Use of Mass Flow and Diffusion Analysis in Predicting Critical N Concentrations Needed at Different Growth Stages

A Dissertation submitted in partial satisfaction of the requirements for the degree of Doctor of Philosophy in Soil Science by Sir El Khatim Hassan Ahmed

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ABSTRACT OF THE DISSERTATION

Use of Mass Flow and Diffusion Analysis in Predicting Critical N Concentrations Needed at Different Growth Stages

by

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Doctor of Philosophy, Graduate Program in Soil Science
University of California, Riverside, December 1984
Professor John Letey, Chairman

Basic information is needed on fertilizer concentrations and amounts to be applied with irrigation water to adequately meet crop needs without excess for potential environmental degradation. \( \text{NO}_3 \) movement to plant roots was analyzed using a transient state mass flow and diffusion model to determine the time that the concentration at the root surface would drop to zero for various uptake rates and initial concentrations. The model assumes constant N uptake rate at the root surface and allows for competition between adjacent roots for N.

A greenhouse experiment was conducted where barley (\textit{Hordeum vulgare}), Swiss chard (\textit{Beta vulgaris}) and lettuce (\textit{Lactuca sativa}) were grown to obtain numerical values for parameters used in the model. These
included water and N fluxes into the root and half the distance between adjacent roots. Calculations were done for a practical range of volumetric water content ($\Theta$), specifically $\Theta = .25$ and $\Theta = .35 \text{ cm}^3/\text{cm}^3$. The sensitivity of N concentrations at the root surface to these parameters was also investigated. N concentration at the root surface was more sensitive to half distance between adjacent roots than to any other soil or plant parameter. Results indicated that, in the absence of mass flow, diffusive flux to plant roots may be large enough to satisfy all N requirements of the plant.

Predicted N concentrations were directly proportional to N flux into the roots, N application interval and inversely proportional to NO$_3$ diffusion coefficient in the soil. In general, results indicated the need for higher initial soil solution concentrations at the initial seedling stage rather than latter crop development stages.
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INTRODUCTION

Recommendations on supplemental N fertilization are usually based on correlations between plant response and total quantity of N fertilizer. In order to maximize crop production, a critical level where there is no significant increase in plant yield with additional fertilizer is often selected and that amount of fertilizer is applied to the soil one or more times during the year. However, maximizing crop production does not necessarily result in maximizing fertilizer use efficiency. This is especially true if N losses by leaching and/or denitrification occur. Besides being a valuable resource loss, N movement below the root zone represents a potential hazard to environmental quality.

Considering the dynamic nature of the crop demand for N, timing as well as the quantity of N application is essential for efficient N fertilizer use. An effective fertilizer management program should provide the nutrient in the quantities necessary for adequate nutrition during the intervening application time period. N application with the irrigation water, especially with drip systems, offers flexibility in timing nutrient applications to crop demand. As water moves through the profile, N could be removed by the plant root system resulting in a relatively low concentration at the bottom of the root system. Results of Miller et al. (1976) indicate that N is used more efficiently when applied through the drip system than when banded and furrow irrigated or banded and drip irrigated.
Knowledge of N concentration at the root surface expected from a certain fertilizer application is very important in determining the minimum N solution concentration needed for adequate N supply to plant roots. Depending on the rate of N uptake relative to the rate of N supply, N accumulation or depletion at the root surface may take place. When N is applied with the irrigation water, the grower would like to apply the minimum N concentration required to maintain N concentration at the root surface above the predetermined critical level needed for optimum growth before the next application. Historically, soil analysis for N has been used as an index for N availability to plant roots. Accordingly, plant growth is related to an average bulk soil solution concentration which may be completely different from N concentration at the root surface. This is probably because of the extreme difficulty encountered in actual measurement of the concentration profile around the roots of growing crops.

An estimate of N concentration at the root surface as a function of time can be obtained from mathematical modeling of nutrient uptake. Such an approach is based on the concepts of the root as a sink towards which N moves through the soil by both mass flow and diffusion. Nakagawa et al. (1976) and Sharma and Chaudhary (1984) used a model originally described by Gardner (1965) to predict N uptake into the roots of corn and wheat, respectively, grown under field conditions as a function of applied N fertilizer. In spite of the gross simplification and assumptions involved in developing the model, agreement between calculated and measured uptake was reasonable.
The main purpose of this study was to quantitatively measure the rate of N uptake per unit root length for three crops at different sampling dates and to use these data in a transient mass flow and diffusion model to predict minimum N solution concentrations required to adequately provide the crop with N at different stages of development.
LITERATURE REVIEW

Mechanisms of Nutrient Supply to Plant Roots

Nutrient uptake from the soil is an essential process for plant growth. For a nutrient to be absorbed it must be in the proper chemical form that the plant root is capable of absorbing. Also, since a plant root only detects and responds to the concentration at its surface, nutrients must be positionally available, i.e., present at the root surface before absorption can take place. This implies that, in the soil, nutrient availability to plant roots will be essentially limited by the rate of nutrient transfer from bulk soil to the root surface. Nutrients reach the plant root by root extension, mass flow and diffusion. Root elongation into undepleted soil volumes results in a continuous supply of nutrients at the root surface. This is particularly significant because root development is stimulated in soil regions where nutrients are locally more abundant (Danielson, 1972). Mass flow is the movement of dissolved nutrients in water flowing to plant roots in response to transpiration. Diffusion is the result of the thermal motion of ions so that there is a net movement in response to concentration gradients at the root surface. The relative contribution of root extension, mass flow and diffusion to the total supply of nutrients to the root surface is very difficult to assess since they interact when occurring simultaneously.

Evidence for root interception was provided by Oliver and Barber (1966a) in a study of Mn uptake by three crops from five soils. Mn
uptake was linearly related to total supply by root interception and mass flow was minimized. However, root interception is still poorly defined and very difficult to quantify unless some assumptions are made. It may be possible for roots to grow through the soil pores without disturbing the solid matrix or roots may displace soil particles as they grow. In the latter case, the volume of displaced soil would be proportional to the root volume and the magnitude of root interception is thus calculated on the basis of root volume (Oliver and Barber, 1966a), the maximum root interception would occur when the roots grow through the soil pores which may have a higher than average nutrient content. Barber et al. (1963) estimated that plant roots grow to a maximum of 3% of the available nutrients in the soil. They also concluded that the actual amount contacted would undoubtedly be much less because roots will tend to push soil away from them as they extend. Estimation of the amount of available nutrients contacted by the root in terms of surface areas of the roots and soil was done by Albrecht et al. (1940) and Passioura (1966). Halstead et al. (1968) evaluated these three methods of calculating the quantity of available nutrients contacted by the roots by determining the relative degree of correlation between the calculated supply and uptake by the plant. The method that estimates the maximum possible root interception gave the highest correlation while the use of a parameter based on root surface area was poorly correlated with uptake.

Oliver and Barber (1966a) conducted two experiments to evaluate methods for estimating relative contribution of root extension, mass
flow and diffusion to the total ion uptake. Mass flow contribution was calculated by multiplying the amount of water uptake by the concentration of ions as determined from analysis of a saturation extract. Root interception was calculated by assuming that roots intercepted an amount proportional to their volume. Diffusion was estimated by the difference between total nutrient uptake and the sum of root interception and mass flow contribution. When most of the uptake was by diffusion, as with K, varying mass flow contribution by altering the transpiration rate had very little effect on uptake. When mass flow supplied most of the uptake, as with Ca, the amount of movement to the plant by mass flow had a large effect on the amount taken up by the plant. Following the same procedure, similar studies were done by Oliver and Barber (1966b), Hiestand et al. (1968), Barber and Olsen (1968) and Brewster and Tinker (1970).

In summary, results indicate that plant roots grow to less than 3% of the available nutrients in the soil. They may grow to much of the plant's Ca and Mg but very little of the plant's need for N, P and K. Mass flow seems to be the major mechanism for the supply of Ca, Mg and N to plant roots while most of the P and K must reach the root by diffusion.

Calculation of mass flow from water uptake and average soil solution concentration tends to overestimate its contribution to total ion uptake. This is because nutrient uptake may continue when the transpiration rate is very low or even absent and roots may continue to absorb water but tend to lose their efficiency in absorbing nutrients as they age (Clarke et al., 1968). Another limitation is the fact that nutrient
Concentration at the root surface should be used instead of an average bulk soil solution concentration (Yue, 1968). Since diffusion is calculated by difference, its contribution will be underestimated. However, such generalizations increase our understanding of the role of each mechanism on nutrient uptake but results must be recognized to be, at best, merely approximations.

Modeling Nutrient Uptake

A plant root is considered as a sink towards which nutrients move by both mass flow and diffusion. A mass balance equation that describes nutrient flow through such a system can be written (see the theory section of this study). Many investigators have given consideration to nutrient movement in the root vicinity in relation to nutrient uptake. Examples of these are Olsen et al. (1982), Passloue (1963), Gardner (1965), Marriott and Yne (1968), Claassen and Barber (1974), Cushman (1979) and Willigen (1981). A common feature to all these studies is that they are all based on solving the nutrient flow equation for different boundary conditions and varying degrees of assumptions. More information about this subject is available in the excellent review on movement of nutrients to plant roots by Olsen and Kemper (1968). The solution of the nutrient flow equation has both soil and plant parameters. These include nutrient and water fluxes into the root, total root length and radius and a value for the diffusion coefficient of the nutrient in soil together with an estimate for the initial bulk soil solution concentration. For some of these models knowledge of the threshold concentration needed at the root surface where nutrient flux is still at its maximum rate is essential.
Nutrient Flux into the Roots

Assuming that nutrient uptake and root length increase in the same ratio during the period between successive harvests and allowing for the exponential nature of the root growth, mean nutrient flux per unit root length could be estimated by (Radford, 1967):

\[ I = \frac{U_2 - U_1}{(l_2 - l_1) (t_2 - t_1)} \]

where \( U \) is the nutrient content of the plant, \( L \) is the root length, \( t \) is the plant age and the subscripts refer to successive harvests. Mengel and Barber (1974) used this equation to calculate N flux into corn roots under field conditions. N flux was greatest at the first sampling date and then decreased rapidly with increased plant age. This was attributed to the rapid increase in root length relative to the increase in the uptake rate. Flux was calculated on the assumption that N uptake is uniform along all segments of the root irrespective of their age. This will tend to underestimate the actual flux since roots tend to lose their efficiency in absorbing nutrients as they age (Rovira and Bowen, 1968).

Water flux into the roots is given by (P. Willigen, 1981):

\[ V = -E / \pi r_0^2 \]

where \( E \) is the transpiration rate per unit root length and \( r_0 \) is the root radius. The negative sign indicates that the flux is in the negative direction of radial distance from root center.
Diffusion Coefficient

To evaluate limitations imposed by the soil properties on nutrient transference through the soil, the diffusion coefficient of the nutrient under consideration must be considered. The diffusion coefficient in the soil is a function of both physical and chemical properties of the system and can be written as (Porter et al., 1960):

\[ D = D_0 \left( \frac{L}{L_e} \right)^2 \Omega \psi y \]

where \( D_0 \) is the diffusion coefficient of the ion in liquid water, \( L \) is the macroscopic distance between two points, \( L_e \) is the actual path length of diffusion, \( \Omega \) is the volumetric water content, i.e., fraction of the total porosity through which ions may move, \( \psi \) is a factor that takes into account the decrease in diffusivity associated with an increase in water viscosity near clay mineral surfaces and \( \gamma \) is a factor included as a measure of negative adsorption of anions. In the above equation, the fraction \( \left( \frac{L}{L_e} \right)^2 \Omega \psi \) is a geometric factor that takes into account the effects of reduced path length for diffusion and restricted total cross-sectional area available for the flow. The product \( \left( \frac{L}{L_e} \right)^2 \Omega \psi \gamma \) is approximately linearly related to water content as shown by Porter et al. (1960) and thus as the water content increases, \( D \) is expected to increase in a hyperbolic manner. Such increase in \( D \) as a result of moisture content increase was reported by Koike and Letey (1959), Porter et al. (1960), Paul (1963), Remman and Bruce (1964) and Warncke (1972). Millington and Quirk (1961) developed a simple equation that relates the diffusion coefficient in the soil to volumetric water content and soil porosity.
The diffusion coefficient is also dependent on the soil solution concentration. Such dependence is probably due to variations in thickness of the diffuse double layer (Graham-Bryce, 1963). Gerald et al. (1964) reported an increase in Rb diffusion coefficient with increasing Rb concentration. This was attributed to a reduced strength of Rb bonding by the soil. Lewis and Quirk (1965) and Hafr et al. (1978) reported a linear relationship between P diffusion coefficient and P concentration.

Boundary Conditions

To solve the nutrient flow equation, a boundary condition that relates nutrient uptake to the concentration at the root surface is needed. This relationship can be obtained from well-stirred solution culture experiments. Such a relationship has been generally described by the Michaelis-Menten kinetic equation (Nye and Tinker, 1977). However, most of these studies have been done with excised roots for a short uptake period and to a lesser degree with intact plants where nutrient uptake and translocation are taking place. Discrepancies in data from experiments with excised roots and intact plants have been reported by Loneragan and Asher (1967) and Edwards (1970).

The most widely used boundary condition in published literature is based on the assumption that nutrient uptake is proportional to the concentration at the root surface. Accordingly, nutrient uptake per unit root length, I, is given by Olsen and Kemper (1968):

\[ I = 2\pi r_0 k C_a \]
where $K$ is a proportionality constant denoted as the root absorbing power and $C_a$ is the nutrient concentration at the root surface. The solution of the nutrient flow equation subject to this boundary condition is used to evaluate the concentration at the root surface as a function of a certain initial soil solution concentration, diffusion coefficient, root absorbing power and time and then the above equation is used to predict nutrient uptake (Cushman, 1979). One limitation of this approach is the fact that the root absorbing power is assumed to be constant but it varies with both concentration and age of the root (Passioura, 1963). Other factors that may influence $K$ include nutrient content of the root, interaction with other ions, pH, kind and degree of microbial growth (Bowen and Rovira, 1966), and possibly bicarbonate concentration (Subcliffe, 1962). In case $K$ changes with concentration, Bouldin (1961) suggested selecting a value of $K$ corresponding to the concentration expected at the root surface after 4 to 8 hours of uptake.

Olsen and Kemper (1968) recommended the use of roots of comparable age, size and nutrient content and to measure uptake from well-stirred solutions of composition and pH similar to those expected in the soil solution.

Usually, the proportional uptake boundary condition is only valid over the narrow range where the concentration at the root surface is limiting nutrient uptake. Over an optimum range of concentration, $K$ tends to be smaller as the concentration increases. Because of this, selecting a constant value for $K$ will tend to overestimate predicted uptake. This limits the applicability of this boundary condition, especially if sought solution is to be used to guide fertilizer recommendations for optimum fertilizer applications.
Moreover, studies cited next have shown that plant growth is independent of N concentration until the concentration at the root surface becomes very low. Edward and Barber (1976) measured the rate of N depletion from nutrient solution by corn roots. N uptake was constant until the solution N concentration reached 4 μM and ceased below this value. Since a situation where the N level outside the root is maintained for any appreciable time around this value is unlikely, they conclude that, under field conditions, plants may be considered as either absorbing N at a rate close to the maximum rate or not absorbing at all. The relative independence of plant growth and N uptake on solution N concentration at the root surface was also reported by Frota and Tucker (1979), Alberta (1965), Wanncke and Barber (1974), and Clement et al. (1975) for different crops. Similar results were also reported by Letey et al. (1982) who recommended the use of a constant uptake boundary condition until the concentration at the root surface becomes essentially zero. It should be noted that these experiments were conducted in solutions essentially free from Cl and due to possible competition between Cl and NO₃, higher solution NO₃ concentrations may be needed in the presence of Cl for adequate N uptake (Karkafi et al., 1982). However, these results indicate that, in the soil, nutrient uptake will be limited by the rate of nutrient supply from bulk soil to the root surface rather than the ability of the plant to absorb nutrients from very low concentrations. They also indicate that the constant uptake boundary condition is a good approximation of actual conditions.
THEORY

Considering a plant root as a cylinder of uniform radius and infinite length having uniform \(\text{NO}_3\) absorbing properties, the change of \(\text{NO}_3\) concentration with respect to time and radial distance from the root is given by solving the equation (P. de Willigen, 1887):

\[
\frac{\partial C}{\partial t} = \frac{D}{r} \frac{\partial}{\partial r} \left( r \frac{\partial C}{\partial r} \right) - V \frac{\partial C}{\partial r} \tag{1}
\]

where

- \(C\) = \(\text{NO}_3\) concentration, mol/cm\(^3\) of solution,
- \(t\) = time, days,
- \(D\) = diffusion coefficient of \(\text{NO}_3\) in soil, cm\(^2\)/day,
- \(r\) = volumetric water content, cm\(^3\)/cm\(^3\),
- \(r\) = radial distance from root center, cm,
- \(V\) = water flux at distance \(r\), \(= E/2\pi r\),
- \(E\) = transpiration rate, cm\(^3\)/day per cm root.

**Boundary Conditions**

1) Constant uptake, i.e., \(\text{NO}_3\) uptake is independent of the concentration at the root surface. Mathematically, this can be written as:

\[
2\pi r_0 \frac{\partial C}{\partial r} - 2\pi r_0 V = I \quad r = r_0, \quad t > 0 \tag{2}
\]

where \(r_0\) is the root radius and \(I\) is \(\text{NO}_3\) uptake per cm root.
2) Competition between adjacent roots can be accommodated by a boundary condition which prohibits water and nutrient transport across the boundary \( r = r_1 \), where \( r_1 \) is the mid-point between adjacent roots, i.e.,

\[
2\pi r_1 D \frac{\partial C}{\partial r} - 2\pi r_1 V C = 0 \quad r = r_1, \quad t > 0
\]

Subject to these boundary conditions along with the initial condition that \( C = \text{initial soil solution concentration}, \ C_0 \) at \( t = 0 \), the general solution of equation (1) is written as (P. de Willigen, 1981):

\[
U = \left[ \frac{x^2}{(2v+2-1)} \right] (u+1) x^2 + \frac{\int (u+1) x^2 \, \frac{\partial}{\partial r} \, \frac{\partial}{\partial C} \, \frac{\partial}{\partial t} \, C \, r \, \partial r}{(2v+2-1)}
\]

\[
+ \frac{\int (u+2v) \, \frac{\partial}{\partial r} \, \frac{\partial}{\partial C} \, \frac{\partial}{\partial t} \, C \, r \, \partial r}{(2v+2) \, (2v+2-1)}
\]

\[
+ \frac{\int (u+1) (1-2v+2) \, \frac{\partial}{\partial r} \, \frac{\partial}{\partial C} \, \frac{\partial}{\partial t} \, C \, r \, \partial r}{(2v+2) \, (2v+2-1)^2}
\]

\[
+ \int (u+1) \, \frac{\partial}{\partial r} \, \frac{\partial}{\partial C} \, \frac{\partial}{\partial t} \, C \, r \, \partial r
\]

\[
+ (Q-2v)X^\forall \, \sum_{n=1}^{\infty} \exp\left( -\frac{\pi^2}{a} \frac{T}{x^2} \right) \, F_n(X, \phi, \nu_n)
\]

\[
+ \frac{2u-2}{(2v+2-1)} \, \sum_{n=1}^{\infty} \exp\left( -\frac{\pi^2}{a} \frac{T}{x^2} \right) \, \frac{\partial}{\partial \nu} \, \frac{\partial}{\partial C} \, \frac{\partial}{\partial t} \, C \, r \, \partial r
\]

\[
+ 2u-2 \, \sum_{n=1}^{\infty} \exp\left( -\frac{\pi^2}{a} \frac{T}{x^2} \right) \, \frac{\partial}{\partial \nu} \, \frac{\partial}{\partial C} \, \frac{\partial}{\partial t} \, C \, r \, \partial r
\]

\[
+ \frac{\partial}{\partial C} \, \frac{\partial}{\partial t} \, C \, r \, \partial r
\]

\[
+ \frac{\partial}{\partial C} \, \frac{\partial}{\partial t} \, C \, r \, \partial r
\]

\[
+ \frac{\partial}{\partial C} \, \frac{\partial}{\partial t} \, C \, r \, \partial r
\]

\[
+ \frac{\partial}{\partial C} \, \frac{\partial}{\partial t} \, C \, r \, \partial r
\]

\[
+ \frac{\partial}{\partial C} \, \frac{\partial}{\partial t} \, C \, r \, \partial r
\]
where \( a_n \) is the \( n^{th} \) root of:

\[
Y_{u+1}(a_n) J_{u+1}(a_n) = Y_{u+1}(a_n) J_{u+1}(a_n) = 0
\]

(5)

\[
F_u(x, \nu, a_n) = \frac{J_{u+1}(a_n) J_{u+1}(a_n) - J_{u+1}(a_n) J_{u+1}(a_n)}{a_n^2 J_{u+1}^2(a_n) - J_{u+1}^2(a_n)}
\]

(6)

and

\[
U = \frac{C}{C_0} \rho \frac{T}{D_0/\rho}
\]

\( r_0 \) = root radius, cm

\( x = r/r_0 \)

\( \rho = r_1/r_0 \)

\( r_1 \) = mid-point between adjacent roots, cm

\( \nu = -E/4\pi D \)

\( Q = -I/3\pi D C_0 \)

\( I = N_{O_3} \) uptake, mol/day per cm root

\( Q = \) volumetric water content, cm\(^2\)/cm\(^3\)

\( J_u \) and \( Y_u \) are Bessel functions of first and second kind, respectively.

and order \( \nu \). See Abramowitz and Stegun (1970) for definition.

Special case of the above solution is when \( N_{O_3} \) transport is by diffusion alone, i.e., \( \nu = 0 \) and this is given by:

\[
U = 1 + Q \left[ \frac{2\pi}{(a^2-1)\rho} - \frac{2\pi}{(a^2-1)} \right]
\]

\[
+ Q \sum_{n=1} \exp(-\frac{\pi^2}{4\rho^2}) \frac{J_1(a_n) J_1(a_n) - J_1(a_n) J_1(a_n)}{a_n^2 J_1^2(a_n) - J_1^2(a_n)}
\]

(7)
The above equation can be used to calculate the time required for the concentration at the root surface (C_d) to decrease to a predetermined critical level for given initial soil solution concentration (C_0) and plant uptake rate (I). This information can be used to guide fertilizer management particularly for frequent fertilizer application with irrigation water such as in a drip irrigation system. If the application interval (t) is known, the necessary C_0 to maintain C_d above the critical level before next application can be calculated.

Knowledge of plant uptake rate (I) is required. This study reports the results of a greenhouse investigation to determine I for 3 crops at different stages of plant growth. The measured values of I are then used in equation (4) to calculate appropriate values of C_0 to maintain maximum plant growth.
MATERIALS AND METHODS

A greenhouse experiment was conducted where barley (*Hordeum vulgare*), Swiss chard (*Beta vulgaris*) and lettuce (*Lactuca sativa*) were grown in plastic pots of about one liter capacity. A sand culture with a full-strength Hoagland's solution (Hoagland and Arnon, 1950), with NO₃ being the only source of N, was used. The experiment consisted of a total of 20 pots which had received essentially the same amount of N. Seeds were first sown on box trays containing sand and 3-day-old seedlings were then transferred to the pots. Only one plant per pot was grown to avoid root interaction except for plants of the first sample where 4 plants per pot were grown to get enough tissue for chemical analysis. Evaporation was minimized by covering the pots and water uptake was measured by weighing the pots before and after watering. Plants of 4 pots were randomly selected for sampling every week for 5 weeks.

Shoots of sampled plants were dried in a forced-air oven at 65°C and subsequently analyzed by the microKjeldahl method for total N. Concurrently, sand was washed from the roots of sampled plants and the line intersection method of Newman (1966) was used to measure the total root length per plant. N flux into the roots was calculated by measuring the slope of the total N accumulation versus time curves using a derivometer and then dividing by the total root length at each sampling date. The same procedure was followed to estimate water uptake rate per unit root length.

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RESULTS AND DISCUSSION

Plant Data

Total N accumulation and water uptake as a function of time for lettuce, Swiss chard, and barley are given in Fig. 1 through 6. Total N accumulation by both Swiss chard and barley showed a rapid steady increase with time. However, in case of lettuce, total accumulated N increased rapidly up to the third week and then at a lower rate during the last two sampling dates. Water uptake as a function of time followed the same trend as nitrogen uptake.

Data on root length, mid-point distance between adjacent roots, water and N fluxes into the roots are given in Table 1. Mid-point between adjacent roots was calculated by assigning each root a uniform zone of exploitation. In fact, the zone exploited will be of irregular shape but may be roughly approximated by an equivalent cylindrical volume of radius r₁ (Nye, 1972). The latter may be defined as \( r₁ = \frac{1}{(\pi w)^{1/2}} \) where w is the root length density, cm root/cm³ soil. Except for the first sampling date where four plants per pot were grown, calculated mid-point between adjacent roots decreased steadily with time and its value ranged from about 1 to .2 cm. Since a mobile ion, like NO₂, can move rapidly through distance of a centimeter a day in moist soils (Barley, 1970), adjacent roots are certain to compete for N.

For the three crops, over the period tested, both water and N fluxes tended to increase up to a maximum value and then decrease. The decrease in water and N fluxes into the roots is due to the rapid increase in root length relative to both water and N uptake rates. Water and N
a.) LETTUCE

TIME (WEEKS)

N(gm x 10^2)

0 0.2 0.4 0.6 0.8 1.0 1.2 1.4 1.6 1.8 2.0

0 1 2 3 4 5 6
b) SWISS CHARD

$N = (0.1 \times 10^2)$

TIME (WEEKS)

0 1 2 3 4 5
c) BARLEY

Time (WEEKS) vs. $N (\text{gm} \times 10^2)$
LETTUCE

WATER UPTAKE (g)

TIME (days)

7 14 21 28 35
<table>
<thead>
<tr>
<th>Crop</th>
<th>Plant age (weeks)</th>
<th>Root length (cm)</th>
<th>Mid-point (cm)</th>
<th>Water flux (cm³/day per cm)</th>
<th>N flux (µM/day per cm)</th>
</tr>
</thead>
<tbody>
<tr>
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<td>0.014</td>
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</tr>
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<tr>
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<td>0.49</td>
<td>0.061</td>
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<td>0.55</td>
<td>0.016</td>
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<td>0.025</td>
<td>0.208</td>
</tr>
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<td>0.059</td>
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<tr>
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<td>0.212</td>
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<td>0.019</td>
<td>0.074</td>
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<td>5</td>
<td>2887</td>
<td>0.23</td>
<td>0.014</td>
<td>0.053</td>
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</tbody>
</table>
fluxes were calculated on the assumption that plant roots are having uniform water and N absorbing properties irrespective of their age. This will underestimate the actual flux since roots tend to lose their efficiency in absorbing nutrients as they age (Novira and Bowen, 1968). Variations in N uptake because of differences in nutrient content between and along plant roots are also possible. Grasmatis and Barley (1969) found that, in stirred solutions, NO$_3^-$ uptake varied by a factor of 4 to 5 along the length of a pea radicle and most of the variation was attributed to differences in protein content of the zone. Water and N uptake rates are expected to be higher during the light rather than the dark period of the day but measuring the uptake rate over a period of a week averages the uptake rate.

N Concentration at the Root Surface

Knowledge of the concentration profile around the root is necessary for a complete description of nutrient supply over the growing season. Unfortunately, direct measurement of nutrient concentration at the root surface is extremely difficult. This problem arises from the complexity of actually making the physical measurements and an extreme lack of information about the ionic environment of roots (Olsen and Kemper, 1968). Moreover, as pointed out by Danielson (1972), even when environmental conditions at point sites become measurable, interpretation of the influence of cultural practices on nutrient availability will be difficult because of complicated interactions and continuous changes with time. Difficulty in direct measurements could be resolved by using equation (4) to estimate nutrient concentration at the root.
surface as a function of plant uptake, soil properties and time. Calculation of the infinite series in equation (4) requires the use of a computer. A computer program was written and it is given, with a short note on its main features, in the Appendix. Calculations were done for a practical range of volumetric water content, namely $q = 0.25$ and $q = 0.35 \text{ cm}^3/\text{cm}^2$. $\text{NO}_3^-$ diffusion coefficient in the soil was estimated by the Millington and Quirk (1961) model based on a value of 1.47 \text{ cm}^2/\text{day} for $\text{NO}_3^-$ diffusion coefficient in liquid water and a measured total porosity of 42% for sand. These correspond to 0.081 and 0.25 \text{ cm}^2/\text{day} for $\text{NO}_3^-$ diffusion coefficient in the soil at $q = 0.25$ and $0.35 \text{ cm}^3/\text{cm}^2$, respectively. A value of 0.05 cm for the root radius was used in the analysis.

The dimensionless concentration, $U$, at the root surface as a function of initial $N$ solution concentration, $C_0$, of 8 mM, volumetric water content of 0.25 $\text{ cm}^3/\text{cm}^3$ and time is shown in Fig. 7. Mid-point distance between adjacent roots, water and $N$ flux values used in the calculations were those given in Table 1 for barley on its first sampling date. Results show that $N$ concentrations at the root surface decreases with time and decreases more rapidly at the lower water level. The effect of volumetric water content on $N$ concentration at the root surface was assumed to be mainly through its effect on the diffusor coefficient of $\text{NO}_3^-$ in the soil rather than reduced water availability to plant roots. Lowering soil volumetric water content translates into a reduced total cross-sectional area available for the flow and a longer distance of diffusion. This results in a lower diffusion coefficient which in turn limits the rate of $N$ supply from bulk soil to the root surface. Clarke and Barley
(1967) studied the effect of volumetric water content on NO$_3$ uptake by plant roots in a system where mass flow was minimized. Over the range tested, i.e., $\theta = 0.03$ to $\theta = 0.12$ cm$^3$/cm$^3$, observed variations in N uptake were largely attributed to changes in the resistance that the soil offered to the diffusion of NO$_3$.

In the present model, the entire root system is considered as a sink for N. The strength of this sink is represented by the magnitude of N flux into the roots. Any increase in N flux during the growing season creates a higher demand for N at the root surface. Figure 8 shows N dimensionless concentration, $U$, at the root surface as a function of time and two N flux values, namely $I = .2$ and $I = .4$ gN/dm per cm root. Other soil and plant parameters were the same as those given in Fig. 7. Doubling N flux resulted in a significantly higher concentration gradient at the root surface. N concentration at the root surface initially decreased exponentially with time but after one day decreased linearly with time. These results indicate that when the crops demand for N is relatively high, higher initial soil solution concentrations are needed to keep N concentration at the root surface at desired levels.

NO$_3$ is a mobile ion in the soil and as nutrient uptake proceeds, adjacent roots may compete for N. Root competition was accommodated by the boundary condition that prohibited water and N transport across mid-point between adjacent roots. i.e., equation (3) of the theory section of this study. The effect of root competition on the dimensionless concentration, $U$, at the root surface is shown in Fig. 9. Calculations were done for $I = .2$ gN/dm per cm and 3 values of mid-point between adjacent roots, namely $r_1 = 1$, .8 and .5 cm. These correspond to
Fig. 7. N dimensionless concentration at the root surface as a function of volumetric water content and time.
Fig. 10. A dimensionless concentration at the root surface as a function of transpiration rate and time.
root densities of 0.32, 0.5 and 1.27 cm root/cm³, respectively. Other
soil and plant parameters were the same as those given in Fig. 7.
Over the range of r₁ tested, N concentrations at the root surface
was very sensitive to competition between adjacent roots and decreased
more rapidly with time as r₁ was decreased from 1 to 0.5 cm.

Figure 10 shows the dimensionless concentration, U, at the root sur-
face as a function E = 0 and E = 0.03 cm³/day per cm root. Other plant
parameters used in the calculations were those attained by barley on its
first sampling date and a value of 0.25 cm³/cm³ for H was used. Except
for the initial period of uptake, N movement to plant roots by diffusion
alone, i.e., E = 0 maintained N concentration at the root surface at
a level very close to that at E = 0.03. This is probably because of
the high concentration gradient developed initially and the relatively
high diffusion coefficient of NO₃ in the soil. This suggests that,
in the absence of mass flow, diffusive flux to plant roots could be high
enough to meet all N requirements of the plant.

Predicted Critical N Concentrations

N flux values given in Table 1 were measured under conditions where
N was not limiting plant uptake. The main objective, now, is to use
equation (4) to predict the minimum N solution concentration that would
still maintain measured flux at its maximum rate. By trial and error,
equation (4) was used to calculate the minimum N solution concentration
required to keep nutrient concentration at the root surface greater than
zero for the whole uptake period, t. Assuming a 7-day N application
interval, predicted critical N concentrations required to supply adequate
N to the roots of lettuce, Swiss chard and barley at different sampling dates are given in Table 2. Plant parameters used were those given in Table 1. Results indicate that higher initial soil solution concentrations are needed at Q = .25 compared to Q = .35 cm$^3$/cm$^3$. These correspond to D (NO$_3$) values of .08 and .25 cm$^2$/day, respectively. At the lower water level diffusion is limiting the rate of N supply to plant roots and hence higher initial soil solution concentrations are needed to keep measured flux at its maximum rate. These results support the views of Olsen and Kemper (1968) who suggested that a more reliable test for N should include an allowance for differences in the diffusion coefficient among soils. They also indicate that equal concentrations of NO$_3$ and NH$_4$ does not mean equal availability to plant roots since these two ions have different diffusion coefficients (Clarke, 1966).

On solving equation (1) both Q and D were assumed to be constant. Thus equation (4) does not predict what might happen under field conditions as the soil dries out. However, NO$_3$ concentration in the soil is inversely proportional to volumetric water content and any decrease in D as a result of soil drying is expected to be partially offset by a proportional increase in concentration unless water and N uptake are proportional. It must be remembered that the effect of volumetric water content on nutrient uptake was assumed to be mainly through its effect on the rate of N transfer through the soil and hence use of low values of Q that might affect physiological processes of the plant must be avoided. A poor soil-root contact at low water levels is also possible (Nye and Tinker, 1977).
<table>
<thead>
<tr>
<th>Crop</th>
<th>Plant age (weeks)</th>
<th>N concentration (µM)</th>
<th>Q = .25</th>
<th>Q = .35</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lettuce</td>
<td>1</td>
<td>1.0</td>
<td>1.2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>1.6</td>
<td>0.9</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>5.4</td>
<td>3.4</td>
<td></td>
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<td></td>
<td>4</td>
<td>3.8</td>
<td>2.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>0.9</td>
<td>0.6</td>
<td></td>
</tr>
<tr>
<td>Swiss chard</td>
<td>1</td>
<td>2.2</td>
<td>1.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>3.2</td>
<td>2.0</td>
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<td></td>
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<tr>
<td></td>
<td>5</td>
<td>22.6</td>
<td>15.2</td>
<td></td>
</tr>
<tr>
<td>Barley</td>
<td>1</td>
<td>4.1</td>
<td>1.6</td>
<td></td>
</tr>
<tr>
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<td>2</td>
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<td></td>
<td>5</td>
<td>9.5</td>
<td>7.0</td>
<td></td>
</tr>
</tbody>
</table>
As was indicated earlier, the boundary condition selected was that N flux into the roots is constant until the concentration at the root surface becomes essentially zero. But if uptake decreases at a N concentration at the root surface which is greater than zero, then that concentration should be added to all concentrations presented in Table 2.

Figures 11 through 16 show N concentration at the root surface as a function of time for different ages of lettuce, Swiss chard and barley, respectively. The concentration at time zero represents the initial soil solution concentration, C_o. Depending on the uptake rate relative to the rate of N supply by mass flow, N accumulation at the root surface during the initial few hours of uptake may take place. In such a case N is moving away from the root by diffusion because of the positive concentration gradient at the root surface. This is well illustrated in Fig. 11 through 16 especially when the initial soil solution concentration is relatively high.

Since N concentration at the root surface is a decreasing function of time, data presented in Fig. 11 through 16 suggest that higher initial soil solution concentrations will be needed if N application interval is greater than 7 days. Likewise, lower critical concentrations will be needed for shorter application intervals. This can be easily verified by plotting predicted critical N concentrations as a function of application interval. Equation (4) was used to investigate this relationship and results are presented in Fig. 17. Plant parameters used in calculations were those attained by barley at its first
Fig. 16. N concentration at the root surface as a function of time and $q = .35$ for barley.
Fig. 17. Predicted N concentrations as a function of N application interval.
CONCLUSIONS

1. Results of the model can be used to obtain basic information on minimum N concentrations to be applied with the irrigation water to adequately meet crop needs without excess for potential environmental degradation.

2. When N application interval is a day or more, which is usually the case, N concentration at the root surface decreases linearly with time and the infinite series part in equation (4) can be neglected.

3. Predicted N concentrations were directly proportional to N flux, N application interval and inversely proportional to the diffusion coefficient of NO₃ in the soil and volumetric water content.

4. N concentration at the root surface was more sensitive to half distance between adjacent roots than to any other soil or plant parameter. This indicates the need for higher N initial soil solution concentrations at higher root densities.

5. Higher values of N flux into the roots at initial growth stages indicate the need for higher soil solution concentrations at this time rather than during latter crop development stages.
LITERATURE CITED


APPENDIX

The computer program used to evaluate equation (4) consisted of two main parts. These were stored in two different files described next as files (12) and (13). File (12) calculates the values of \( a_n \), that satisfy equation (4) of the theory section and stores them in a data file.

Asymptotic expansions were used to evaluate Bessel functions. The subroutines ASS1 (Line 62) and ASS2 (Line 67) are polynomial expansions given by Abramowitz and Stegun (1970) to evaluate \( J_1(x) \) and \( Y_1(x) \), respectively, for \( x \geq 3 \). When \( x \geq 3 \) these functions are evaluated by Lines (46) through (51) which are sine-cosine expansions given by McLachlan (1955). By trial and error a number of 50 terms was found to be enough to approximate the infinite series summation in equation (4).

The second part of the program stored in file (13) recalls calculated \( a_n \) values and evaluates the complete solution. A choice of printout or a plot for \( N \) concentration of the root surface is available. Results indicated that the series summation is important for evaluating initial \( N \) buildup or depletion around the root. However, when \( t \geq 1 \) day, \( N \) concentration at the root surface decreases linearly with time and the infinite series part of equation (4) can be neglected.