate by increasing their inflow rates, total uptake over a given interval will always be less where only a fraction of the roots are exposed to nitrate. Claassen and Barber (1977) have also verified the general form of Equation 6 for potassium inflow but show that it tends to underestimate the increases in inflow when X_r/X_b is small (< 0.3). The same deductions may also be made from the results of similar experiments with nitrate (Edwards and Barber, 1976b).

Because both physiological and morphological adaptation can only occur when the plant becomes deficient in N, some interference with the growth of plant is inevitable when nitrate is restricted to a limited region of roots (Edwards and Barber, 1976b). Results suggest that this interference takes the form of a temporary check in growth rather than a permanent change in relative growth rate (Drew and Saker, 1975). Once the physiological and morphological compensation mechanisms have been induced, plants are able to resume growth at the same relative growth rate as the control. The length of the induction period is, therefore, governed by whether the uptake rate can be restored to its previous level by the more rapid method of increasing inflow rate, or whether the slower root proliferation mechanism is also necessary. At the relative growth rates (ca 0.2 d^{-1} for maize and ca 0.165 d^{-1} for rice) observed in the experiments of Gile and Carrero (1917), a period of induction of little more than a day during which no growth occurred is all that is necessary to explain the differences in yield between treatments. Such differences are small and it is doubtful if they could be distinguished for most crops grown in the field where exponential growth is not maintained until maturity.

Thus, although there is likely to be a temporary check in growth when the proportion of roots exposed to nitrate is reduced, the plant rapidly adapts to enable a smaller quantity of roots to satisfy its entire demands for N. Drew and Saker (1975) found that this was achieved with ca 35 per cent of the root system of barley plants grown in solution culture, whilst Edwards and Barber (1976b) found that ca 28 per cent was sufficient in similar experiments with maize.

Other results suggest that even smaller proportions of the roots may be satisfactory in field conditions. Ohlrogge (1957, 1958, 1962) showed that a single root which was allowed to proliferate in nitrate-rich soil was sufficient to support luxuriant growth of maize. Photographs of the root showed that it comprised only a relatively small proportion of the total root mass of the mature crop. Wiersum (1967) demonstrated a similar effect with spring wheat, broad beans and a brassica crop, using a root training technique (de Roo and Wiersum, 1963) in which the roots of each plant were grown down a length of narrow tubing (containing a soil mixture of minimal fertility) before emerging into a zone of moist well-fertilized soil. The results were compared with a control in which no tubing was used. Although the quantity of roots in the fertilised soil declined as the length of tubing increased, their rate of inflow increased. The largest effects were observed with wheat, where the biggest inflow rate was more than ten times that of the control. Although this figure may have been exaggerated because of the greater proportion of older suberized roots present in the fertilized zone for the control plants, it suggests that as

little as 10 per cent or less of the roots were capable of supporting growth in this experiment.

The ability of small fractions of the root system to absorb the total plant N requirements from different depths in the soil profile has also been demonstrated in placement experiments with winter wheat (Daigger and Sander, 1976), with maize (Herron *et al.*, 1968; Gass *et al.*, 1971) and with established grass swards (Kernick, 1960; Garwood and Williams, 1967; Hodgson, 1970; Ogus and Fox, 1970). The results of Daigger and Sander (1976) are summarised in Fig. 1. These show that as the crop approached maturity, recovery of fertilizer N became almost independent of the depth of placement (even to 150 cm) within the root zone. Since Kmoch *et al.* (1957) have shown that *ca* 90 per cent of wheat roots are typically contained in the surface metre of these soils, it is clear that a small proportion of roots in the region between 100 and 150 cm were able to support the demands of the crop. Similar results were obtained for maize (Gass *et al.*, 1971) provided residual levels of N were not excessive. Ogus and Fox (1970) found greatest recoveries were obtained from surface applications of fertilizer N to established bromegrass, although recoveries from deeper applications remained approximately constant (at a slightly reduced value) until the proportion of the root system exposed fell below *ca* 9 per
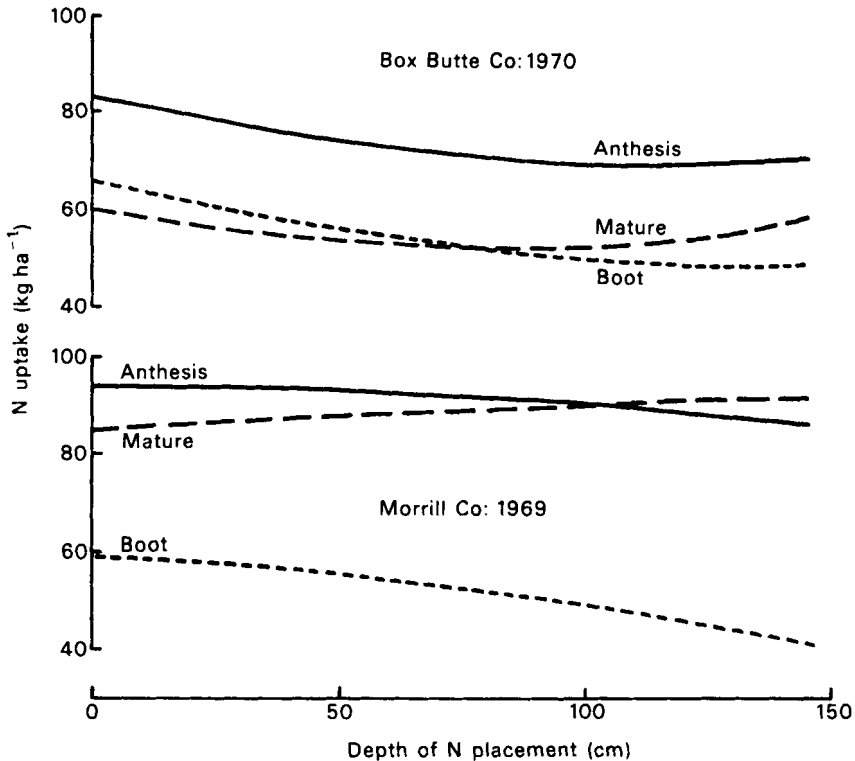

FIG. 1. Variation in N uptake by winter wheat with depth of placement of N fertilizer (after Daigger and Sander, 1976).

cent, when uptake declined rapidly. Uptake per unit weight of roots in the subsoil was found to be up to 300 times that in the surface region. Similar results were obtained by Kernick (1960) for the recovery of fertilizer N by the shallower-rooted cocksfoot and red fescue grasses over a somewhat narrower range of placement depths, and by Hodgson (1970) for established ryegrass swards. Garwood and Williams (1967), and Herron *et al.* (1968) showed that N recoveries from subsoil applications within the root zone could even exceed those from equivalent surface dressings when the top soil was dry.

Thus, although there is some variability in these results, it seems likely that relatively small proportions of the roots (probably as little as 10 per cent or less) are capable of absorbing most of the plants requirements for nitrate if the soil conditions are satisfactory. In this respect, nitrate appears to behave like phosphate (see Wiersum, 1967), for which it has been shown that under favourable conditions more than 60 per cent of the total P requirement of alfalfa can be supplied from the subsoil by little more than 2 per cent of its roots (Fox and Lipps, 1960, 1964).

The model

This examination of the literature shows that under moist conditions it is not the average concentration of nitrate in the soil solution which is likely to limit uptake, but the proportion of roots which have access to it. It follows, therefore, that the soil can be visualised as consisting of a series of nitrate-containing and nitrate-free zones, and that crop response will be determined by the proportion of root system which is exposed to each.

When nitrate is restricted to a fraction of the root system, plants attempt to optimize uptake initially by increasing their inflow rates and subsequently by increasing root development in the zones containing nitrate. Thus, in practice there is often considerable latitude in the way in which root systems may be distributed between nitrate-containing and nitrate-free regions before uptake is affected. The compensatory effect of these processes is reflected in the results of Kernick (1960), Herron *et al.* (1968), Ogus and Fox (1970), Gass *et al.* (1971) and Daigger and Sander (1976) who showed that nitrate recoveries remained approximately constant (except occasionally from surface applications) over a wide range of placement depths within the rooting zone.

However, inflow rates cannot be increased indefinitely when the proportion of roots exposed to nitrate is decreased, and N uptake must become dependent on root length when the proportion of roots exposed is small. The problem is to define the minimum quantity of roots required for normal growth. For the purpose of this paper it has been assumed that this critical root length (L_c) is reached when increases in inflow become limited by the permeability of the root membranes. L_c was then estimated from the ratio of the uptake (*i.e.* N demand) to this maximum inflow rate. Using maximum inflow data from Barley (1970) and an average value of 5.56 kg N ha^{-1}d^{-1} for the daily N demand for a number of crops (Greenwood, personal communication), the critical root length was estimated to be 7.3 cm^{-1} for the linear period of growth. The ratio of this figure to total root length data (estimated from the root distribution measurements of Gerwitz

TABLE 3

Root lengths and effective rooting depths for various crops at or near maturity. Values were estimated from the data of Gerwitz (personal communication) and Welbank et al. (1974)

Crop (experimental no.)	Treatment/variety	Harvest no.	Critical root length† (% of total)	Effective rooting depth (cm) :	
				Measured	Calculated
Broad bean	—	4	44.7	24	35
Cauliflower	—	5	5.0	77	60
Leek	0 kgN/ha	—	22.4	23	15
	200 kgN/ha	—	17.8	29	15
Lettuce	—	3	22.3	15	20
Onion	—	4	35.0	20	25
Parsnip	—	3	12.5	50	45
	—	4	13.5	69	100
Pea	—	3	13.2	37	55
	—	4	13.3	45	50
Turnip	1974	4	4.6	94	80
	1975; dry	7	4.2	86	65
	1975; wet	7	3.0	77	80
Barley (4)	—	4	5.4	122	105
Oats (4)	—	4	6.2	91	105
Spring wheat (4)	—	4	6.3	88	105
Winter wheat (4)	—	4	5.7	124	110
Winter wheat (5)	Cappelle-Desprez	5	3.7	90	110
	Maris Ranger	5	3.6	115	110
	TL 363/30	5	3.2	120	110
	TL 365a/25	5	3.2	103	105
	TL 365a/34	5	3.5	118	110
	TL 365a/37	5	3.8	121	105
Winter wheat (6)	Cappelle-Desprez	4	4.3	100	90
	Maris Ranger	4	4.0	98	90
	TL 363/30	4	4.1	98	95
	Maris Nimrod	4	5.0	84	90
	TL 365a/34	4	4.4	80	85
	TL 365a/37	4	4.8	92	85

†Critical root length is the estimated minimum length of root required for normal growth expressed as a percentage of the total root length below the crop.

*Measured values of effective rooting depth were estimated from the critical root length; calculated values were determined to the nearest 5 cm using Equation 7.

(personal communication) and Welbank *et al*. (1974)) for a range of mature crops is given in Table 3. The results confirm the previous conclusion that most crops can continue growing normally with less than 15 per cent of their roots supplied with nitrate, although the values for individual crops will vary to some extent with changes in both demand and maximum inflow rate as the crop ages.

Using this information, it is possible to construct a simple model in which soil nitrate is assumed to be uniformly available as it is leached through the profile until it reaches a depth below which there are insufficient roots exposed to recover all of the N required by the plant. Only when nitrate is leached into the regions beyond this point (where $L < L_c$) will uptake decline with depth. This behaviour is illustrated in Fig. 2. It is evident from this diagram that the predicted changes in N availability may be represented approximately by a simple step function which assumes that nitrate is totally available above a set depth (h) and totally unavailable below it. Consequently, this function has been used to characterise the effective rooting depth for the recovery of nitrate. Since substantial nitrate uptake will occur in the region where $L_c > L > 0$ (and may be enhanced by subsequent root proliferation), h was assumed to correspond with the depth at which uptake declined to half its maximum rate (see Fig. 2).

The effective rooting depths of various drops grown at Wellesbourne and Rothamsted have been estimated from root distribution data (Gerwitz, personal communication; Welbank *et al*., 1974) for various stages in their development. The maximum values (given in Table 3) were always observed as they approached maturity. However, because of sampling errors in the root distribution measurements the results for each crop are
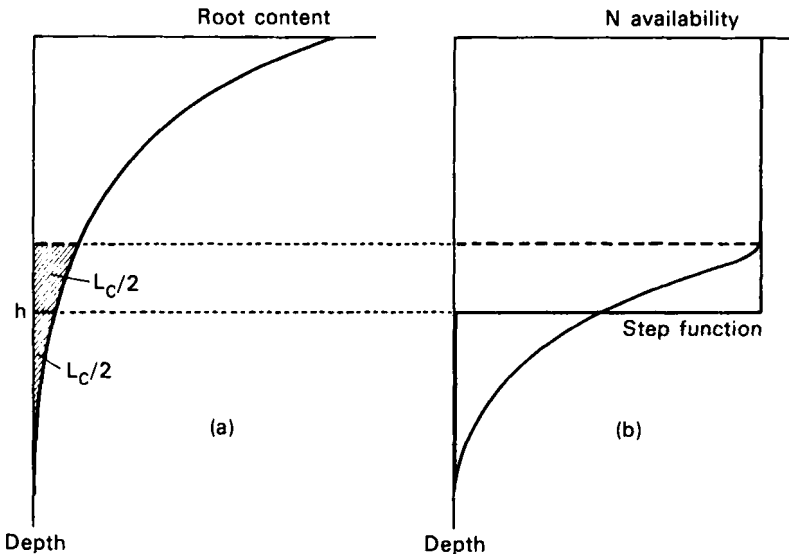

FIG. 2. Diagramatic representation of the changes in root content (a) and N availability (b) with depth in moist soil.

extremely variable. Nevertheless, real differences between most of the crops do occur, and although some of these effects may be attributed to the different soil conditions at the two sites, the general pattern of results is not dissimilar to that for the corresponding depths of water extraction (Rijtema, 1969; Anon, 1974). The results for cereals also agree with measurements of the depths to which mineralized N can be extracted by winter wheat in Germany (Jungk and Wehrmann, 1978).

Examination of the data for all of the crops at every stage of development revealed that the effective rooting depth (h cm) tends to increase with the above-ground dry weight (W t ha^{-1}) and population density (ρ plant ha^{-1}) of the crop, and decrease with the average cross-sectional area of their roots. Of the models tested the following simple regression equation was found to give the best fit to the data:

$$h = 6.082\, W + 1.52 \times 10^{-5}\, \rho + (1.81 \times 10^{-3}/a^2) - 2.1 \qquad (7)$$

where a is the average radius of the roots (cm). For root crops the dry weight of the tap root is also included in W. Average values of a for cereals were taken from Brewster and Tinker (1972) and for vegetable crops from Gerwitz (personal communication), and were assumed to remain constant throughout the life of each crop.

The equation shows that in most cases crop weight and the cross-sectional area of the roots govern rooting depth, and plant population only becomes important for closely-spaced crops such as cereals. Thicker-rooted crops tend to be more shallow rooting than those with fine ones, because not only are there fewer pores of suitable diameter to allow unimpeded growth of the thicker roots (Wiersum, 1957) but such crops cannot produce the same length of root per unit of dry matter as finer-rooted types. The small positive effect of population density in Equation 7 implies that the roots of more closely-spaced plants tend to explore deeper regions of the soil in search of water or nutrients, in response to competition from their neighbours. This is in agreement with the findings of Kirby and Rackham (1971) and Verheij (1970) for low to average population densities, although their results show that rooting depth may also decline at very high densities due to poor top growth (which affects W).

Although this equation has little theoretical basis, and conceals many of the effects from different soil conditions and changing weather patterns on root growth, it still gave a highly significant fit to the data ($P<0.001$) with more than 77 per cent of the variance accounted for. It may therefore be useful in representing the plant factors that influence rooting depth. Rooting depths calculated by Equation 7 are plotted against the corresponding experimental values estimated from the critical root length for the twelve crops at various stages of growth in Fig. 3, and the results for mature crops are also given in Table 3.

Equation 7 enables the rooting depths of crops, for which detailed root distribution data is not available, to be estimated at almost any stage of growth using data which can be measured relatively easily. However, for many leaching calculations it may be sufficient only to know the rooting depth for the mature crop. Although this may result in an underestimation
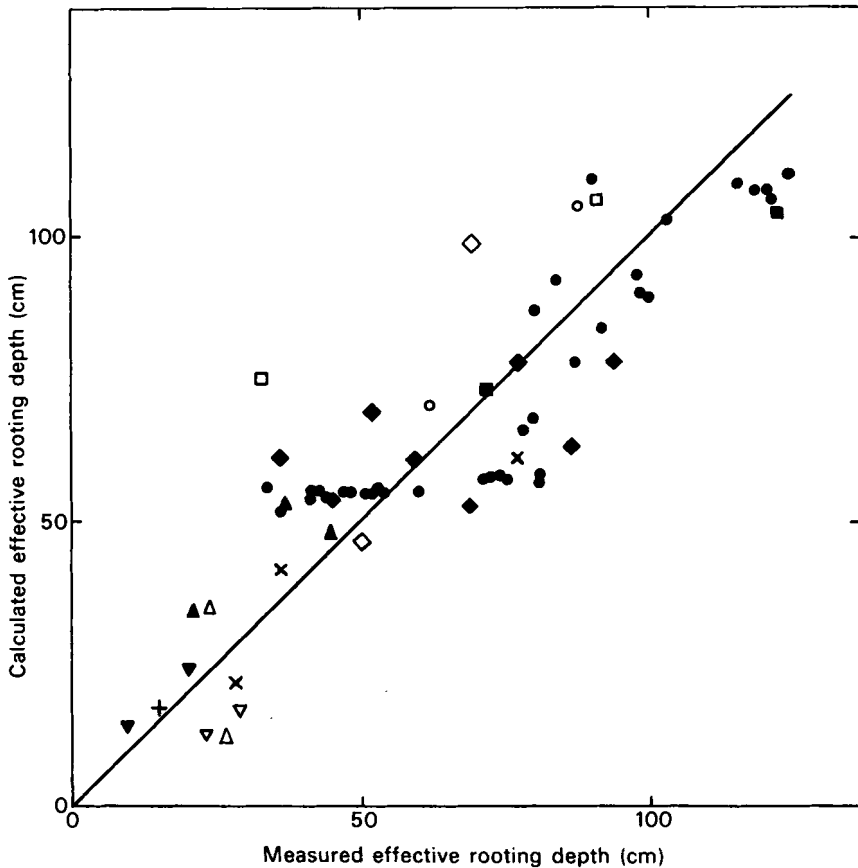
FIG. 3. Plot of calculated vs measured values of effective rooting depth for 12 crops. The calculated data were obtained using Equation 7; the measured data were determined from the average critical root length using root distribution measurements from Gerwitz (personal communication) and Welbank *et al.* (1974). Key: △ broad bean; X cauliflower; ▽ Leek; + Lettuce; ▼ Onion; ◇ Parsnip; ▲ Pea; ◆ Turnip; ● Winter Wheat; ○ Spring Wheat; □ Oats; ■ Barley.

of losses when leaching occurs from the rooting zone of a young crop, this may not be unduly important in Britain because N is seldom completely displaced from the topsoil (especially when both ammonium and nitrate have been applied), and some nitrate can usually be recovered by the few primary roots which penetrate quite rapidly to the lower regions of the rooting zone. Thus, the developing crop may be able to acquire sufficient N to alow it to continue growing until the main body of roots catches up with any nitrate leached into the lower regions of the rooting zone.

If the model is correct, it should be possible to predict the effects of nitrate leaching on the N fertilizer needs of different crops by a simple 3-step procedure:

(1) Determine the effective rooting depth from Equation 7.

(2) Estimate the amount and distribution of nitrate within this depth of soil at the onset of leaching.

(3) Calculate the amount of nitrate leached below this depth using a suitable model.

The validity of this procedure for estimating the effects of leaching which occurs either during or before the growing season will be examined in following papers (Burns, 1980a, b).

Acknowledgements

REFERENCES

ADDISCOTT, T. M. 1977. A simple computer model for leaching in structured soils. Journal of Soil Science 28, 554–563.

ALBERDA, TH. 1965. The influence of temperature, light intensity and nitrate concentration on dry-matter production and chemical composition of Lolium perenne L. Netherlands Journal of agricultural Science 13, 335–360.

ANONYMOUS 1974. In Irrigation: booklet for BP landwork 1974. Gleadthorpe Experimental Husbandry Farm, ADAS, MAFF.

ASHER, C. J. and EDWARDS, D. G. 1978. Critical external concentrations for nutrient deficiency and excess. Proceedings of the 8th international Colloquium on Plant Analysis and Fertilizer Problems, Auckland, 1978. Volume 1, pp. 13–28. N.Z. DSIR Information Series No 134, Wellington, New Zealand.

BALDWIN, J. P. 1975. A quantitative analysis of the factors affecting plant nutrient uptake from some soils. Journal of Soil Science 26, 195–206.

BALDWIN, J. P., NYE, P. H. and TINKER, P. B. 1973. Uptake of solutes by multiple root systems from soil. III. A model for calculating the solute uptake by a randomly dispersed root system developing in a finite volume of soil. Plant and Soil 38, 621–635.

BARBER, S. A. 1962. A diffusion and mass-flow concept of soil nutrient availability. Soil Science 93, 39–49.

BARBER, S. A. 1974. Properties of the plant that influence fertilizer practice. Proceedings of the 7th international Colloquium on Plant Analysis and Fertilizer Problems, Hanover, 1974, Volume 1, pp. 25–33. German Society of Plant Nutrition, Hannover, Federal Republic of Germany.

BARLEY, K. P. 1970. The configuration of the root system in relation to nutrient uptake. Advances in Agronomy 22, 159–201.

BHAT, K. K. S. and NYE, P. H. 1973. Diffusion of phosphate to plant roots in soil. I. Quantitative autoradiography of the depletion zone. Plant and Soil 38, 161–175.

BOUMA, D. 1967a. Nutrient uptake and distribution in subterranean clover during recovery from nutritional stresses. I. Experiments with phosphorous. Australian Journal of biological Sciences 20, 601–612.

BOUMA, D. 1967b. Nutrient uptake and distribution in subterranean clover during recovery from nutritional stresses. II. Experiments with sulphur. Australian Journal of biological Sciences 20, 613–621.

BRESLER, E. and HANKS, R. J. 1969. Numerical method for estimating simultaneous flow of water and salt in unsaturated soils. Soil Science Society of America Proceedings 33, 827–832.

BREWSTER, J. L. and TINKER, P. B. H. 1972. Nutrient flow rates into roots. Soils and Fertilizers 35, 355–359.

BROUWER, R. 1954. The regulating influence of transpiration and suction tension on the water and salt uptake by the roots of intact Vicia faba plants. Acta Botanica Neerlandica 3, 264–312.

BURNS, I. G. 1974. A model for predicting the redistribution of salts applied to fallow soils after excess rainfall or evaporation. Journal of Soil Science 25, 165–178.

BURNS, I. G. 1975. An equation to predict the leaching of surface-applied nitrate. Journal of agricultural Science, Cambridge 85, 443–454.

BURNS, I. G. 1976. Equations to predict the leaching of nitrate uniformly incorporated to a known depth or uniformly distributed throughout a soil profile. Journal of agricultural Science, Cambridge 86, 305–313.

BURNS, I. G. 1980a. A simple model for predicting the effects of leaching of fertilizer nitrate during the growing season on the nitrogen fertilizer need of crops. Journal of Soil Science 31, 175–185.

BURNS, I. G. 1980b. A simple model for predicting the effects of winter leaching of residual nitrate on the nitrogen fertilizer need of spring crops. Journal of Soil Science 31, 187–202.

CLAASSEN, N. and BARBER, S. A. 1974. A method for characterizing the relation between nutrient concentration and flux into roots of intact plants. Plant Physiology 54, 564–568.

CLAASSEN, N. and BARBER, S. A. 1977. Potassium influx characteristics of corn roots and interaction with N,P, Ca and Mg influx. Agronomy Journal 69, 860–864.

CLEMENT, C. R., HOPPER, M. J., CANAWAY, R. J. and JONES, L. H. P. 1974. A system for measuring the uptake of ions by plants from flowing solutions of controlled composition. Journal of experimental Botany 25, 81–99.

CLEMENT, C. R., HOPPER, M. J. and JONES, L. H. P. 1978. The uptake of nitrate by Lolium perenne from flowing nutrient solution. I. Effect of NO_3^- concentration. Journal of experimental Botany 29, 453–464.

COLLANDER, R. 1959. In Plant physiology (ed. F. C. Steward), Volume II, pp 3–102. New York: Academic Press.

COOKE, G. W. 1979. Some priorities for British Soil Science. Journal of Soil Science 30, 187–213.

CRAM, W. J. 1973. Internal factors regulating nitrate and chloride influx in plant cells. Journal of experimental Botany 24, 328–341.

DAIGGER, L. A. and SANDER, D. H. 1976. Nitrogen availability to wheat as affected by depth of nitrogen placement. Agronomy Journal 68, 524–526.

DE ROO, H. C. and WIERSUM, L. K. 1963. Root training by plastic tubes. Agronomy Journal 55, 402–405.

DE WIT, C. T. 1953. A physical theory on placement of fertilizers. Verslagen van Landbouwkundige Onderzoekingen No 59.4, pp. 1–71.

DOLL, E. C., CHRISTENSON, D. R. and WOLCOTT, A. R. 1971. Potato yields as related to nitrate levels in petioles and soils. American Potato Journal 48, 105–112.

DREW, M. C. 1975. Comparison of the effects of a localized supply of phosphate, nitrate, ammonium and potassium on the growth of the seminal root system, and the shoot, in barley. New Phytologist 75, 479–490.

DREW, M. C., SAKER, L. R. and ASHLEY, T. W. 1973. Nutrient supply and the growth of the seminal root system in barley. I. The effect of nitrate concentration on the growth of axes and laterals. Journal of experimental Botany 24, 1189–1202.

DREW, M. C. and SAKER, L. R. 1975. Nutrient supply and the growth of the seminal root system in barley. II. Localized, compensatory increases in lateral root growth and rates of nitrate uptake when nitrate supply is restricted to only part of the root system. Journal of experimental Botany 26, 79–90.

DREW, M. C. and SAKER, L. R. 1978. Nutrient supply and the growth of the seminal root system in barley. III. Compensatory increases in growth of lateral roots, and in rates of phosphate uptake, in response to a localized supply of phosphate. Journal of experimental Botany 29, 435–451.

DUNHAM, R. J. and NYE, P. H. 1974. The influence of soil water content on the uptake of ions by roots. II. Chloride uptake and concentration gradients in soil. Journal of applied Ecology 11, 581–596.

DUNHAM, R. J. and NYE, P. H. 1976. The influence of soil water content on the uptake of ions by roots. III. Phosphate, potassium, calcium and magnesium uptake and concentration gradients in soil. Journal of applied Ecology 13, 967–984.

DUTT, G. R., SHAFFER, M. J. and MOORE, W. J. 1972. Computer simulation model of dynamic bio-physicochemical processes in soil. Technical Bulletin 196. Agricultural Experiment Station, University of Arizona, Tucson, USA.

EDWARDS, J. H. and BARBER, S. A. 1976a. Nitrogen uptake characteristics of corn roots at low N concentration as influenced by plant age. Agronomy Journal **68**, 17–19.

EDWARDS, J. H. and BARBER, S. A. 1976b. Nitrogen flux into corn roots as influenced by shoot requirement. Agronomy Journal **68**, 471–473.

EPSTEIN, E. 1972. *Mineral nutrition of plants: Principles and perspectives*, pp 128–129 New York: John Wiley and Sons, Inc.

EPSTEIN, E. and HAGEN, C. E. 1952. A Kinetic study of the absorption of alkali cations by barley roots. Plant Physiology **27**, 457–474.

EPSTEIN, E. and RAINS, D. W. 1965. Carrier-mediated cation transport in barley roots: Kinetic evidence for a spectrum of active sites. Proceedings of the National Academy of Science **53**, 1320–1324.

FAGERIA, N. K. and WILCOX, G. E. 1977. Effect of nitrogen and phosphorus on rice growth. Lavoura Arrozeira **30**, (301) 24–26, 28; see Soils and Fertilizer **42**, 2583 (1979).

FERRARI, TH, J. and CUPERUS, J. L. 1973. Dynamic simulation of vertical non-adsorbed anion transport. Plant and Soil **38**, 425–438.

FOX, R. L. and LIPPS, R. C. 1960. Distribution and activity of roots in relation to soil properties. Transactions of the 7th international Congress of Soil Science, Madison, Wisconsin **3**, 260–267.

FOX, R. L. and LIPPS, R. C. 1964. A comparison of stable stronthium and P^{32} as tracers for estimating alfalfa root activity. Plant and Soil **20**, 337–350.

FRISSEL, M. J., POELSTRA, P. and REINIGER, P. 1970. Chromatographic transport through soils. III. A simulation model for the evaluation of the apparent diffusion coefficient in undisturbed soils with tritiated water. Plant and Soil **33**, 161–176.

FRISSEL, M. J. and REINIGER, P. 1974. *Simulation of accumulation and leaching in soils*. Wageningen, Pudoc.

FROTA, J. N. E. and TUCKER, T. C. 1978. Absorption rates of ammonium and nitrate by red kidney beans under salt and water stress. Soil Science Society of America Journal **42**, 753–756.

GARDNER, W. R. 1965. In *Soil nitrogen* (eds. W. V. Bartholomew and F. E. Clark), pp 550–572. American Society of Agronomy, Madison, USA.

GARWOOD, E. A. and WILLIAMS, T. E. 1967. Growth, water use and nutrient uptake from the subsoil by grass swards. Journal of agricultural Science, Cambridge **69**, 125–130.

GASS, W. B., PETERSON, G. A., HAUCK, R. D. and OLSON, R. A. 1971. Recovery of residual nitrogen by corn (*Zea mays* L.) from various soil depths as measured by ^{15}N tracer techniques. Soil Science Society of America Proceedings **35**, 290–294.

GILE, P. L. and CARRERO, J. O. 1917. Absorption of nutrients as affected by the number of roots supplied with the nutrient. Journal of agricultural Research **9**, 73–95.

GRASMANIS, V. O. and BARLEY, K. P. 1969. The uptake of nitrate and ammonium by successive zones of the pea radicle. Australian Journal of Biological Sciences **22**, 1313–1320.

HARMSEN, G. W. and KOLENBRANDER, G. J. 1965. In *Soil Nitrogen* (eds. W. V. Bartholomew and F. E. Clark), pp 43–92. American Society of Agronomy, Madison, USA.

HERRON, G. M., TERMAN, G. L. DREIER, A. F. and OLSON, R. A. 1968. Residual nitrate nitrogen in fertilized deep loess-derived soils. Agronomy Journal **60**, 477–482.

HOAGLAND, D. R. and BROYER, T. C. 1936. General nature of the process of salt accumulation by roots with description of experimental methods. Plant Physiology **11**, 471–507.

HODGSON, D. R. 1970. In *Nitrogen nutrition of the plant*. (ed. E. A. Kirkby), pp 201–214. University of Leeds.

HONERT, T. H. VAN DEN and HOOYMANS. J. J. M. 1955. On the absorption of nitrate by maize in water culture. Acta Botanica Neerlandica **4**, 376–384.

HOPKINS, H. T. 1956. Absorption of ionic species of orthophosphate by barley roots: effects of 2,4 dinitrophenol and oxygen tension. Plant Physiology **31**, 155–161.

JACKSON, W. A., VOLK, R. J. and TUCKER, T. C. 1972. Apparent induction of nitrate uptake in nitrate - depleted plants. Agronomy Journal **64**, 518–521.

JUNGK, A. 1974. Phosphate uptake characteristics of intact root systems in nutrient solution as affected by plant species, age and P supply. Proceedings of the 7th international Colloquium on Plant Analysis and Fertilizer Problems, Hanover, 1974, Volume 1, pp 185–196. German Society of Plant Nutrition, Hannover, Federal Republic of Germany.

JUNGK, A. and BARBER, S. A. 1974. Phosphate uptake rate or corn roots as related to the proportion of roots exposed to phosphate. Agronomy Journal **66**, 554–557.

JUNGK, A. and WEHRMANN, J. 1978. Determination of nitrogen fertilizer requirements by plant and soil analysis. Proceedings of the 8th international Colloquium on Plant Analysis and Fertilizer Problems, Auckland, 1978, Volume 1, pp 209–224. N. Z. DSIR Information Series No. 134, Wellington, New Zealand.

KERNICK, M. D. 1960. The recovery of fertilizer nitrogen from various depths below swards. Journal of the British Grassland Society **15**, 34–40.

KIRBY, E. J. M. and RACKHAM, O. 1971. A note on the root growth of barley. Journal of applied Ecology **8**, 919–924.

KMOCH, H. G., RAMIG, R. E., FOX, R. L. and KOEHLER, F. E. 1957. Root development of winter wheat as influenced by soil moisture and nitrogen fertilization. Agronomy Journal **49**, 20–25.

LASTUVKA, Z. and MINAR, J. 1970. The relation between nutrient solution concentration and growth and ion absorption of peas. (*P sativum*, L). II. Accumulation, distribution and utilization of nitrogen, phosphorus and potassium. Plant and Soil **32**, 412–423.

LAVY, T. L. and BARBER, S. A. 1964. Movement of molybdenum in the soil and its effect on availability to the plant. Soil Science Society of America Proceedings **28**, 93–97.

LYCKLAMA, J. C. 1963. The absorption of ammonium and nitrate by perennial rye-grass. Acta Botanica Neerlandica **12**, 361–423.

MAFF 1973. *Fertilizer recommendations*. Bulletin No. 209. London:HMSO.

MENGEL, D. B. and BARBER, S. A. 1974. Rate of nutrient uptake per unit of corn root under field conditions. Agronomy Journal **66**, 399–402.

NYE, P. H. and TINKER, P. B. 1977. *Solute movement in the soil-root system*. Oxford: Blackwell Scientific Publications.

OGUS, L. and FOX, R. L. 1970. Nitrogen recovery from a soil profile by *Bromus inermis*. Agronomy Journal **62**, 69–71.

OHLROGGE, A. J. 1957. How to get sufficient uptake of nutrients from fertilizer bands. Proceedings of the 12th Hybrid Corn Industry-Research Conference, pp 55–62.

OHLROGGE, A. J. 1958. How roots tap a fertilizer band. Plant Food Review, pp 4–8.

OHLROGGE, A. J. 1962. Some soil-root-plant relationships. Soil Science **93**, 30–38.

OLSEN, C. 1950. The significance of concentration for the rate of ion absorption by higher plants in water culture. Physiologia Plantarum **3**, 152–164.

OLSEN, S. R. and KEMPER, W. D. 1968. Movement of nutrients to plant roots. Advances in Agronomy **20**, 91–151.

PLACE, G. A. and BARBER, S. A. 1964. The effect of soil moisture and rubidium concentration on diffusion and uptake of rubidium - 86. Soil Science Society of America Proceedings **28**, 239–243.

PORTER, L. K., KEMPER, W. D., JACKSON, R. D. and STEWART, B. A. 1960. Chloride diffusion in soils as influenced by moisture content. Soil Science Society of America Proceedings **24**, 460–463.

REISENAUER, H. M. 1969. A technique for growing plants at controlled levels of all nutrients. Soil Science **108**, 350–353.

RIJTEMA, P. E. 1969. Soil moisture forecasting. Nota 513, Instituut voor Cultuurtechnick en Waterhuishouding, Wageningen, pp 1–28.

VERHEIJ, E. W. M. 1970. Spacing experiments with Brussels sprouts grown for single-pick harvests. Netherlands Journal of agricultural Science **18**, 89–104.

WARNCKE, D. D. and BARBER, S. A. 1974. Nitrate uptake effectiveness of four plant species. Journal of environmental Quality **3**, 28–30.

WARRICK, A. W., BIGGAR, J. W. and NIELSEN, D. R. 1971. Simultaneous solute and water transfer for an unsaturated soil. Water Resources Research **7**, 1216–1225.

WATANABE, F. S., OLSEN, S. R. and DANIELSON, R. E. 1960. Phosphorus availability as related to soil moisture. Transactions of the 7th international Congress of Soil Science, Madison, Wisconsin **3**, 450–456.

WELBANK, P. J., GIBB, M. J., TAYLOR, P. J. and WILLIAMS, E. D. 1974. Root growth of cereal crops. Rothamsted Experimental Station Report for 1973, Part 2, pp 26–66.

WIERSUM, L. K. 1957. The relationship of the size and structural rigidity of pores to their penetration by roots. Plant and Soil **9**, 75–85.

WIERSUM, L. K. 1958. Density of root branching as affected by substrate and separate ions. Acta Botanica Neerlandica **7**, 174–190.

WIERSUM, L. K. 1967. Potential subsoil utilization by roots. Plant and Soil 27, 383–400.
WINSOR, G. W. 1969. In *Nitrogen and soil organic matter*, MAFF Technical Bulletin 15, pp 109–128. London: HMSO.

(Received 6 September 1979)