Nutrient Uptake by Competing Roots in Soil

by

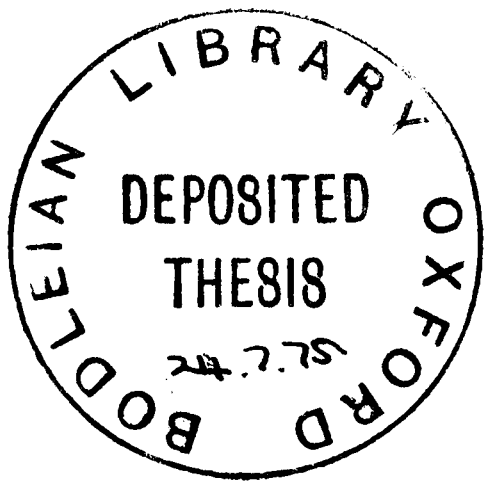
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Abstract

It is postulated that definitions of the availability of nutrients in soil, for plant uptake, will not be satisfactory, unless there is consideration of the plant's role as the absorber.

The amount of nutrients absorbed by plants from soil can be related to i) the initial concentration in the soil solution, ii) the capacity of the soil to maintain this concentration (the buffer power), iii) the ease of movement of the nutrient to an absorbing root, and iv) the plant demand. These ideas are the foundation of models which successfully describe the nutrient uptake by single roots, growing in an infinite quantity of soil.

The aim of the present work was to extend the approach used to explain uptake by single roots, to complete root systems.

The requirements for the work are:

i) a theoretical description of nutrient flow to an absorbing, multiple root system

ii) experiments for examining the proposed hypotheses.

When a root absorbs a nutrient, there is a depletion in the nutrient concentration at the root surface. In a system of many roots, the zones of nutrient depletion around each root overlap. This reduces the effective initial concentration in the soil solution. So, in a multiple root system, the soil around each root is limited. The extent of overlap depends on the diffusion coefficient of the nutrient, the plant demand, and the interroot distance. The consequence is a lowering of the concentration at each root surface, below that of a similar root absorbing alone.

An electrical analogue (Sanders et al. 1971) of diffusion of solutes to groups of absorbing roots was used to simulate nutrient uptake by plants

from soil. The analogue was particularly useful for investigating the general consequences of different plant and soil conditions. To interpret specific plant uptake data, a more flexible computer model of diffusion and mass flow to a root system of variable density, with any specified uptake properties, was developed. For workers interested in an accuracy of ± 20%, an equation for calculating uptake, by systems similar to those which the computer model treats, is presented, which can be solved on a desk calculator.

To test the model, experimental data on nutrient uptake, root dimensions and distribution, and soil conditions, during the growth of whole plants in soil was obtained.

The computer model predicted the measured plant uptake well, when values of the plant demand coefficient (which relates uptake rate to the external solution concentration) given in the literature, from solution culture work under similar conditions, were used. It is concluded that the theory is an adequate representation of the simple plant-soil system used in the experiments.

The expression, relating plant demand to concentration in the soil solution, was simulated on the electrical analogue. The effects of pattern, density, radius and demand coefficient of roots, on the course of uptake of solutes, of varying degrees of mobility, were investigated. Quantitative interrelations between soil and plant characteristics were established, which are discussed in the light of earlier concepts of mobility and availability of nutrients in soil.

The uptake of a solute by any root system is roughly determined by the plant demand coefficient and the product of the solute diffusion coefficient, D, the absorption time, t, and the root density, L. The product DtL, for potassium, may often be in the range where root pattern

affects uptake. This can be estimated graphically.

Theory suggests that the uptake rate of N and K in the plant experiments was reduced by interroot competition. In both experiments, if supply was by physical processes only, the plants were absorbing K from the soil near to a maximum rate, which was set by transport through the soil. In these circumstances, the rate of uptake into a plant is limited by the length of root. Movement through the soil was easily able to supply the plant's requirement of N, until the total quantity was exhausted. It is deduced that this will usually be the case in British arable soils.

A major problem, in the experimental determination of plant uptake from soil, results from the inaccessibility of the roots. A technique was devised for estimating the length and pattern of living roots of individual plants, without excessive labour. Radioactive roots are detected by autoradiography as they intersect planes of soil, and the root length per unit volume and rooting pattern follow easily. If two plants are labelled with different isotopes, their root systems can be distinguished. Any spatial interactions between the root systems are detected by the method, and the causes can be inferred. If the roots are extracted from the soil, their length can be automatically measured with an Image Analysing Computer.

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List of Symbols

D = diffusion coefficient of solute, cm^2/sec

D_l = diffusion coefficient of solute in free solution, cm^2/sec

F = flux of solute ions, $mol/cm^2/sec$

v = water flux at root surface, $ml/cm^2/sec$

C = total concentration of diffusible solute, mol/cm^3 of soil

C_i = initial concentration of diffusible nutrient, moles/ml

C_a = concentration of diffusible nutrient at root surface, moles/ml

C_l = concentration of solute in solution, mol/ml of solution

C_{l_i} = initial solution concentration of solute, mol/ml of solution

C_{l_a} = solution concentration at root surface, mol/ml of solution

C_{l_r} = solution concentration at distance r cm, mol/ml of solution

$\overline{C_l}$ = average concentration in solution, mol/ml of solution

a = root radius, cm

r = radial distance from root, cm

r_{av} = value of r where solution concentration = average solution concentration, cm

b = buffer power of soil = dC/dC_l

$\overline{b}_t$ = time averaged buffer power

t = time, sec

L = root density, cm/cm^3

$\overline{L}_t$ = time averaged root density, cm/cm^3

M_t/M_∞ = fractional uptake to time t

v_l = volumetric moisture content of soil

$\overline{v_{l_t}}$ = time averaged v_l

f_l = impedance factor

$\overline{f_{l_t}}$ = time averaged f_l

A = constant, $mole/cm^2/sec$

B = constant, $mole/cm^3$

h = distance parameter on analogue

ρ = N = density of root intercepts on a plane, cm^{-2}

V/M = variance/mean ratio

$\bar{y}$ = mean nearest neighbour distance, cm

I = inflow, moles/cm/sec

U = nutrient uptake by a plant, moles

X = nutrient per cent in plant tissue

γ = instantaneous flux parameter

G = average flux parameter

W = plant weight, g.

RGR = relative growth rate = $\frac{1}{W}\frac{dW}{dt}$

M = water inflow, ml/cm/sec

Q/I = Quantity/Intensity relation

$\overline{\alpha a}$ = root demand coefficient cm^2/sec

α = root absorbing power, cm/sec

$\frac{\alpha a}{Db}$ = relative sink strength

a_{x^+} = activity of x^+

Whenever the'$F = \alpha C_{la}$ condition' is discussed, α is assumed constant unless specified otherwise.

Any local useage, or departures from this scheme are specified in the text.

Chapter 1

Introduction

1.1. For many years, scientists have been interested in characterising the nutrient supplying power of a soil. In the early part of this century, it was felt that the total quantity of nutrient available to plants was the most appropriate guide to a soils ability to support crops. This idea is formulated in Liebig's law of the minimum, which states that the nutrient present in the least amount relative to the requirement, is the limiting nutrient. The first attempts to measure the fertility of a soil by chemical methods were, therefore, based on the idea that the chemical method should simulate plant feeding and remove amounts similar to those taken by crops. Dyer's (1894) citric acid method for measuring the available nutrients is based on this principle.

In the fifties, Schofield (1955) and Woodruff (1955) departed from this classical approach, and expressed the view that it was not the amount of nutrient that controls the uptake, but the work required to withdraw the nutrient from the labile pool, and accumulate it in the plant. Nutrients are generally absorbed from the solution in the soil (Lagerwerff 1960), and a suitable measure of the work, for K for example, is the activity ratio of the cations in solution, or the intensity (Beckett 1964), which in most British agricultural soils is $a_{K^{+}} / \sqrt{a_{Ca^{++}} + a_{Mg^{++}}}$.

Nye (1968) has calculated that the energy requirement is unlikely to be important - plants have no lack of energy for accumulating salts. However, an important advance followed from Schofield's work viz. that the concentration in the soil solution measures the 'immediately' available nutrient, and for this concept to be of any value, the ability

of a soil to maintain a given concentration against depletion must be considered. This may be expressed in the Quantity/Intensity or Q/I curve. The slope of the Q/I gives the decrease in solution concentration which follows as a result of a decrease in total concentration of labile nutrient, and is called the buffer power of the soil. The buffer power and the equilibrium solution concentration are a measure of the fertility of a soil in relation to growth over a season.

Plant roots are discrete entities and may not deplete the soil uniformly. To measure the nutrient supplying power at any time, therefore, it is necessary to include a space parameter in the availability concept. This was expressed by Tepe and Leidenfrost (1958), when they wrote "To obtain a realistic estimate of availability of plant nutrients in soil, due consideration should be given to the degree of mobility of ions and their proximity to an absorbing surface". Barber (1962) went one step further than this when he claimed that "plant nutrient availability in a soil is principally governed by the rate at which nutrients move through the soil to the root surface". This appears to be a contradiction of earlier ideas. Bray (1954) was more perceptive when he assessed the influence of nutrient mobility on the total quantity needed in a soil for optimum yield. He formulated the following concept,

"As the mobility of a nutrient in the soil decreases, the amount of that nutrient needed in the soil to produce a maximum yield (the soil nutrient requirement) increases from a variable "net" value, determined principally by the magnitude of the yield and the optimum percentage composition of the crop, to an amount whose value tends to be a constant. The magnitude of this constant is independent of the magnitude of the yield of the crop, provided the kind of plant, planting pattern and rate, and fertility pattern remain constant, and provided relatively similar soil and seasonal conditions prevail."

This may be summarised as follows: if a nutrient in soil is mobile, any root system is able to absorb all of it, provided there are no leaching or microbial losses, and the total amount present determines uptake; if a nutrient is immobile, the amount removed by a crop is a function of the length of root produced, the total present usually being far in excess of that removed in any season.

This was the first attempt to bring together ideas of nutrient mobility, nutrient quantity and plant "foraging" power. The object of this thesis is to place these notions in a quantitative framework. The macro-nutrients N, P and K only are treated in deta l, but the principles which are established may well apply to other solutes in soil.

1.2. Nutrient transport processes

It has been established that the physical processes of nutrient movement in soil to roots are diffusion in response to a concentration gradient, and mass flow of water moving in the transpiration stream. Olsen and Kemper (1968) have presented a very thorough review of the subject. An understanding of the processes has shown the extent to which concepts of nutrient availability based on quantity and intensity were incomplete.

First consider transport by diffusion alone. Following Nye (1968), the quantity of nutrient diffusing to a planar sink in contact with an infinite source of soil is given approximately by

$$Q_t = \frac{2}{\sqrt{\pi}} \Delta C_l \sqrt{\frac{\Delta C}{\Delta C_l}} \sqrt{v_l f_l} \sqrt{D_l t} \quad \ldots\ldots 1.i$$

where Q_t = quantity moving into the sink

ΔC_l = difference in concentration between the bulk soil solution and the sink solution

ΔC = corresponding difference in total concentration of diffusible ion

$\Delta C/\Delta C_l$ = buffer power of the soil

v_l = volume fraction of soil moisture

f_l = impedance factor

D_l = diffusion coefficient of ion in free solution

t = time

An equation of a similar kind may be deduced for cylindrical flow of nutrient, but the planar case is simpler. It illustrates how the flow of nutrients to a root depends directly on the soil solution concentration, and how this is maintained against depletion - ideas which follow from Schofield's work. Notice that $\Delta C / \Delta C_l$ enters as a square root term. Equation 1.1 was derived assuming an infinite source of soil where the initial solution concentration remains constant. Clearly, if the source is limited, as might occur if there are multiple sinks, or roots, the buffer power will be more important - it governs the rate at which the initial solution concentration decreases. Equation 1.1 also involves the physical properties of the soil. These are expressed in v_l and f_l. The moisture term arises because the effective cross section for diffusion is reduced when the moisture is reduced - nearly all the diffusive flux occurs along the solution pathway. The impedance factor depends primarily on moisture content, but also on soil texture, and arises because of the increased path length caused by the presence of soil particles.

The second nutrient transport process is mass flow of soil solution in the transpiration stream. Marriott and Nye (1968) have shown that, if there is a depletion at the root surface, the mass flow contribution to the flux is approximately equal to the quantity of nutrient that the water flow brings into the zone of nutrient disturbance i.e. vC_{ll} where v = water flux mls cm^{-2} sec^{-1}. This again emphasises the importance of solution concentration of nutrient. The relation between mass flow and total flux is modified in a finite system, where the water uptake causes

drying, as there is a decrease in diffusive flux.

As ideas of quantity, intensity and mobility are linked together, it becomes clear that the nutrient concentration at any point in soil is related to the proximity of an absorbing root surface, and is not, therefore, a characteristic of the soil.

The state of the nutrient concentration distance relation depends on the balance between soil supplying power and plant demand. To express this quantitatively, a boundary condition is required at the root surface which gives the rate of loss of solute from the soil. It has been demonstrated that plant roots take up nutrients from the soil solution (Lagerwerff 1960). Epstein and Hagen (1952) have shown that roots take up nutrients from solution culture according to a Michaelis-Menten relation,

i.e. $$\frac{dU}{dt} = \frac{\alpha C_1}{1 + \frac{\alpha C_1}{\left(\frac{dU}{dt}\right)_{max}}} \qquad \ldots\ldots\ldots 1.ii$$

where $\frac{dU}{dt}$ = uptake rate

$\left(\frac{dU}{dt}\right)_{max}$ = maximum rate of uptake attainable

C_1 = solution concentration of nutrient bathing the roots

α = plant parameter called the root absorbing power.

This reduces to $\frac{dU}{dt} = \alpha C_1$ 1.iii

when $\frac{dU}{dt} << \left(\frac{dU}{dt}\right)_{max}$

It seems reasonable to apply Epstein and Hagens (1952) results to the soil solution. Equation 1.iii is the more attractive since it involves 1 constant only, but must break down when C_1 is high. Kautsky et al. (1968) have compared equations 1.ii and 1.iii as boundary conditions for the diffusion equation, and conclude that 1.iii is a satisfactory

approximation for the major nutrients in soil, especially under conditions of nutrient deficiency. Some workers (van den Honert and Hooymans 1955, Olsen 1950, and Lyoklama 1963), however, have reported a constant flux of NO_3^- into plant roots at concentrations above 10^{-4} M, which is below normal agricultural concentrations. Various authors have used a constant flux boundary condition for solving diffusion equations (e.g. Olsen and Watanabe 1966).

A number of workers have attempted to define nutrient supply in soil in terms of the transport processes. A brief historical account of their mathematical development follows which will show more specifically how the ideas apply to plant roots in soil, and lead up to the present state of knowledge.

1.3 Application of transport equations to isolated roots

In 1961, Bouldin applied diffusion equations developed in work on heat transfer, to the supply of nutrients existing solely in the soil solution, to roots, with and without root hairs, which were taking up nutrients at a rate proportional to the concentration in solution at the root surface. He over emphasised the importance of root hairs by neglecting the fact that soil in the root hair zone is rapidly depleted to a fairly uniform level. Passioura (1963) recognised this latter point, and also suggested that the diffusive and mass flow fluxes may be considered as additive, thus combining both transport processes in a single expression. His calculation of diffusive flux is based on contradictory assumptions regarding the boundary condition at the root surface i.e. he first assumes that C_{1a} is constant and measures the flux due to $(C_{1i}-C_{1a})$, and then assumes that $F = {}^{w}_{A} C_{1a}$, where C_{1a} is the solution concentration at a, the root radius, and F is the flux into the roots, (see Passioura 1965), Nye and Spiers 1964), but Drew (1966) has shown that after reasonable times very little error follows as a result. Marriott and Nye (1968) tested the approximation that the fluxes were additive, and concluded that when $v < \alpha$

i.e. there is a depletion at the root surface, Passioura's (1963) suggestion gives results within 10% of the exact ones, but where $v > \alpha$ the Passioura model underestimates the total flux, especially when D is low.

Nye (1966a) extended Bouldin's (1961) work to include diffusive supply of adsorbed ions, introducing ideas of quantity and intensity into the nutrient mobility story.

Drew et al. (1969) and Drew and Nye (1969), using 1 cm leek or ryegrass roots tested Nye's (1966a) theory experimentally. They found good agreement between theoretical calculations and observed uptake of P and K when supply by mass flow was minimised. Clarke and Barley (1968) using a similar technique, reported that diffusion theory could account for the uptake of NO_3 by a .5 cm length of an intact wheat root.

1.4 Extension of the transport equations for single roots to whole root systems

The theory outlined so far is restricted to the uptake by a single root exploiting an infinite volume of soil. However, these single root studies have shown that the transport mechanisms can be used to define the conditions which apply during plant uptake in simple circumstances. They have also afforded some evidence that the plant properties are sufficiently predictable for the analysis to be extended to whole root systems.

The Passioura (1963) model gives a good approximation of the nutrient flux to a single root, and it formed the basis of the first attempt to treat complete root systems (Brewster and Tinker 1970). The equation is

$$F = \frac{(C_i - C_a)D\gamma}{a} + vC_{li} = \alpha C_{la} \qquad \ldots\ldots\ldots \quad 1.iv$$

where F = flux to roots moles $/cm^2/sec$

C_{li} = initial solution concentration moles/ml

C_{la} = solution concentration at root surface moles/ml

C_i = initial concentration of diffusible nutrient, moles/ml

C_a = concentration of diffusible nutrient at root surface moles/ml

D = diffusion coefficient in soil cm^2/sec

a = root radius cm

γ = function of Dt/a^2, where t = time

v = water flux mls/cm^2/sec

α = root absorbing power cm/sec

Equation 1.iv gives the radial flux of nutrients to a single isolated root which has lowered the concentration of diffusible nutrient from C_i to C_a at the root surface. This flux decreases with time as γ does, which is rather slowly (see fig. 1.1). The average flux up to any time is obtained by integrating γ to give G, the average flux parameter (Nye 1966a). The time dependency of γ and G are shown in fig. 1.1. Equation 1.iv is more useful when expressed as Inflow per cm of root per sec, when it is less sensitive to an exact value of root radius.

Thus $I = 2\pi(C_i - C_a)D\gamma + MC_{li} = 2\pi(\alpha a)C_{la}$

where $M = 2\pi av$.

If diffusion is restricted to the solution phase, where the diffusion coefficient is linearly related to the buffer power,

$$D = D_1 v_1 f_1 \frac{dC_1}{dC} = D_1 v_1 f_1 \frac{(C_{li} - C_{la})}{(C_i - C_a)}, \text{ and}$$

$$I = 2\pi D_1 v_1 f_1 (C_{li} - C_{la}) D\gamma + MC_{li} = 2\pi \alpha a C_{la} \quad \ldots\ldots\ldots 1.v$$

(Brewster and Tinker 1970). The mean Inflow during any period is

$$\bar{I} = 2\pi D_1 v_1 f_1 (C_{li} - C_{la}) G + MC_{li} = 2\pi \overline{\alpha a} C_{la} \quad \ldots\ldots\ldots 1.vi$$

This equation may be used to calculate the mean root surface concentration of a whole root system, if the root length with time relation is known. The root system is divided into segments of a particular age, and a value of G appropriate to each, is multiplied by the root length in each segment, to give a weighted mean $\bar{G}$. Details of the exact computation of G for each segment are given by Brewster (1971), but a value of γ taken at the mean age is often satisfactory. Brewster and Tinker used equation 1.vi to

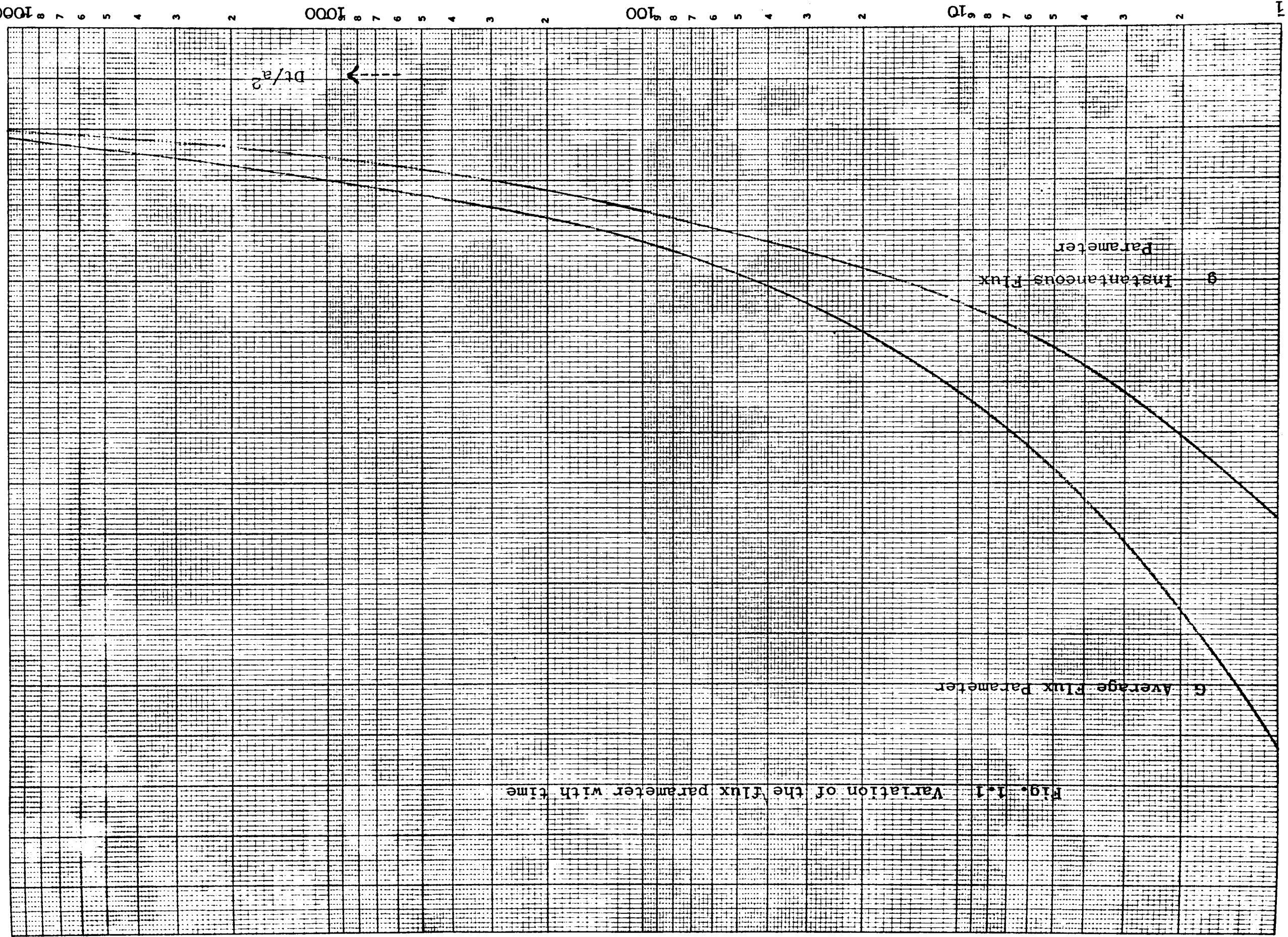


Fig. 1.1 Variation of the flux parameter with time

calculate values of the mean $\overline{\alpha}_a$ of a hole root system.

This mean $\overline{\alpha}_a$ is the α_a which would apply if the inflow and root radius were uniform over the whole root system. It is the arithmetic mean of the different α_a in various parts of the root system, only if the external root surface solution concentration is constant throughout the root system, as may obtain when the local depletion around roots is small. It is reasonable to apply the concept of $\overline{\alpha}_a$ to all soil data, as each root will have roughly the same history of C_{la}. In such studies, we investigate the behaviour of an average root, although no actual root may be like it. Thus, $\overline{\alpha}_a$ has a hypothetical value which can be used in models of the uptake process, to allow intellectual understanding of the role of the various factors involved, and estimations of total plant uptake under different conditions to be made.

Such estimations will be possible only if $\overline{\alpha}_a$ is constant, or varies in a regular or predictable way for a given root in defined conditions. As yet, there is no conclusive evidence on the variability of α_a of different roots, or on the effect of age, external solution concentration, transpiration rate, moisture stress or nutrient stress on the uptake rate of different root regions. There seems little reason to doubt that all regions of young roots can take up nutrients (e.g. Grasmanis and Barley (1969), using NO_3 and NH_4, Rovira and Bowen 1966, using P, and Clarkson and Sanderson 1970, who used K). Brouwer (1965 p.256) has given a lucid review of current theories on the influence of v on α, but no definite relation between the two emerges.

It is important to note here, that when the root surface concentration is reduced to below 0.1 of the average concentration, the value of $\overline{\alpha}_a$ has little effect on uptake rate; in such circumstances, transport through the soil is the rate determining step in the uptake process (Nye 1966a).

Since both K and P may have deep depletion zones when the bulk solution concentration is low (see 1.5.c), an exact knowledge of αa or $\bar{\alpha} a$ for these two elements may not be required.

$\bar{\alpha} a$ may be calculated from the plant nutrient uptake, U, and root length, L, against time curves, and equation 1.vi.

Instantaneous inflow = $\frac{1}{L} \frac{dU}{dt}$ (analogous to instantaneous assimilation rate of plant physiologists), and mean inflow over a period can be found if the U v t and L v t relations are known, or of there is an integrable relation between U and L. If U and L are linearly related,

$$\bar{I} = \frac{(U_2 - U_1)}{(t_2 - t_1)} \quad \frac{\ln L_2/L_1}{(L_2 - L_1)} \qquad \text{..... 1.vii}$$

Note that if U is related to L^2, instead of L, and if $L_2 \leqslant 2L_1$, the mathematical error in using 1.vii is < 4% (Coombe 1960). The formula in this case should be

$$\bar{I} = \frac{2(U_2 - U_1)}{(L_2 + L_1)(t_2 - t_1)}$$

Radford (1967) considers other relations between U and L.

This calculated value of Inflow gives the value of C_{la} from equation 1.vi and $\bar{\alpha} a$ follows.

The great value of this approach to nutrient uptake from soil is its simplicity. The data required for the calculation of inflow and $\bar{\alpha} a$ are 1) the relation between nutrient uptake and root length - this may often be assumed linear without much error, 2) the root length v time relation - required in the calculation of $\bar{C}$. Since C is rather insensitive to time, an exact relation is not essential, 3) the uptake and root length at 2 times, 4) volume fraction of moisture in the soil, from which the impedance factor may be inferred. An analysis of the factors limiting plant growth can be made with very little effort.

The above arguments are no longer valid when roots cannot be considered to exist in isolation. This will occur when the zones of nutrient disturbance around each root overlap sufficiently to affect the nutrient uptake rate, and is the major topic of this thesis.

1.5 The mechanism of interroot competition

It is useful to distinguish three possible competition mechanisms. The first includes any effect whereby the spatial arrangement, or the morphology of the root system is altered. This certainly arises with those species which exude chemicals which can inhibit the development of roots near them (Bonner 1950). It may also result from nutrient gradients in the soil caused by absorption, since roots will branch most in zones of highest nutrient concentration (Duncan and Ohlrogge 1958). Secondly, it is possible that such toxic exudates will alter the physiological properties of a root so that it absorbs less rapidly. Thirdly, a root usually absorbs at a rate which is related to the concentration of nutrient around it; and if this concentration is decreased due to the absorption by a competing root, then the uptake rate of the first root must decrease. In terms of the theory of the transport of ions to roots, this is equivalent to saying that the depleted zones around the two roots have overlapped, and it is this type of competition which is discussed here. Depleted zones cannot be defined exactly, and in theory there is competition between any two roots in the same soil volume at all times. We are concerned with the degree of this competition, and the question of when, and under which conditions it becomes important.

In this section, we see how the magnitude of the competitive effect is a function of the depth and radial spread of the zones of disturbance around roots, and the interroot distance.

1.5 a) Nutrient supply by diffusion only

When a plant root in soil absorbs nutrients, the concentration in the

solution around the root decreases below that in the bulk, and a zone of depletion spreads out as a result of diffusion. This is shown diagrematically in fig. 1.2a. The flux to the root depends primarily on the diffusion coefficient of the ion and the difference in root surface and initial nutrient concentration, ΔC_l. If we assume uptake rate is proportional to the root surface concentration C_{la}, it declines rapidly at first, but afterwards rather slowly as C_{la} approaches a fairly constant value (Nye 1966a). If there are two roots in close proximity, the zones of depletion will overlap, as shown on fig. 1.2b. This reduces the effective C_{li} and ΔC_l, and so the flux to the roots, causing a reduction in C_{la} and a consequent reduction in uptake rate into the plant. The importance of this effect will depend on the degree of zone overlap, which is a function of the spread and depth of the diffusion zones, and the interroot distance.

The spread of a diffusion zone is given approximately by $\sqrt{Dt}$ cm, which is the radial distance corresponding to .5 times ΔC. The maximum intensity of depletion, or depth, of a zone may be derived from the Passioura (1963) model:

Since $$F = \frac{D_l \theta_l f_l (C_{li} - C_{la})\gamma}{a} = \alpha C_{la},$$

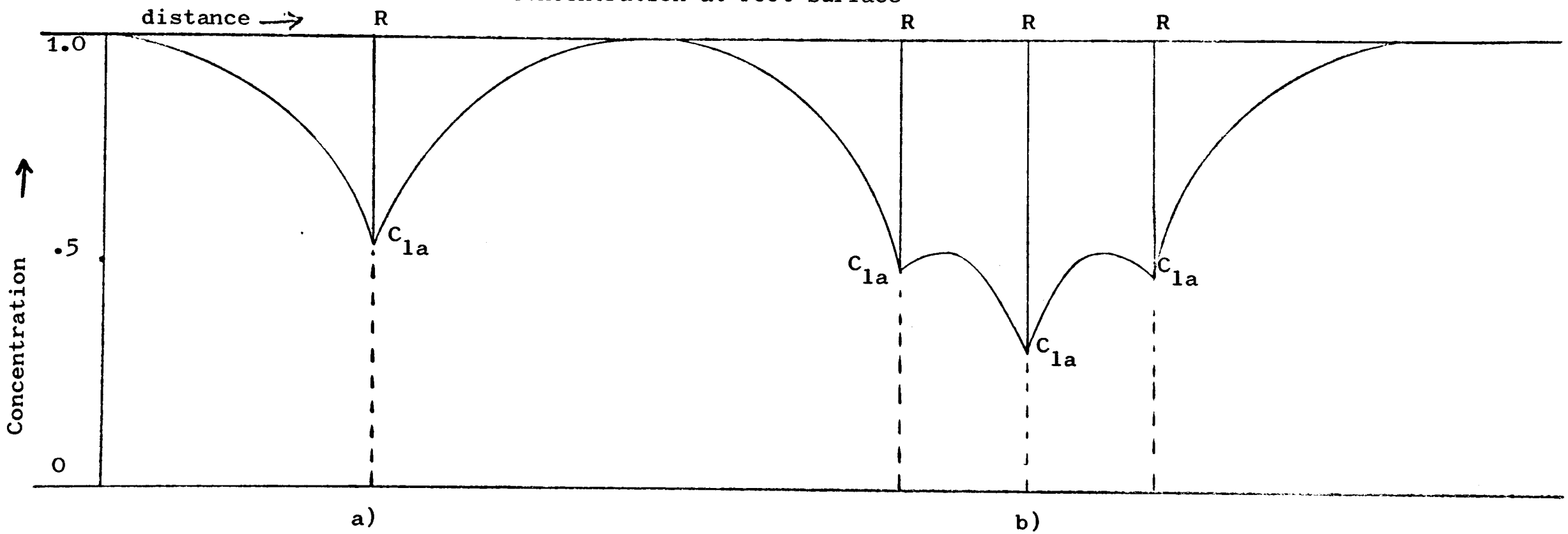
$$\frac{C_{la}}{C_{li}} \simeq \frac{1}{1 + \frac{\alpha a}{Db\gamma}} .$$

γ decreases slowly when $Dt/a^2 > 1$ (see fig. 1.1), and C_{la}/C_{li} is a function of $\alpha a/Db$. This term has been called the relative sink strength.

1.5.b) Supply by diffusion and mass flow

In this paragraph, we assume, for simplicity, that nutrient and water uptake occur simultaneously, in the same parts of the root system. Nye and Marriott (1969) have considered the theoretical distribution of

Fig 1.2 Concentration distance profile to show effect of overlap of diffusion zones on concentration at root surface



R denotes a root

solutes around a root when mass flow and diffusion are operating. No simple guide to the depth and spread of the zones emerges. If $v < \alpha$ the major effect is to compress the depletion zone. In this case C_{1a}/C_{1i} is given approximately by

$$\frac{C_{1a}}{C_{1i}} \simeq \frac{\frac{av}{Db\gamma} + 1}{\frac{a\alpha}{Db\gamma} + 1}$$

This equation becomes increasingly inaccurate as v/α increases (Marriott and Nye 1966).

Some maximum values of $\hat{2\pi}av$ have been calculated by Newman (1969), from transpiration rates, $\hat{E}$, (assuming complete plant cover), and lengths of root per unit area of ground, L_A. If $\hat{E}$ is 1 cm/day, av will reach 0.1 $cm^3/cm/day$, or 1.16×10^{-6} $cm^3/cm/sec$, only when $L_A < 10$ cm/cm^2 (which is a low value). Typical values of $\sqrt{\alpha}$ are given in 1.5.c, from which we may conclude that, in a moist soil, i) if v is of sufficient magnitude to affect C_{1a}/C_{1i}, the local depletion, and, hence, competitive effect, if v were zero, would have been small, and ii) the effect of mass flow on C_{1a} will be small when the magnitude of the local competition is large. This conclusion, together with the information that water uptake is usually low in the early part of the growing season when nutrient requirement is high, enables us to profitably continue on the basis that $a\alpha/Db$ and $\sqrt{Dt}$ are the major factors governing the shape of a depletion zone in competitive situations.

The remaining factor is interroot distance. Clearly this will depend on the pattern and density of the roots.

1.5. c) Values of $\sqrt{Dt}$ and $a\alpha/Db$ for the macronutrients

a) $\sqrt{Dt}$. The diffusion coefficient of an ion in soil may be expressed by

$$D \simeq \theta_1 v_1 f_1 \frac{dC_1}{dC} + F_s$$

where dC/dC_1 is the buffer power and F_s is the contribution to diffusive flux along the exchange surfaces (Nye 1966b). F_s is usually negligible

in soils (Rowell et al. 1967, Tinker 1968). For N, P and K, D_1 is 1.92, .89 and 1.98 x 10^{-5} cm^2/sec respectively, and dC/dC_1 is approximately equal to v_1, 100 and 10 respectively. Thus in a moist soil where $v_1=f_1=.25$, D for N, P and K is roughly $5x10^{-6}$, $5x10^{-9}$ and 10^{-7} respectively. It follows that the value of $\sqrt{Dt}$ when $t = 10^6$ secs is 2.2 cm, .07 cm and .32 cm for N, P and K. An interroot distance of $2\sqrt{Dt}$ will result in a significant decrease in uptake rate due to overlapping depletion zones (see 2.7). The length per unit volume, of parallel, regularly dispersed plant roots having a mean interroot distance of $2\sqrt{Dt}$ corresponding to the values of $\sqrt{Dt}$ given above is .052. 51 and 2.44 cm/cm^3. Newman (1969) presents data showing that a root length per unit volume of 10 cm/cm^3 is fairly typical for crops and grasses in the early part of a season. Therefore, for both N and K, there is likely to be considerable overlap of depletion zones in the root systems of these species after a few days, but overlap of P diffusion zones remains unlikely, unless the root density is very high.

b) α/b

Db is approximately equal to $D_1v_1f_1$, (Rowell et al. 1967) and is roughly the same for N and K, both being twice as great as for P. Db varies from 10^{-6} cm^2/sec in moist soils to 10^{-8} cm^2/sec in dry soils.

Values of the mean $\overline{\alpha}$a, the root demand coefficient (Nye and Tinker 1969), may be derived from experiments in solution culture in which the uptake into whole plants has been measured over a period of days. The data in table 1.1a, b and c has been calculated from results presented in a recent review (Brewster and Tinker 1972), from values given by Nye and Tinker (1969) and from the literature itself in some cases.

Note that these measurements were made on healthy growing plants. $\overline{\alpha}$a may well be different when the plants are deficient or diseased. The factors affecting $\overline{\alpha}$a, and the likely short term fluctuations are

Table 1.1a

Values of the root demand coefficient, $\overline{\alpha_a}$, and Inflow for potassium, determined from solution culture experiments

Author	Species	Age at start days	Uptake Period	Root radius cm	Inflow mol/cm/sec $\times 10^{-13}$	Solution concentration molarity	$\overline{\alpha_a} \times 10^{-6}$ $cm^2\ sec^{-1}$
Williams (1961)	Barley	42	35d	.025	11.4	2.6×10^{-6}	70
Williams (1961)	Barley	42	35d	.025	13	2.6×10^{-6}	8.0
Williams (1961)	Barley	42	35d	.025	16	13×10^{-4}	.20
Brewster (1971)	Leek	49	24h	.03	16	4×10^{-4}	.64
Asher and Ozanne (1967)	Vetch	10	31d	.02	3.1	2.8×10^{-6}	3.8
Asher and Ozanne (1967)	Capeweed	10	31d	.02	13	9.5×10^{-6}	2.8
Bange (1959)	Maize	20	1h	.02	13	2×10^{-4}	1.2
Brewster (1971)	Leek	14	53d	.03	11	4×10^{-4}	.43
Hackett (1969)	Barley	7	7d	.025	11	4×10^{-4}	.43
Hackett (1969)	Barley	7	14d	.015	1.8	4×10^{-4}	.06
Lasturka and Minar (1970)	Pea	0	42d	.02	4.3	3×10^{-4}	.23
Minar and Lasturka (1969)	Maize	0	32d	.02	11	3×10^{-3}	.06
Freeman (1970)	Red beet	22	1h	.02	14	10^{-4}	2.2
Johansen et al. (1968)	Barley	5	20d	.02	7.3	10^{-4}	1.2

Table 1.15

Values of the root demand coefficient, $\overline{\alpha}a$, and Inflow for nitrate, determined from solution culture experiments

Author	Species	Age at start days	Uptake period	Root radius cm	Inflow mol/cm/sec x_{10-13}	Solution concentration molarity	$\overline{\alpha}a$ $x10^{-7}$ cm^2 sec^{-1}
Brouwer (1954)	Broad bean	42	8-24h	.05	21	10^{-2}	.33
Graemanis and Barley (1969)	Pea	8	30 min	.04	5.5	$1.5x10^{-3}$	.58
Brewster (1971)	Leek	14	53d	.03	13	$22x10^{-3}$	.94
Hackett (1969)	Barley	7	7d	.025	12	$21x10^{-4}$	.91
Lastuvka and Minar (1970)	Pea	0	42d	.02	13.5	$8.0x10^{-4}$	2.7
Minar and Lastuvka (1969)	Maize	0	32d	.02	31	$3.3x10^{-3}$	1.5
Kuhlman-Falk (1961)	Wheat	7	2-24h	.02	28	$2x10^{-3}$	2.2
Lastuvka and Minar (1970)	Pea	0	42	.02	20	$8x10^{-3}$	.40

Table 1.1c

Values of the root demand coefficient, $\overline{\alpha}_a$, and inflow for phosphate, determined from solution culture experiments

Author	Species	Age at start days	Uptake period	Root radius cm	Inflow mol/cm/s $\times 10^{-13}$	Solution concentration molarity	$\overline{\alpha}_a \times 10^{-6}$ $cm^2\ sec^{-1}$
Bowen (1969)	Pinus radiata	21	20 min	.05	7	5×10^{-6}	2.2
Rovira and Bowen (1966)	Wheat	4	15 min	.02	3	5×10^{-6}	9.5
Brewster (1971)	Leek	49	24h	.03	.26	10^{-6}	.41
Scott-Russell and Sanderson (1967)	Barley	21	24h	.02	.15	3×10^{-6}	.80
Brewster (1971)	Leek	14	53d	.03	1.0	10^{-5}	1.6
Hackett (1969)	Barley	7	7d	.025	1.7	10^{-4}	.27
Hackett (1969)	Barley	7	14d	.015	.8	10^{-4}	.13
Lastuvka and Minar (1970)	Pea	0	42d	.02	.93	1.4×10^{-4}	.11
Lonergan and Asher (1967)	Mean of 8 pasture sp.	10	18d	.02	1.4	5×10^{-6}	4.4
Minar and Lastuvka (1969)	Maize	0	32d	.02	4.2	1.4×10^{-3}	.48
Robson et al. (1970)	Medicago Truncata	6	20d	.02	1.46	1.9×10^{-6}	12.2

discussed in the next section.

The general conclusions from these tables are:

i) $\overline{\alpha a}$ for NO_3 is very roughly 10^{-7} cm^2/sec, when the N concentration is $< 10^{-2}$ M.

ii) $\overline{\alpha a}$ for P is approximately 10^{-6} cm^2/sec, when the P concentration is $< 10^{-3}$ M.

iii) $\overline{\alpha a}$ for K is approximately 10^{-6} cm^2/sec, when the K concentration is $< 10^{-4}$ M.

The relative constancy of $\overline{\alpha a}$ for each nutrient under a wide set of conditions and for different crops should be noted.

Summarising this section: $\overline{\alpha a}/Db$ will be roughly .1, 1 and 1 for N, P and K respectively in a moist soil, with higher values in dry soils, unless $\overline{\alpha a}$ decreases due to moisture stress (as found by Dunham 1971). Inspection of Fig. 1a, section 2.6 shows that these values give rise to C_{1e}/C_{1i} of .7, .3 and .3 respectively, after reasonable times.

1.5.d Factors affecting $\overline{\alpha a}$

Since the concept of $\overline{\alpha a}$ is central to these discussions on root competition, its likely behaviour throughout a growing season is considered here.

Nye and Tinker (1969) have discussed the notion of $\overline{\alpha a}$ at length. They showed that it is related to the physiological state of the plant by

$$\overline{\alpha a} = \frac{1}{2\pi} \cdot \frac{w}{L} \cdot \frac{X}{C_{1a}} \left(\frac{1}{w} \frac{dw}{dt} + \frac{1}{x} \frac{dx}{dt} \right) \quad \ldots\ldots \text{1.viii}$$

where w = dry weight of plant g

L = total length of root system cm

X = mean concentration of nutrient in whole plant g/g

C_{1a} = concentration of ion in solution at the root surface g/cm^3

$\frac{1}{w} \frac{dw}{dt}$ = relative growth rate

$\frac{1}{X} \frac{dX}{dt}$ = relative concentration change rate

A consideration of each of these terms gives some guide to the variability of $\overline{\alpha}a$, but it is noted that change in any term is likely to cause a change in the others, as well as in $\overline{\alpha}a$.

In actively growing plants, $\frac{1}{W}\frac{dW}{dt}$ tends to be much greater than $\frac{1}{X}\frac{dX}{dt}$. This latter term is usually negative, but may not decrease by more than a factor of 2 during a whole growing season. If a nutrient deficiency limits growth $\frac{1}{X}\frac{dX}{dt}$ will change more rapidly, but the maximum change in X is unlikely to be greater than times L. Thus for healthy plants

$$\overline{\alpha}a \sim \frac{1}{2\pi} \cdot \frac{W}{L} \cdot \frac{r}{C_{la}} \cdot \frac{1}{W} \cdot \frac{dW}{dt}$$

If growth is logarithmic $\frac{1}{W}\frac{dW}{dt}$ is constant. If $\frac{W}{L}$ is constant, as found by Brouwer (1962) for a particular plant species in each phase of growth under any set of conditions, $\overline{\alpha}a$ will depend on X/C_{la}. After short times C_{la} is approximately constant (see section 2.6), and thus X/C_{la} is roughly constant. It follows from this that $\overline{\alpha}a$ is unlikely to vary suddenly, or by several orders of magnitude during a growing period.

In conditions of nutrient deficiency, the story is not so simple, as the parameters in equation 1.viii vary more. However, trends may be evident. Consider equation 1.viii in detail:

a) $\frac{W}{L}$. This term is the major adaptive variable in plants. Brouwer (1962) reported the shoot; root fresh weight ratio, which will reflect changes in W/L, decreased under conditions of nutrient or water stress. This is as expected, the plant tending to maintain the overall uptake rate.

b) X/C_{la}. A usual consequence of nutrient deficiency is a decline in X. C_{la} will also decline as the soil is depleted. No definite conclusions can be drawn regarding the behaviour of the ratio X/C_{la}. It may rise because C_{la} decreases more and more rapidly as it gets smaller.

c) $\frac{1}{W}\frac{dW}{dt}$. relative growth rate usually declines in conditions of nutrient deficiency. However it is always positive whilst the plant is still growing.

d) $\frac{1}{X}\frac{dX}{dt}$. If the nutrient percent in the tissue declines linearly with time, $\frac{1}{X}\frac{dX}{dt}$ will become increasingly negative. It seems clear that this term will not be positive.

We may make the tentative conclusion from this analysis that $\overline{\alpha a}$ will decrease with time when nutrient deficiency limits growth, but again the decrease should not be erratic. It must be stressed here that it is a hypothetical $\overline{\alpha a}$ over the whole root system that is being considered. αa in different parts of the root system may be varying widely.

1.3.c <u>The influence of pattern and density on the uptake of the major nutrients</u>

1) The depletion zones of nitrate are wide but not very deep. There will be a tendency towards complete overlap of the depletion zones in any pattern of roots, and uptake will depend more on root density than root pattern. This generalisation may require modification if there is a constant flux of NO_3 into roots above 10^{-4} M, as suggested by van den Honert and Hooymans (1955). The approximate ΔC_1 required to give the typical N inflow of 10^{-12} moles/cm/sec (Brewster and Tinker 1971) is 3×10^{-4} M in a moist soil. The depletion zones in the constant flux case, therefore, will be shallow when the bulk solution concentration is greater than 10^{-3} M.

2) Depletion zones of phosphate are narrow and deep. There is little likelihood of serious overlap of P depletion zones and uptake will be a function of root density, unless thorough ramification in the soil is prevented, for example by adverse soil structure (which may lead to roots proliferating in the soil cracks).

not relevant if constant flux
only dependent on C

3) Depletion zones of potassium are fairly wide and long. Serious overlap of the zones will be common, and the effect on nutrient uptake may be large. The K uptake potential of a root system will be sensitive to root pattern as well as density.

1.5.f The interroot distance

The interroot distance is a function of the length of root per unit volume, and the spatial orientation of these roots. For parallel roots in a regular hexagonal array, the interroot distance is constant at $1/\sqrt{\rho}$; for roots distributed randomly, the mean interroot distance = $.5/\sqrt{\rho}$ (Clark and Evans 1954). ρ is the number of intercepts between the roots and a plane, and equals $\frac{1}{2}L$, where L = length per unit volume, when the root orientation is random (see section 3.5.E) The effective interroot distance will be reduced by the presence of root hairs.

The value of L in soil under well established crops or pastures decreases with depth, the order of magnitude (cm^{-2}) ranging from 10 in top soils, through 1 at .5 m to .1 at 1 m depth. Deep rooted plants frequently sustain L values approaching 1 cm^{-2} to depths of 1m. Some typical values are given in table 1.2, and the quantitative relations between the members of a mature cereal root system are shown in fig. 1.3.

There is relatively little information available regarding the 3-dimensional spread of a root system. The main primary roots of dicotyledons tend to grow vertically downwards in response to gravity. The main seminal and nodal roots of grasses are also geotropic but the angle to the vertical, the liminal angle, varies widely among species, ranging from 10° to 30°. These roots often radiate around the base of the plant (Kutschera 1960), and the preferred direction of growth is maintained despite any deflection of the root tip due to soil heterogeneity (Wilson 1967). First-order laterals grow at an obtuse angle to the subtending main root; initially the liminal angle is usually high. The

Table 1.2

Values of L (root length per unit volume of soil) for Plants in the Field

Species	Depth (cm)	L_V (cm^{-2})
Herbs: Gramineae		
Poa pratensis	0–15	50
Cereals (oats, rye, wheat)	0–15	5–25
	25–50	4
	75–100	2
Herbs: Non-Gramineae		
Stylosanthes gracilis	0–10	30
	40–50	3
	90–100	1
Medicago sativa	0–10	20
Glycine max	0–15	4
Woody plants		
Tea *(Camellia sinensis)*	0–2.5	4
	45–47.5	1
	68.5–70.0	0.5
Pinus radiata	0–8	2
	25–45	0.8
	91–106	0.4

Barley (1970)

Fig 1.3

Quantitative relations between the members of a mature cereal root system

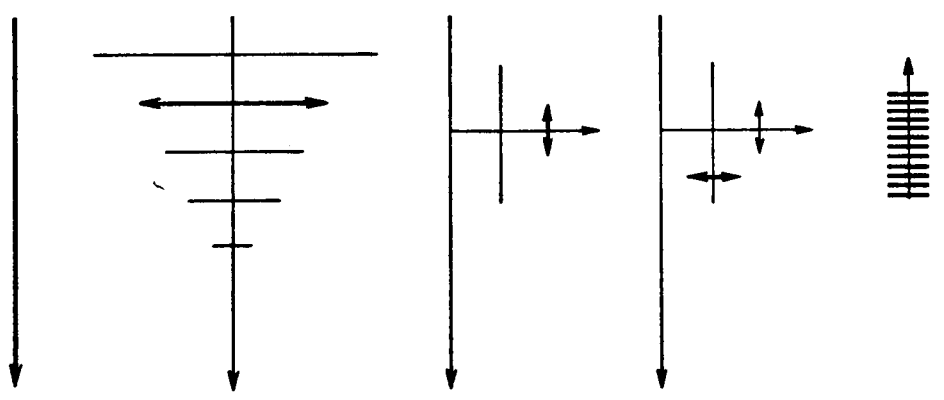


FIG. 1. The constituent parts of the plant root system. The geometical data pertain to roots of cereals in topsoils.

Barley (1970)

horizontal development of first order laterals often depends on the density of the plant cover, since interpenetration of similar root systems seems rare. This was well illustrated by Raper and Barber (1970). Higher-order laterals follow a roughly random path in finely structured soils, filling in the array of main roots and first-order laterals (Barley 1970).

It is clear from the above that the average interplant distance under established crops growing in well structured soils is of the order of millimeters. When these conditions obtain, a consideration of nutrient transport processes appears unwarranted, except perhaps for P. However, the success of a crop often depends on its behaviour in the early stages of growth. In these circumstances, rooting density will be much lower, and transport processes more important.

So far, we have been discussing uniformly well structured soils, where lateral root development is radially symmetrical. Although omnidirectional root systems may be the norm, Pittman (1964) has observed magnetotropism in cereals - he reported that the majority of wheat roots are oriented parallel to the horizontal component of the earths magnetic field. The result of this is an uneven root density distribution, or clumping. In addition, roots tend to follow the path of least mechanical stress, and thus clumping of roots will arise in fissured soil. An extreme example of this is shown in fig. 1.4. It is interesting to note here that conventional methods of measuring root weight or length may not detect such features, and the efficiency of the root system might be grossly overestimated. A less extreme example is the local clumping of roots found in soils with a cloddy structure, where soil peds are too dense to allow thorough root exploitation. Weaver (1958) has discussed this at length in relation to grass root development. Muller (1946) has presented a very thorough account of the effect of different soil

Fig 1.4

The effect of Soil Conditions on Root Development

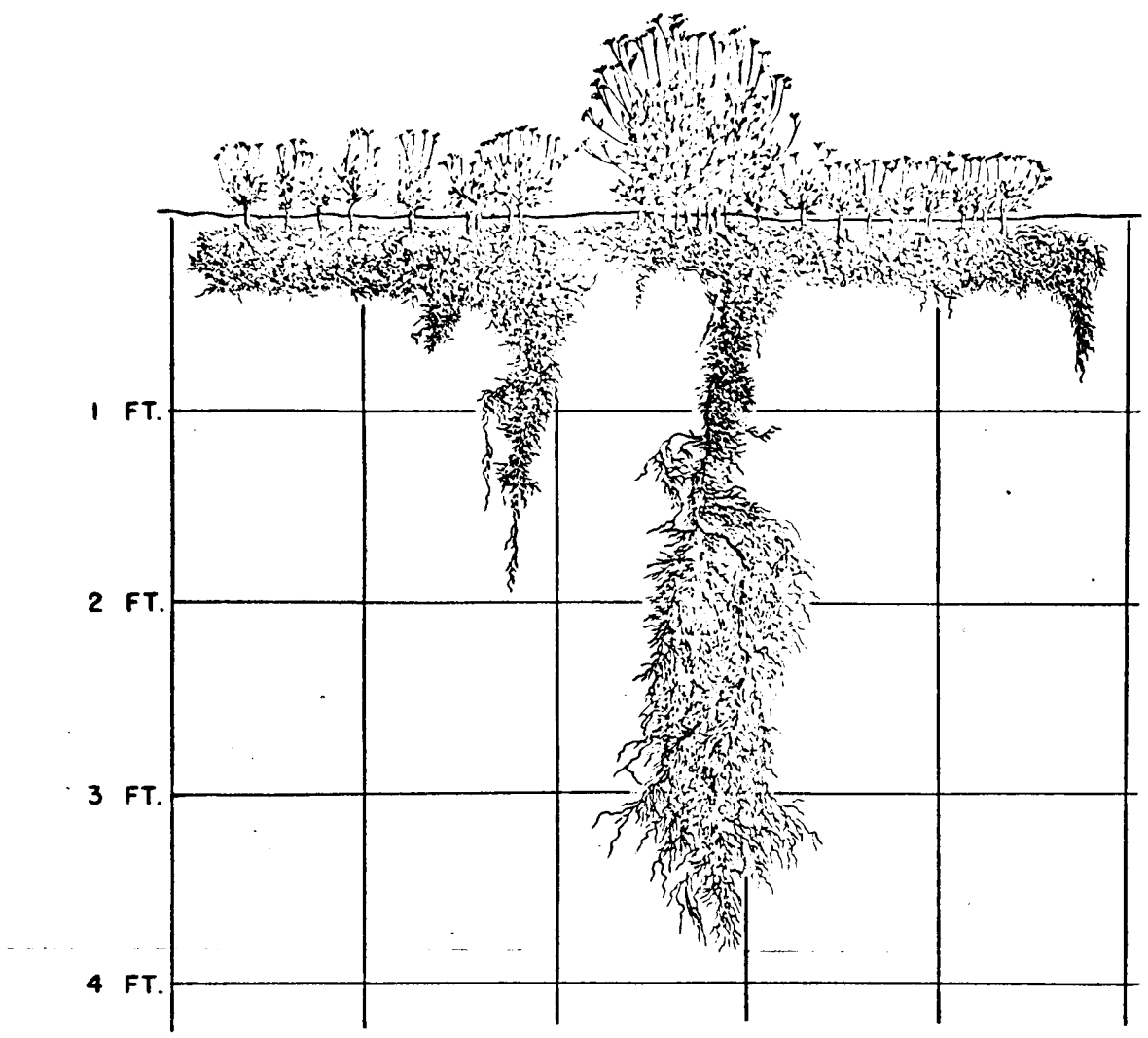


FIGURE 69.—One-year-old guayule plants adjacent to the site of those shown in figures 65 and 66. The highly developed hard layer of soil was softened only locally by the winter rains, and most of the plants remained root-bound. Note the normal root development below the 1-foot level and the larger tops of the plants thus freed.

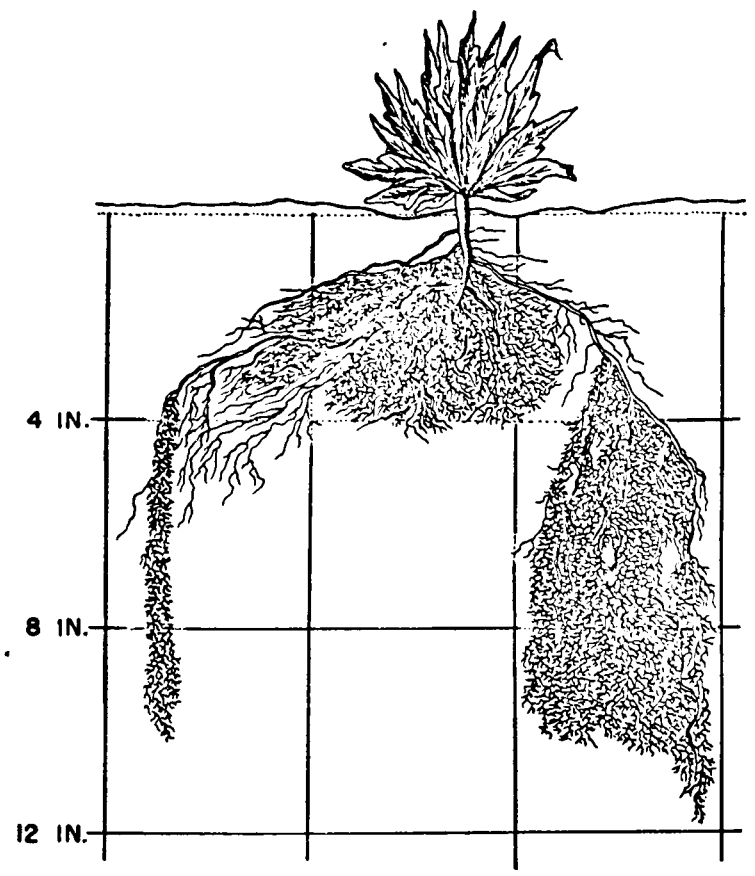


FIGURE 67.—The middle guayule plant shown in figure 66 viewed in the direction of the row. The coralloid mat on the left occupied an old chisel track parallel to the row; that on the right, a crack transverse to the row.

Muller (1946)

conditions on the root system morphology of guayule.

Wiersum (1962) has studied the N and P nutrition of young tomato plants growing amongst prismatic soil blocks. As we may have expected from ideas already mentioned, P but not N uptake decreased when roots were restricted to the interpod voids. In the field, Cleverings (1955) reported a low phosphate uptake by a crop whose roots were restricted to the soil between large impenetrable peds.

Heterogeneity of root system development may be the result of an uneven nutrient distribution throughout the profile. For example, it is well known that roots proliferate around fertiliser granules (Duncan and Ohlrogge 1958). It is less certain whether individual roots can detect local nutrient concentration differences, which then influences their direction of growth. If this were the case, root systems in uniform soil may be expected to develop regularly, as each new root tries to avoid the depletion zone of an existing root, or in a clumped way if roots of one plant make the local environment more favourable to those of another. Litav and Harper (1967) looked for both these effects, but found no evidence of either. Undermixing (i.e. regularity) may also occur when substances exuded from the roots of one plant, e.g. guayule (Bonner 1950), are injurious to those of another - again this has not been demonstrated in soils. The technique suggested in Chapter 3 should facilitate this type of study. More data are certainly required on the local pattern of plant roots growing through soil. There seem to be many instances where root clumping, may occur, and an analysis of nutrient transport within multiple root systems would be incomplete without due consideration of the effects of root pattern.

1.6 Qualitative investigations of interroot competition

There is very little evidence available in the literature which relates exactly to this discussion. Various workers have demonstrated

how the uptake of N and P is a function of the contrasting mobility of these elements. Thus it has been shown that the uptake per unit volume of soil of P but not N decreases with a decreasing root density (Cornforth 1968). Andrews and Newman (1970) varied root density by pruning a plant's root system, and compared the behaviour of the pruned root system with unpruned plants. As expected, N uptake was unaffected by the treatment, but pruning reduced P uptake. The work was extended by growing the unpruned and pruned plants together. In this case, the N uptake by each plant was in proportion to its root length whereas P uptake was unaffected by the association. This follows the reasoning of the last section; in a competitive situation both N and P uptake are functions of root density. The difference between the competitive and non-competitive cases, with regard to N uptake, is one of time scale.

That competitive ability is not solely a function of root density was well demonstrated by Raper and Barber (1970a) when they compared the growth of Aoda and Harosoy 63 soybean. Harosoy 63 develops the much denser root system, but Aoda has a greater capacity per unit length of root to absorb K from high solution concentrations. When these plants were grown together, Aoda initially absorbed more K, but the differences had disappeared by the end of the growing season. The probable explanation is that the greater root density finally outweighed the disadvantage of a low root absorbing power. Since both root systems absorb K at the same rate from low solution concentrations, Harosoy 63 may be expected to be more successful in nutrient deficient conditions.

1.7 Quantitative investigations of interroot competition

It follows from the earlier discussion that a quantitative description of interroot competition requires a mathematical treatment of the nutrient flow in whole root systems.

1.7.1 Nutrient transport in multiple root systems

An exact analysis of nutrient transport in multiple root systems is possible only for a regularly dispersed system of parallel roots whose density does not vary with time. Barley (1970) has suggested a procedure whereby the accurate analysis of diffusive transport can be extended to root systems of varying degrees of dispersion. Dispersion is a measure of the spatial relations between roots. Barley concluded from his study that dispersion had very little effect on uptake by any density of roots.

Barley's (1970) procedure for calculating the uptake by an irregular root system when nutrient supply is by 2-dimensional diffusion is as follows:

1. each root is assigned an area of soil which contains all points in space nearer to that root than any other. If the roots are distributed randomly in a plane, the regions so defined are Voronoi polygons. An example of these polygons is in fig. 1.5.

2. each polygon is substituted for a circle of equal area with the root at the centre, and a frequency distribution of the radii of the equivalent circles is constructed.

3. for a random pattern of roots this frequency distribution approximates to a gamma distribution. Different orders of clumping are effected by changing the skewness, but not the variance or the mean, of this frequency distribution by applying the transformation

$$B_i' = B_i - \phi(s^2-(B_i-\bar{B}^2)$$

where B_i' = the transformed radius

B_i = the radius for a random pattern

ϕ = constant

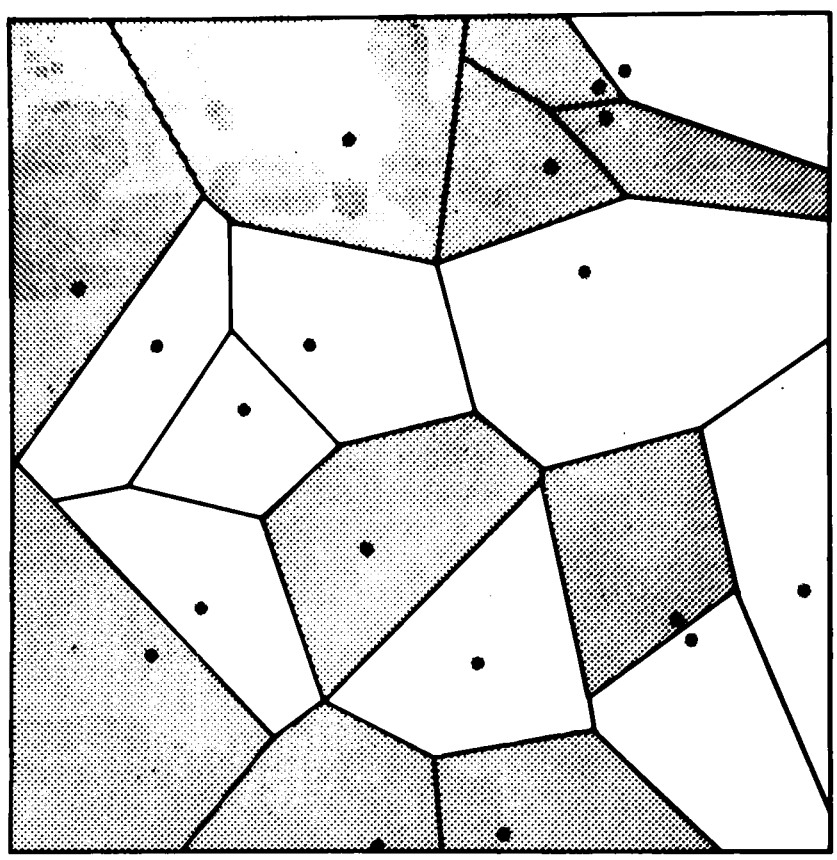
s^2 = variance of random pattern

$\bar{B}$ = mean of random pattern

4. the problem of diffusion in a finite hollow cylinder is solved by the method of Youngs and Gardner (1963) for the range of values of radii.

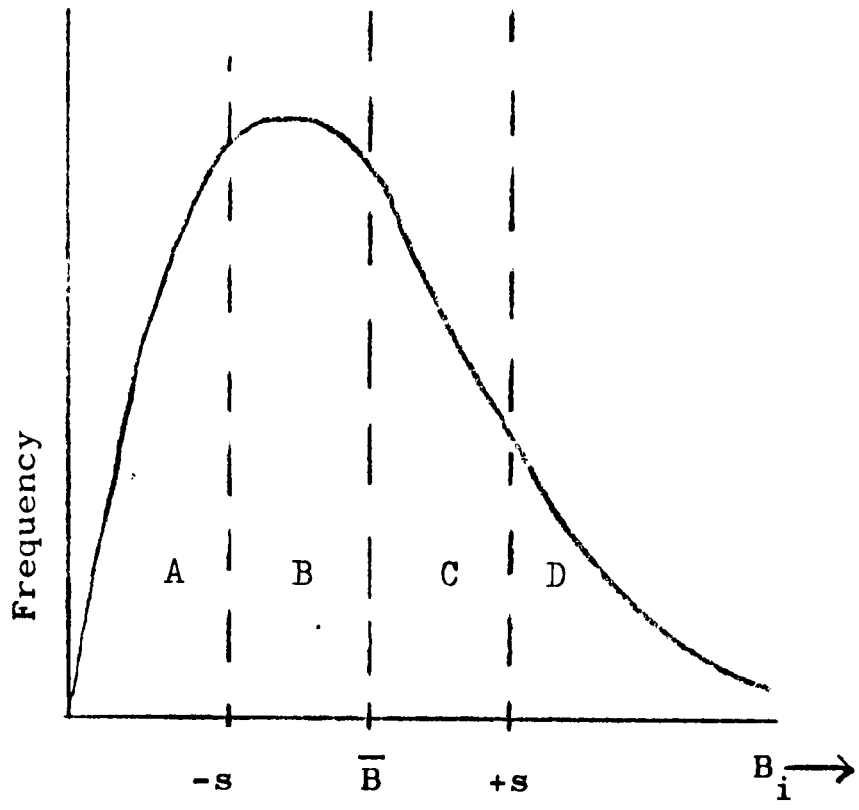
Fig 1.5

A random pattern of points, with the associated Voronoi polygons

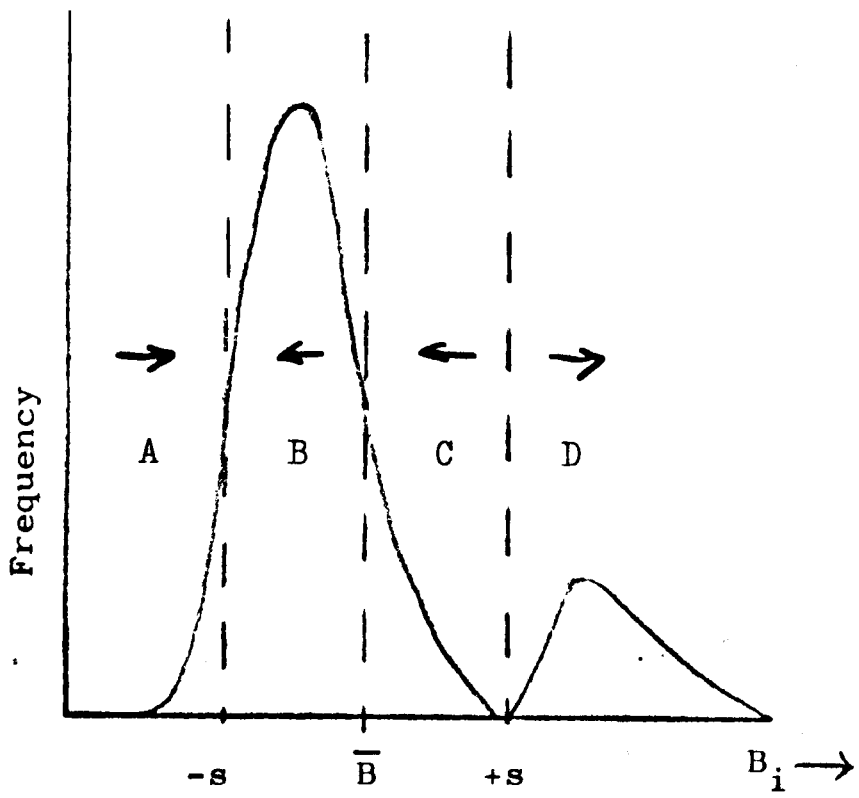


A random-sets mosaic or "S-mosaic."

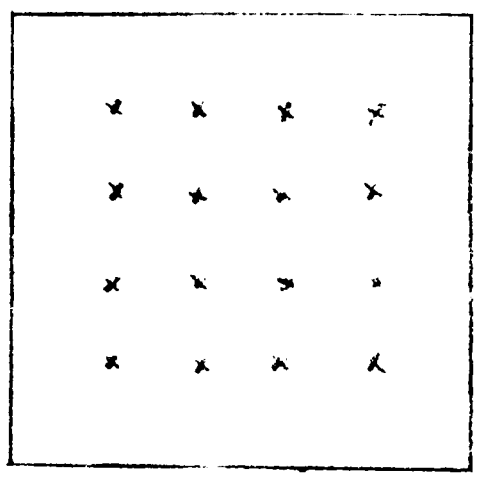
a)


Frequency
A
B
C
D
-s
$\bar{B}$
+s
B_i

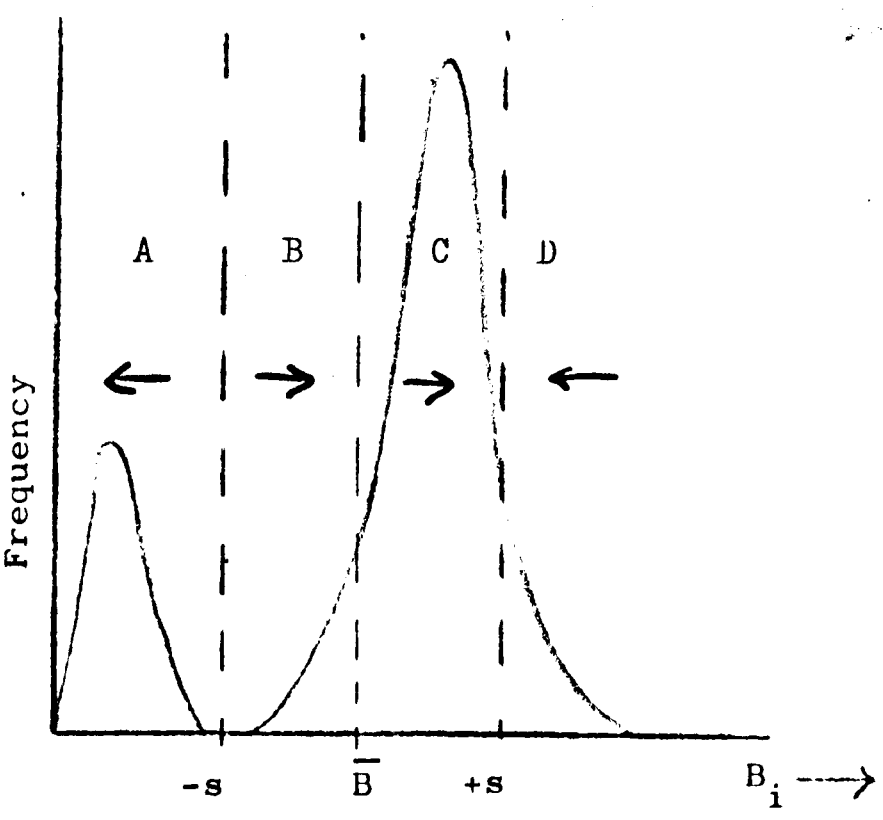
b)


Frequency
A
B
C
D
-s
$\bar{B}$
+s
B_i

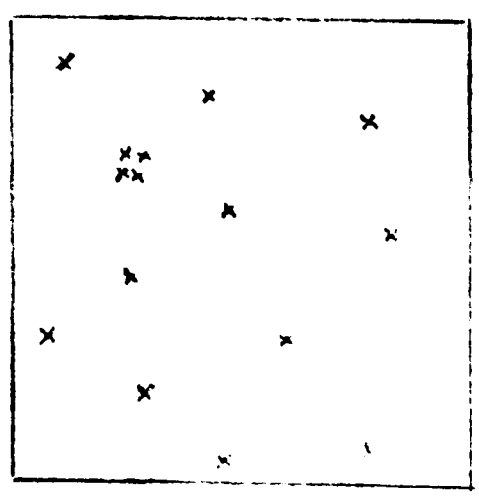
c)



d)


Frequency
A
B
C
D
-s
$\bar{B}$
+s
B_i

e)



3. the uptake after a given time for specified root and soil properties, for each radius, is multiplied by the appropriate frequency, and the total obtained by summation.

Since the method of clumping changes only the 3rd. moment of the frequency distribution, whereas it is the variance which is usually more sensitive to points being clumped, Barley's conclusions, on the effect of pattern on uptake, should not be accepted without further consideration. Let us look in more detail at the nature of the root patterns resulting from the suggested transformation. The frequency distribution for a random pattern of roots divided into 4 regions by the standard deviation, s, is outlined in fig. 1.6a.

a) if ϕ is +ve:

With reference to fig. 1.6a, each value of B_i in sections A and D becomes greater, and each value of B_i in sections B and C becomes smaller. The effect of this is to decrease the number of short equivalent radii and increase the number of long and intermediate ones. The frequency distribution in fig. 1.6b is an extreme example of this transformation, which might occur with the root pattern in fig. 1.6c.

b) if ϕ is -ve:

Referring to fig. 1.6a., each value of B_i in A and D becomes smaller and each value of B_i in B and C becomes greater. The effect is to increase the number of very short distances, and increase the number of fairly long distances, but decrease the very long distances. Fig. 1.6d is an extreme example and coincides with a root pattern of the type shown in fig. 1.6f. A small - ve. ϕ will give a symmetrical distribution of B_i.

The conclusion which follows from the previous discussion is that Barley's suggested transformation does not clump the roots to any large extent; it is not surprising that he recorded no effect.

Further disadvantageous features of the suggested procedure are 1) as pointed out by Barley (1970), the model is unsatisfactory if the centres of equivalent circles deviate widely from those of the corresponding polygons.

2) error must be introduced if the polygon shape is widely different from that of a circle, which is common even for randomly dispersed roots (see fig. 1.5).

In view of the possible criticisms of the above approach, I was unable to accept that the effects of pattern could be ignored.

Sanders (1971) has also investigated the influence of pattern on nutrient uptake by roots in soil. He used an electrical analogue (Sanders et al. 1971) of the soil- root system to compare the theoretical supply by diffusion to a group of 7 roots, 1 cm long, with results obtained from a plant experiment. In the plant experiment, nutrient uptake, and profiles of the soil solution concentration around roots were measured. The analogue (further details are in chapter 2) gave a satisfactory prediction of both root surface concentration and nutrient uptake, and he concluded that the diffusion model provided a good explanation of the mechanism of interroot competition.

The above discussion has summarised the present state of knowledge on the application of the concepts of nutrient flow to estimates of soil supplying power and nutrient uptake by crops.

1.8 Objectives of the present study

The aim of the present study was to extend the precise mathematical statements of nutrient transport, to whole root systems where the individual roots may be influencing each other, and to investigate experimentally whether the "transport process" approach is useful for analysing nutrient uptake by plants from soil, if the plant development is given.

1.9 Plan of Work

a) To develop a theoretical model of nutrient flow to a developing root system.

b) To use this theory to identify the factors influencing interroot competition, and quantify their interrelations.

c) To develop techniques to perform plant experiments which may be analysed by the theoretical model.

d) To investigate experimentally the uptake by a root system growing in soil.

e) To determine experimentally whether a simple relation describing rate of uptake of solute from different zones of soil exists.

f) To investigate the possibility of using the theoretical model for predicting the nutrient uptake by a specified root system.

Chapter 2

A theoretical model describing nutrient supply to whole root systems

2.1 An analysis of the nutrient uptake by whole plant root systems requires precise information on the nutrient supply to individual roots, and a knowledge of the boundary conditions at the root surfaces describing the rate of nutrient loss from the soil. These two factors cannot be varied independently. Therefore, a theoretical model of nutrient supply to plant roots is required, which can be used to calculate nutrient uptake consequent upon different values of the boundary condition at the root surface. A comparison of theoretical and observed uptakes will give information about the actual boundary conditions operating when plants grow in soil. If a complete analysis is possible, the rate limiting step in the process of nutrient uptake from soil can be identified in any conditions. This may be of general interest.

An analytical solution of diffusion in two-dimensions to multiple root systems has been given (Youngs and Gardner 1963), and a numerical method has been presented for solute supply by diffusion and mass flow (Passioura and Frere 1967). These solutions apply only to roots of constant density, arranged in a hexagonal array. Earlier (section 1.7.4) it was concluded that for any given root density, individual root position may affect the total uptake, especially for K. It was desirable, therefore, that the effects of pattern at different densities be investigated quantitatively, and if necessary included in a theoretical model of nutrient supply.

In the absence of any acceptable solution of nutrient transport to irregular root arrays, an electrical analogue of the soil-root system has been used. This analogue (Sanders et al. 1971) simulates diffusive

transport only, but since K^+, the ion which is likely to be most influenced by rooting pattern, is mainly supplied by diffusion (Barber et al. 1963), this limitation is not serious.

2.2 Electrical analogue of diffusion to roots

Solute diffuses in soil if there is a gradient in chemical potential; current flows through a resistor if there is a gradient in electrical potential. Since the driving force in both processes is, in effect, the gradient in electrochemical potential, the equations describing the flow of current, are formally similar to those describing diffusive flow of solute. This principle is the basis of the electrical analogue described by Sanders et al. (1971). The physical system simulated is a flat slab of uniform soil. Roots grow through this slab at right angles to the surface, and concentration gradients occur in two dimensions only.

Ideally, the analogue would consist of a uniform sheet of material with electrical resistance and capacity, so that it can be charged above earth potential. The total charge represents the amount of solute in the soil, and the potential at any point represents the concentration of solute in the soil solution. In practice, it was more convenient to approximate to the homogeneity of a sheet with a network of resistors and capacitors. Thus the analogue consists of 585 junctions or nodes; each is joined to 4 neighbours by a resistor, and to one plate of a condenser. The other plate of the condenser is earthed. A diagram of the wiring at one node is in fig. 2.1. If a conductor, S, is connected to a node, A, and to earth, charge will flow out of the analogue at a rate dependent on the characteristics of S, and the resistance and capacity of the sheet. This process is analogous to the uptake of solutes by plant roots from soils. Several uptake functions can be

Fig 2.1

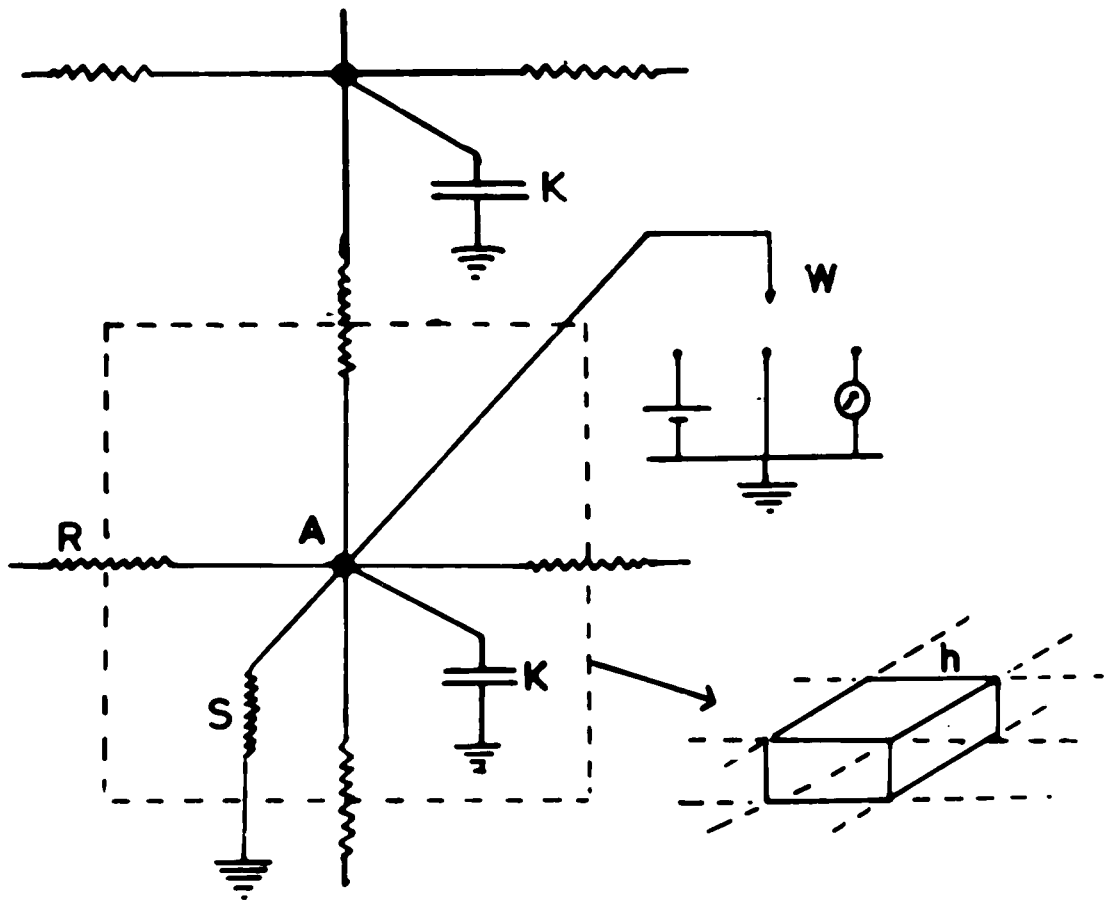


Fig. 2. Circuit diagram for two nodes of the analog, showing sink resistor S, and equivalent portion of soil slab.

simulated (Sanders et al. 1971 p.465), and if S is a resistor, the current flowing through S is directly proportional to the potential at node A. This is analogous to the boundary condition for plant uptake given by $F = \alpha C_{la}$, and is the system used in this work. The potential at A, which represents the nutrient uptake rate, can be continuously monitored on a chart recorder, and the decrease in total charge on the analogue after any time, which represents the uptake M_t/M_∞, is measured with a Vibron electrometer.

From a series of trials, it was found that up to 50 conductors may be attached to the sheet at any one time. At numbers greater than this, the assumption that the fine network of resistors and capacitors approximates a continuous sheet is no longer satisfactory. However, this is a sufficient number to investigate the mutual effects of roots on their rate of uptake, and to compare the efficiency of different root patterns with respect to total uptake.

The following equivalences, which are given by Sanders et al. (1971), are helpful to an understanding of results obtained with the analogue.

S = value of sink resistor = $\frac{10^6}{2\pi} \cdot \frac{Db}{\alpha a}$ ohms

t = physical time simulated secs

t_e = electrical time on the analogue = $\frac{Dt}{h^2}$ secs

h = length of one side of the square element of soil simulated by one node, cm

a = root radius = $\frac{2h}{\pi e}$ cm, if S is connected directly to a node.

The variables on the analogue are t_e and S, and a can be varied if necessary.

2.3 Assumptions implicit in the use of the analogue

a. The solution concentration in the soil is initially uniform.

b. The diffusion coefficient of an ion does not vary in space or in time during nutrient depletion. If D depends on concentration, an effective, average D over the concentration range is appropriate.

c. The diffusive flux of solute occurs only through the liquid pathway. This has been shown to be the case in soils (Mott and Nye 1968, Rowell et al. 1967, Tinker 1968), although several workers have demonstrated a flux of adsorbed cations in pure clays (e.g. Shainberg and Kemper 1966 van Shaik et al. 1966, Kemper and Quirk 1972).

d. Nutrient supply to plant roots is restricted to diffusion. This will always be untrue if there is water uptake and nutrient uptake by the same portions of root. However, several workers have shown that diffusion is the predominant supply mechanism for K and P. Diffusion of nitrate may be important in the early part of the season, when the transpiration rate is low, and the plant demand is high.

e. In the work here, it is assumed that nutrient uptake rate is directly proportional to the solution concentration of nutrient at the root surface.

All these assumptions are acceptable in an attempt to establish principles regarding the effects of inter-root competition.

2.4 Studies using the analogue

1. An illustration of root competition as it is affected by $\alpha\, a/Db$, $\sqrt{Dt}$ and the interroot distance. This is discussed in section 2.6.

2. nvestigations into the influence of the density of a root system on the time course of uptake, as it is affected by various soil and plant properties. This is treated in section 2.7, and 2.11.

3. An investigation into the influence of rooting pattern on uptake for high and low values of $\alpha\, a/Db$. Results for high values of $\alpha a/Db$ are given in section 2.8; results for low values of $\alpha a/Db$ are in section 2.12.

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2.5 UPTAKE OF SOLUTES BY MULTIPLE ROOT SYSTEMS FROM SOIL

II. THE THEORETICAL EFFECTS OF ROOTING DENSITY AND PATTERN ON UPTAKE OF NUTRIENTS FROM SOIL

by J. P. BALDWIN, P. B. TINKER*, AND P. H. NYE

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a

SUMMARY

The analog described in Part I is used to investigate quantitatively the the effects of pattern and density on the uptake and uptake rate of nutrients which move to plant roots by diffusion. The uptake by two roots is considered first, to illustrate the competitive effect. The results for multiple root systems are given for a variety of different soil and plant parameters at different times and demonstrate the importance of pattern and density in the uptake of different plant nutrients in both competitive and non competitive situations. Pattern can decrease the uptake by root systems by at least 75 per cent, depending on the value of the diffusion coefficient, time, and root density. Graphs of two indices of dispersion against uptake are given so that the effect of any pattern can be estimated. A procedure is outlined which enables the uptake after any time by a developing root system to be predicted and compared with a theoretical maximum. If the uptake is known, then the graphs show whether soil or plant parameters are limiting uptake.

b

INTRODUCTION

The concept of a root as a 'sink' towards which nutrients move through the soil is now well established. Several authors have given theoretical treatments of the diffusive transport of ions to single roots, and of the depleted zones which form in the soil around them. (See Part I of this series [19].) Up to the present, only one attempt [3] appears to have been made to extend this type of treatment to the real situation, in which a number of roots are distributed throughout a soil and compete with each other for the nutrients in it.

Plant competition has also received much attention [8 18], but the

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Throughout this paper, r signifies root radius.

exact study of competition between roots, either belonging to one plant or several, has proved difficult, and little is still known about how it occurs. It is useful to distinguish three possible competition mechanisms. The first includes any effect whereby the spatial arrangement, or the morphology of the root system is altered. This certainly arises with those species which exude chemicals which can inhibit the development of roots near them [4]. It may also result from nutrient gradients in the soil caused by absorption, since roots will branch most in zones of highest nutrient concentration [9]. Secondly, it is possible that such toxic exudates will alter the physiological properties of a root so that it absorbs less rapidly. Thirdly, a root usually absorbs at a rate which is related to the concentration of nutrient around it; and if this concentration is decreased due to the absorption by a competing root, then the uptake rate of the first root must decrease. In terms of the theory of the transport of ions to roots, this is equivalent to saying that the depleted zones around the two roots have overlapped, and it is this type of competition which we discuss here. Depleted zones cannot be defined exactly, and in theory there is competition between any two roots in the same soil volume at all times. We are concerned with the degree of this competition, and the question of when and under which conditions it becomes important.

In this paper we investigate the theory of the diffusion of material to a series of linear sinks dispersed in a medium such as soil. No general analytical solution of the diffusion equation for such a system is known to us, and it appears unreasonable to expect that one will be produced in an acceptable form. We have therefore used the electrical analog described in Part I of this series [19]. The results are only relevant to ions transported by diffusion, and do not apply directly to ions moved mainly by mass flow of soil solution. However, they may be of interest for work on movement of water to plant roots, since similar general considerations may apply. Hitherto, water uptake has been treated in terms of a single root in an infinite medium or as a group of parallel equally spaced roots [7 11 16].

The final destination of the absorbed nutrients is not considered here. Later we hope to distinguish between the uptake of roots which all belong to the same plant, and the uptake into interpenetrating root systems. In the former case the major consideration is the efficiency of the whole root system; in the latter, it is which of the root systems is the most effective competitor.

List of symbols

D = diffusion coefficient of a nutrient, cm^2/sec.
F = flux of nutrient ions, mole/cm^2/sec.
C = total concentration of diffusible nutrient, mole/cm^3 of soil.
C_l = concentration in liquid phase, mole/cm^3 of solution.
A = constant, mole/cm^2/sec.
B = constant, mole/cm^3
t = time, sec.
r = root radius, cm.
α = root absorbing power, cm/sec.
h = distance parameter on analog – real distance corresponding to 1 internode, cm.
ρ = density of root intercepts on a plane, cm^{-2}.
V/M = variance/mean ratio.
$\bar{y}$ = mean nearest neighbour distance, cm.
b = buffer power of soil.

Some of the properties of the analog are briefly outlined here to make it easier to understand the results obtained with it.

1. The analog represents a flat slab of uniform soil of unit thickness and with constant diffusion coefficient; only transfer in two dimensions can be simulated (but see p. 706).

2. Resistors which connect the analog to earth simulate roots penetrating the slab of soil normal to the surface, and absorbing nutrients according to the equation $F = \alpha C_l$: the size of the resistance simulates the magnitude of the relative 'sink strength', $\alpha r/bD$.

3. Different dimensions in the slab of soil can be simulated by varying the scale factor which relates 'analog time' to real time.

Considerable flexibility is possible in simulations of particular assemblies of roots, *e.g.* the uptake characteristics, the number, or the distribution of the roots can be varied during the run. However, to produce results in a simple and general form, we have assumed that all roots have the first order uptake relationship given above, with constant α, and that they all commence absorbing from the soil simultaneously. Roots entering at different times will be considered later. Real roots have variable uptake properties which are most closely approximated by a relationship of the form $F = AC_l/(B + C_l)$ [10]. Therefore, at high concentrations the roots will tend towards a 'constant flux' situation, and no competition in our sense is then possible. As the concentration becomes less, the root property tends towards the 'first order' type given above, and our results therefore represent the largest degree of competition which can normally occur.

2.6 *Competition between two parallel roots.*

The mutual effect of two roots at varying distances from each other in an infinite volume of soil illustrates the basic competitive situation. It may readily be simulated on the analog by inserting resistors, representing roots, at varying distances apart. An even simpler method is to place the resistors at a fixed distance apart, and let this represent different real distances by varying the time scale factor, but this is less accurate, since the simulated root radius will in effect vary also [19].

Results for this simple situation are not available elsewhere, and we therefore give them in some detail. Fig. 1a gives the relative concentration at the root surface, which is proportional to the uptake rate, plotted against Dt/r^2 for various values of $\alpha r/Db$, and distances between the roots, the latter being expressed in units of r. Distance units may be given in terms of r because there is a constant relationship between h, the distance parameter on the analogue, and r, namely $r = 2h/\pi e$ [19]. Fig. 1b gives the mutual effects of two near 'zero sink' roots (large value of $\alpha r/Db$) in terms of the percentage reduction in uptake for each root, plotted against their distance apart, again in units of r, for different values of Dt/r^2. For our purposes, we define the competitive effect as the reduction in uptake rate due to the overlap of depletion zones relative to the rate of a single root in similar conditions.

The general conclusions that can be drawn from these curves are:
(a) Fairly obviously the competitive effect depends upon t and upon D.
(b) The competitive effect depends upon $\alpha r/Db$, but does not appear to differ very greatly as long as the relative concentration at the root surface is less than 0.25. (Fig. 1a – *note* log scale.)
(c) Uptake into zero-sink roots is reduced approximately by 10 per cent at the point when $\sqrt{Dt}$ equals the inter-root distance. If effects of less than 10 per cent can be ignored, we can make the useful approximation that roots further apart than $\sqrt{Dt}$ will not affect each other in this way. Since the effective mean radius of the depleted zone around an isolated root is $\sqrt{Dt}$ [14], an inter-root distance of $\sqrt{Dt}$ corresponds to an appreciable overlap of their depletion zones. The dimensionless quantity Dt/r^2 can be regarded as the area of the depleted zone (πDt) in units of the cross-sectional area of the root (πr^2).

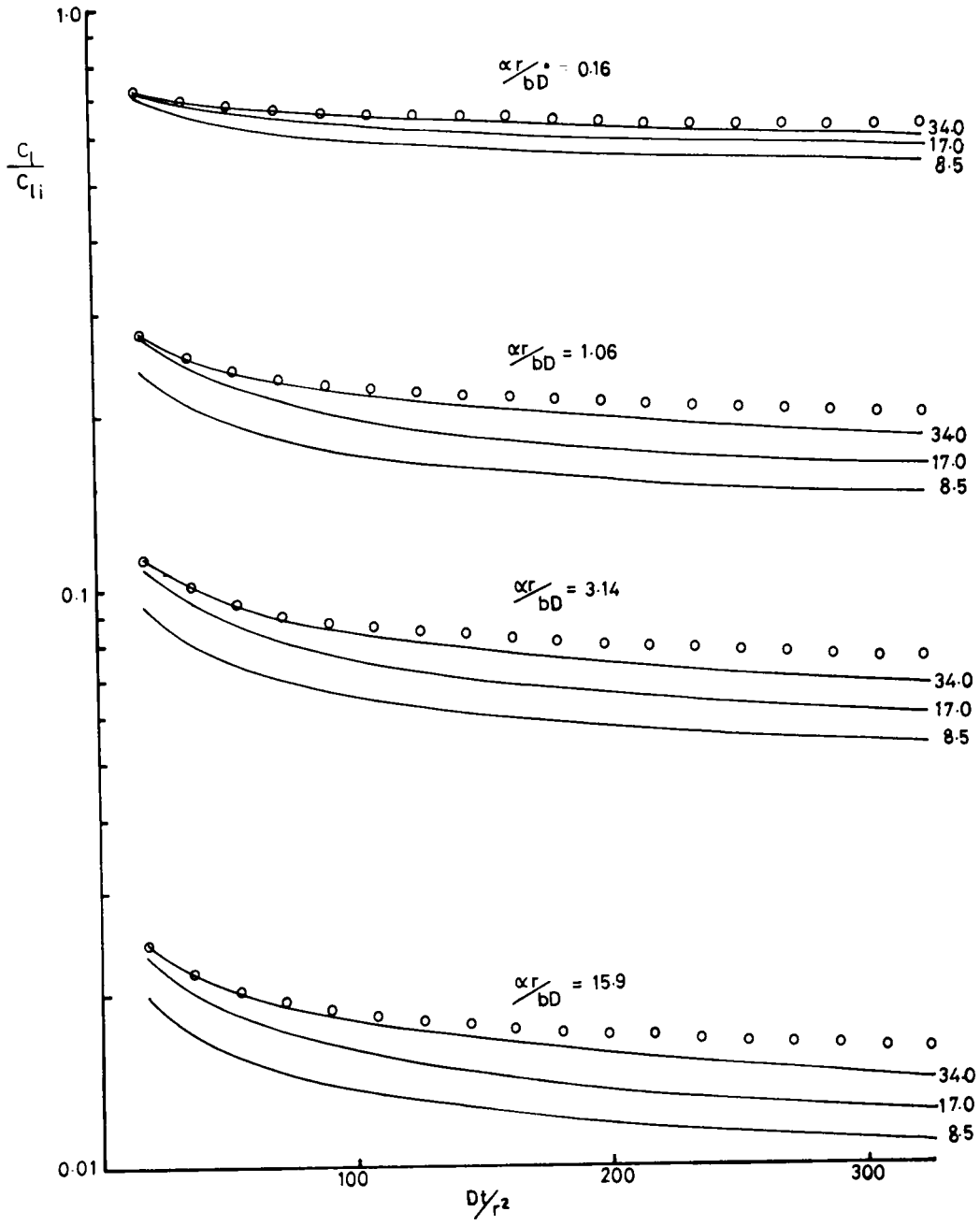


Fig. 1a. Effect of interroot distance on the change in the relative concentration at the root surface, C_l/C_{li} (which is proportional to uptake rate)with Dt/r^2, for different values of $\alpha r/Db$. The interroot distance for each curve is given by nr, where n is the number on the curve. Circles represent results for $n = \infty$

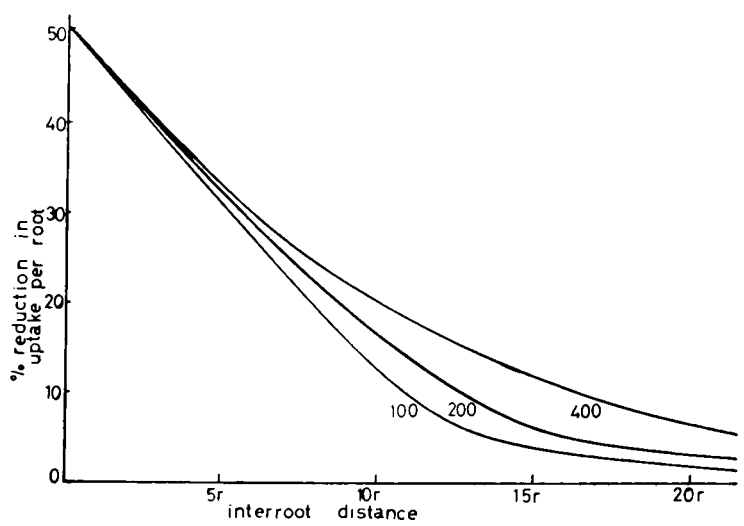


Fig. 1b. Reduction in total uptake by a pair of roots, expressed as a percentage of uptake of two isolated roots, plotted against interroot distance. Numbers on curves are Dt/r^2. All results are for $\alpha r/Db = 15.9$, which is near a zero sink; the maximum reduction is therefore 50 per cent.

(d) The competitive effect increases with both $\alpha r/Db$ and Dt/r^2. The former is a measure of the depth of the depletion zone, and the latter a measure of the spread. Thus nitrate, which often has a relatively small α and a high D, will in these circumstances have shallow, extensive depletion zones, and the solution concentration will be relatively independent of root position. Phosphate, on the other hand, has a large α, and very small D, and thus no overlap of depletion zones, and therefore no competition, would be expected unless the root system is very dense. Potassium, with a large α and a moderate D will be the most affected by competition, as the depletion zones will be deep, but fairly wide, and hence their interaction will be dependent on root position.

2.7 THE EFFECT OF DENSITY IN REGULAR ARRAYS OF PARALLEL ROOTS

The previous section illustrates the nature of competition and outlines the important parameters. It is likely to cover the case of very sparse root systems which can be regarded as pairs of root in a large volume of soil. However it is more usual in the field situation for large numbers of roots to be distributed throughout the soil, and we must therefore deal with whole populations rather than individual pairs. This population can be described in terms of $\alpha r/bD$, which is again assumed constant, the density of roots and their pattern. We

deal with the last two parameters in turn here. First consider an infinite array of roots equally spaced from each other. Each root can be considered to exploit a volume of soil around it which is defined by the zero-transfer boundary between it and the rest of the soil. The problem then approximates to one of diffusion in a cylinder towards a central sink. Analytical solutions of the diffusion equation for this system have been given [5 20], and Barley [3] has given results for uptake by such a regular assembly for particular values of density and other parameters.

The properties of the analog make it easy to produce general results for any root and soil system of this type, and we give some here, since it may be preferable to read the results off the graphs rather than perform the tedious calculations needed for the analytical solution. The analog can be used to simulate this situation in two ways: sink resistors can be inserted in a regular pattern over the whole analog, or a single resistor can be inserted in the centre of the analog, which is then regarded as the area within the zero-transfer boundary around a single root. Both methods gave closely similar results when compared, but the second method was used to get the results given here since it is more accurate and simpler.

The real area represented by the analog can be any size, and the reciprocal of this is the root density, ρ cm^{-2}. Since the area of the analog can also be specified in terms of h^2, the time dimension on the analog, Dt/h^2, [19] can consequently be written as $Dt\rho$. The results of a single run can therefore be applied to any root density. However, any change in ρ implies a corresponding change in r for any one set of circuit connections, and a correct choice of ρ may imply an incorrect r. The uptake is therefore plotted in Fig. 2a against $Dt\rho$ for 5 different r–ρ relationships, and results for other values can readily be found by interpolation.

These curves give changes with D and t directly, with ρ held constant. However, they do not give a correct indication of how uptake varies when ρ is not constant, since all changes in ρ imply a change in r. The curve giving the true change with ρ, for any chosen D, t and r, can be constructed from those given. An example is shown dotted in Fig. 2a. The method was also found to agree well with the curves given by Barley [3] for uptake at different values of ρ and particular values of D, t, α and r. Initially, the uptake increases linearly with ρ, but falls off when the depletion zones overlap significantly. For

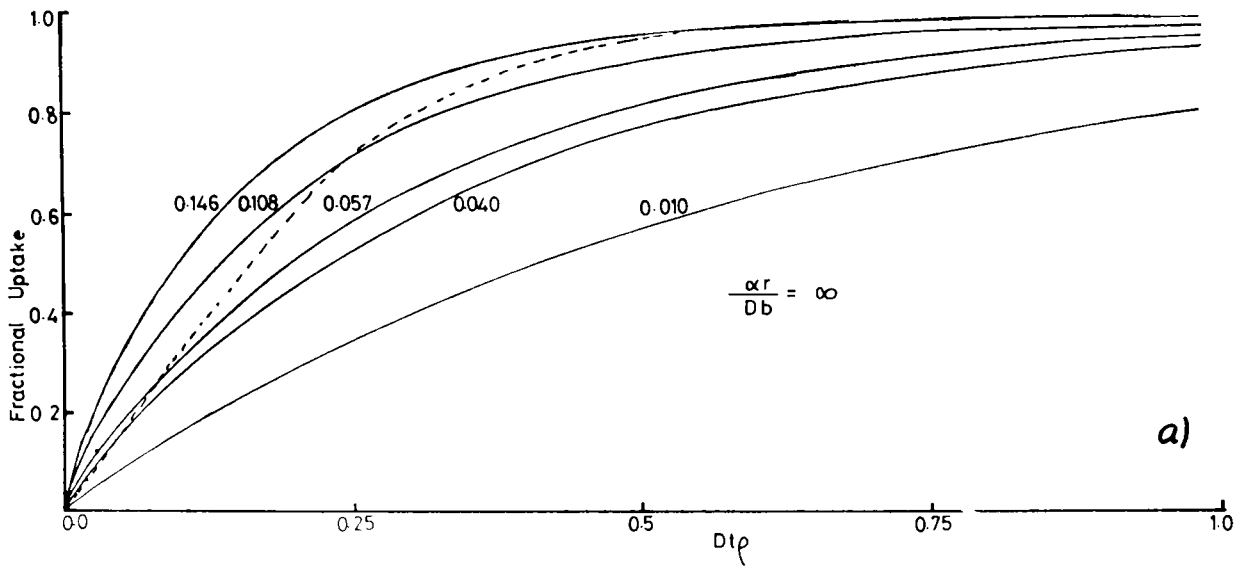
the dotted curve the value of $Dt\rho$ which gives a 10 per cent reduction from the linear curve is 0.25, and this corresponds to an interroot distance of $2\sqrt{Dt}$. This illustrates the additive effect of additional sinks, recalling that the equivalent interroot distance for the two root case was $\sqrt{Dt}$. These two figures are likely to be useful limits for rough estimations of the importance of interroot competition.

Curves showing the uptake from systems of this type by roots with different $\alpha r/Db$ are given in Fig. 2b, but for only one $r-\rho$ relationship. An increase in $\alpha r/Db$ above 2.5 does not greatly affect the uptake. Variations in percentage uptake resulting from different $r-\rho$ relationships are essentially similar for all $\alpha r/Db$ values above 2.5, and corrections can therefore be made using Fig. 2a. The curves tend asymptotically towards 1, or complete exhaustion of the nutrient in the soil, and systems with any value of ρ will approach this state given sufficient time. Relatively short times are needed for nitrate, with large D, and very long times for phosphate, with very small D. If the expected values of D, ρ and t for any given situation are such that the flatter portions of the curves will be reached, then there is little advantage to the crop in producing more roots to increase ρ. This agrees with the intuitive expectation, and the experimental finding [6] that nitrate uptake from a soil is not greatly dependent upon ρ, whereas that of phosphate is. The implication that plants need only small root densities to absorb nitrate effectively, may well be true in general, but in a competitive situation there is still an advantage in a high ρ, as it allows the plant to absorb more rapidly than its competitor [1 13].

Real root systems will not, of course, establish a given root density instantaneously, but we suggest that the uptake by the real system up to any time can be found by using the real total time of absorption and the time average $\bar{\rho}$, this latter being used to determine the $r-\rho$ relationship. This is being investigated further.

2·3 THE EFFECT OF PATTERN IN IRREGULARLY SPACED ARRAYS OF PARALLEL ROOTS

The major purpose of this work was to enquire into the effects of spatial distribution or pattern of roots on nutrient uptake. Mechanisms have been suggested which would cause roots to have regular or contagious patterns, and methods are now available for determining



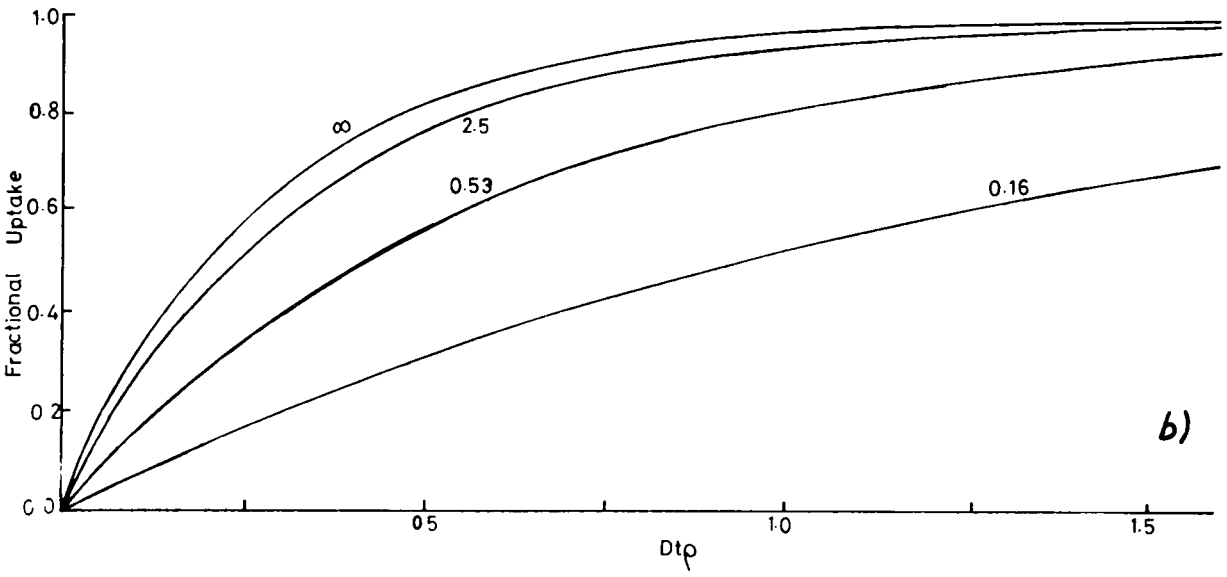


Fig. 2. **a**. Fractional uptake by a regular array of parallel roots with $\alpha r/Db = \infty$ plotted against D t ρ. Numbers on curves are the $r\sqrt{\rho}$ product. Curves are correct for constant ρ and r and variable t or D. The effect of change in ρ, for Dt = 0.25 cm^2 and r = 0.1 cm, are in the derived curve, shown dotted. **b**. Fractional uptake by a regular array of roots plotted against D t ρ, for $r = 0.057\sqrt{\rho}$. Different values of $\alpha r/Db$ are indicated on the curves. The curve for $\alpha r/Db = 15.9$ was indistiguishable from that for ∞.

these [2], but no experimental information is yet available. It appears to us that the immediate need is to predict the magnitude of the effects of root pattern, at different densities, on nutrient uptake and to decide whether they are large enough to merit serious attention.

With the analog it is easy to investigate the effects of any particular arrangement of parallel roots, whose intercepts make a defined pattern on a plane normal to the roots. It is desirable, but more difficult, to express the results in a generalised way, so that the effect of any particular distribution of roots can be inferred directly without using the analog. The basic problem is to describe the pattern of roots by some index of dispersion which can be related to the competitive effect. The pattern of points on a surface has been discussed frequently [12 17] and a variety of parameters for describing it has been proposed. It is well recognised that no single number can define pattern accurately, and that some form of frequency distribution is ideally required. Since it is preferable to avoid such complexity until it can be shown to be essential, we have used the simplest single-value indices of dispersion available. There is no necessary connection between these and the competitive effect between roots, and any relationships found are regarded as empirical. The indices chosen were the variance-mean ratio (V/M), *i.e.* the variance of the number of points in a sample square of chosen size compared with the mean, and the mean nearest neighbour distance ($\bar{y}$); and these indicate whether the root pattern is regular, random or clumped. For a random pattern $V/M = 1$. For more regular patterns $V/M < 1$, and for more clumped patterns $V/M > 1$. In terms of nearest neighbour distance, for a completely regular pattern $\bar{y} = 1/\sqrt{\rho}$; for a random pattern $\bar{y} = 0.5/\sqrt{\rho}$; and for a clumped pattern $\bar{y} < 0.5/\sqrt{\rho}$.

A total of 14 patterns of 40 points were prepared manually to span the range from regularity to extreme clumping, and the resistors on the analog were arranged according to these. The analog then represents a sample from a large area on which the selected pattern of roots is continually repeated, and the sample edge is therefore a zero-transfer boundary. The variance–mean ratio and the mean nearest neighbour distances were determined for each pattern; V/M was easy to determine, by placing a grid with 59 squares marked on a transparent sheet over the pattern, counting the

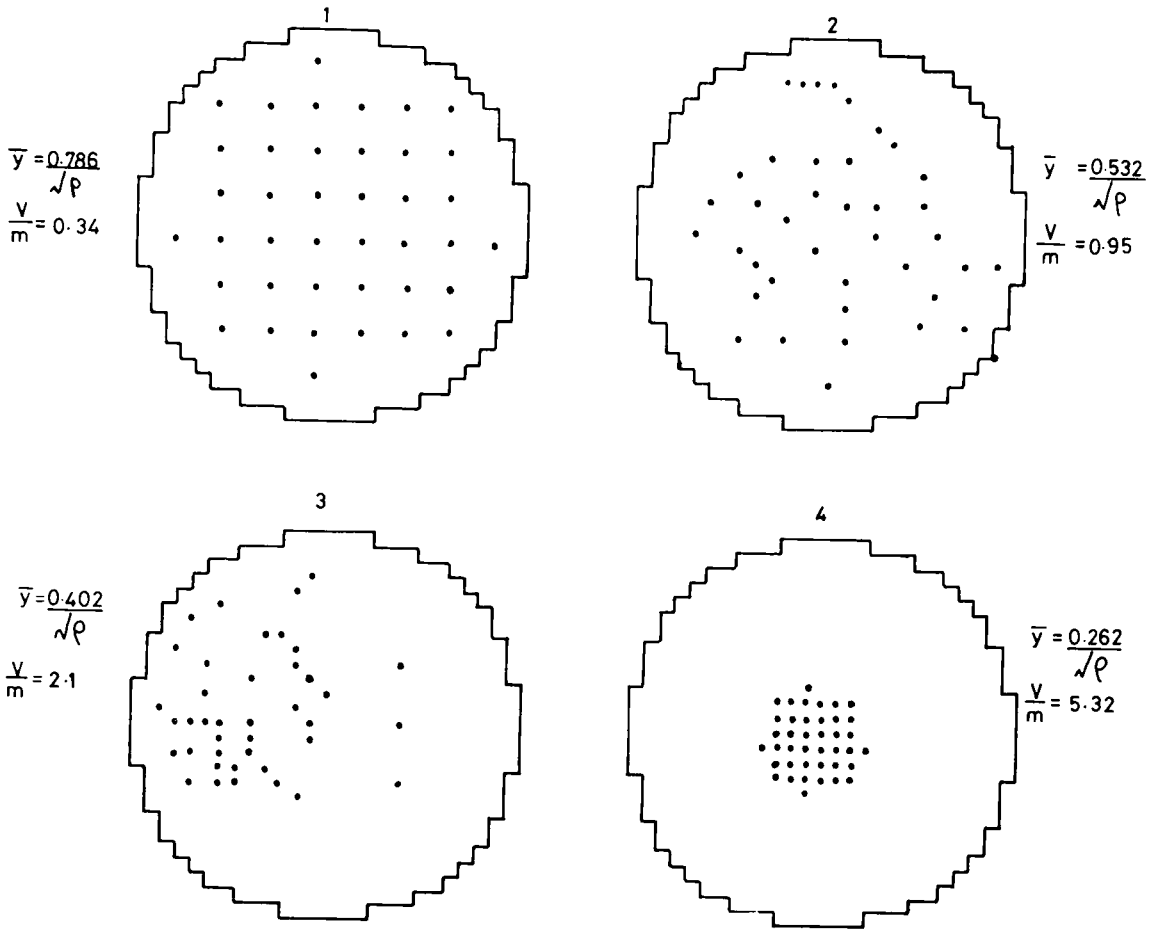


Fig. 3. Regular, random, clumped and highly clumped patterns with their indices of dispersion.

number of points in each square, and determining the variance of these numbers. The result depends upon the size of grid squares chosen [12] and we suggest that this should be of the order of $\sqrt{Dt}$, which is roughly the distance at which a root can influence its neighbours (see p. 696). Changes in V/M therefore reflect changes in the numbers of roots within this distance of each other. The nearest neighbour distance was found by direct measurement from each root in turn.

The effects of changes of pattern (Fig. 3) on the rate of uptake are illustrated in Fig. 4. Uptakes by other patterns can be found by interpolation on this figure. The following points are clear from inspection:

a) The degree of competition depends upon D, t and ρ, as for the regular distributions in Fig. 2a and b.

b) There are relatively small differences in uptake between regular and random patterns.

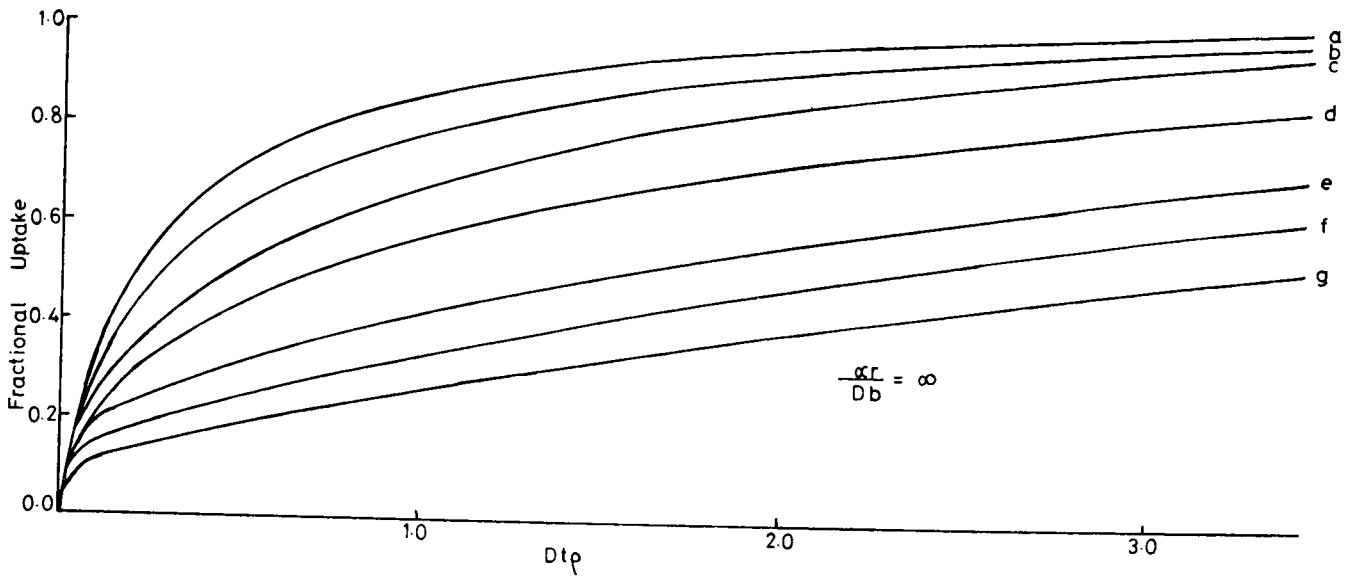


Fig. 4. Fractional uptake by different patterns of zero sink roots plotted against D t ρ, for r = $0.057/\sqrt{\rho}$.

Letters on curves	a	b	c	d	e	f	g
V/M	0.34	0.95	1.6	2.4	2.6	4.4	5.3
$\bar{y}$ (in $\rho^{-\frac{1}{2}}$)	0.79	0.53	0.41	0.34	0.31	0.28	0.26

c) Very large differences in uptake can be caused by clumping, the effect again depending upon time.

Results for all the 14 patterns are in Figs. 5a and b in which fractional uptake is plotted against the dispersion parameter for different values of Dtρ. Neither V/M nor $\bar{y}$ are exact measures of the effect of pattern since the points on the graph are scattered, but they give quite a good indication of important effects. There is little to choose between these two parameters, but the relation of V/M to competitive effect is more linear, which is useful.

Barley [3] is the only other author who has considered the effects of root pattern. His method was to construct Voronoi polygons around each root and then replace each of these with a circle of equivalent area with the root at the centre. As he states, the results must be in error if the root is near the edge of the polygon. There will also be error if the polygon shape is very dissimilar to that of a circle, which is common even with randomly distributed roots. His results are not given in detail, but he concluded that the difference in uptake rate between the most clumped and the most regular pattern used was not greater than 5 per cent. Our results are thus completely different, since we find reductions in uptake rate of over 75

per cent for similar uptake times. We have not been able to compare results from the two methods for identical patterns, but even a random pattern can give a 20 per cent reduction according to our results. Barley does not state the time at which his comparison was made, and it may be very early or very late in the uptake period. He states that all the patterns had the same variance-mean ratio, but this is not possible for a fully regular reference pattern, which should have a V/M of zero. In his treatment, different patterns were

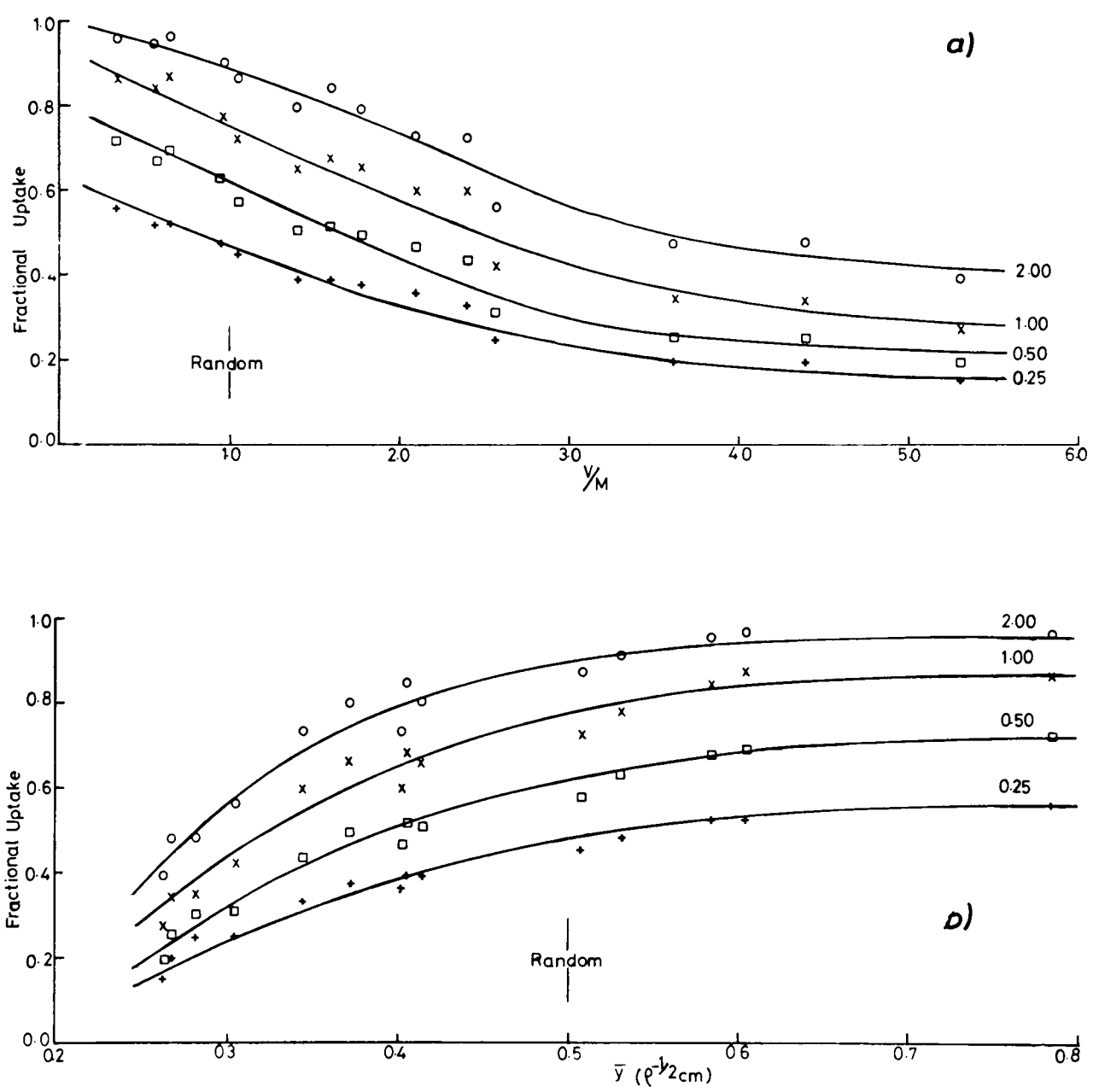


Fig. 5. **a**. Fractional uptake plotted against V/M for zero sink roots. Numbers on the curves are values of D t ρ. **b**. Fractional uptake against $\bar{y}$ (units of $\rho^{-\frac{1}{2}}$) for zero sink roots. Numbers on the curves are values of D t ρ.

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generated by altering the skewness of the frequency distribution of the radii of the equivalent circles, but not the variance or the mean, whereas it is these which are most likely to affect uptake.

2.9 APPLICATION OF RESULTS TO 3-DIMENSIONAL ROOT SYSTEMS

To be of use, these results must be applicable to 3-dimensional root systems. It is not practicable to build a similar 3-dimensional analog, and an approximate transformation must be used. A plane cut through a root system in soil will reveal a set of root ends, which will have a pattern of the type discussed here. Patterns with a different index of dispersion may be found on the two planes at right angles to the first. A suitable index of dispersion for the 3-dimensional distribution may be obtained from an average, weighted according to the number of intercepts on each plane. The measured intercept density on the planes cannot be used directly in relation to our results, since the analog model assumes parallel roots, which will have an intercept density equal to the length per unit volume. This is not true for roots which are differently oriented in space. The relation between root length and intercept density has been discussed in detail by Baldwin, Tinker and Marriott [2]. To overcome this, a real root system is considered equivalent to a parallel array, with the same total length per unit volume, the same index of dispersion for intercepts on the surface and ρ equal to the length per unit volume. Since, for a random but not necessarily isotropic distribution, the mean distance from a random point to the n^{th} nearest root is the same for the 2- and 3-dimensional cases (Marriott, submitted to Biometrics), this transformation seems reasonable. The results given are then directly applicable to a 3-dimensional system.

2.10 CONCLUSIONS

The results given here establish that the spatial distribution or pattern of strongly-absorbing roots can affect the uptake rate greatly. Root systems which are confined to cracks and gaps between peds are therefore likely to be inefficient in the absorption of at least some ions.

The effect of pattern varies with density. At low densities, it is unlikely to be important as the uptake rate per root is already very

much decreased by the time competition takes effect. On the other hand, at very high densities, the value of Dt ρ may be such that even the most clumped pattern will exhaust the soil. In this latter case, although the pattern itself is not important, it is evident that the root system is inefficient.

With the graphs given here, or similar ones which could readily be made, it is possible to determine the approximate uptake or uptake rate by any given root system from a soil of known properties. We recapitulate the steps to be carried out in practice, recalling that the results may be less accurate for $\alpha r/bD$ less than 2.5:

a) Determine the total length per unit volume and the index of dispersion (V/M or $\bar{\gamma}$) for the roots in the defined soil volume, by methods such as those of Baldwin, Tinker and Marriott [2], at two or more times after roots enter it. If the index of dispersion differs on the three planes, then an average, weighted according to the number of intercepts per plane, is taken.

b) Calculate Dt $\bar{\rho}$. ρ at any time is taken equal to the root length per unit volume. Plot ρ against t, and integrate to get $t\bar{\rho}$, hence Dt $\bar{\rho}$.

c) With an estimated value of $\alpha r/bD$, determine fractional uptake of diffusible nutrient from Fig. 2b, for a regular array with $r = 0.057/\sqrt{\rho}$, at the correct value of Dt$\bar{\rho}$.

d) Correct for effect of pattern, by obtaining a percent correction factor from Fig. 5a or b, or from Fig. 4a by interpolation. This assumes that the index of pattern remains constant as the density develops.

e) Correct for the fact that r–ρ relationship is different from $r = 0.057/\sqrt{\bar{\rho}}$, which is used in Fig. 2b and 4a. Calculate the correct r–ρ relationship and estimate a per cent correction factor by interpolation on Fig. 2a at the appropriate Dt$\bar{\rho}$.

Thus with a knowledge of the development of root length with time and a value of $\alpha r/Db$, the uptake after any time can be estimated. This can be compared with a maximum possible uptake and so give a measure of the root system efficiency. Alternatively, if the uptake is known after any time, the time-density relationship can be used to give an estimate of $\overline{\alpha r}$ for the root system, using a reversed procedure. This latter is a measure of whether the soil properties or the plant properties are limiting uptake [15].

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2.11 Investigation into the effects of root density

It seems obvious that the greater the density of a root system, the more nutrient it will take up in any one time from any block of soil. This must be expressed quantitatively if we are to analyse the behaviour of any root system, to develop ideas on root system efficiency, or to predict the effect that adverse physical, chemical or biological conditions may have if they restrict the development of an optimum rooting density.

The analogue procedure for varying root density is described in paragraph 2 section 2.7.

2.11.i Details of the method for changing root density

Root density is varied by making the physical size of the analogue smaller in relation to a given root radius. This is achieved by increasing the number of nodes which simulate a single root.

Sanders et al. (1971) have discussed the situation where one node represents a root, and calculated the root radius a to be $a = .234h$ cm. The additional systems used here are shown in fig. 2.2. Following Sanders et al (1971), we consider the root to be a square of side r, in which the resistance is zero, and calculate the remaining internode resistance.

In fig. 2.2 a

Resistance of shaded area should be $= \int_{j=\frac{r}{2}}^{j=\frac{\sqrt{2}h}{2}} \frac{R}{2} \frac{dj}{j} = \frac{R}{2} \ln \frac{\sqrt{2}h}{r/2}$

In fact,

Resistance $= \frac{R}{6}$

$\therefore \ln \frac{\sqrt{2}h}{r/2} = \frac{1}{3}$

$\therefore r = 1.52h$

and if $2\pi a = 4r$

$a = 0.97h$

In fig. 2.2 b

Resistance of shaded area should be $= \int_{J=\frac{r}{2}}^{J=\frac{3h}{2}} \frac{R}{2} \frac{dJ}{J} = \frac{R}{2} \ln \frac{3h}{r}$

In fact, it is $\frac{R}{2} \times \frac{1}{3}$

$\therefore \ln \frac{3h}{r} = \frac{1}{3}$

$\therefore r = 2.15h$

and $a = 1.37h$

The root radius for figs. 2.2 a and d was calculated directly from the perimeter of the excised areas, which gave values of $a = 2.62h$ and $a = 3.52h$ respectively.

All these values of a were checked by comparing the uptake given by the 5 different systems into a root of the same real radius after the same real time. Comparisons were made at times sufficiently short, such that the roots behaved as isolated absorbers in infinite soil The trials indicated that the calculated a-h relations were correct.

2.11.ii Results of uptake by regular root systems of differing density

The results and conclusion for a root system of high α a/Db are given in section 2.7. Note that fig. 2a, section 2.7, is a plot of uptake ve sus time for roots of varying radius but constant α a/Db. If we consider the root radius to be constant, the plots become uptake versus time for roots of varying density, but the real time axis for each root system is different.

Fig. 2b, section 2.7, is a plot of uptake versus time for root systems of different α a/Db, for a single a-p relation. For values of

$\alpha a/Db > 2.5$, these curves can be converted to any $a-\rho$ relation using fig. 2a. The curves corresponding to fig. 2a for a range of values of $\alpha a/Db$ are given in fig. 2.4 i to iii. These additional curves extend the usefulness of fig. 2b, section 2.7.

2.12 The effect of pattern on the uptake by parallel roots of any density

The influence of rooting pattern on the uptake by any density of roots when $\alpha a/Db$ is high is discussed in 2.8. However, it is evident from fig. 1a section 2.6, that the magnitude of the effect is dependent on the value of $\alpha a/Db$. Graphs corresponding to figs. 4, 5a and 5b in section 2.8 have been constructed for $\alpha a/Db = .16$, and are shown in figs. 2.5 and 2.6 i and ii, respectively.

It is clear from inspection that pattern can seriously reduce uptake, even at low values of $\alpha a/Db$. The conclusions discussed in 2.10 apply equally to results where $\alpha a/Db$ is low. Table 2.1 has been prepared to allow an easier comparison of the effects of pattern for the two values of $\alpha a/Db$. It can be seen that when the effect of pattern is great, the difference caused by a large change in $\alpha a/Db$ is fairly small - the maximum difference being a factor of 2. Effects of pattern at other values of $\alpha a/Db$ may be estimated with reasonable accuracy by interpolation, either linearly, or non-linearly using fig. 2b section 2.7.

2.13 A model for calculating uptake by root systems developing in a finite volume of soil, when nutrient supply is by diffusion and mass flow

The procedure given in section 2.10 for calculating the theoretical uptake by any given root system from a soil of known properties is made more generally useful with the additional data given here. The more complete procedure is:

a) Measure the total length per unit volume and the index of dispersion

(V/M or $\bar{y}$) for the roots in the defined soil volume at two or more times after roots enter it. If the dispersion index differs in three mutually perpendicular planes, an average, weighted according to the number of intercepts per plane is taken.

b) Calculate $Dt\bar{\rho}$. ρ at any time is taken equal to the root length per unit volume. Plot ρ against t, and integrate to get $t\bar{\rho}$, hence $Dt\bar{\rho}$. The suitability of a time-averaged root density is discussed in section 2.22.2.

c) With an estimated $\alpha a/Db$ (tables 1.1a, b and c may be helpful), determine the fractional uptake of diffusible nutrient from fig. 2b, by a regular array of roots with $a = .057/\sqrt{\rho}$, at the value of $Dt\bar{\rho}$.

d) Correct for the effect of pattern at the appropriate $\alpha a/Db$, by interpolating from figs. 5a or b and 2.6 i and ii, or from fig. 4a and fig. 2.5. If the observed value of $\alpha a/Db$ is roughly 16 or .16, step c may be omitted, and the fractional uptake can be obtained from fig. 4a and 2.5 respectively. These curves may be appropriate for phosphate and nitrate respectively. Potassium may also have a high value of $\alpha a/Db$.

This step assumes that the index of pattern remains constant as the density increases.

e) Correct for the fact that the $a-\rho$ relation is different from $a = .057/\sqrt{\rho}$, by interpolating in figs. 2a, 2.4 i or 2.4 ii according to the value of $\alpha a/Db$, at the appropriate $Dt\bar{\rho}$.

This gives the uptake, expressed as a fraction of the total diffusible nutrient, after any time when the predominant mechanism of nutrient supply is by diffusion. Mass flow may be incorporated into this scheme, by adding an 'apparent' mass flow contribution, $v\bar{C}_1$, where $\bar{C}_1$ is the average concentration in the soil block, to the diffusive flux. This suggestion is tested for regular root systems of constant

density in section 2.[illegible]. It seems reasonable to apply it to clumped root systems, since, when mass flow increases uptake significantly, the effects of interroot competition will be reduced.

In the present work, a reversed procedure to that given above has been used, and a mean $\overline{\alpha a}$ for a root system estimated by measuring the root length development with time, and the uptake after consecutive times.

2.14 These results from the electrical analogue are a quantitative demonstration of the importance of root pattern, root density, root absorbing power and soil diffusion properties on the nutrient uptake by a plant after any time. However, a more versatile treatment for specific developing root densities, which included both nutrient supply mechanisms, i.e. diffusion and mass flow, would be of more general use for calculating or predicting uptake by different plant root systems. Such a treatment is developed in section 2.15. The results are applicable only to root systems which develop randomly in space. Until the importance of severe root clumping in the field is assessed, and until field data can be obtained more accurately than at the present, it is unwarranted to conclude that the model outlined in section 2.15 is severely limited, in that it applies only to random patterns of roots. The analogue may be used to obtain an empirical correction factor for clumping, if necessary.

Fig. 2.2 Circuit arrangements for varying root radius

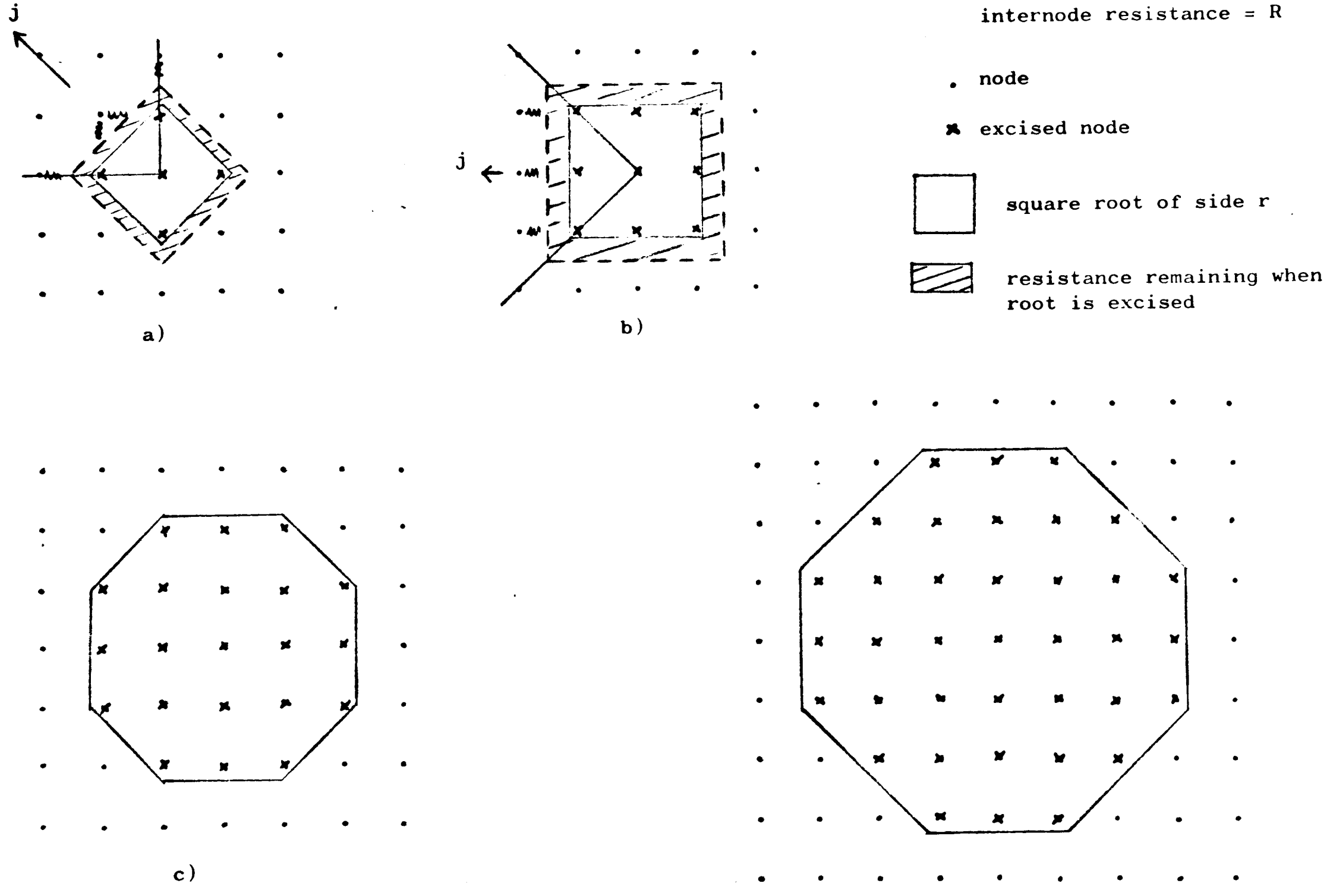


Fig 2.4i Fractional uptake by a regular array of parallel roots with $\alpha = a/Db = 2.5$ plotted against $Dt\rho$. Numbers on the curve are the $a\sqrt{\rho}$ product. Curves are correct for constant ρ and a, and variable t or D.

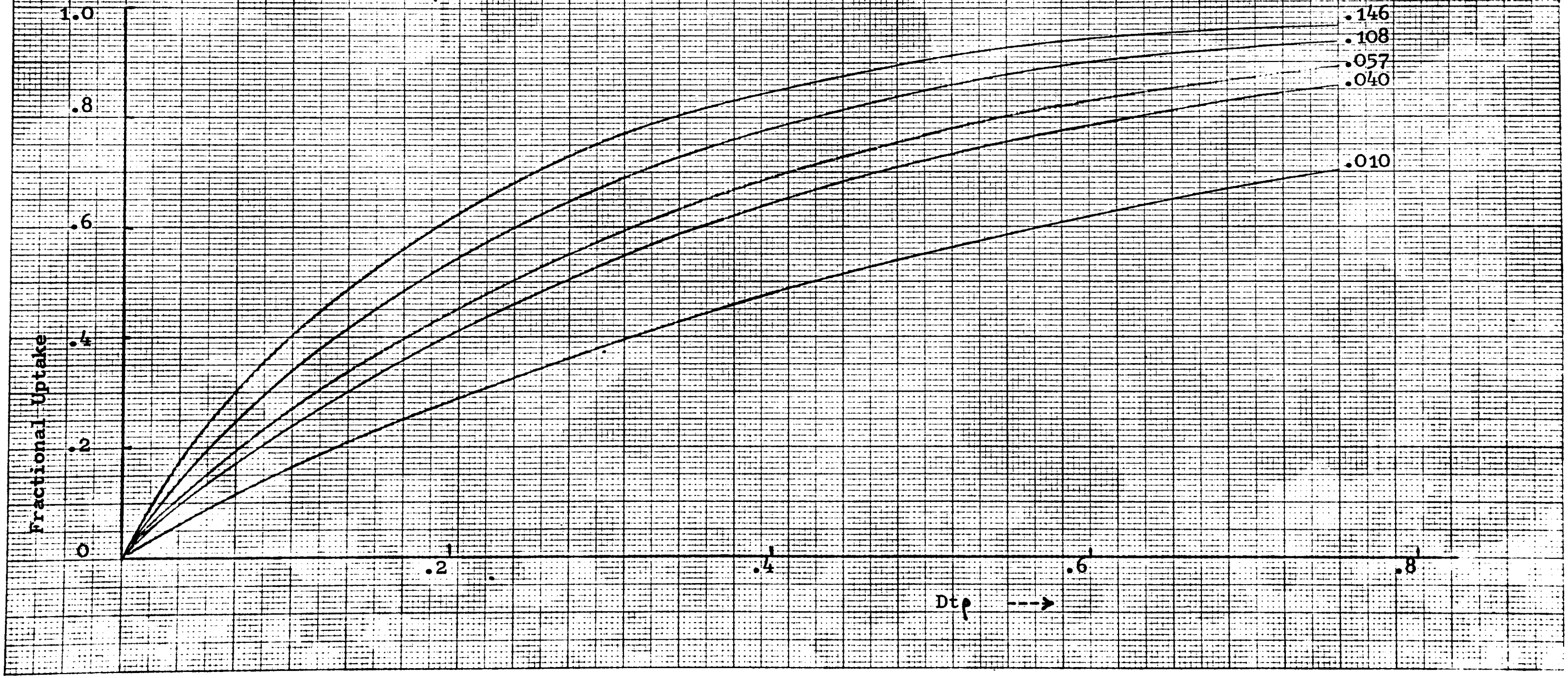


Fig 2.4ii Fractional uptake by a regular array of parallel roots with α a/Db=.53 plotted against Dtρ .Numbers on the curve are the a/ρ product. Curves are correct for constant ρ and a, and variable t or D.

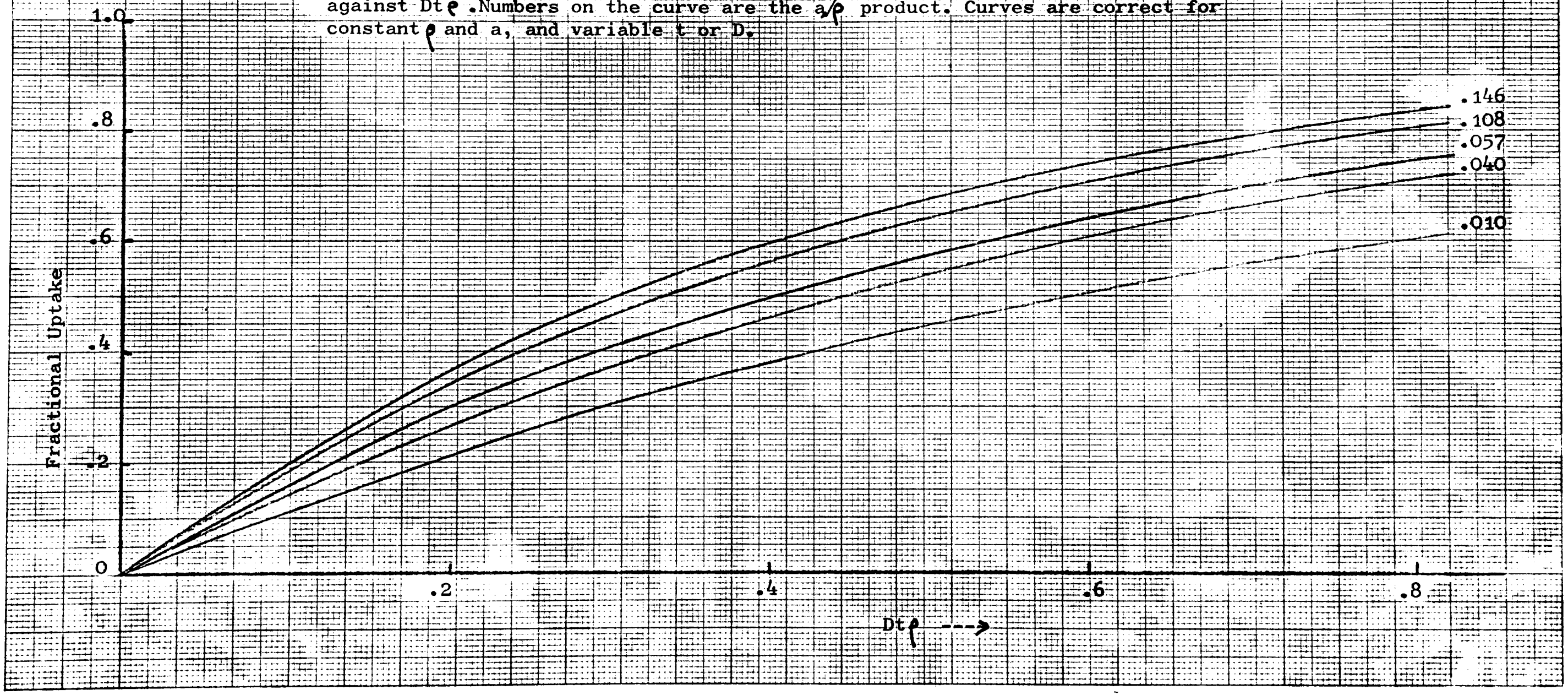


Fig 2.4iii Fractional uptake by a regular array of parallel roots with $\alpha a/Db = .16$ plotted against $Dt\rho$. Numbers on the curve are the $a\rho$ product. Curves are correct for constant ρ and a, and variable t or D.

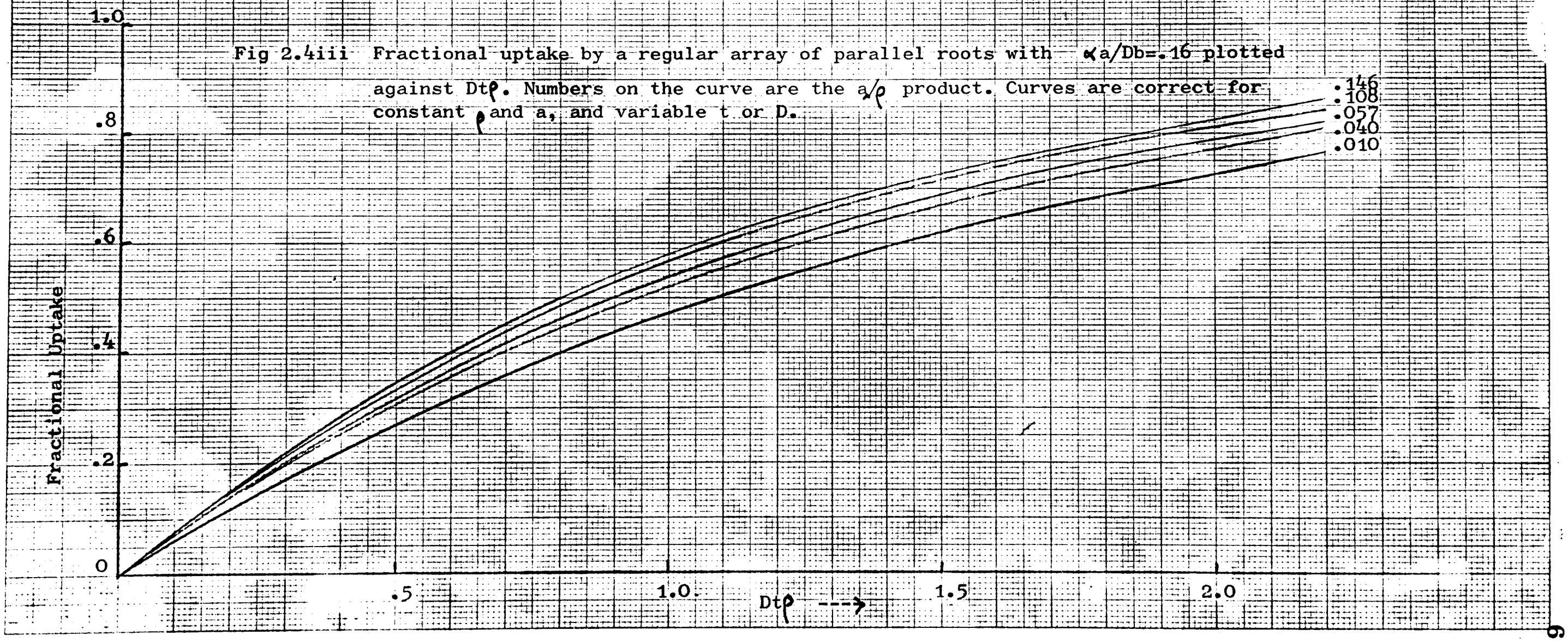


Fig 2.5 Fractional uptake into different patterns of roots, plotted against $Dt\rho$, for $a = .057/\sqrt{\rho}$

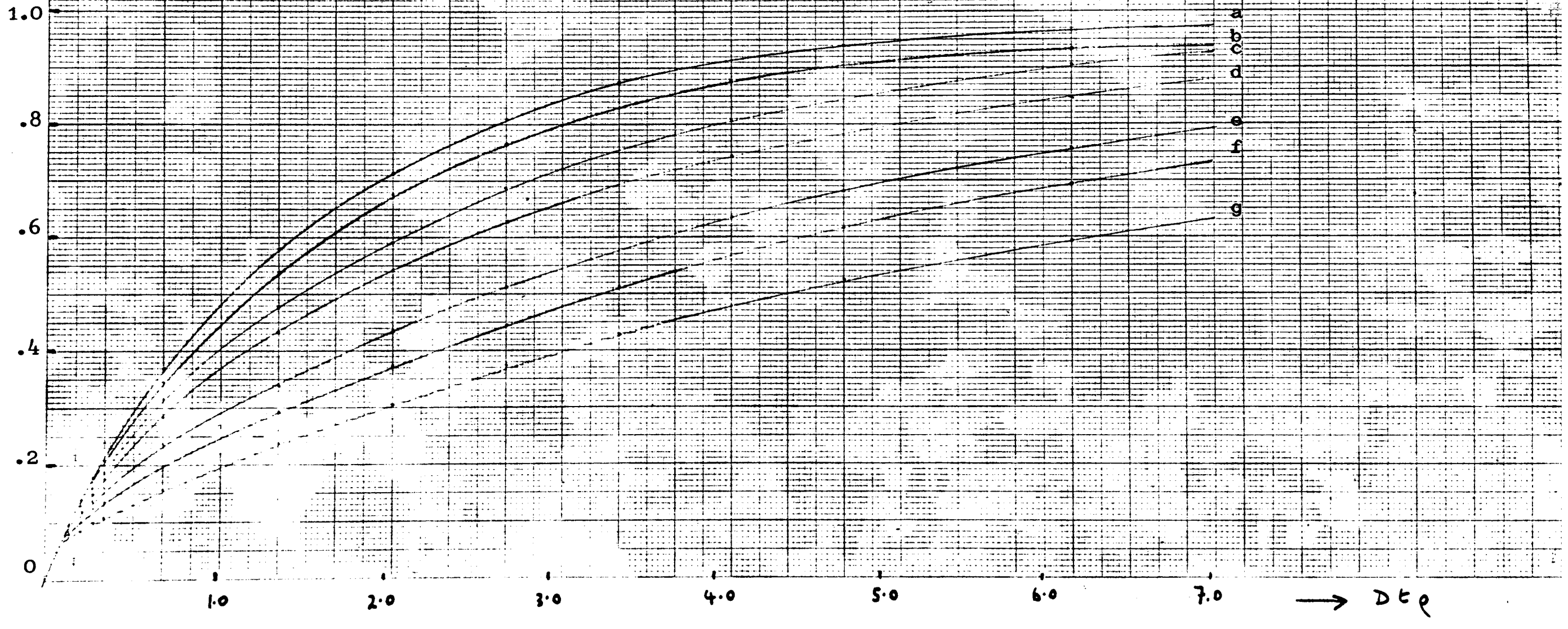


Fig 2.6i Fractional uptake plotted against V/M, $\alpha a/Db = .16$

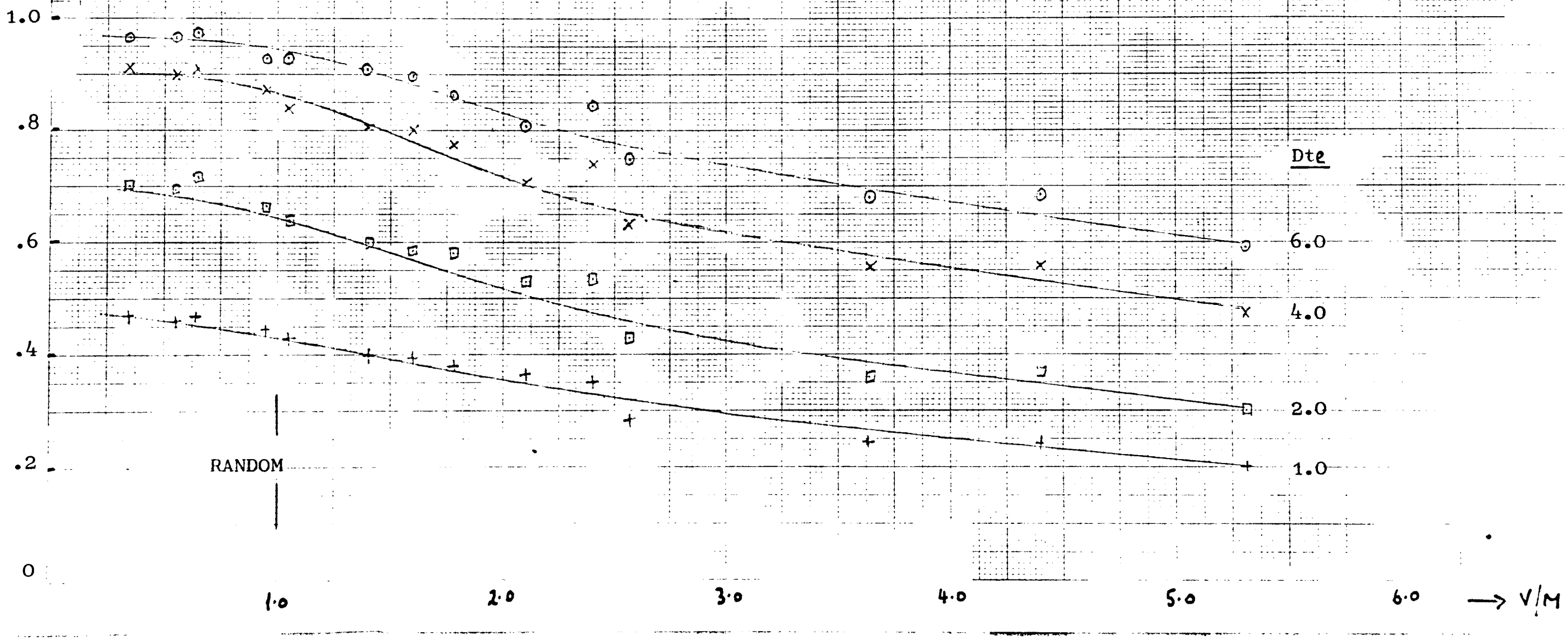


Fig 2.6ii Fractional uptake plotted against $\bar{y}$, $\alpha a/Db = .16$

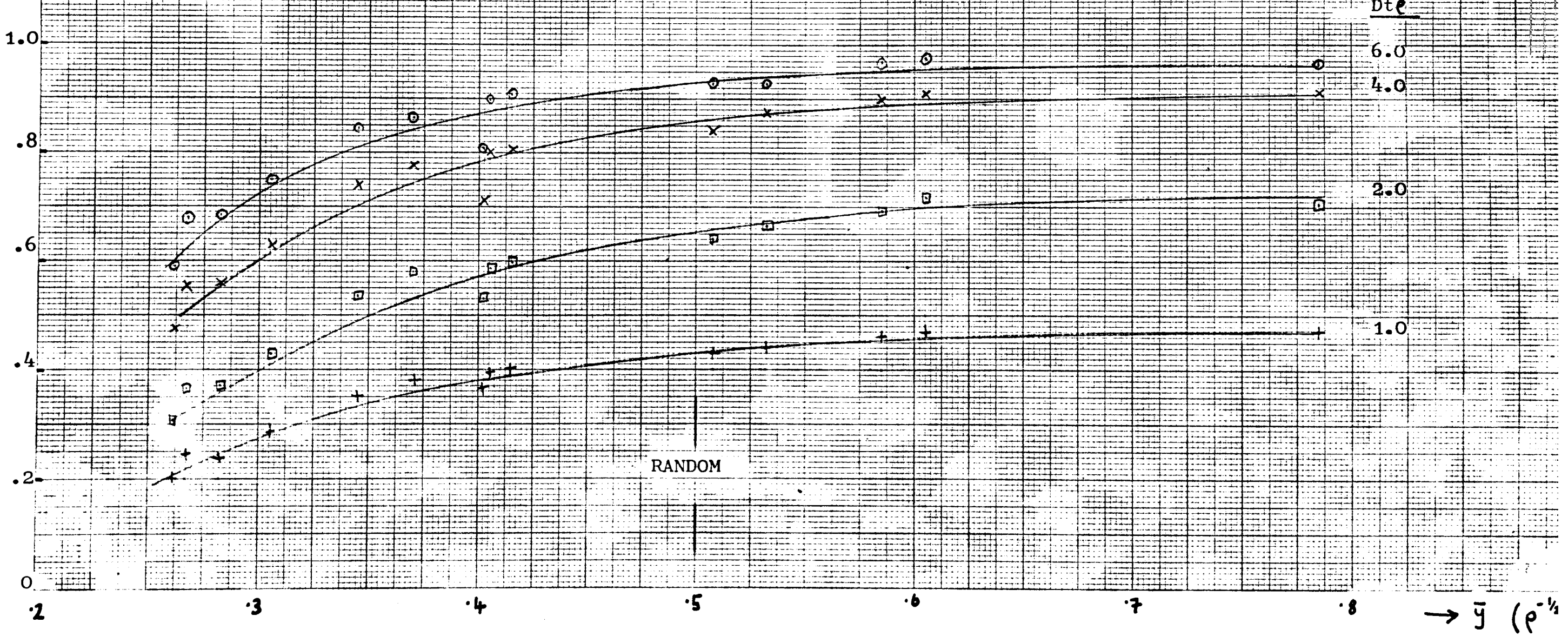


Table 2.1

Reduction in uptake caused by rooting pattern, expressed as a per cent of the uptake by a regular pattern, as it is affected by α a/Db.

The patterns are those used in Fig. 4a and 2.5, and results are given for two values of α a/Db, at 3 values of M_t/M_∞

M_t/M_∞	0.4		0.6		0.9	
α a/bD	15.9	0.159	15.9	0.159	15.9	0.159
pattern reference						
b	12.5	7.5	13.5	6.7	8.0	4.5
c	27.5	15.0	30.0	17.5	18.9	12.8
d	38.0	22.5	40.8	24.8	30.4	19.7
e	47.5	37.5	55.8	41.2	48.9	32.0
f	57.5	47.5	65.3	49.3	57.8	39.4
g	70.0	58.8	73.3	59.3	66.1	48.9

2.15 # 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.

by J.P. Baldwin, P.H. Nye and P.B. Tinker

2.16 ## Summary

A procedure is put forward for calculating the plant uptake of solutes supplied by diffusion and mass flow to the randomly dispersed roots of a developing root system. The model was tested as follows: (a) for a constant root density, and both transport processes - against a more accurate numerical solution of the same system (b) for an increasing root density, and for supply by diffusion only - by electrical simulation using the analog described in Part I. In both cases, results obtained by the two types of calculation were in close agreement.

A more approximate method which includes both supply mechanisms and does not require a computer is presented, and compared with an electrical simulation when there is no mass flow. Agreement is within 20%.

The model should be useful for predicting plant nutrient uptake from soil, and may be of special interest to modellers of the whole plant system.

Numbered equations in the text are <u>not</u> preceded by 2.

2.17 Solutes are supplied to plant roots by the processes of diffusion and mass flow. In part II[1] of this series we considered the effect of root density and pattern on the uptake of solutes supplied by diffusion only. The results applied strictly to root systems of constant density, but an averaging procedure was suggested for calculating the uptake when root density was changing. In this paper we present a general method for calculating the uptake of solutes supplied by both diffusion and mass flow to a randomly distributed developing root system.

In a system of many roots, we assume each root exploits a finite volume of soil, the size of which depends on the root density. For a regular array of parallel roots of constant density, the problem approximates to one of 2-dimensional transfer by mass flow and diffusion within a cylinder of soil around each root of radius $r = x$, where $x = 1/\sqrt{\pi L}$, subject to the conditions $dC/dr = 0$, $r = x$, $t > 0$, and to specified conditions at $r = a$. Passioura and Frere[7], and Nye and Marriott[5] have given numerical solutions of this problem. For an irregular root system, the volume of soil available to each root is not easily specified, and if the root system develops, it will decrease with time. Thus, the extension of the exact solution from constant to time dependent density is difficult. We have derived a simple approximate solution, involving only a first order differential with respect to time, which is sufficiently accurate for most practical purposes.

The approximate solution has been tested as follows:
a) For a regular array of roots of constant density - for diffusion without mass flow in a limited soil volume -

against a more exact numerical solution.

b) For a regular array of roots of constant density - for diffusion with mass flow in a limited soil volume - against a more exact numerical solution.

c) For randomly dispersed roots of increasing density - for diffusion alone - against results obtained using an electrical analog of the system[9].

List of Symbols

D = diffusion coefficient of solute, cm^2/sec

D_l = diffusion coefficient of solute in free solution, cm^2/sec

F = flux of solute ions, $mol/cm^2/sec$

v = water flux at root surface, $ml/cm^2/sec$

C = total concentration of diffusible solute, mol/cm^3 of soil

C_l = concentration of solute in solution, mol/ml of solution

C_{l_i} = initial solution concentration of solute, mol/ml of solution

C_{l_a} = solution concentration at root surface, mol/ml of solution

C_{l_r} = solution concentration at distance r cm, mol/ml of solution

$\overline{C_l}$ = average concentration in solution, mol/ml of solution

a = root radius, cm

r = radial distance from root, cm

r_{av} = value of r where solution concentration = average solution concentration, cm

α = root absorbing power, cm/sec

b = buffer power of soil = dC/dC_l

$\overline{b}_t$ = time averaged buffer power

t = time, sec

L = root density, cm/cm^3

$\overline{L}_t$ = time averaged root density, cm/cm^3

M_t/M_∞ = fractional uptake to time t

v_l = volumetric moisture content of soil

$\overline{v_{l_t}}$ = time averaged v_l

f_l = impedance factor

$\overline{f_{l_t}}$ = time averaged f_l

2.18 Model to calculate uptake by a developing root system where the roots are distributed randomly in a given volume

Boundary conditions for the transport processes around a given root.

The first is $t = 0,\ a \leq r \leq x,\ C_l = C_{l_i}$

The second relates rate of solute uptake into the plant to the solution concentration at the root surface. We have used $F = \alpha C_{l_a}$ with α constant, but other relations between F and C_{l_a} could be used, and could include the physiological influence of v on α, if known.

The boundary at r = x is defined as being where $dC/dr = 0$. The problem is to find the appropriate value of $r = x$ as the number of roots increases. In reality, each root may be considered to draw solute from a volume of soil, the size and shape of which depends on a) the number and position of all other roots and b) the length of time that it, and the others have been absorbing. In a 2-dimensional treatment, Barley[2] pointed out that these exploited areas are Voronoi polygons, but as the boundaries of these will change due to a) new roots entering and b) non-uniform depletion over the soil block as time progresses, we have not been able to develop this approach. Since the equations for transport within irregularly shaped bodies are not available, we have considered each root to exploit an average effective volume of soil, which is assumed to be a cylinder round each root. In reality, some will have more than this, others less. Thus the outside

boundary condition is $\frac{dC}{dr} = 0$, $r = x = \frac{1}{\sqrt{(\pi L)}}$, $t > 0$, $L = f(t)$. Although these conditions are for transport in 2-d, the results apply directly to roots distributed at random, though not necessarily isotropically, in 3-d[4].

2.19 Nutrient supply by diffusion - Constant density of regular roots.

First consider uptake associated with transport by diffusion alone with a constant density of regularly distributed roots. Since $F = \alpha C_{l_a}$ at $r = a$, the problem is to find the concentration at $r = a$ as a function of t, given the boundary conditions. We assume the concentration-distance profile develops in time in a stepwise manner and that at each step it approximates to the steady state profile. This approach has been used previously for water uptake[3]. The steady state profile is derived as follows.

Since solute is conserved in the steady state, the quantity of solute diffusing across any radial boundary is equal to the amount taken up by the root.

If $F = \alpha C_{l_a}$ at $r = a$, since, by definition, $F = -D\frac{dC}{dr}$

$$2\pi r Db \frac{dC_l}{dr} = 2\pi\alpha a C_{l_a} \qquad 2\cdot(i)$$

$$\therefore \int_{C_{la}}^{C_{lr}} Db\, dC_l = a\alpha C_{l_a} \int_a^r \frac{dr}{r}$$

If we assume Db, which is approximately equal to $D_l v_l f_l$[8] is constant,

$$C_{l_r} = C_{l_a} \left(1 + \frac{\alpha a}{Db} \ln \frac{r}{a}\right) \qquad 2.(ii)$$

and $$C_{l_x} = C_{l_a} \left(1 + \frac{\alpha a}{Db} \ln \frac{x}{a}\right)$$

The average value of C_{l_r} is given by

$$\overline{C_l} = \frac{\int_a^x 2\pi r\, C_{l_r}\, dr}{\pi(x^2 - a^2)}$$

$$= C_{l_a}\left(1 - \tfrac{1}{2}.\frac{\alpha a}{Db} + \frac{x^2\,\frac{\alpha a}{Db}}{x^2 - a^2}\ln\frac{x}{a}\right) \quad 2.\text{(iii)}$$

If $x^2 \gg a^2$, then equation (iii) reduces to

$$\overline{C_l} = C_{l_a}\left(1 + \frac{\alpha a}{Db}\ln\frac{x}{1.65a}\right)$$

Thus the value of r such that $C_l = \overline{C_l}$ is approximately $\frac{x}{1.65}$.

The rate of uptake equals the rate of loss of solute, i.e.

$$\frac{dC_l}{dt} \times \frac{b}{L} = -2\pi a\alpha C_{l_a} \quad 2.\text{(iv)}$$

Eliminating C_{l_a} from (iv) using (iii) gives

$$\frac{d\overline{C_l}}{\overline{C_l}} = \frac{-2\pi a\alpha L}{b}\cdot\frac{dt}{\left(1 - \tfrac{1}{2}\frac{a\alpha}{Db} + \frac{x^2\,\frac{a\alpha}{Db}}{x^2 - a^2}\ln\frac{x}{a}\right)}$$

For constant L and assuming b is constant, integration gives

$$\frac{\overline{C_l}}{C_{l_i}} = \exp\left(\frac{-2\pi a\alpha L t}{b\left(1 - \tfrac{1}{2}\frac{a\alpha}{Db} + \frac{x^2\,\frac{a\alpha}{Db}}{x^2 - a^2}\ln\frac{x}{a}\right)}\right) \quad 2.\text{(v)}$$

and $\frac{M_t}{M_\infty} = 1 - \frac{\overline{C_l}}{C_{l_i}}$ can be calculated directly.

Note that if only solution phase ions are mobile then $Db = D_l v_l f_l^8$. The buffer power b then enters only to divide t, i.e. doubling the buffer power serves to double the time taken to reach a given fractional depletion of the soil volume.

Test of equation (v)

To test equation (v), the numerical computer solution given by Nye and Marriott[5] was modified to allow for $dC/dr = 0$ at $r = x$, i.e a finite system.

The essential difference between the steady state and true solution is shown in fig. 1, which compares the concentration distance profiles generated by Nye and Marriott's method with those calculated from equations (ii) and (iii). Note that the value of r where $C_l = \overline{C_l}$ is approximately the same in the two methods, except at short times.

Equation (v) was tested by comparing the value for uptake by a constant density of roots with that calculated by the more exact numerical method[5]. The calculations, for a range of values of $\alpha a/Db$ are given in figure 2. Agreement is very good at values of $\alpha a/Db < 5.0$. The difference reaches a maximum of 15% for the very high value of $\alpha a/bD$. This error is caused by the fact that the model assume the radial flux is constant at all values of r; the larger $\alpha a/Db$ is, the less correct is this assumption.

Agreement between the two methods may depend on the root density. The steady state model assumes that the depletion zone instantly reaches the boundary, which will be less true as x increases. However, as x increases, so the mean concentration in the soil volume decreases relatively more slowly. These two factors therefore compensate for each

other. Figure 3 is a plot of the relative rates of uptake, at the same M_t/M_∞, given by the steady state solution and true solution against root density for a high $\alpha a/bD$, which will show the maximum effect of density. For any density, this relative uptake rate is constant up to an M_t/M_∞ of 0.9. Thus the accuracy of the method is insensitive to density over the range considered.

2.20 Nutrient supply by diffusion and mass flow - Constant density of regular roots.

Where there is a mass flow of solvent, the mass balance equation for solute is

$$\frac{1}{r}\frac{\partial}{\partial r}\left(r.D.b\frac{\partial C_l}{\partial r} + a.v.C_l\right) = \frac{\partial C}{\partial t} \qquad 2.(vi)$$

(Nye and Spiers[6], eqn. (6)). This assumes D is independent of v.

In the steady state $\frac{\partial C}{\partial t} = 0$, and the equation can be solved for constant mass flow of solvent to give (Nye and Spiers[6], eqn. (8) and (10)).

$$\frac{C_{l_r}}{C_{l_a}} = \frac{\alpha}{v} + \left(1 - \frac{\alpha}{v}\right)\left(\frac{r}{a}\right)^{-\frac{av}{Db}} \qquad 2.(vii)$$

We note that in the case of a root in an infinite volume of soil, as considered by Nye and Spiers[6], no steady state is attained unless $\frac{av}{Db} > 2$. However, for a finite volume of soil, in which solution of appropriate concentration is supplied at the outer boundary, a steady state can always be attained[3].

Note that, by writing (as Gardner[3]), $\left(\frac{r}{a}\right)^{-\frac{av}{Db}} =$

$\exp\left(\frac{av}{Db} \ln \frac{r}{a}\right) = 1 - \frac{av}{Db} \ln \frac{r}{a}$ if the exponent is small, we obtain

$$\frac{C_{l_r}}{C_{l_a}} = 1 + \frac{\alpha a}{Db} \ln \frac{r}{a} - \frac{av}{Db} \ln \frac{r}{a}$$

which reduces to equation (ii) when v = 0.

We now proceed to find the average value of C_{l_r} as before.

$$\frac{\overline{C_l}}{C_{l_a}} = \frac{\int_a^x \left[\frac{\alpha}{v} + (1 - \frac{\alpha}{v})(\frac{r}{a})^{-\frac{av}{Db}}\right] 2\pi r dr}{\pi(x^2 - a^2)}$$

$$= \frac{\alpha}{v} + (1 - \frac{\alpha}{v}) \frac{2}{2 - \frac{av}{Db}} \left[(\frac{x}{a})^{2 - \frac{av}{Db}} - 1\right] \Big/ \left[(\frac{x}{a})^2 - 1\right] \quad 2\text{(viii)}$$

Note that if $\frac{av}{Db} = 2$, $\frac{2}{2 - \frac{av}{Db}} \left((\frac{x}{a})^{2 - \frac{av}{Db}} - 1\right) = 2 \ln \frac{x}{a}$

Solute uptake using this formula is calculated by a stepwise procedure. For unit volume of soil, the uptake rate, $2\pi a\alpha LC_{l_a}$, is calculated from the value of $\overline{C_l}$, which is the mean concentration in the block at the beginning of each time step, the value of x, which equals $1/\sqrt{\pi L}$, and the value of av/Db. In step 1, uptake = $2\pi a\alpha LC_{l_{a_1}} t_1$ and $\overline{C_{l_1}} = C_{l_i}$. This uptake reduces $\overline{C_l}$ by an amount equal to that uptake divided by b. Therefore, for step 2, $\overline{C_l} = \overline{C_{l_2}} = (\overline{C_{l_1}} - \frac{1}{b}(2\pi a\alpha LC_{l_{a_1}} . t_1))$. By proceding in small time steps, the uptake after any time can be computed.

The steady-state concentration-distance profile given by equation (vii) was used to calculate the course of uptake from the following model system. It was compared with the more exact results derived from Nye and Marriott's[5] numerical

solution applied to the same model. The root system of constant density and regular array exploits a volume of soil and no water or nutrient crosses the boundary. In addition, the hydraulic conductivity is sufficiently high that it can be assumed that as transpiration depleted the soil moisture, no appreciable gradients of soil moisture were set up, i.e. v_1 depended on time only and not on distance.

As in the previous section, we assume the concentration-distance relation during depletion approximates to the steady-state profile given by equation (vii). The results, for the range of values of $\alpha a/Db$ and water flux that are normally found, are in Table 1. The percent increase in uptake due to mass flow given by the two methods is in close agreement. Note that the effect of mass flow on uptake depends on $\frac{\alpha a}{Db}$, and in particular, that there is a small effect when $\frac{\alpha a}{Db}$ is high. Gaps in the table occur when the soil dried out too much for uptake to continue, i.e. when $v_1 < 0.1$.

2.21 Root system of increasing density

The model for uptake using equation (viii) may be extended to include a developing root system by letting $x = 1/\sqrt{\pi L}$, where $L = f(t)$. The model assumes that each new root samples the mean nutrient concentration in the zone, i.e. that the roots are entering the block at random positions. In this treatment, the volume of soil considered is not a whole root system, but is a zone sufficiently small for the root density to show no average gradient over it. For a complete root system, the uptake in different zones can be calculated, and the total obtained by summation.

The program used to calculate uptake from equation (viii) in Fortran, is available on request from the Department of

Agricultural Science, Oxford.

Comparison with analog solution - Diffusion only

The model was tested by comparing results obtained from a step-wise solution as described in the previous section, but using, instead of equation (viii), equation (iii) when $x = f(t)$, with those obtained using an electrical analog[9]. The root and soil properties were identical in the two cases. An increasing root density is easily simulated on the analog by increasing the number of connections between the charged network and earth, as time progresses. The positions of the roots on the analog were chosen from random number tables. Root density was assumed to increase exponentially with time, i.e. $L = L_o e^{kt}$. The results for $k = 2.4$ and 0.85 day^{-1}, for $D = 3 \times 10^{-6}$ cm^2/sec, and for $\alpha a/bD = 13.25$ are in figure 4. Electrical time on the analog is a function of D and real time[9], and thus k and D are inversely related.

Initially, the approximate method underestimates uptake, but later the calculated uptake rate is greater than it should be, and the two curves cross over. This behaviour is the result of two approximations with opposing effects. Real uptake initially is more rapid because the model tends to underestimate uptake rate, as shown in figure 2. Real uptake later is slower, because the contribution per root to the total uptake by the more regularly dispersed roots becomes successively greater as the effect of competition in the clumps increases. In the model, these more regularly dispersed roots are given a lower value of $r = x$ than they should have, and therefore their uptake rate is being calculated greater than it should be. The result of these two factors is the very good agreement

between the model and the analog results.

Since the analog does not provide for mass flow, it is not possible to test the model in this way when mass flow is included.

2.22 Approximations not requiring a numerical solution

1. For a simple estimation of uptake by a randomly dispersed root system with density varying in a known way with time in a finite volume of soil, the following method may be used. The calculation includes nutrient supply by diffusion and mass flow.

Following the argument on page 6, eliminating C_{l_a} from (iv) using (viii) gives

$$\frac{d\overline{C_l}}{dt} = \frac{-2\pi a\alpha L}{b} \cdot \frac{\overline{C_l}}{\frac{\alpha}{v} + \left((1 - \frac{\alpha}{v})\left(\frac{2}{2 - \frac{av}{Db}}\right)\left((\frac{x}{a})^{2-\frac{av}{Db}} - 1\right)\right)\Big/\left((\frac{x}{a})^2 - 1\right)} \quad \text{2.(ix)}$$

This equation cannot usually be integrated directly, since L and $Db \simeq D_l v_l f_l$ vary with time. For a non-adsorbed ion $b = v_l$, and also varies with time. It may, however, be sufficiently accurate to use time averaged values, calculated by integrating the respective time curves. Hence, for non-adsorbed ions

$$\frac{\overline{C_l}}{C_{l_i}} = \exp\left[\frac{-2\pi a\alpha \overline{L}_t t}{\overline{b}_t\left(\frac{\alpha}{v} + \left((1 - \frac{\alpha}{v})\left(\frac{2}{2 - \frac{av}{\overline{D}_t\overline{b}_t}}\right)\left((\frac{x}{a})^{2-\frac{av}{\overline{D}_t\overline{b}_t}} - 1\right)\right)\Big/\left((\frac{x}{a})^2 - 1\right)\right)}\right]$$

.....2.(x)

where $x = 1/\sqrt{\pi \bar{L}_t}$, and M_t/M_∞ follows. For adsorbed ions, if $\overline{C_1} = f(C)$ we have $\frac{dC}{dt} = -2\pi a \alpha C_{1_a} L$ and

$$\frac{dC}{\overline{C_1}} = \frac{dC}{f(C)} = \frac{-2\pi a \alpha \bar{L}_t . dt}{\frac{\alpha}{v} + (1 - \frac{\alpha}{v})\left(\frac{2}{2 - \frac{av}{\bar{D}_t \bar{b}_t}}\right)\left((\frac{x}{a})^{2 - \frac{av}{\bar{D}_t \bar{b}_t}} - 1\right) \Big/ \left((\frac{x}{a})^2 - 1\right)}$$

which may be integrated to give C in terms of t.

The results obtained using equation (x) are compared with the electrical simulation described previously, in figure 5. In this approximation we are considering a developing root system to behave similarly to a static root system with the time-averaged density. Thus the results should apply to root systems which develop regularly. However, since the method underestimates uptake, we may consider the results to apply to a root system which in reality develops randomly. This method gives better results than method (2), but cannot be applied to clumped patterns of roots.

2. In part II[1] we suggested a procedure for calculating the uptake by any root system which develops with time when solute supply is by diffusion. Again a time averaged root density and diffusion coefficient is used. The value of M_t/M_∞ by roots of any pattern at the appropriate $Dt\bar{L}_t$ is derived from fig. 4 of Baldwin et al.[1], and when this is adjusted for the $a\sqrt{\bar{L}_t}$ relation, the uptake is obtained. The results using this method for the random patterns used earlier are also in figure 5. The method underestimates uptake by up to 25%. The use of a time averaged root density becomes less valid the more the density at the beginning and end of the

period differs from the mean. This is because roots are relatively more efficient at the beginning of their period of uptake. The example chosen shows a greater difference than normally found in plant root systems and the error, therefore, will probably be greater than that found in practice.

2.23 Conclusion

The method presented for calculating the relation between the concentration at the root surface, C_{1_a} and the mean solution concentration $\overline{C_1}$ has been used to estimate the nutrient uptake as a function of time by a root system of constant density and a developing random root system, and has given results in close agreement with the exact ones, where these are available. The model includes supply by diffusion and mass flow, and should prove a useful tool for interpreting experimental data.

The method should be specially useful in modelling and predicting plant nutrient uptake from specified zones of soil, since it links plant properties, namely the root demand coefficient, $\overline{\alpha a}$, the water inflow and the geometry and growth of roots, to readily comprehensible and measurable soil properties, namely the average soil solution concentration and the soil buffer power.

Acknowledgements

We are grateful for computer facilities provided by St. Cross College, and the Atlas Laboratory.

The computer programmes to calculate uptake using equation 2.viii, and Nye and Marriott's modified solution, are in appendices 1 and 2 respectively.

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Figure Captions

1. Plot of the concentration-distance profile given by Nye and Marriott's method ——— compared with that given by the steady state method – - – – for 4 values of M_t/M_∞ .
   o are the positions of r_{av} for the more exact method.
   r_{av} =0.162 cm for the steady state method
   $\alpha = 2 \times 10^{-4}$ cm sec^{-1}, $a = 5 \times 10^{-2}$ cm, $D = 3 \times 10^{-6}$ cm^2 sec^{-1}
   $b = 0.3$, $L = 5.3$ cm^{-2}

2. Plot of fractional uptake against time given by Nye and Marriott's method ——— and that given by equation (v), o.
   Numbers on the curve are of $\alpha a/Db$
   $a = 5 \times 10^{-2}$ cm, $Db = .09 \times 10^{-5}$ cm^2 sec^{-1}
   $\alpha = 2 \times 10^{-4}$, 10^{-5}, 10^{-6} and 10^{-7} cm sec^{-1}, $L = 5.3$ cm^{-2}

3. Plot of relative uptake rates given by the approximate and more exact solutions for diffusion in a finite volume against root density. $\frac{\alpha a}{Db} = 11.1$

4. Plot of fractional uptake against time by a randomly dispersed root system developing in a finite volume of soil. ———, mean of two replicates obtained using electrical analog, x, results calculated using equation (iii) when $x = f(t)$

   $\alpha = 5.52 \times 10^{-4}$ cm sec^{-1}, $a = .0216$ cm, $v = 0$,
   $D_1 = 10^{-5}$ cm^2 sec^{-1}, $v_1 = 0.3$, $f_1 = 0.3$

5. Comparison of fractional uptake against time calculated using the electrical analog ———, a time-averaged density and the analog △,▲, and a time-averaged density and equation (x) o,●. Root and soil properties the same as in fig. 4.

Fig 1

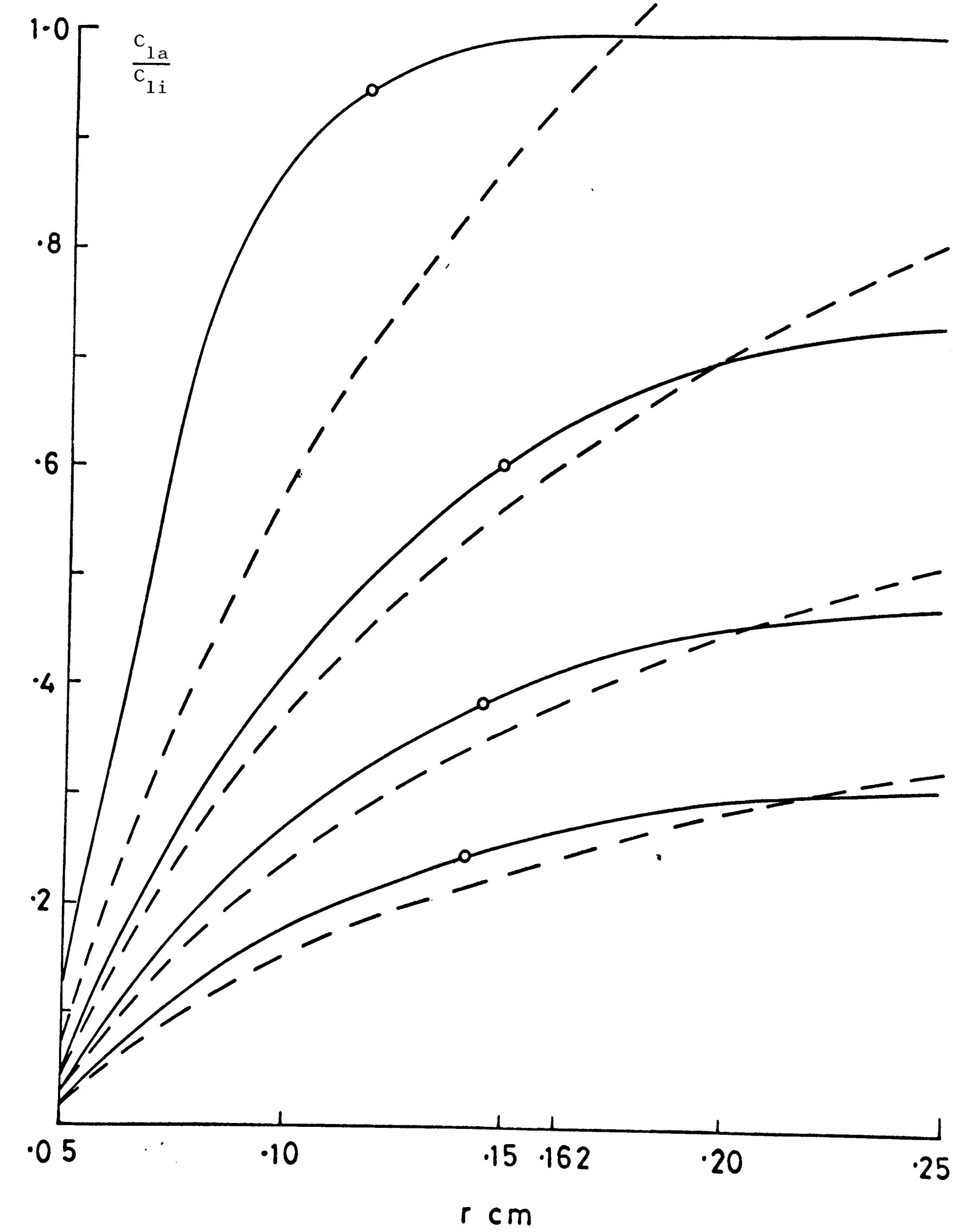


Fig 2

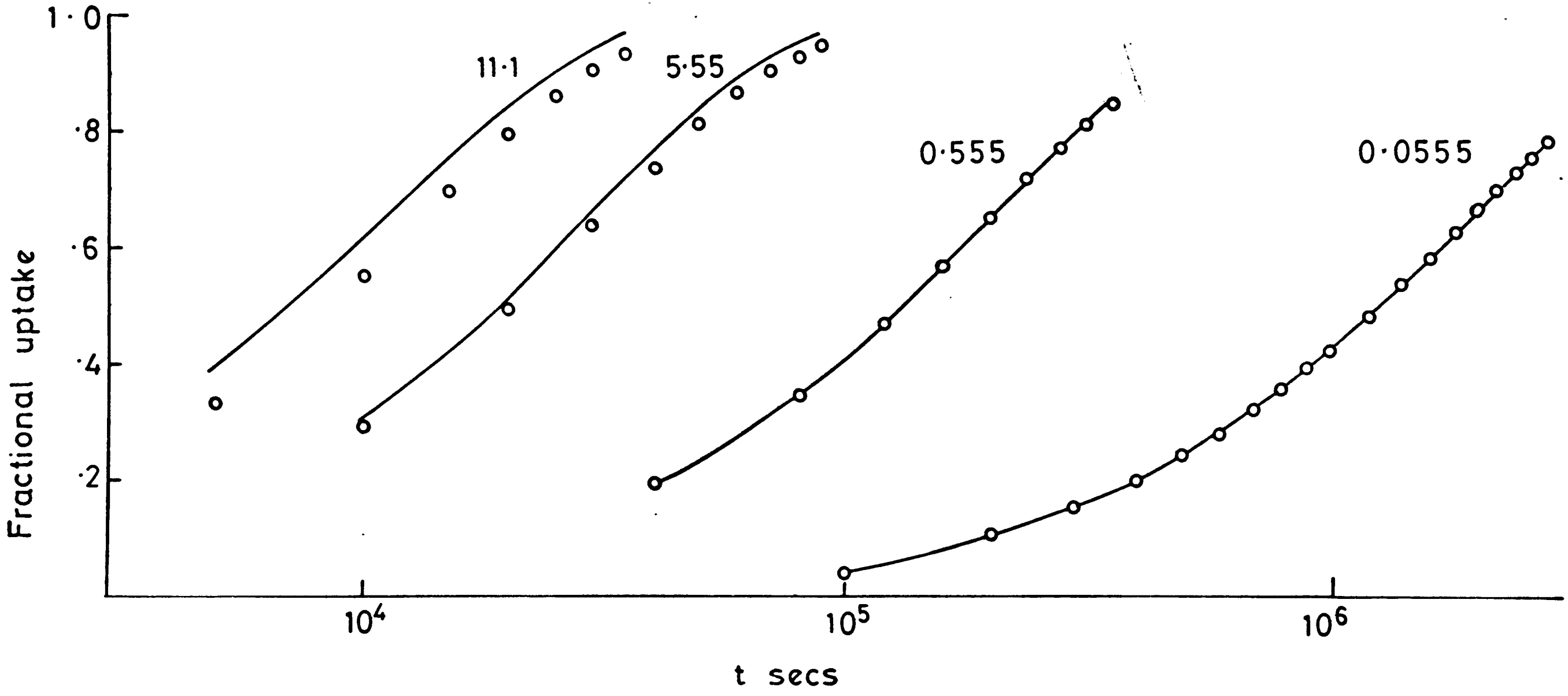

1·0
·8
·6
·4
·2
Fractional uptake
11·1
5·55
0·555
0·0555
10^4
10^5
10^6
t secs

Fig 3

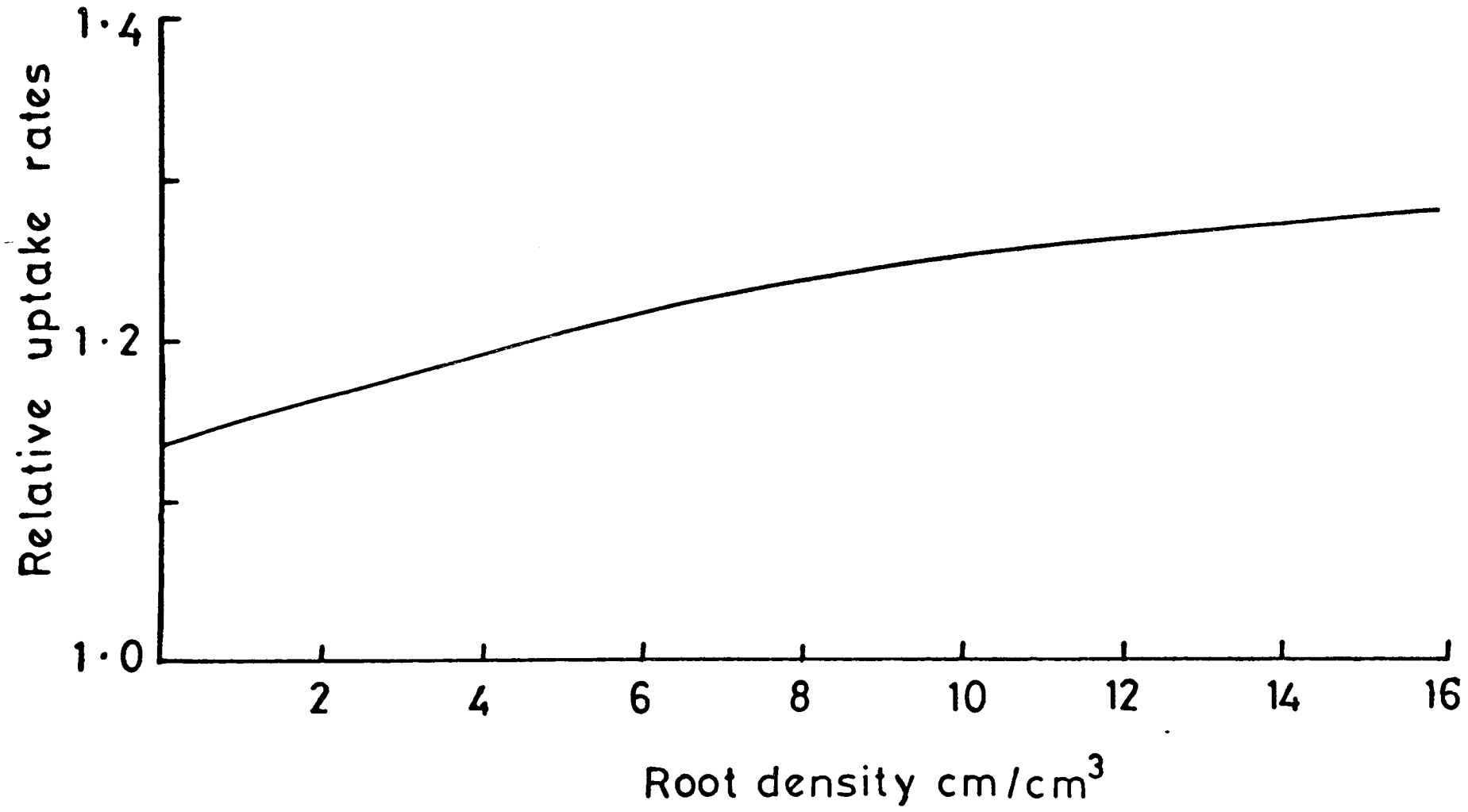

Relative uptake rates
1·4
1·2
1·0
2
4
6
8
10
12
14
16
Root density cm/cm3

Fig 4

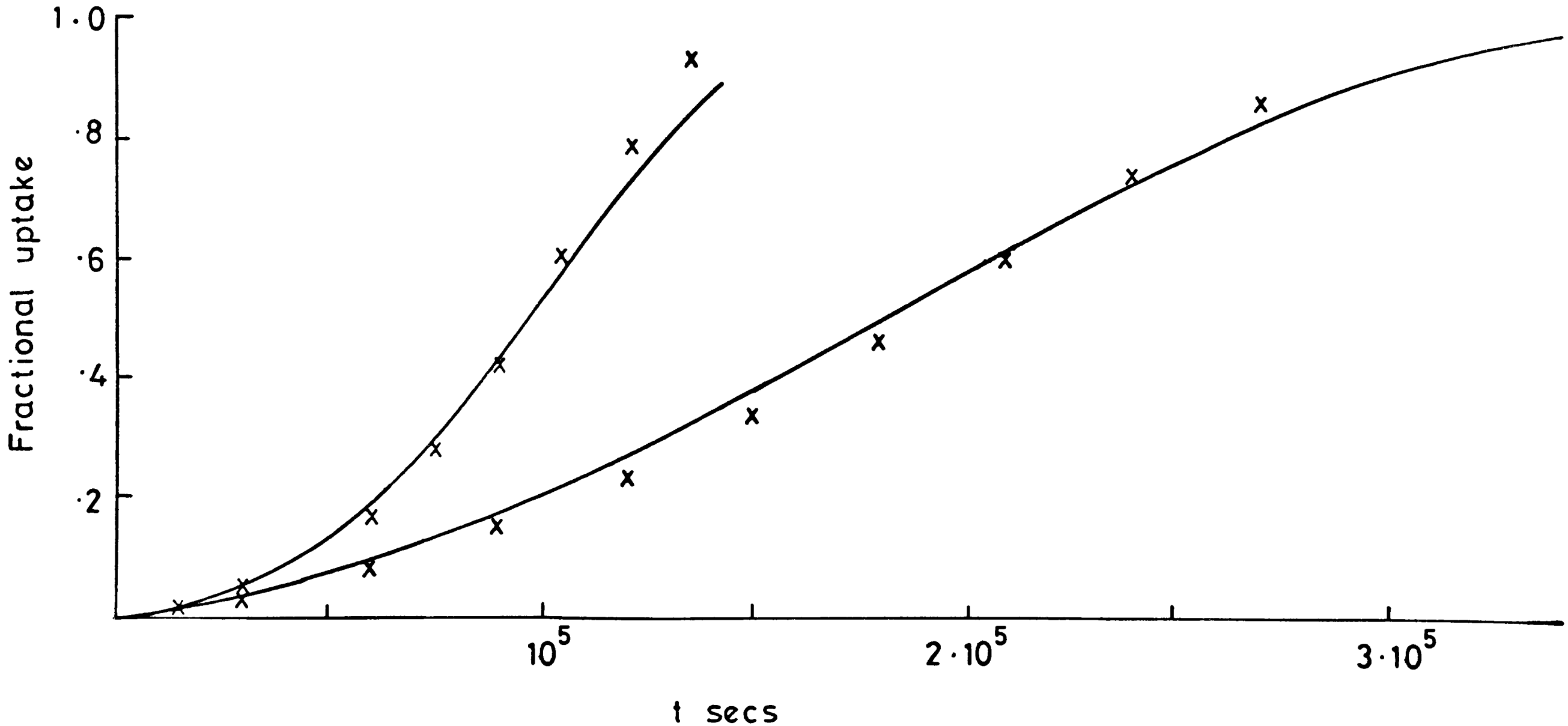


Fig 5

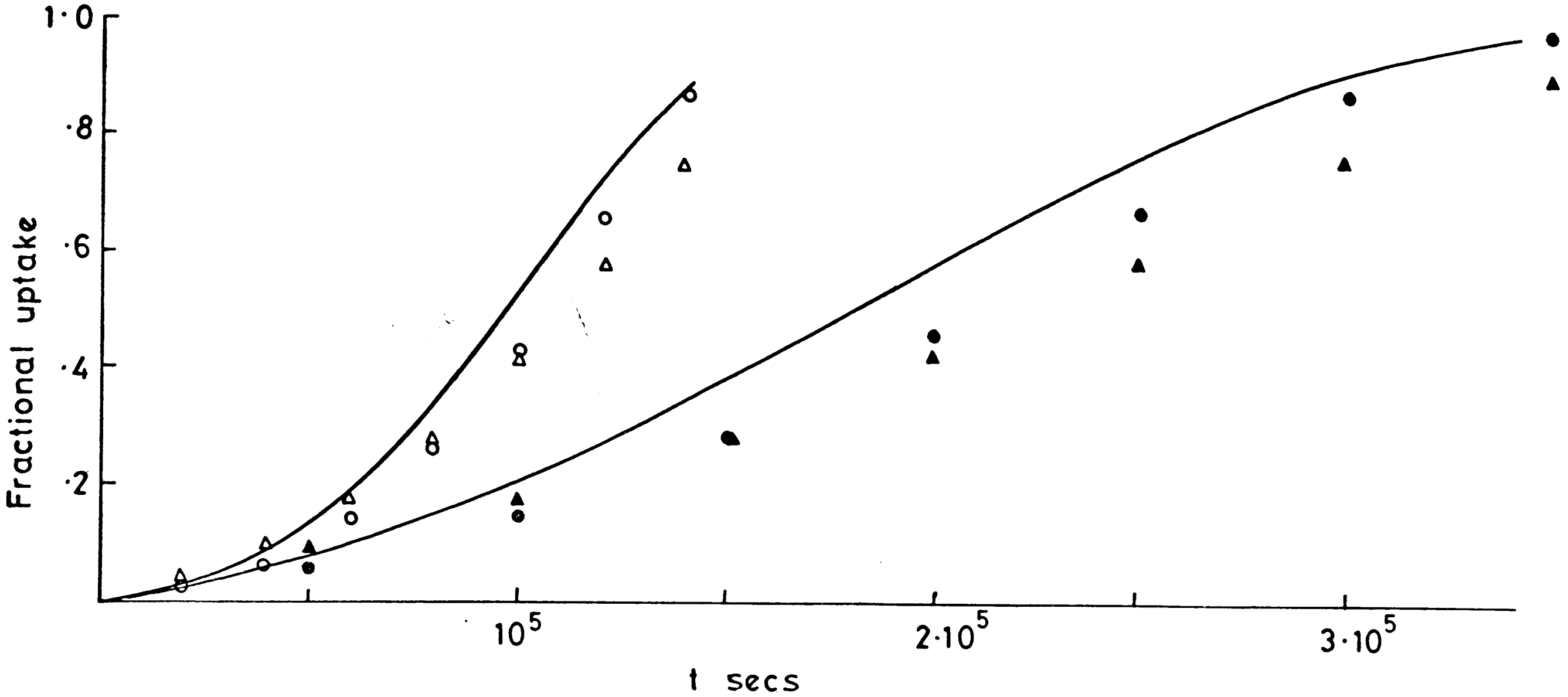


Table 1

Values of M_t/M_∞ for a range of values of $\frac{\alpha a}{bD}$ and water flux

v cm sec^{-1}	0		5×10^{-7}		1×10^{-6}		2.5×10^{-6}		5×10^{-6}	
α cm sec^{-1}	Exact soln.	Steady State	Exact Soln.	Steady State	Exact Soln.	Steady State	Exact Soln.	Steady State	Exact Soln.	Steady State
2×10^{-4}	.397	.332	.399 (.5)	.335 (.9)	.401 (1.0)	.338 (1.8)	.410 (3.3)	.348 (4.8)	.424 (6.8)	.368 (10.8)
	.756	.701	.756 (0)	.701 (0)	.756 (0)	.701 (0)	.754 (0)	.704 (.4)	.761 (0.71)	.723 (3.1)
10^{-5}	.307	.289	.314 (2.3)	.296 (2.4)	.320 (4.2)	.304 (5.2)	.343 (11.7)	.328 (13.5)	.391 (27.4)	.381 (31.8)
	.518	.495	.528 (1.9)	.506 (2.2)	.539 (4.05)	.518 (4.6)	.578 (11.6)	.559 (12.9)	.671 (29.5)	.660 (33.3)
10^{-6}	.191	.189	.205 (7.3)	.204 (7.9)	.223 (16.7)	.222 (17.5)	.323 (69.1)	.332 (75.7)		
	.345	.343	.385 (11.6)	.384 (11.9)	.443 (28.4)	.444 (29.4)				
	.472	.467	.542 (14.6)	.539 (15.4)	.666 (41.1)	.667 (42.8)				
10^{-7}	.0218	.0218	.0239 (9.6)	.0239 (9.6)	.0263 (20.6)	.0266 (22.0)	.0438 (100.0)	.0468 (114.7)		
	.0537	.0538	.0650 (21.0)	.0651 (21.0)	.0869 (61.8)	.0892 (65.8)				
	.104	.105	.157 (50.0)	.157 (49.5)						

a = 0.05 cm, $D_1 = 1 \times 10^{-5}$ cm^2 sec^{-1}, initial $v_1 = 0.3$,

$f_1 = v_1$, L = 5.3 cm^{-2}

A comparison of values of M_t/M_∞ obtained using Nye and Marriott's method, and equation (viii), for a range of values of $\alpha a/Db$ and water flux. The numbers in parentheses are the percent increase in uptake due to mass flow. Value in any horizontal line are after the same time.

In thesis, this is referred to as Table 2.2

2.24 Test of the analogue model of nutrient uptake when supply is by diffusion and mass flow.

The analogue model which calculates uptake when nutrient supply is by diffusion and mass flow is:

Uptake = Diffusion term obtained + ml taken up by plant X 2.xi

by procedure in 2.13 average solution concentration in soil

For a constant density of roots in a regular array, the diffusion term in equation 2.xi may be calculated by the approximate solution of the correct diffusion equation, given in section 2.19. In addition, the system represented by 2.xi may be described by the method given by Nye and Marriott (1969), modified for use in section 2.20. Therefore, the analogue model could be tested by comparing the results obtained by the exact method (Nye and Marriott 1969) with those calculated by:

$$I = \underbrace{\frac{2\pi\ Db(C_{lr}-C_{la})}{\ln\frac{r}{a}}}_{\text{steady state diffusion + mass flow}} + 2\pi a v\bar{C}_l = 2\pi\alpha a C_{la} \qquad \text{..... 2.xii}$$

see section 2.19 eqn. ii

From which,

$$\frac{C_{lr}}{C_{la}} = \frac{1+\frac{\alpha a}{Db}\ln\frac{r}{a}}{1+\frac{va}{Db}\ln\frac{r}{a}} \qquad \text{where } r = r_{av} \qquad \text{..... 2.xiii}$$

The value of r, where $C_{lr} = \bar{C}_l$ is found by assuming r_{av} is unaffected by v. Therefore, from equations 2.ii and 2.iii, section 2.19,

$$\ln\frac{r}{a} = \frac{x^2}{x^2-a^2}\ln\left(\frac{x}{a}\right) - \frac{1}{2}$$

Hence,

$$\frac{\bar{C}_l}{C_{la}} = \frac{\left(1+\frac{x^2}{x^2-a^2}\frac{\alpha a}{Db}\ln\frac{x}{a} - \frac{1}{2}\frac{\alpha a}{Db}\right)}{\left(1+\frac{x^2}{x^2-a^2}\frac{va}{Db}\ln\frac{x}{a} - \frac{1}{2}\frac{va}{Db}\right)} \qquad \text{.....2.xiv}$$

Table 2.3 A comparison of values of M_t/M_∞ obtained using Nye and Marriott's (1969) method, and equation 2.xiv, for a range of values of $\alpha a/Db$ and water flux. The numbers in parentheses are the per cent increase in uptake due to mass flow. Values in any horizontal line are after the same time. Constants as in table 2.2.

v cm sec^{-1}	0		5×10^{-7}		1×10^{-6}		2.5×10^{-6}		5×10^{-6}	
α cm sec^{-1}	Exact soln.	Steady State	Exact Soln.	Steady State	Exact Soln.	Steady State	Exact Soln.	Steady State	Exact Soln.	Steady State
2×10^{-4}	.397	.332	.399 (.5)	.338 (1.8)	.401 (1.0)	.345 (3.9)	.410 (3.3)	.366 (10.3)	.424 (6.8)	.403 (21.4)
	.756	.701	.756 (0)	.706 (.7)	.756 (0)	.712 (1.6	.754 (0)	.730 (4.2	.761 (0.71)	.773 (10.3)
10^{-5}	.307	.289	.314 (2.3)	.298 (3.1)	.320 (4.2)	.307 (6.3)	.343 (11.7)	.335 (15.9)	.391 (27.4)	.392 (35.6)
	.518	.495	.528 (1.9)	.508 (2.6)	.539 (4.05)	.522 (5.5)	.578 (11.6)	.570 (15.1)	.671 (29.5)	.682 (37.8)
10^{-6}	.191	.189	.205 (7.3)	.204 (7.9)	.223 (16.7)	.222 (17.5)	.323 (69.1)	.323 (70.9)		
	.345	.343	.385 (11.6)	.384 (11.9)	.443 (28.4)	.444 (29.4)	—			
	.472	.467	.542 (14.6)	.540 (15.6)	.666 (41.1)	.667 (42.8)				
10^{-7}	.0218	.0218	.0239 (9.6)	.0239 (9.6)	.0263 (20.6)	.0265 (21.6)	.0438 (100.0)	.0436 (100.0)		
	.0537	.0538	.0650 (21.0)	.0645 (19.9)	.0869 (61.8)	.0882 (63.9)			—	
	.104	.105	.157 (50.0)	.156 (48.6)			—			

The programme which calculates uptake by equation 2.xiv is in appendix 3. Table 2.3 compares the results obtained using equation 2.xiv and the more accurate solution, for the same soil and plant data used in table 2.2. Agreement between the two approaches to the calculation is very good, especially when mass flow makes a significant contribution to uptake. Equation 2.xiv approximates to equation 2.viii when $\frac{av}{Db}$ is small; in the systems tested in table 2.3, $\frac{av}{Db}$ reaches 2.5 (a is usually .05 cm or less, v is unlikely to be greater than 2.3×10^{-6} cm^2/sec (Newman 1969), and Db ranges from 10^{-6} cm^2/sec in moist soils to 10^{-8} cm^2/sec in dry soils. Table 2.3, therefore, covers an important range of conditions).

2.25 The maximum nutrient supply to a plant root system

Equation 2.x may be used to calculate the theoretical maximum supply by diffusion and mass flow of nutrients to the root system of a plant at any time. For maximum plant uptake rate, $\alpha \; a \rightarrow \infty$, and

$$\frac{M_t}{M_\infty} = 1 - \frac{\bar{C}_l}{C_{li}} \rightarrow 1 - \exp\left[\frac{-2\pi \frac{va}{Db} \; Dt\,L}{1 - \left(\frac{2}{2 - \frac{va}{Db}}\right)\left(\left(\frac{x}{a}\right)^{2 - \frac{va}{Db}} - 1\right) \Big/ \left(\left(\frac{x}{a}\right)^2 - 1\right)}\right] \quad \cdots 2.xv$$

Also, as $v \rightarrow 0$, from equation 2.v

$$\frac{M_t}{M_\infty} = 1 - \frac{\bar{C}_l}{C_{li}} \rightarrow 1 - \exp\left[\frac{-2\pi \; Dt\,L}{\frac{x^2}{x^2 - a^2} \ln \frac{x}{a} \quad - \frac{1}{2}}\right] \quad \cdots\cdots 2.xvi$$

and if $x^2 \gg a^2$, 2.xvi becomes

$$\frac{M_t}{M_\infty} \rightarrow 1 - \exp\left[\frac{-2\pi \; Dt\,L}{\ln \frac{x}{1.65a}}\right] \quad \cdots\cdots 2.xvii$$

where $x = 1/\sqrt{\pi L}$.

These equations hold where $\frac{\alpha a}{Db} \gg 1$, or > 10.

If we wish to consider the supplying power of the soil alone, it is useful to investigate, and include, the case when $\frac{\alpha a}{Db}$ is low, either because of low plant demand or high diffusivity through the soil.

As $\frac{\alpha a}{Db} \rightarrow 0$

$$\frac{M_t}{M_\infty} \longrightarrow 1 - \exp\left[\frac{-2\pi \frac{\alpha a}{Db} Dt L}{\left(\frac{2}{2-\frac{va}{Db}}\right)\left(\left(\frac{x}{a}\right)^{2-\frac{va}{Db}} - 1\right) \Big/ \left(\left(\frac{x}{a}\right)^2 - 1\right)}\right] \quad \cdots 2.xviii$$

and if $v \rightarrow 0$

$$\frac{M_t}{M_\infty} \longrightarrow 1 - \exp\left[-2\pi \frac{\alpha a}{Db} Dt L\right] \quad \cdots 2.xix$$

Corresponding equations for a concentration dependent D may also be derived.

The equations given above may be useful for characterising the maximum supplying power of a soil. They are quantitative statements of Bray's (1954) concept of nutrient mobility and emphasise the properties which need to be measured before estimations can be made on whether a particular soil can supply a particular crop with any particular nutrient. The total quantity of diffusible nutrient enters directly as M_∞, and also, with the solution concentration, as the buffer power - which is inversely proportional to D. Equations 2.xiv and 2.xix stress the interrelation between D, t, L and the plant demand.

Chapter 3

This chapter describes the experiments carried out to support the theory put forward in chapter 2.

3.1 Information required from experiments

The model of nutrient supply will calculate the time course of uptake by a plant growing in uniform soil, given the root length, root radius and rooting pattern in different zones of a soil block at successive times, an appropriate boundary condition at the root surface, and the soil properties which influence diffusion and mass flow. Experiments were carried out to obtain this plant and soil data in order to test possible root surface boundary conditions, and investigate whether the model could be used to predict the uptake if the above mentioned plant and soil properties were known. The experimental measurements and a complete growth curve were obtained from sequential harvests of plants in soil.

3.2 Type of plant required

Plant roots are considered to behave as cylindrical sinks for nutrients which move to them by diffusion and mass flow. The analysis is simplified if nutrient supply is restricted to diffusion to roots without root hairs, which are of constant radius, and are uniformly active along their length for long periods. Limiting nutrient supply to diffusion also avoids the difficulties of water supply; pots cannot be watered without modifying the pattern of nutrient depletion.

The roots of onions are long, generally unbranched in the young plant, of fairly uniform radius and show no root hair development under favourable soil conditions. Drew (1966) has shown that the roots continue absorbing for at least 16 days. Since onion behaviour under experimental conditions is well known, it seemed the ideal choice.

Three varieties, Mustang, Abundance and Elba Globe, of F_1 hybrid onions were tested for inter plant variability, in a growth chamber experiment. Germination of each variety was 95% and Elba Globe was the most variable at the seedling stage. Nine seedlings of each cultivar were selected for uniformity, and grown in aerated nutrient solution (for composition see Table 3.1) at 19° ± 1° C, 1500 foot candles of continuous light, for 13 days, when five were chosen at random and removed. The remaining four were left for 34 days. The number and lengths of each root and leaf (the latter is a measure of the assimilating area) were measured daily for 13 days and then at 3 more times. The results are summarised in Table 3.2. There is little difference in suitability between Mustang and Abundance, and Mustang was chosen because of the slightly more uniform top growth.

3.3 Growing Conditions

A Type of Soil

The following properties were required

1. The soil does not release K from non-exchangeable forms when it is depleted by plant uptake. This would cause two complications a) uptake could not be measured by loss from the soil and b) the depletion zones around absorbing roots would fill in by an incalculable amount.
2. There is no change in the nitrate level of the soil due to nitrification or denitrification during a plant growth experiment.
3. The soil forms a stable structure over the range of moisture contents experienced in plant growth, so that it can be sliced and handled without crumbling for the autoradiography described in section 3.5.a.ii.1
4. The soil has sufficient water holding capacity such that plants do not require watering during growth.

Begbroke Sandy Loam (B.S.L.) was found to satisfy these requirements (see sections 3.7.1.b and 3.7.2.a)and has been used throughout. The moisture characteristic is in fig. 3.1 and Table 3.3 gives details of some soil properties.

B. Environmental conditions

The electrical anlogue described in section 2.2 simulates nutrient supply by diffusion only, and so it was necessary to minimise transpiration and, hence, nutrient supply by mass flow. It has been suggested that antitranspirants are useful in plant experiments which require low transpiration rates (Gale and Polyakoff-Mayber 1963).

There are two types of antitranspirants

(i) chemicals that interfere with stomatal physiology causing stomata to close when they are sprayed on the leaves, e.g. phenyl mercuric acetate (PMA), dodecenyl-succinic acid and nonenylsuccinic acid. The effective concentration ranges of these chemicals are very small and their influence is ephemeral (Parkinson, 1970). Cooking and Tukey (1970), using P.M.A. on chrysanthemums, found that, whenever P.M.A. was effective, the antitranspirant effect was short lived, and there was some permanent damage to the plants.

(ii) chemicals which form a complete film over the leaves when sprayed on, and thus act as a physical barrier to water loss. Parkinson (1970) has used dimethyl silicones, but reported that photosynthesis, as well as transpiration, was reduced.

In both cases, rapidly growing plants will need frequent spraying to cover new leaf surfaces, and in view of the possible damage, and the possible lack of uniformity of the application, antitranspirants were not used in these experiments.

Transpiration rate depends on the humidity, and the relative humidity of the atmosphere, and can, therefore, be controlled by growing

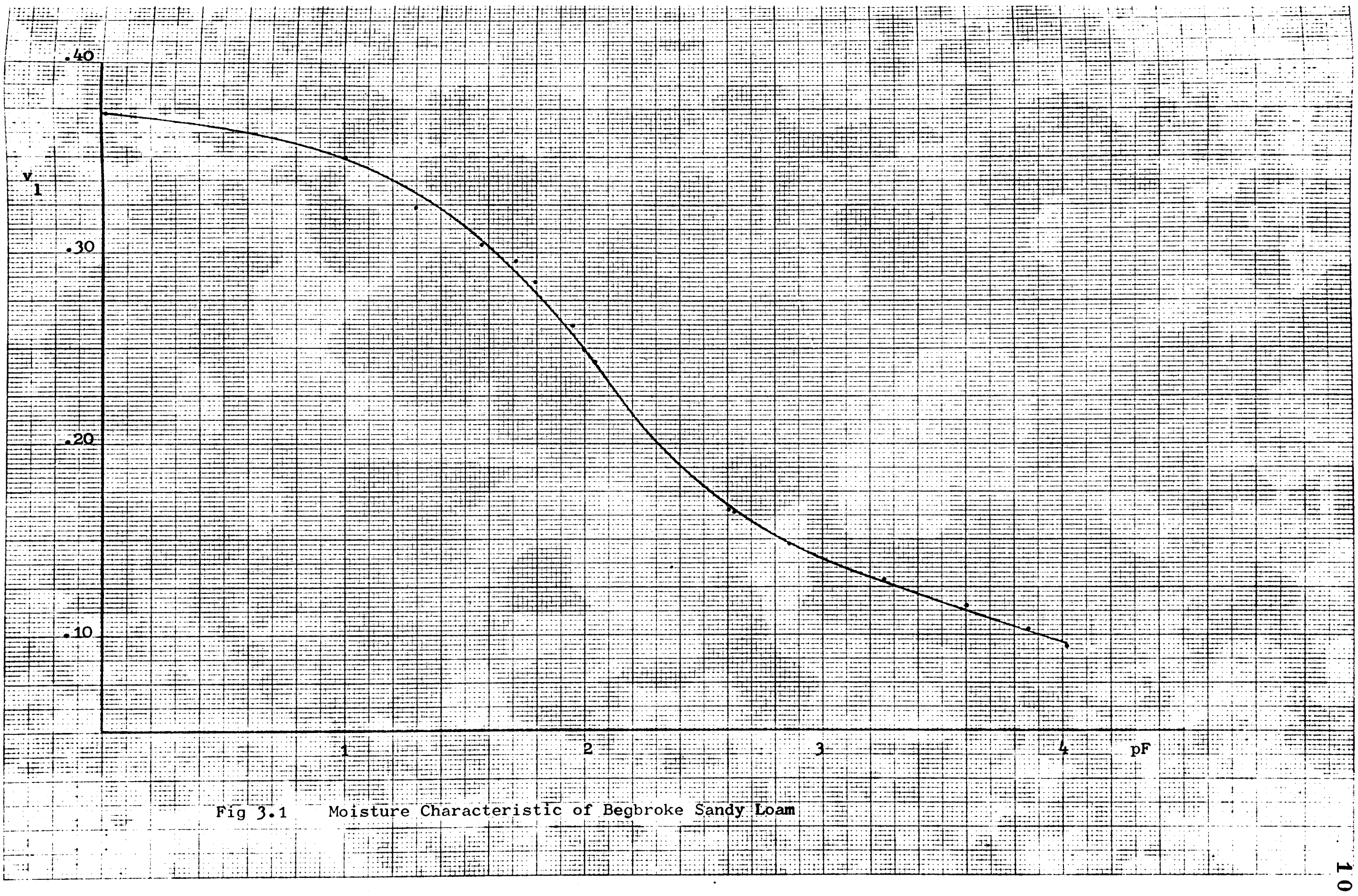


Fig 3.1 Moisture Characteristic of Begbroke Sandy Loam

Table 3.2.

Comparisons of the lengths cm and standard deviations of roots and leaves of 3 onion varieties

A - Abundance B - Mustang C - Elba Globe The 1st figure in a column is length, the 2nd is standard deviation.

t days after germination	Roots			Cotyledon			1st leaf			2nd leaf			3rd leaf		
	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
4	4.9 .88	5.3 .64	5.1 1.4	5.8 .7	4.6 .61	5.3 .97									
6	9.7 1.0	9.5 1.9	9.9 2.7	7.7 1.1	5.8 .80	6.9 1.0									
8	15.5 2.1	14.4 3.0	14.9 3.7	8.5 1.1	6.3 .75	7.5 1.0	1.2 1.1	1.9 .94	1.3 1.3						
10	22.7 2.9	20.7 3.8	20.9 5.7	8.7 1.1	6.3 .75	7.8 .88	4.4 1.8	3.1 1.4	4.0 2.4						
13	34.6 6.3	33.6 7.1	31.0 9.7	8.7 1.1	6.3 .75	7.8 .88	11.0 2.6	10.5 1.6	9.5 3.2						
16	81.8 11.0	60.4 10.8	60.4 7.6				17.1 2.4	13.8 1.9	18.0 2.8	3.9 2.0	4.4 1.1				
25	169 41	138 22.3	141 15.0				18.0 2.6	15.1 .90	19.0 1.1	20.2 1.2	22.3 2.1		8.5 3.1	9.7 2.5	8.0 1.4
34	285 46	263 37	254 15				18.0 2.6	15.3 .96	19.0 1.1	28.0 1.3	24.5 2.5		32 3.3	32.5 2.9	30.7 3.5

Table 3.1.

Composition of nutrient solution used in all solution culture experiments

Salt	wt. in gl^{-1}
KNO_3	.40
$Ca(NO_3)_2$	.66
$Mg\ SO_4\ 7H_2O$	.37
$NaH_2PO_4\ 2H_2O$	.21
Fe EDTA	.031
$Mn\ SO_4\ 4H_2O$	.022
$Cu\ SO_4\ 5H_2O$	.0025
$Zn\ SO_4\ 7H_2O$	.0029
H_3BO_3	.031
Na Cl	.059
$Na_2MoO_4\ 2H_2O$	.0012

Table 3.3.

Some Properties of Begbroke Sandy Loam BSL

Coarse Sand	2000μ - 200μ	38%
Fine Sand	200μ - 50μ	21%
Coarse Silt	50μ - 20μ	15%
Fine Silt	20μ - 2μ	12%
Clay	$<2\mu$	14%
Free $CaCO_3$		trace
pH in 1:2.5 N/100 $CaCl_2$		6.5
Cation Exchange Capacity		12 meq/100 g soil
% Mineral N as NH_4^+ in moist equilibrated soil		3%
Bulk density of air dry soil		1.11

Fig 3.2 Melinex Antitranspiration Chamber

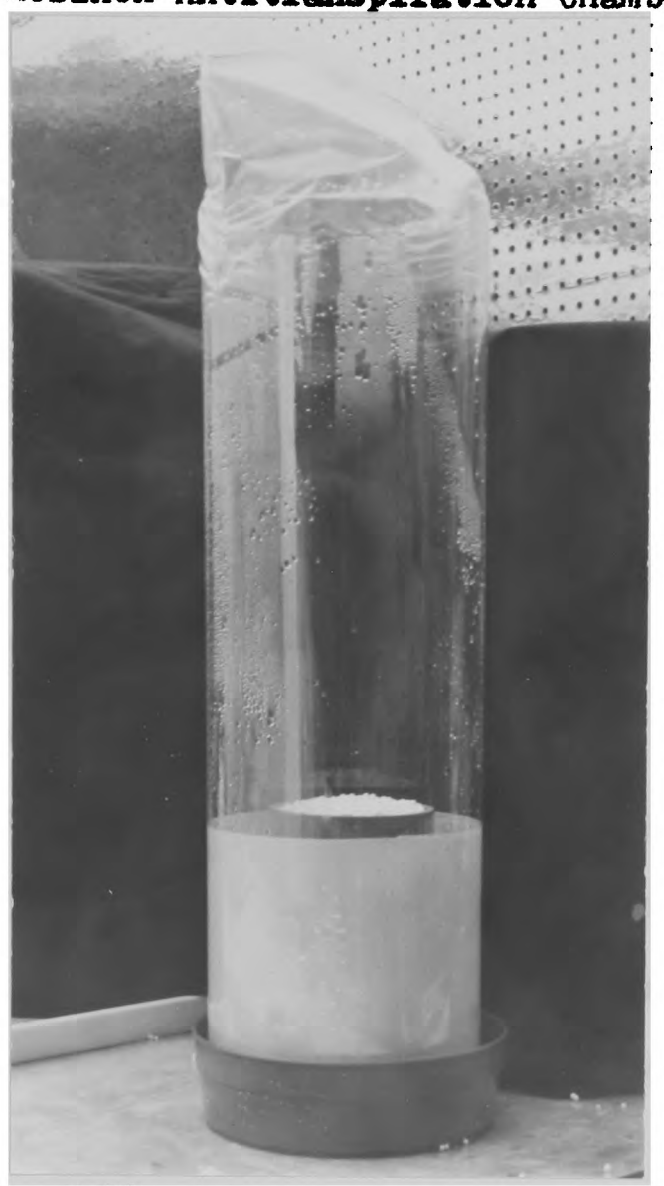


Table 3.4

Table 1. Summary of the mean values of root length, standard deviations, and coefficient of variation for the various methods of estimating root length. Root length is reported as the mean of three estimates per sample.

Sample	Methods								
	Direct count			Inch counter			Line intercept		
	Length	SD*	CV*	Length	SD	CV	Length	SD	CV
	cm	cm	%	cm	cm	%	cm	cm	%
1	1,201	32.9	2.74	1,126	16	1.47	1,253	50	4.04
2	758	1.8	0.24	745	50	6.79	851	82	9.69
3	1,367	54.1	3.96	1,145	47	4.10	1,488	83	5.61
4	777	21.8	2.80	745	9	1.21	802	28	3.50
5	831	11.6	1.39	832	10	1.23	867	50	5.76
6	783	9.2	1.18	734	6	0.91	821	38	4.62

* SD -- Standard deviation, CV -- Coefficient of variation.

plants in a humid environment at a low temperature. It has proved satisfactory to enclose each pot in a chamber of melinex (Type O), which has a lining of moist filter paper up to the level of the top of a pot. The melinex cylinder and lining (fig. 3.2) stand in water, and there was no improvement in transpiration control by heating this water 10° C above ambient. During an experiment the chamber was removed and aerated daily to prevent depletion of CO_2 or O_2. This system does not stop transpiration, and diurnal fluctuations in the mass flow contribution to nutrient supply were eliminated by growing plants in continuous light, supplied by fluorescent tubes. Light intensity was 1500 foot candles and the ambient temperature was kept constant at 19° C. Water loss by evaporation from the soil surface was prevented by a 1 cm layer of white polystyrene granules. These were on top of a single layer of black polypropylene granules, which were necessary to prevent the growth of moss.

3.4 The plant and soil measurements

3.5 Measurement of root properties in soil

Requirement: Density, spatial pattern and orientation, and radius of roots in different zones of the soil after different times.

3.5.a Methods for estimating root length

The methods for measuring root length in soil fall naturally into two groups; direct measurements on extracted roots and indirect measurements from which root length can be inferred.

3.5.a.i Measurements on extracted roots

A major problem in the measurements on extracted roots is the great lengths which can occur in small volumes of soil - 100 m per l of soil is a low figure for annual plants (Newman 1969). This makes both

extraction and measurement laborious. Direct measurement with a ruler is time consuming, and difficult with heavily branched samples, and a map measuring wheel run over a photographic print of the roots has been suggested. rrors are likely when lifting and resetting the wheel for each new root. If the volume or surface area of the roots is known, the total length can be estimated from the mean radius. Where there are several classes of roots wit. different radii, the proportion in each class must be estimated from measurements at random positions in the sample. The length is obtained from

$$L = \frac{V}{\pi\left(\sum (r_i^{2} p_i)\right)} = \frac{SA}{2\pi \sum (r_i p_i)}$$

where V = root volume

SA = root surface area

r_i = radius of i^{th} class of root

p_i = proportion of root in i^{th} class

Root volume is obtained from the fresh weight of roots centrifuged at 180 g for 3 mins (Ellis and Barnes, 1968), or by displacement of paraffin oil (Evans 1938). Surface area has been estimated by titration of absorbed HCl (Wilde and Voigt 1949), or gravimetrically using $Ca(NO_3)_2$ solution (Carley and Watson 1966). If there is more than one class of root, a large number of measurements of radius are required, and it may be easier to estimate the length by spreading the roots out in a plane and counting the intersections between roots and randomly placed transects. An estimate of length is given by

$$L = \frac{\pi N A}{2 H}$$ (Newman 1966)

where L = length of root

N = number of intersections

A = Area covered by sample

H = total length of transect

This result always holds if either the transects or the roots can be considered as short randomly oriented elements. When the transects are random (as Newman, 1966), it is tedious to estimate the total length of transect within the sample area; at the edge only a certain fraction of each transect will be within the sample area. It is more convenient, therefore, for the roots to be randomly dispersed, and the intersections with a superimposed rectangular grid counted. Then, $L = \frac{\pi NA}{2H} = \frac{\pi Na^2}{4a^2}$

$= \frac{\pi}{4} N$ (Marsh, 1971)

where a = side of the square.

If the roots are not randomly dispersed, rotation of the grid through 180° with measurements at regular intervals, is satisfactory. Should this be necessary, however, it will be simpler to randomise the transects and proceed as Newman (1966).

Reicosky et al. (1970) used the grid procedure on soybean roots and compared the results with those obtained using a ruler and an inch counter. Their results are in table 3.4. Their value of N was 0.142 L, or c.115 and c.170 for the 800 cm and 1200 cm lengths respectively. The time taken per sample for the 3 measurements was approximately 1.0, 5.5 and 7.5 man hours respectively. When small numbers of samples are being measured it seems that the transect method using a grid is the most suitable. I adopted the following procedure as routine. The roots are dispersed in water over the bottom of a transparent plastic petri dish, and then the excess water drained off, fixing the roots in position. The petri dish is

placed on top of graph paper and the intersections between the lines on the graph paper and the roots are counted using a stereoscopic microscope. If the numbers of intersections with each set of parallel lines composing the grid differed by more than 10 , the sample was rotated 45° with respect to the grid and recounted. All 4 readings were used in calculating the length of root. Each sample takes about 20 minutes using this procedure. After about 1½ hours, the operator suffers from e e strain, which can be a disadvantage with large numbers of samples. In these cases the Quantimet should prove ideal. This is an image Analysing Computer which can measure the number, area, area distribution, length and length distribution of detected features, and was developed primarily for metallurgical research.

The details of the Quantimet method and its accuracy are in section 3.5.a.b. Each sample requires 5 minutes in preparation for photography and 1 minute for measurement of length. If the number of samples is large, the time per sample spent developing the film is small. Although the method is more accurate than the transect method, the latter is more convenient for small numbers of samples (less than 10 at any one time).

3.5.a.ii Indirect estimations of root length

Indirect attempts at measuring root properties have been prompted by a) the labour of root extraction and measurement, and that which follows because the method is destructive, b) uncertainties in the effectiveness of the extraction procedure, c) the desire to distinguish living roots of a particular plant with dead roots, or living ones from other plants.

If the uptake of a nutrient from a zone of soil is related to the root activity within it, this can be used as a measure of root activity. Thus Hall et al. (1953) suggested labelling a zone of the soil with ^{32}P. By using a number of test plants with a different part of their rooting zone labelled, a picture of the root distribution is obtained. Nye and Foster

(1960) showed how the technique could be used to give quantitative data on the relative uptake of a nutrient from different compartments of a plant's root zone. If measurements are taken at different times, the pattern of root activity and distribution may be inferred. However, the method is not useful for experiments where the pattern of nutrient uptake is to be inferred from root data.

Race et al. (1964) have suggested that living root volume in different parts of soil can be estimated by injecting the plant with ^{32}P, and subsequently radioassaying soil cores. The activity in each core will be a measure of the root volume, only if the isotope is uniformly distributed throughout the root mass, and if a given activity corresponds to a known root volume. Halstead and Nennie (1965) reported that the soil moisture stress, the plant age and the number of tillers injected markedly influences the per cent of the injected ^{32}P which moves into the root system, and they concluded that the level of activity in roots cannot be used directly as an index of root weight. However, they found that the translocated ^{32}P was uniformly distributed throughout the root system, and they were able to determine the relative root distribution throughout the soil profile. Because of the low penetrating power of the β radiation from ^{32}P, it is possible to detect only the roots in 10 g samples of soil at any one time. Roots from larger volumes may be detected by injecting the plant with a γ emitter. Thus Ellis and Barnes (1968) have studied the distribution of ^{86}Rb throughout the root system of barley plants. They injected all the tillers of their plants with ^{86}Rb and, after a 60 hour equilibration period, divided the root system into 12 equal subsamples and assayed each subsample for radioactivity. The coefficient of variation of measurements of activity per unit fresh weight was 20% or less, which they concluded was satisfactory, in view of the errors associated with

other methods for estimating the distribution of roots. The errors incurred as a result of injection and sampling were a minor source of the total experimental error. The percent of the injected ^{86}Rb translocated depended on plant age and method of injection, and the method gives only the relative root distribution throughout a profile. If either of these labelling methods are to be quantitative, the activity per unit mass of root must be constant throughout the root system. Tests reported in section 3.3.B.b showed this not to be the case with onions.

Helhuish (1968) has presented a method for determining the length of root per unit soil volume and the precise spatial pattern of these roots as they intersect two dimensional planes. This method offers the information that is required for a study of nutrient transport to plant roots, (i.e. the exact positioning of the roots). The three-dimensional orientation may be inferred from the pattern and density recorded on 3 mutually perpendicular planes. The method, as improved by Helhuish and Lang (1968), involves vacuum impregnation of oven dry soil cores with Plastrene 47 incorporating 0.05% berberine hydrogen sulphate. Next, plane surfaces are prepared by surface grinding. The roots intersecting the planes are counted using a stereomicroscope, and the root length is obtained by the principles of geometrical probability; in particular, the theoretical relationship between the number of random lines intersecting a plane of unit area, and the probable total length of line per unit volume. If the roots are randomly oriented then $L = 2N$, where L = length per unit volume, N = number of intercepts per unit area. The live root density is calculated by counting only light brown roots which exist in a root void. (Helhuish and Lang (1968) suggested that a live root shrinks on oven drying, leaving a void in the soil of the same size as the live root. Also, the colour of live roots does not alter appreciably on oven drying). Although this method is very attractive in principle, it

appeared rather tedious in practice, and there seems a high possibility of incorrectly analysing some of the soil voids. An alternative way to count the roots intersecting a plane is to label them with a suitable isotope, and analyse an autoradiograph of a cut soil surface.

3.5.a.ii.1 The autoradiographic technique for measuring root length and spatial pattern

The principle of the technique is to label the roots with radioactivity and then detect them by taking autoradiographs of planar soil surfaces. Each root appears as a black spot on the film. The root length per unit volume and the spatial pattern of the roots as they intercept the soil plane are obtained directly from the autoradiographs.

The roots are labelled by applying isotope to the tops, and allowing it to be translocated throughout the root system.

3.5 A. Factors governing the choice of isotope

(i) the isotope must label the whole root system

(ii) the half life. This should be of the order of 10 to 50 days so that a) a very high specific activity at the time of injection, which may cause injury, is not required to give suitable levels of activity for the autoradiographs, and b) the isotope will decay completely within a reasonable time so that there is no long term hazard, and the soil may be used again.

(iii) the initial energy of emission. This affects the efficiency and, therefore, the exposure time, and resolution of the autoradiograph. It is convenient if the film can be handled in its envelope and exposed in about 12 hours, yet the resolution must be such that individual roots are always distinguishable.

The β particle energy has two distinct effects on the efficiency of an autoradiograph. Firstly, with a source of finite thickness, more β particles from an isotope with low maximum energy will be absorbed within

the source itself. On the other hand, lower energy β particles have a higher rate of energy loss and, thus, a greater probability of causing a latent image in every crystal of silver bromide along their track. For example, the efficiency, in this respect, of ^{14}C : ^{32}P is in the ratio 2:0.8. (Hers, 1959).

Emission energy affects resolution - an increase in maximum energy resulting in a greater number of particles producing silver grains at a distance from the source.

(iv) movement of isotope which leaks out of cut roots should be a minimum.

^{32}P seemed to be a suitable isotope. It is a major plant nutrient and is likely to label the whole root system; the $t_{\frac{1}{2}}$ is 14 days; the maximum β energy of emission is 1.7 MeV; any ^{32}P which leaks out of cut roots is immobilised in the soil; there is no γ emission.

There has been considerable interest in the fate of fertiliser P applied to foliage, but Raos et al. (1964) were the first to check on the completeness of distribution of the label throughout the root system. More detailed experiments were reported by Halstead and Rennie (1965). These workers grew wheat in a box which had a transparent side. The box was inclined at 45° and after injection the roots which grew along the transparent window were assayed by autoradiography. A better method is to grow the plant in solution culture, and then analyse every root for activity. This method is satisfactory only if there is no leakage of ^{32}P into the solution.

3.5.B. Experiments to test the completeness of labelling of the onion root system

a) Details of Procedure

1. Method of application of the isotope.

Koontz and Biddulph (1959) using bean plants, found that spraying the leaf or injecting the leaf vein with isotope were equally satisfactory. Placing a droplet at the leaf base was less effective. Raos et al. (1964)

injected the label into the wheat stem with a micro litre syringe. For thin-stemmed species, e.g. grasses, they recommended abrasing the leaf and curling the end into a small tube containing the isotope.

The onion leaf is hollow and the label can easily be injected into it, with a syringe.

2. Level of activity

The requirement is that all roots intersecting the cut soil surface will be sufficiently active to blacken the X-ray film. Approximately 10 million β particles are required to blacken 1 cm^2 of film (Lamerton and Harriss 1954). Therefore, a root of radius a lying normal to the film must emit $\sim \frac{\pi a^2 \times 10^7}{12 \times 60 \times 60}$ β particles per sec into the film to give blackening in 12 hours. For ^{32}P, infinite thickness corresponds to a density of 700 mg cm^{-2}, and the density for 50% self absorption is 310 mg cm^{-2}. Thus, to calculate the activity in root tissue, we consider roughly a 0.2 cm length of root. Approximately 1/6 of the β particles will emerge to hit the film, and therefore we require $\frac{\pi a^2 \times 6 \times 10^7}{12 \times 60 \times 60}$ β per sec from $0.2 \pi a^2$ g root or $.72 \times 10^4$ β per sec per g of root, which gives 0.2 μc per g of root.

About 2.5% (within a factor of 2) of the activity injected into plant tops is distributed to the root system (Rennie and Halstead 1965, Ellis and Barnes 1968). Therefore, if the shoot:root ratio is 7:1, we need to inject 1.0 μc ^{32}P per g fresh weight of plant to give the necessary activity in the roots. In practice, 2 μc per g fresh weight was used, and this was found satisfactory in all cases.

3. Use of carrier in injecting solution.

Koontz and Biddulph (loc cit.) found a nearly linear increase in the per cent of the applied P translocated when the P concentration of the injecting solution was increased from 0.3→10mM. Of the salts tested,

NaH_2PO_4 was the most effective, and they attributed this to a longer drying time of the solution on the leaf surface. Hygroscopic agents added to other salts were sometimes beneficial, but never gave better results than using NaH_2PO_4 alone. Halstead and Rennie (loc cit.) reported a marked decrease in translocation when $NH_4H_2PO_4$ or H_3PO_4 was used at a concentration of 5.16 M phosphate. Loughman (pers. comm.) recommended using the physiological concentration of phosphate, i.e. 5×10^{-6} M.

4. Use of a wetting agent.

A range of cationic, anionic and nonionic wetting agents have been tried, but none of them increased the per cent of the applied P translocated (Koontz and Biddulph 1957). A wetting agent was not used in the present experiments.

5. Site of injection.

Koontz and Biddulph (l.c.) using beans, reported that the oldest leaves translocated the greatest percentage of the applied phosphate, and that very young leaves often do not translocate any phosphate. Halstead and Rennie (1965), using wheat, recorded a linear increase in the specific activity of root material by increasing the number of tillers injected per plant. Each tiller was injected between the first and second node.

b) Details of injection experiments

In the following experiments the activity in the roots was monitored by either a chromatogram scanner with a 0.5 cm slit, or autoradiography. In some cases, portions of active roots were digested with nitric acid, and the total activity per cm of root calculated.

(1) Experiments in solution culture

In all experiments, onions were grown at 19° C continuous light in a growth chamber. A growth cell is shown in fig. 3.3. Plants were injected after four weeks growth, when they had 3 leaves and about 10 roots. In all cases, 0.05 mls ^{32}P in 5×10^{-6} M NaH_2PO_4 were injected into the

leaves with a syringe. The specific activity was adjusted so that each plant received about 2 μc per g fresh weight. After harvest, each solution was sampled for radioactivity leaking from the roots. In no case was it above background.

A series of experiments showed that:

i) activity in one or two roots is no indication that the whole root system is labelled.

ii) after 18 hours from injection, there is little increase in the amount of ^{32}P translocated to the roots

iii) there is no translocation to roots if the youngest leaf only is injected.

iv) if isotope is injected into the oldest leaf, or divided equally between all the leaves, then all roots are labelled.

v) activity was not constant along the length of a root. A typical scan is in fig. 3.4, where the activity differs by a factor of 2 between base and tip. Fig. 3.5 is an autoradiograph of 4 roots with the roots themselves shown slightly displaced. The numbers on the figure are values of the relative activity, obtained by scanning densitometry. From a series of scans or roots, the activity per cm of root between different roots of a single root system was found to vary by up to a factor of 4.

2. Experiments in soil

Onions (var. Mustang) were grown in the growth cabinet in boxes of soil. There was one plant per box, and the box was inclined at 45° to the vertical to encourage the roots to grow down one side. This side had a polythene cover which was held in place by a removable wooden panel. There were six replicate boxes.

Four weeks after germination, the onions were injected with ^{32}P at 2 μc per gram fresh weight. All leaves were injected with equal volumes

of a solution of 5×10^{-6} M NaH_2PO_4. Immediately after injection, the wooden panel was removed and X ray film was placed against the polythene film. Autoradiographs were taken from 0 → 10 hrs, 12 hrs → 22 hrs, 24.5 hrs → 35 hrs, 54 → 65 hrs and 128 → 141 hrs. The set from one box is shown in figure 3.6 a-e, together with a photograph of the root system 3.6g, which was taken after 160 hours. Unfortunately two roots were disturbed whilst the polythene film was adjusted for photography and, therefore, these two do not coincide exactly in the photograph and the autoradiographs in fig. 3.6 a-e. Fig. 3.6.f was taken after the photograph, to demonstrate that the roots had in fact moved and the difference was an artefact. A comparison of the autoradiographs and photograph shows that all roots were labelled by the injection technique. The numbers on the autoradiographs are measures of the radio-activity at the different points, and were obtained from a scanning densitometer. The densitometer scans indicated there was no increase in the activity of established roots after 12 hours from the time of injection. Roots which grew after the injection were much more active than the other roots. Thus, if the activity in any soil zone is taken as a measure of relative root mass, the measurement should be taken as soon as possible after the injection time. The 5-day interval suggested by Baez et al. (1964) seems unnecessarily long.

c) Conclusions from experiments on labelling onion roots with ^{32}P

If ^{32}P in 0.05 mls. of 5×10^{-6} M NaH_2PO_4 is injected into either the oldest, or all the leaves of an onion plant up to 2 months old at a rate of 2 μc per g fresh weight of plant, all the roots will become labelled by 10 hours. There is little increase in the activity of the root system after 12 hours. The activity is not constant along the length of root, but may vary by a factor of 2. The activity between roots of a single plant may vary by a factor of 4.

Fig 3.4 Distribution of ^{32}P along the length of a root, as measured by a chromatogram scanner

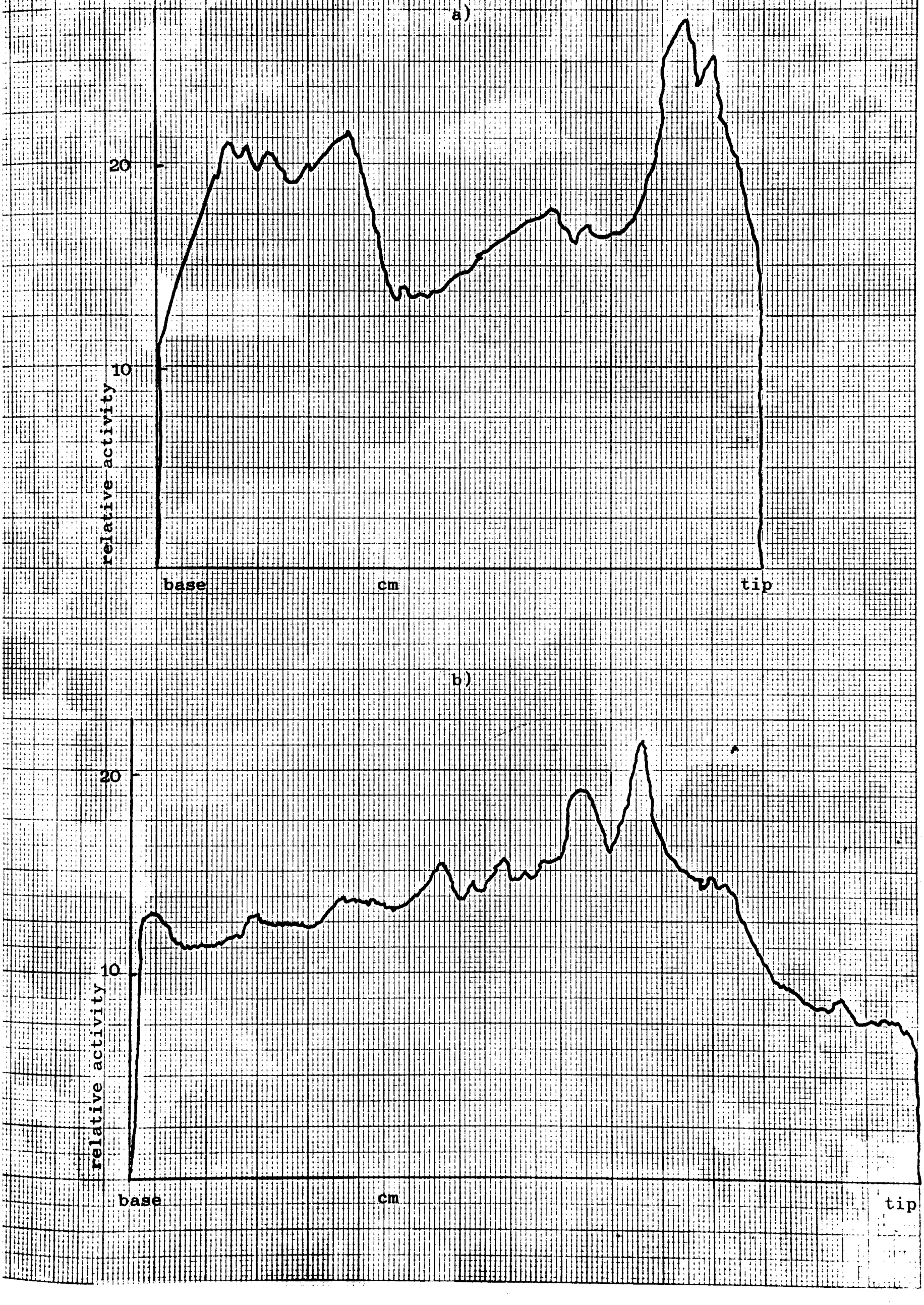


Fig 3.3 Growth cell used for testing injection methods

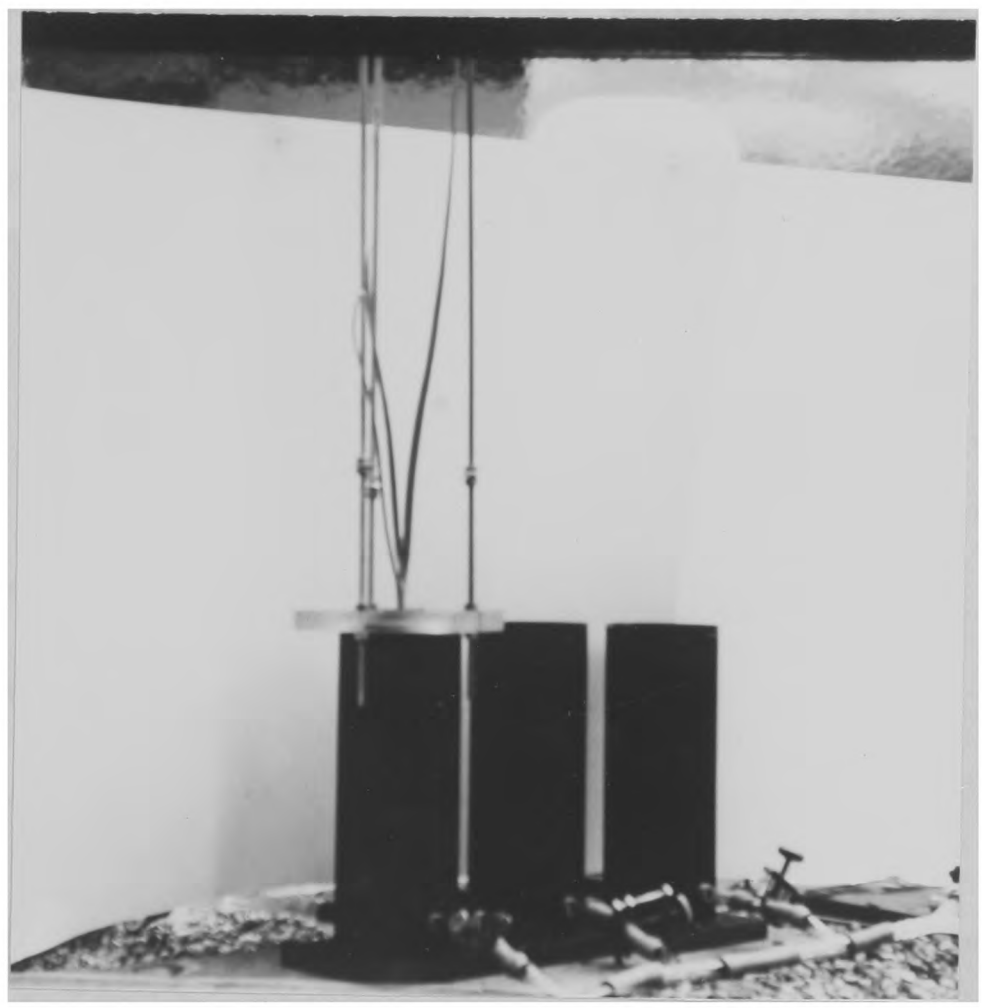


Fig 3.5 Radioactive onion roots, and the corresponding autoradiographs. The numbers are the relative activity of ^{32}P in the positions marked by the lines.

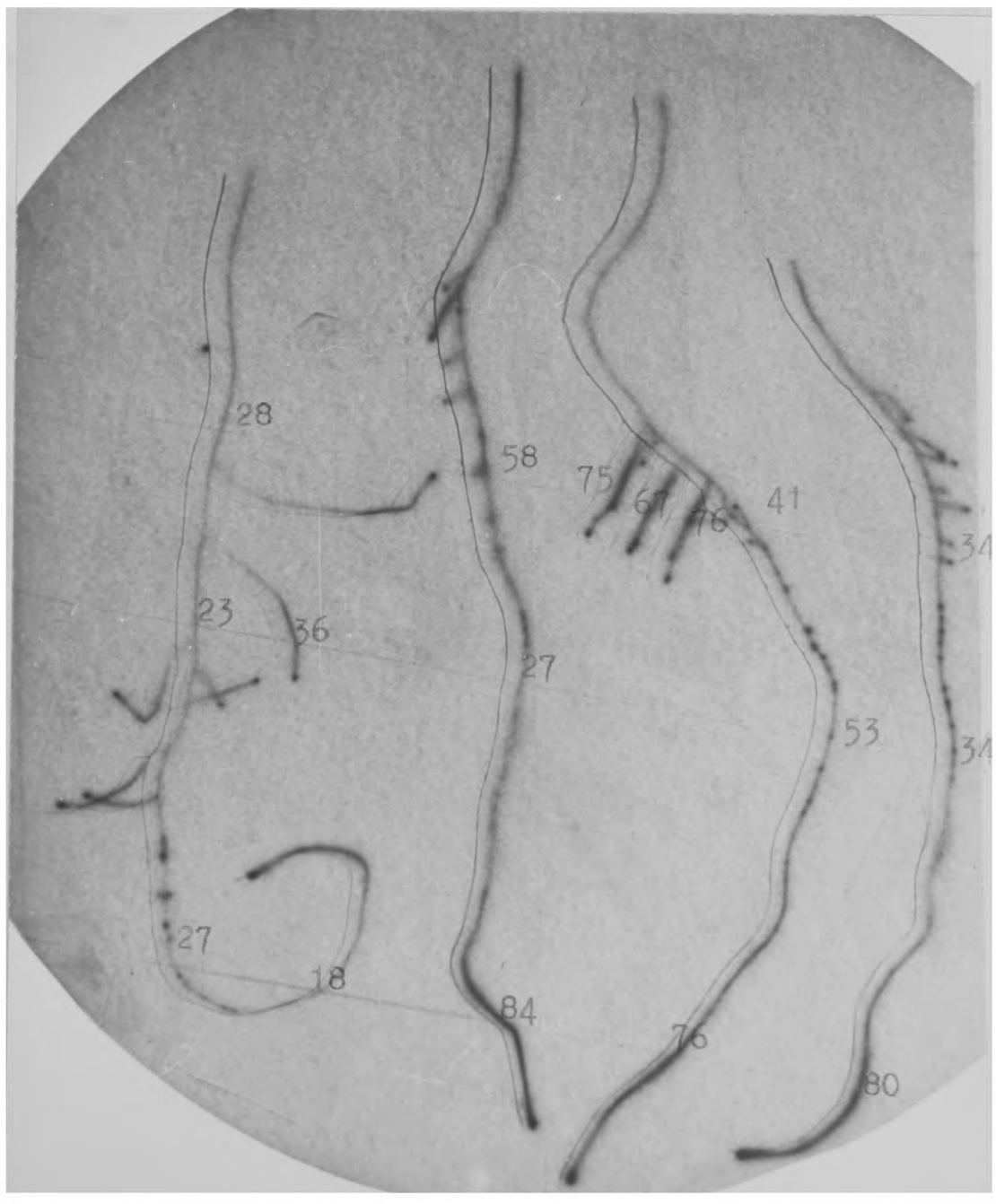
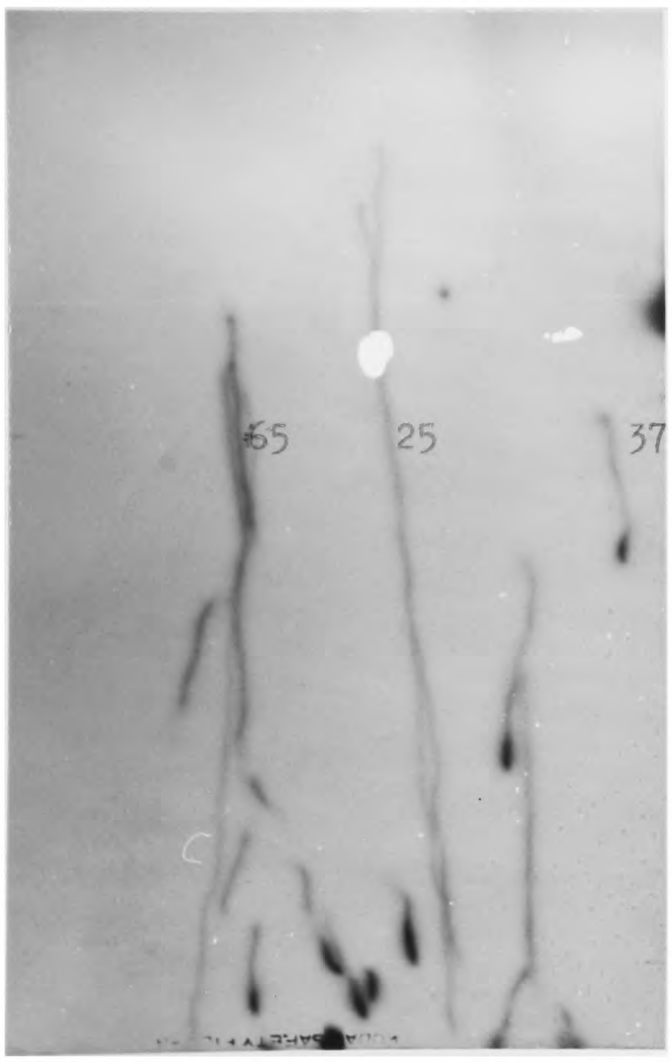
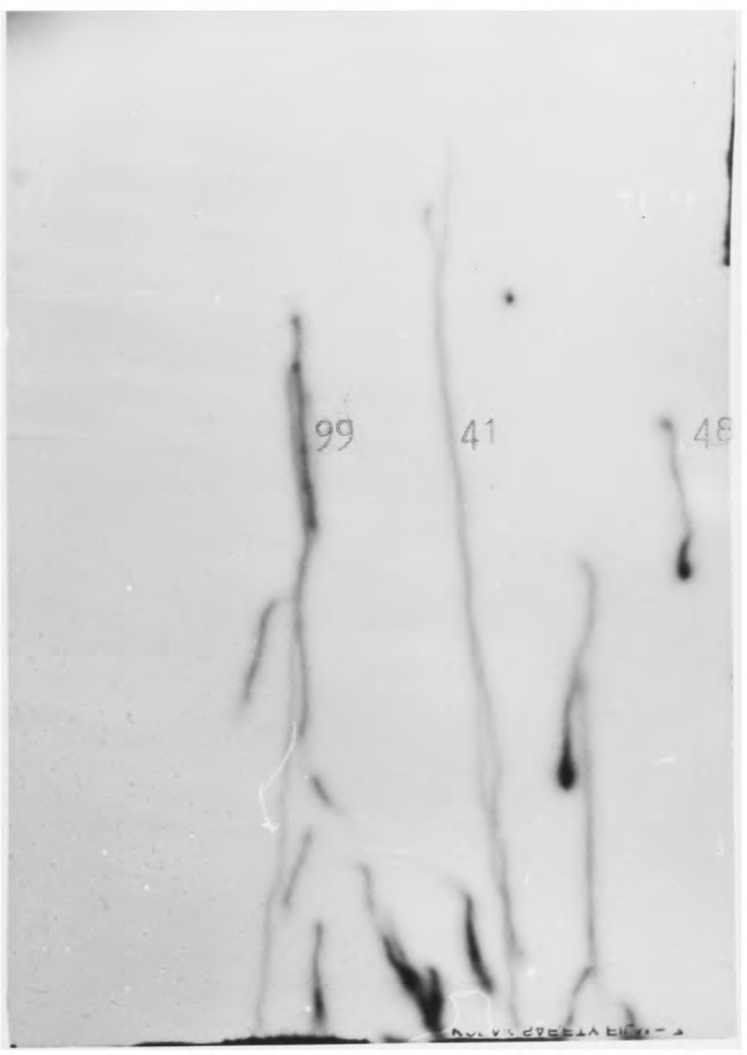


Fig 3.6 Autoradiographs of roots in soil, taken at different times after the plants had been injected with ^{32}P. Numbers on the figures are relative activity of isotope.

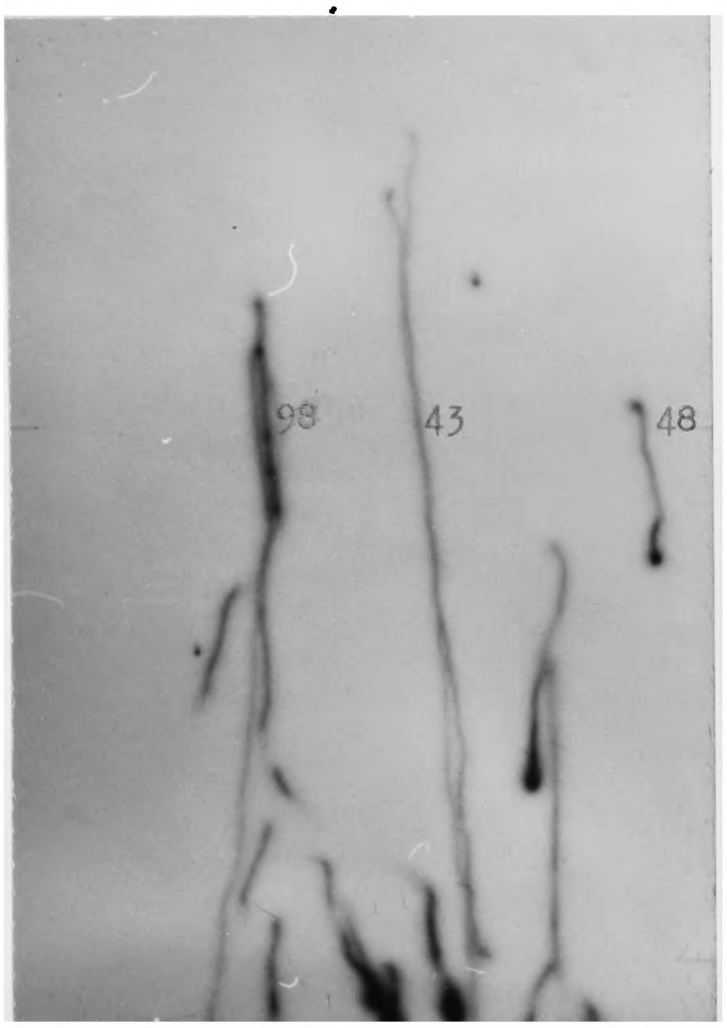
a) 0-10h



b) 12-22h



c) 24·5-35h



d) 54-65h

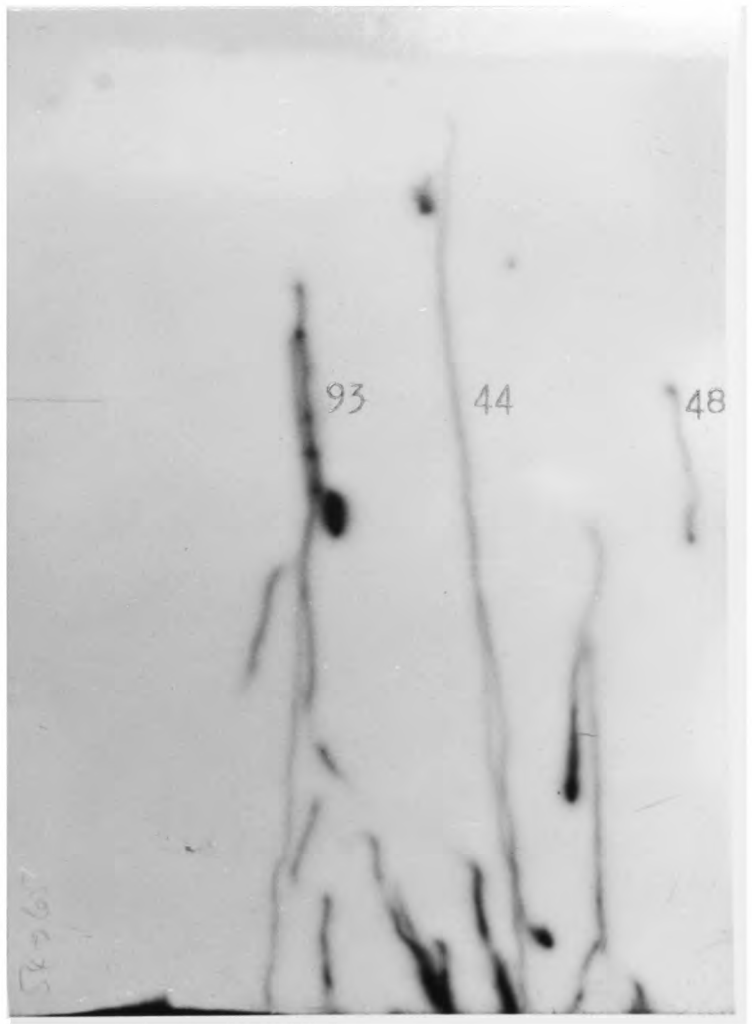
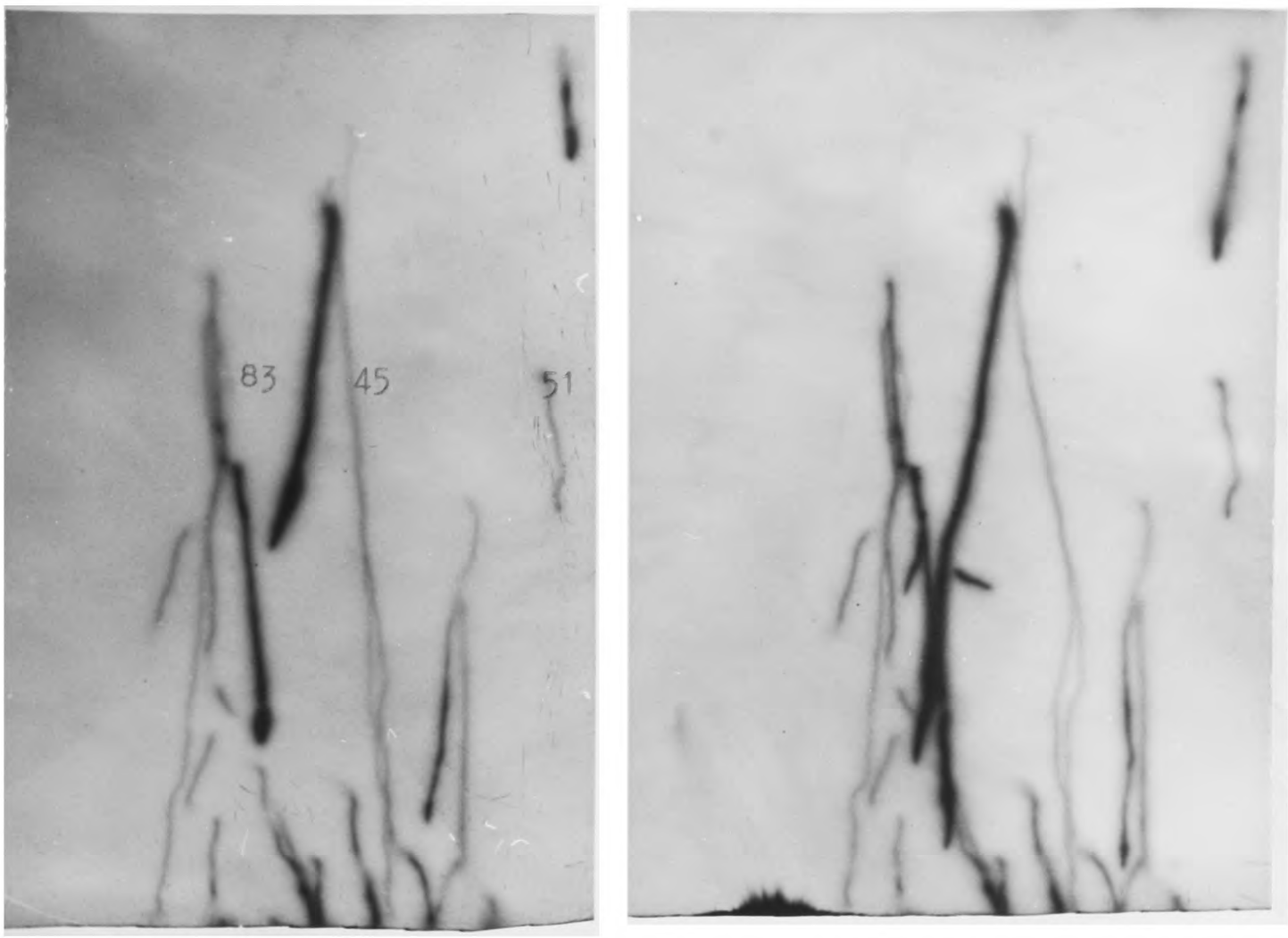


Fig 3.6 (cont)

e) 128-141h

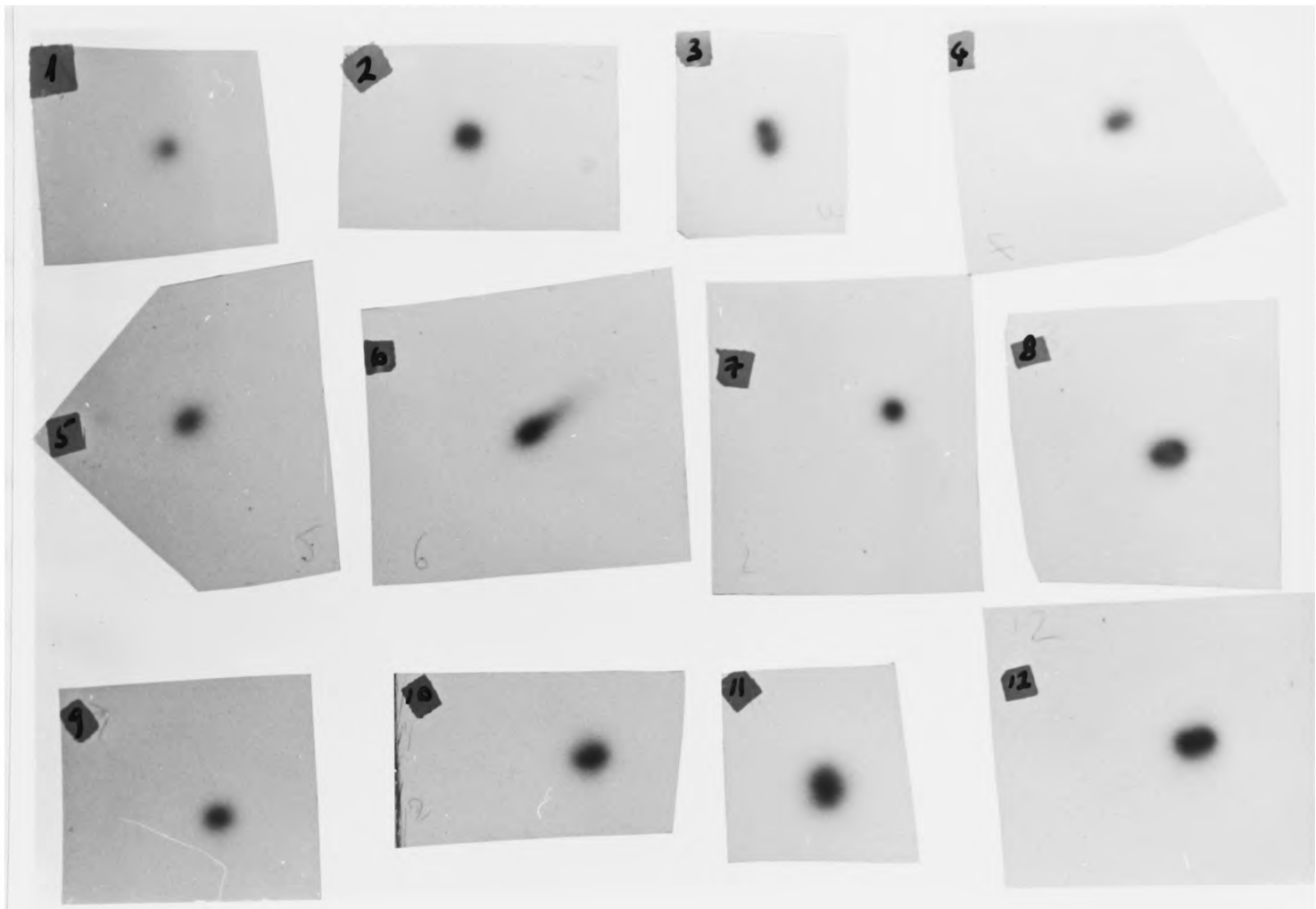
f) 162-172h



g) photograph of the roots in situ, 160h



Fig 3.7 To show the resolution of spots, obtained by autoradiographing soil into which radioactive roots have been placed.



Key

All distances are from root centres, and all roots are normal to the soil surface, unless specified otherwise.

1. single root
2. two adjacent roots
3. two roots, ·15 cm apart
4. two roots, ·1 cm apart
5. single root, inclined at 45°
6. single root, inclined at 5°
7. single root
8. two roots, ·1 cm apart
9. two adjacent roots
10. three roots, in ∧ shape
11. two roots, ·15 cm apart
12. two roots, ·15 cm apart

3.5.C. Investigations on resolution of autoradiographs of soil grown roots labelled with ^{32}P

The most important single factor influencing resolution in a grain density autoradiograph is the distance between the source and the emulsion (Rogers 1967). In the case of roots in soil, a protective layer is needed to keep the film dry, and the film must, of course, be kept in the dark. Aluminium foil (thickness 40 μ) satisfies these requirements admirably, but tears easily. Satisfactory results for onion roots in the present experimental conditions were obtained using envelope wrapped film in a thin polythene bag. Better resolution may be required in denser root systems.

The other major controllable factor is the exposure period. This should be sufficiently short that the probability of silver halide crystals directly over the source being hit by more than one particle is not significant. If exposure continues after this, the grain density over the source will not increase proportionally to the increase occurring away from the source.

A less important factor is the crystal size in the emulsion. A film with smaller crystals gives better resolution, but requires a longer exposure time, which may be a disadvantage. Three types of film, Kodirex, Industrex D and Crystallex, with relative exposure times of 100, 200 and 400, were tested by exposing them for equivalent periods using ^{32}P on cotton and on soil. Crystallex is significantly better than Kodirex, but Industrex D is the best compromise.

3.5.C.1 Determination of the resolution of radioactive roots in a soil block

If the root length is to be obtained from the number of spots on an autoradiograph, it is essential that each root produces a distinct spot. This was tested by inserting 1 cm lengths of radioactive onion roots

(diam. 2.5 X 10^{-2} cm) into a block of soil at differing distances apart to simulate roots growing in soil. With roots $\angle$ 1 mm apart, it was difficult not to disturb the soil between the roots, and, in these cases, the resolution may be poorer than it would be under natural conditions. The results obtained with envelope wrapped Kodirex in a polythene bag are in fig. 3.7

The following points are clear from inspection.

1) Roots with more than 1 mm between their centres can generally be distinguished.

2) The shape of the spot may indicate whether it represents one or two roots. For example, compare 1, which is round, with 2 which is oval. However, not all oval spots indicate more than 1 root. The shape of 5 is similar to that of 2.

3) If a root lies at a small angle to the film, it is easily distinguished as only one root by its tail (see 6).

If this degree of resolution is insufficient, it may be improved by using ^{33}P (β energy 0.25 MeV, $t_{\frac{1}{2}}$ = 25 days). An example of the use of ^{33}P is given in fig. 3.14 where rye grass roots are detected. ^{32}P gives adequate resolution for sparse root systems such as onions.

A summary of the laboratory and field procedure for the method is in section 3.5.2.

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3.5.D

THE MEASUREMENT OF LENGTH AND DISTRIBUTION OF ONION ROOTS IN THE FIELD AND THE LABORATORY

BY J. P. BALDWIN, P. B. TINKER AND F. H. C. MARRIOTT

Soil Science Laboratory and Biomathematics Department, Oxford University

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S. D. a

INTRODUCTION

There has been much descriptive work on plant root systems (Weaver 1926; Schuurmann & Goedewaagen 1965; Rogers & Head 1968) in the past, but quantitative studies have lagged behind equivalent work on plant tops, probably because of the practical difficulties of measuring underground organs.

Recently better and simpler techniques of measurement have become available (Whittington 1969), most of which have involved the use of radioisotopes. The earliest method was the labelling of limited zones of the soil with isotope, followed by monitoring of the plant tops for activity. The presence of isotope in the tops implies that there are roots in the labelled zone (Nye & Foster 1961). More recently Racz, Rennie & Hutcheon (1964) suggested that the amount of root in a volume of soil could be measured by injecting the plant top with ^{32}P, and determining the activity arising from the roots in soil samples. Russell & Ellis (1968) have developed a similar method using ^{86}Rb in which the γ emission from a soil gives the volume of root in it. Any quantitative results for root volume or mass depend on the isotope being distributed fairly uniformly throughout the root system.

Work on nutrient uptake in water culture (Russell & Sanderson 1967) has shown that root volume may determine uptake rate. However, with roots in soil the uptake may be limited by the rate at which ions diffuse through soil, rather than by the root properties. Theoretical work (Nye & Tinker 1969) indicates that where this diffusion process is the rate limiting step, it is root length and not root volume which is important for uptake. Most real situations will fall between these extreme cases, but uptake limitation by the diffusion process is most likely for nutrient deficient plants, and root length may thus be of particular interest in such circumstances. The roots of onions, which we have used, are very uniform in diameter, and it is therefore not necessary to distinguish between length and volume in this particular case. Other species may require a more detailed consideration of this point, and separate measurements of both quantities may be needed, or morphological data may allow one to be derived from the other.

Root length has normally been measured by excavating soil and washing out roots, and then using a map measuring wheel, a ruler, or the transect method (Newman 1966) on the cleaned roots or a photograph of them. These techniques may be laborious, inaccurate or both (Brewster & Tinker 1970). A great improvement in such direct length measurements is now possible by using the 'Quantimet' Image Analysing Computer, the application of which is described below.

Melhuish & Lang (1968) have recently published an indirect method for determining both length and distribution of roots in a block of soil, from an examination of the roots exposed on the surface of a soil block. The principle is very attractive, but the method

requires impregnation of the block with resin and preparation of a plane surface prior to root analysis, which appears tedious.

We have developed a simpler method for measuring root length and distribution for plants, which uses the same basic principle as that of Melhuish and Lang, but the procedure is easier, and it has the advantage of detecting only living roots belonging to a selected plant or set of plants. This paper describes the use of the method in the field and laboratory, and compares the results with those obtained from direct measurements with the 'Quantimet', which we take as our standard method. The complications which may arise through non-random orientation and distribution of roots are also considered.

3.5.D.b DIRECT MEASUREMENT BY 'QUANTIMET'

The 'Quantimet' Image Analysing Computer* determines space and shape parameters, in any given pattern with sufficient optical contrast, by a scanning technique. Our requirement is simply the total length of a set of roots, on a 35 mm photographic slide. The machine operates by measuring the total projection of the roots in one direction. If the roots are placed at random on the slide, length $= \pi/2 \times$ projection (Kendall & Moran 1963). However, even if all roots lie parallel to each other, the formula gives a result which is 99·5 % of the correct value, if the slide is rotated with respect to the 'Quantimet', the projection measured systematically every 20°, and the average value taken. This procedure was adopted as routine. In effect, the total boundary length on the slide is measured, which will include the end boundary (diameter) as well as the side boundary (length) of each piece of root, but the error caused by this is usually negligible.

For the instrument to detect the roots, they must be photographed against a strongly contrasting background. White roots can be photographed on black filter paper (Whatman 29) but better contrast may be obtained by dyeing the roots with 1 % Azo Black and then photographing them on white filter paper, if necessary. This is useful for old or discoloured roots.

In practice, the onion roots were removed from the soil, cleaned in 'Calgon' solution and then poured with water on to a large tension table lined with black filter paper. The roots were separated and arranged in water to minimize clumping and overlapping, the excess water was sucked away, and the roots photographed (Plate 13b). The 35 mm slides obtained were then mounted on a specially made rotatable holder, as the epidiascope attachment on the 'Quantimet' was not available to us. A parallel light beam from a microscope lamp with condenser was directed through the slide, and focused by a lens mounted on two $\frac{1}{4}$ in. (0·6 cm) extension tubes fixed to the 'Quantimet' (Model QTM B) camera.

Slides of known total length of black cotton or of roots grown in solution culture were used to test the accuracy of the method, and results were always within 2 % of the correct value. The coefficient of variation of a set of values was ◆1·7 %.

3.5.E INDIRECT MEASUREMENT BY AUTORADIOGRAPHIC METHOD

(a) *Laboratory procedure*

The principle is to tag the roots with a radioisotope and then detect them by autoradiography. The roots are labelled by injecting ^{32}P into the plant top and allowing it to

* Manufactured by Image Analysing Computers Ltd, a subsidiary of Metals Research Ltd, Royston, Herts.



(a) Autoradiograph of roots 3 cm below surface of pot containing nineteen onion seedlings—horizontal plane. (b) Slide of roots prepared for 'Quantimet' measurement.

(*Facing p.* 544)

become distributed through the root system. For pot-grown plants in the laboratory, the roots can then be detected by slicing the soil with a steel wire, and placing X-ray film against the cut face. The pots must, of course, be sectioned before filling to allow the soil to be cut. The translocated ^{32}P causes a black dot where each root touches the film, and thus a permanent record is obtained of the distribution and number of all roots in that plane. If the roots are equally oriented in all directions, the length per unit volume L is related to the average number of intersections of roots with unit area of any plane (N, the intercept count) by the equation

$$L = 2N \qquad (1)$$

(Kendall & Moran 1963; Melhuish & Lang 1968). Root systems with preferred orientation are considered later.

For the method to work, all roots must be sufficiently active to cause film blackening, but the spots formed must be small enough to allow closely spaced roots to be distinguished. Extreme differences between the activity in different parts of the root system may therefore cause difficulty. Several methods of labelling the roots were considered, and injection into the hollow onion leaf with a hypodermic syringe was finally chosen as it was simple and gave reproducible results. The presence of carrier phosphate had little effect on translocation of ^{32}P. ^{32}P injected into the young leaves was not translocated throughout the root system, but injection into older leaves normally labelled all roots, as shown by autoradiographs and photographs of the complete root system. The uniformity of labelling was tested by injecting plants grown in solution culture, and passing the individual roots lengthwise under a scanning counter to measure the activity. The level of activity in 0·5 cm lengths along a single root varied by a factor of up to 2, and between different roots on one plant by up to 4. Equal intensity of labelling cannot therefore be assumed in onion roots, but gross differences are unlikely with this procedure.

If the spots on the autoradiographs are too large and too close, they cannot be separated. Tests of spot resolution were made by inserting short pieces of ^{32}P labelled roots into a prepared soil surface at measured distances apart, and taking an autoradiograph. Average sized spots could easily be distinguished if the distance between the centres of roots with diameter 0·5 mm was greater than 1 mm; at smaller distances a double spot could be mistaken for a large single spot. This distance seemed adequate for sparse root systems, such as that of the onion, but might not be sufficient in very dense systems, as immediately below a grass sward. To improve resolution, the weak β-emitter ^{33}P could be used, which would give much sharper spots, though the radiation might be absorbed by any soil smeared over the end of the cut root.

Excellent results were obtained with onions by injecting 2 μCi of ^{32}P/g fresh weight of plant in 0·03 ml of 5×10^{-5} M sodium phosphate, the isotope being divided equally among all leaves to promote uniform labelling. Isotope reached all parts of our plants, which were up to 2 months old, within 12 h, but 48 h was usually allowed between injection and sampling. An exposure time of 18 h was required with envelope-wrapped Kodirex film enclosed in a polythene bag.

Labelling procedure must clearly be tested for any other species investigated by this method, but the method of Racz *et al.* (1964) has been used successfully on several other species (J. W. B. Stewart, personal communication).

(b) *Field procedure*

The method appears promising for field use, though it was designed for the laboratory.

It is possible to dig a small trench near injected plants, trim the soil surfaces flat, and press X-ray film against them, but this method is destructive of the soil–plant system, and it is difficult to get good soil–film contact, which is essential for clear autoradiographs. Instead, we designed a film holder, made of a sheet of 1 mm mild steel. The side and top edges were bent over and flattened to strengthen the sheet, and the lower edge was sharpened. A sheet of 'Melinex' Type 226 125 μ thick, was glued with 'Bostik' to the lower edge immediately above the sharpened edge, and the 'Melinex' sheet fitted under the bent side edges. This is a particularly tough type of 'Melinex', and was chosen to reduce the chance of tearing or pressure effects on the film. Simple rubbing and pressure tests in the laboratory showed none of the latter, and no indication of them was found in the field tests. The film, in its black paper folder and covered with aluminium foil, fitted into the pocket between steel plate and 'Melinex'. This sampling plate could then be hammered into the soil in the vicinity of injected plants and left for 18 h, after which the film was withdrawn and developed. Good soil–film contact was always obtained, and the placing of a thin sheet of plastic foam between the steel plate and the film gave no improvement. Plates of sizes 30×15 and 30×10 cm were made. The greatest depth of the lower edge of the film in the soil was 20 cm. Stony or compacted soil made insertion of the sampling plate more difficult, but narrower plates could be used, which penetrated more easily. The soil and plants were largely undisturbed with this method, though roots were of course cut.

RESULTS AND DISCUSSION

The main test of the autoradiographic method was made by comparing root lengths measured by the 'Quantimet' and by the autoradiographic method in four layers of each of twelve pots in which nineteen onion seedlings were growing. Short rings of 3 cm length were cut from 7·6 cm diameter PVC drainpipe, and four of the rings were taped together to make a completed pot. At harvest a steel wire was used to cut through the soil between each pair of rings after injecting the plants, and an autoradiograph was taken on the lower face of each block. The soil block was then extruded from the ring and sliced vertically. One half was autoradiographed, and the other half was sliced again vertically at right angles to the first cut, and an autoradiograph was taken of this new face. The roots were picked out of the soil, which was relatively easy with the short 3 cm soil cylinders and the straight poorly-branched root habit of onions, and the total length measured on the 'Quantimet'.

It was obvious by inspection that the roots were not oriented at random, but were mainly vertical, and it was therefore necessary to consider non-random distributions.

Non-random orientation of roots

Melhuish & Lang (1968) pointed out that equation (1) was not correct if roots were distributed with preferred directions, but considered that their root directions, and probably those found in the field, were sufficiently random for it to be acceptable if counts in three mutually perpendicular planes were averaged. The root systems investigated by us were extremely non-random, and it seems likely that this may be the case whenever roots are extending into fresh soil, and have not yet branched heavily. The treatment of this problem is complicated, and we only deal with certain aspects here.

The root elements may be considered to have a given probability P of being directed in

any particular direction. If P is constant, then the distribution is random. The other possibilities are:

(a) P varies irregularly with direction, as might happen with a mixture of horizontal roots and sinkers, of the type described by Rogers & Head (1968, Fig. 2). This cannot be treated, and it must be approximated by some combination of regular distributions.

(b) P varies regularly and smoothly, but has different values in the directions of the three major axes. We do not attempt to deal with this here. It is likely that most such distributions can be regarded as being of type (c) without great error.

(c) P varies regularly, but its value along one fixed axis is different to that along the other two; the distribution is thus symmetrical about this axis. There may be a preferred direction or a preferred plane for the roots, depending upon whether P along the fixed axis is greater or less than along the other two axes. Our root systems had a strongly preferred direction, but preferred planes may be found where roots develop in a favourable soil layer or in wide fissures.

It is necessary to know how P varies with direction, and two functions of this type are discussed in detail in the Appendix. Other functions could be assumed, but it is unlikely that the results would differ greatly as long as they defined a smooth distribution. The first assumes that $P \propto 1 + K'\cos 2\phi$, where ϕ is the angle between the fixed axis and the direction considered, and $|K'| \leqslant 1$. The correct result for the root length is obtained by using the average intersect count in (1), or

$$L = 2/3\ (N_1 + N_2 + N_3) \tag{2}$$

where N_{1-3} are the counts on any three mutually perpendicular planes. This function can only define moderately non-random populations, as the ratio N_2/N_1 (the preference ratio) cannot be less than 0·5.

The function

$$P \propto e^{K\cos 2\phi} \tag{3}$$

where $\infty > K > -\infty$, is more useful, as it can define root distributions from completely parallel to completely planar, depending upon the value of K. The fixed axis in such a population is here taken to be vertical, and it is sampled by horizontal and vertical planes with intercept counts N_H, N_{V1} and N_{V2} respectively, when N_{V1} and N_{V2} are in theory equal. It is shown in the Appendix that, for each given value of K, there is a single value for N_V/N_H, and also for the ratio between the root length calculated from

$$L = 2/3\ (N_H + 2N_V) \tag{4}$$

and the true length. The relation between these is in Fig. 1. The greatest errors occur for a parallel population ($N_V/N_H = 0$) and a planar population ($N_H/N_V = 0$). In practice, this error can probably be neglected where the preference ratio lies between 0·25 and 1, and certainly where it lies between 0·5 and 1. This graph can be used to correct results where required. For example, if the measured counts/cm^2 are N_H 50, N_{V1} 12, N_{V2} 8, N_V/N_H is 0·2, and the estimate of length from equation (4) is 48 cm/cm^3. From Fig. 1 the error factor is 0·88, and the true length equals 48/0·88, or 53 cm/cm^3.

The true root lengths measured in our experiments are compared with lengths estimated from the counts on the sampling plates in Fig. 2. The use of (4) alone gave fair results (Fig. 2a), but there was considerable bias for populations with preference ratios less than 0·25. The results were appreciably better after correcting by the method described above (Fig. 2b). This improvement, and the absence of a systematic deviation of

the experimental data from the theoretical line on Fig. 1, indicate that equation (3) describes the actual root distribution reasonably well.

It is assumed in the use of equation (3) that the axes used for describing the root distribution are normal to three mutually perpendicular sampling plates. In practice, this may not be so, and the results will depend upon the angle α between the fixed axis and the normal to the horizontal sampling plate. For example, a parallel population might be sampled by three plates each making the same angle with the roots; the counts on each plate would then be equal, and it would appear that the distribution was random. The preference ratio N_V/N_H and the length calculated by (4) have been found (Appendix) for a parallel population for various values of α. It is possible to be quite mistaken about the randomness of the population, but the maximum error in the root length is 15% with the worst possible distribution and alignment. Strongly oriented populations, and their preferred directions, can usually be detected by simple inspection, and it is shown in the Appendix that errors are negligible for small values of α. It is only likely to cause difficulty where the preferred direction changes rapidly with position, as might happen close to the base of a plant.

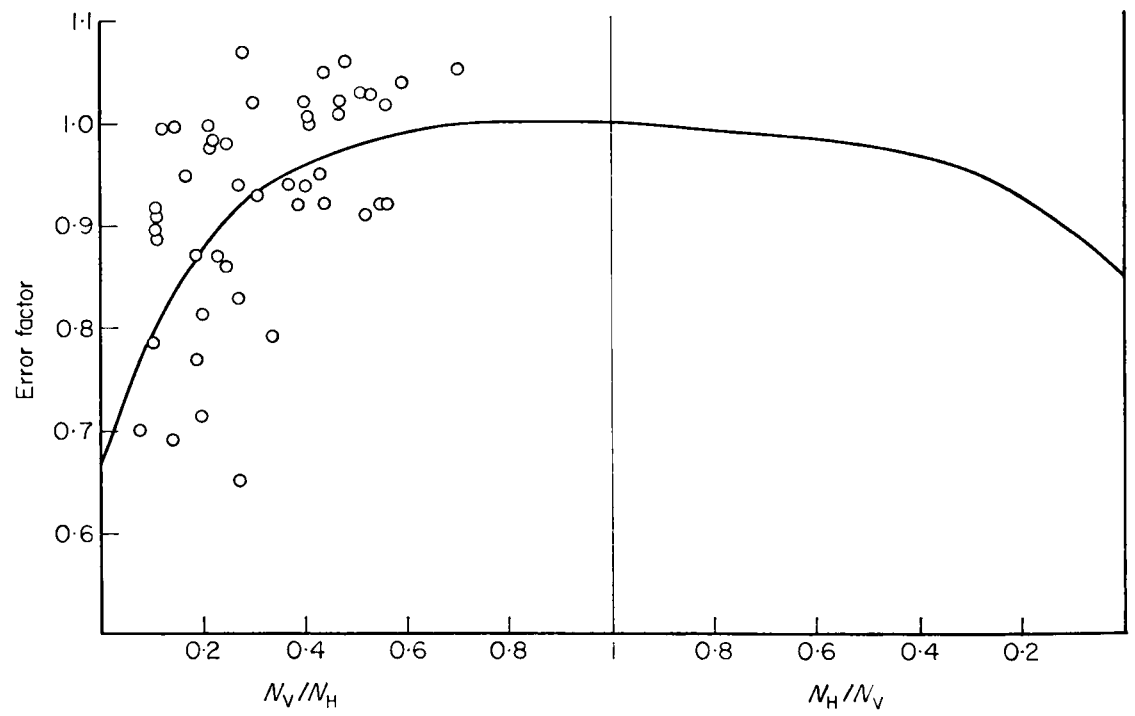


FIG. 1. Relationship between N_V/N_H or N_H/N_V and the ratio of 2/3 (N_H+2N_V) to the true root length, (the error factor). ———, Theoretical line for a distribution defined by $P\alpha e^{K\cos^2\phi}$. ○, Experimental points, taking the 'Quantimet' measurements as the true length.

3.5.F.ii *Intercept distribution*

Irrespective of the distribution of their directions, roots may or may not be positioned at random in a given volume. Inter-root competition, and hence the efficiency of the root system as a whole may depend greatly upon position (Sanders, Tinker & Nye 1971). It is a particular advantage of this type of method that it allows this spatial distribution also to be tested. The intercept distribution on a plane can be either regular, random, or contagious (Greig-Smith 1964). Theoretical reasons can be adduced for expecting either regularity or contagion: any tropic response to water or nutrients, or any toxic root exudates, will tend towards the former, whereas any soil heterogeneity, in chemical composition or mechanical resistance, will tend towards the latter.

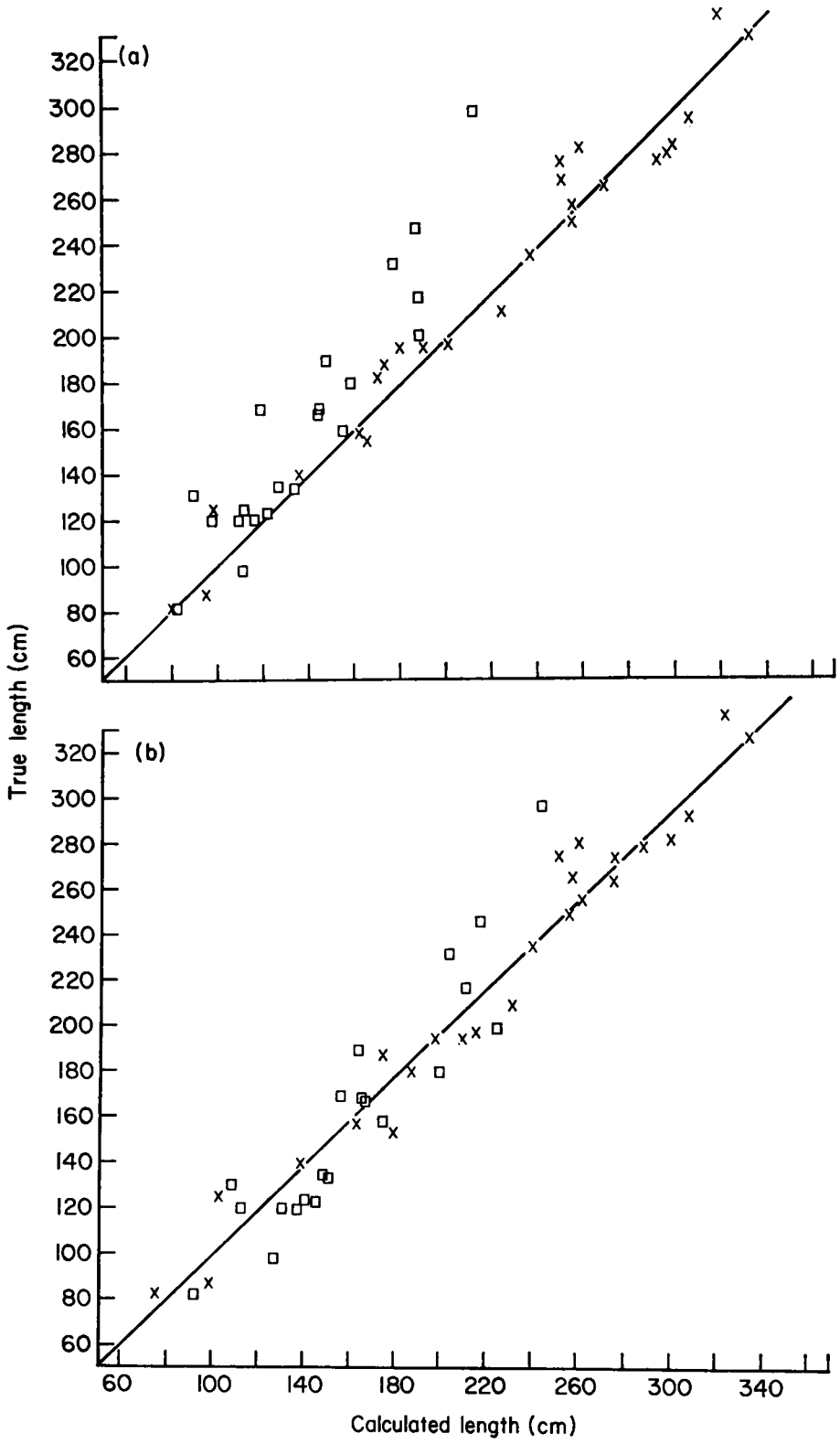


FIG. 2. (a) Comparison of root lengths measured by the 'Quantimet', and calculated by equation (4). (b) As in (a) but with a correction from Fig. 1. ×, Root systems with N_V/N_H greater than 0·25; □, where it is less.

Field results

A test was made of the field method to discover any unexpected difficulties. Fifty onions in a row, part of a crop at the National Vegetable Research Station at Wellesbourne, were injected with ^{32}P and plates were inserted around them in positions as shown in Fig. 3. Horizontal plates cannot be inserted without digging a trench, and instead one plate was forced into the soil at 20° to the soil surface. The preference ratio was greater than 0·25, and the simple average of counts in three planes was therefore used to calculate root lengths (Table 1). This is encouraging, though more field testing is required.

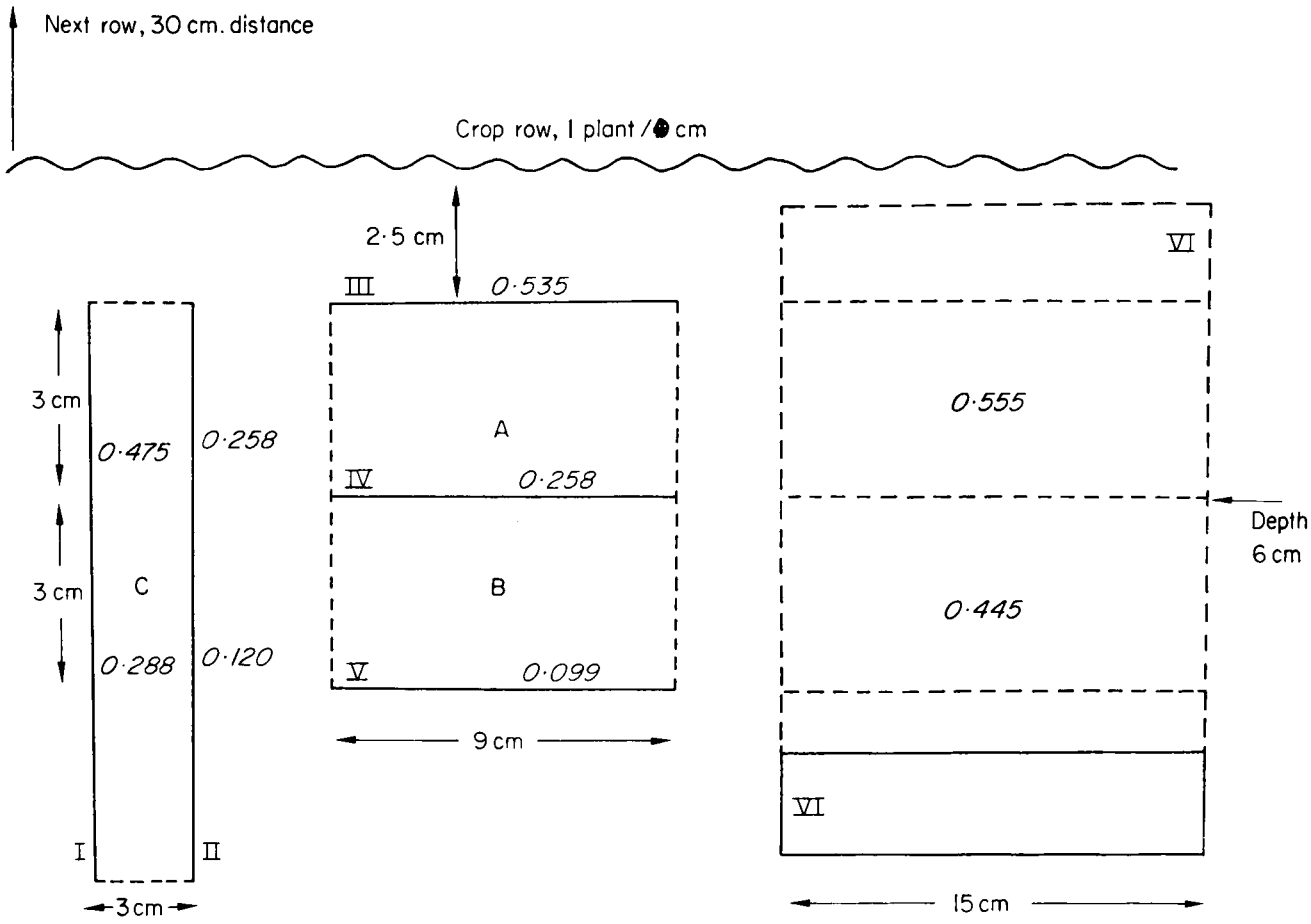


FIG. 3. Arrangement of sampling plates around a row of onion plants in the field. I–V indicate the position of vertical sampling plates, and VI shows the final position of a plate inserted at 20° to the horizontal, the dotted outline being the portion underground. Italic numbers give counts found on the plates (cm^{-2}) and other numbers indicate distances (cm).

Table 1. *Comparison of lengths of root in the field from direct measurement and from autoradiographs (mean counts from the appropriate horizontal and two vertical plates were used in equation* (1)*; see* Fig. 3 *for plan and counts*)

Part measured	True length (cm)	Calculated length (cm)
A	285	269
B	138	164
A+B	423	435 (all plates)
C	290	295

3.5.9. *Conclusion*

The method may be of value for ecological work. Competition between species for nutrients is an important factor (Bradshaw 1969) and root length and distribution in the soil must affect competitive ability greatly. This method has the advantage that the root systems of different species, or different plants of the same species, can be studied separately without excessive labour. Work on double labelling techniques, which will allow interpenetrating root systems (Litav & Harper 1967) to be investigated simultaneously, is now in progress.

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SUMMARY

3.5.H.

The 'Quantimet' Image Analysing Computer has been used to measure the length of roots washed out from soil, and gave quick and accurate results. A new autoradiographic method for measuring root length in the soil is described, in which ^{32}P was injected into onion leaves. After translocation, the soil containing the roots was cut into blocks, and autoradiographs made on each cut surface. Each cut root gave a spot, and there is a simple relationship between the number of spots per unit area and the length of root per unit volume, if the root directions are random. An adaptation of the method for field work used steel plate film holders, which could be driven into the soil around injected plants.

The root systems in experimental pots were found to be non-random, and the theory of such populations is considered for situations where the probability of roots having a given direction is different along one axis from that along the other two. Two functions describing the distribution of root directions have been used, and methods are given for deriving the true root length of such systems from spot counts on three mutually perpendicular autoradiographs. Good agreement was found between the length of roots measured by the 'Quantimet' and by the new method.

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3.5.I.

APPENDIX

Buffon's problem in three dimensions

Buffon, in 1777, first solved the classical problem now know as 'Buffon's Needle' (Kendall & Moran, 1963). A line of length l is placed at random on a plane ruled with parallel straight lines unit distance apart. The mean number of intersections can be shown to be $2l/\pi$, and the result can be used to estimate the length of irregular outlines. The corresponding result in three dimensions is also well known, but since it is seldom possible to intersect a spatial system by *random* planes, it can only be used when the system is itself assumed to be random. If this is not the case, the solution must be modified.

A linear system of length l per unit volume is intersected by parallel planes unit distance apart. The problem is to find the mean number of intersections per unit area of the planes.

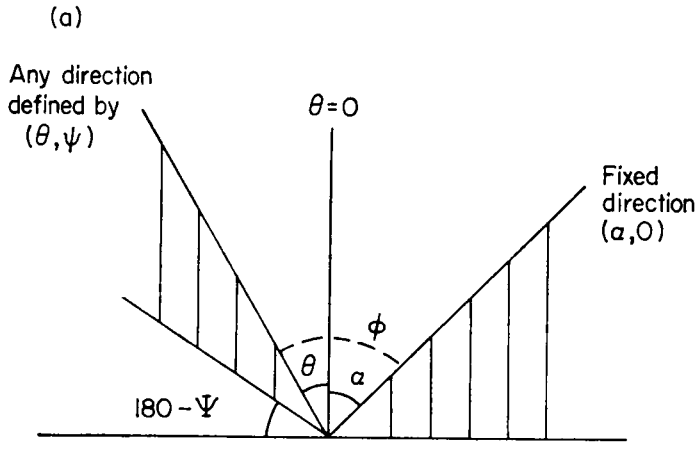


FIG. 1A. (a) $\theta = 0$ is the normal to the planes. The fixed direction defines the plane $\psi = 0$ and makes an angle α with $\theta = 0$. The direction (θ, ψ) makes an angle ϕ with the fixed direction and the planes defined by each of these two lines and $\theta = 0$ make an angle ψ. Thus θ, ψ, ϕ and α form a spherical triangle as shown in (b) and $\cos\phi = \cos\theta\cos\alpha + \sin\theta\sin\alpha\cos\psi$.

In general, the linear system can be thought of as made up of equal straight elements whose direction can be specified. The probability of a given direction can be described by a frequency distribution. The only types of distribution considered here will be those symmetrical about a fixed direction. In this case, the probability of any direction is proportional to $f(\phi)$, a function of the angle ϕ that it makes with the fixed direction.

Suppose spherical polar coordinates are defined with the normal to the planes as $\theta = 0$ (the z axis), and the fixed direction in the plane $\psi = 0$ (the xz plane) making an angle $\theta = \alpha$ (Fig. 1Aa). Any direction given by (θ, ψ) makes an angle ϕ with the fixed direction, where

$$\cos\phi = \cos\theta\cos\alpha + \sin\theta\sin\alpha\cos\psi \quad \text{(Fig. 1Ab)}$$

Now the theoretical mean number of intersections N per unit area is the projection of the length l on the line $\theta = 0$. This is the expected value of $l \cos\theta$, in terms of the frequency distribution specified by $f(\phi)$. Since the area element can be written $\sin\theta \mathrm{d}\theta \mathrm{d}\psi$ (Kendall & Moran 1963, p. 77)

$$N = l\int_0^{2\pi}\int_0^{\pi} f(\phi)|\cos\theta|\sin\theta \,\mathrm{d}\theta\,\mathrm{d}\psi \Big/ \int_0^{2\pi}\int_0^{\pi} f(\theta)\sin\theta\,\mathrm{d}\theta\,\mathrm{d}\psi$$

Here the denominator is a normalizing factor for the distribution.

In general, N depends on $f(\phi)$ and on α. In the next sections various possible distributions will be discussed.

(i) $f(\phi) = 1$

The directions of the elements are completely random. As is well known, $N = l/2$.

(ii) $f(\phi) = 1 + K' \cos 2\phi \qquad |K'| \leqslant 1$

This distribution (cf. Marriott 1969) has a simple form and describes adequately many systems in which the departure from randomness is not very strong. When $K = 0$, it gives the random distribution. Positive values of K correspond to grouping about a preferred direction, negative values to a preferred plane. Integration gives $N = \frac{1}{2}l(1-\frac{1}{4}K'+\frac{1}{4}K'\cos 2\alpha)/(1-\frac{1}{3}K')$. It will be seen that the ratio of counts on sections giving $\alpha = 0$ and $\alpha = \pi/2$ cannot exceed 2:1 for $K' = 1$ nor fall below 2:3 $K' = -1$. For ratios outside these limits, the distribution does not give a satisfactory fit to the data. If it is acceptable, however, the result shows that the mean count on any three mutually perpendicular planes gives an unbiased estimate of $\frac{1}{2}l$. If the planes give angles α_1, α_2 and α_3, these angles correspond to direction cosines. Then $\cos 2\alpha_1 + \cos 2\alpha_2 + \cos 2\alpha_3 = -1$, and the result follows.

(iii) $f(\phi) = \mathrm{e}^{K\cos 2\phi}$

When $|K|$ is small, this distribution approximates to the previous one, but large values correspond to greater departures from the random distribution. When $K \to +\infty$, the elements are all parallel; when $K \to -\infty$, they lie in a plane.

The calculations involved in evaluating N are difficult, but are considerably simplified by considering only the cases $\alpha = 0$ and $\alpha = \frac{1}{2}\pi$. The corresponding values of N, say N_H and N_V, can be reduced to forms involving only single integrals, which can be evaluated numerically.

If counts are taken on three planes, of which one is normal to the fixed direction, the mean is $\frac{1}{3}(N_H + 2N_V)$. This will depend on K. Each value of K gives a corresponding ratio $N_V : N_H$, and Fig. 1 shows the error factor $X = \frac{1}{3}(N_H + 2N_V)/\frac{1}{2}l$ plotted against N_V/N_H for $K > 0$ (when there is a preferred direction) or N_H/N_V for $K < 0$ (when there is a preferred plane).

Provided the ratio is greater than 0·5, the error in using the mean is less than 3%, and for 0·25 it is still less than 10%. When $K \to \infty$, $N_H = 1$ and $N_V = 0$ and the mean is $\frac{2}{3}$ of the value for a random distribution ($X = \frac{2}{3}$). When $K \to -\infty$, $N_H = 0$ and $N_V = 2/\pi$, and $X = 8/3\pi = 0{\cdot}85$.

In practice, given actual counts n_H, n_{v1}, n_{v2}, an unbiased estimate of l is obtained by dividing $\frac{2}{3}(n_H + n_{v1} + n_{v2})$ by the mean error corresponding to n_H/n_V or n_V/n_H read from Fig. 1.

(iv) The discrete distribution $P(\phi) = 1$ when $\phi = 0$, $P(\phi) = 0$ otherwise.

The procedure suggested in the last section depends on a knowledge of the critical fixed direction. As an extreme case, suppose the distribution is strictly parallel, but that the critical direction is unknown. If N_H corresponds to $\theta = \alpha$ and N_V is taken on planes

symmetrically placed with respect to the fixed direction, $N_H = l \cos \alpha$, $N_V = l \sin \alpha/\sqrt{2}$.

The error when l is estimated using Fig. 1A is small when N_V/N_H is small. When the ratio increases, the error rises to about 15%. This happens when the planes are symmetrically placed about the direction of the elements, which are therefore judged to be nearly random. When N_V/N_H is 0·2, 0·3 or 0·4, the error is 3, 6 or 9% respectively, and corresponds to values of α of 11·4, 23 or 29·5°. A moderate angular error in estimating the fixed direction thus has very little effect on the estimate of length.

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3.5.J. Additional details of the field test

Fig. 3.8 is a photograph of the site of the field test. After each plant was injected, it was marked with a drop of collodion. This shows up white in fig. 3.9. Fig. 3.9 shows the relative positions of the film holders, and corresponds with Fig. 3, section 3.5.F.iii. Fig. 3.10 shows the metal jig, which was used for inserting the angled plate.

3.5.K. Non random orientations of roots

The formula $L = 2N$ applies only to random lines intersecting a cube. However, non-random lines can be treated if they have a known probability P of lying in any particular direction. This is discussed in section 3.5.F.i. Melhuish and Lang (1970) have suggested anisotropic root orientation may be represented by an ellipsoidal probability distribution. Their calculations have been corrected by Marriott (1972). The error factor assuming the ellipsoidal distribution is compared with that given in fig. 1, section 3.5.F.i, in fig. 3.11. The ellipsoidal model suggests a slightly larger correction factor, but agreement is generally good. However, the ellipsoidal model is limited to the extent that it cannot satisfactorily represent a distribution in which all the lines have nearly the same direction. In fact, the limiting N_V/N_H (see section 3.5.F.i.) is 0.64 (Marriott 1972). The majority of my results have given an N_V/N_H less than this. Melhuish and Lang (1971) have, unwittingly, given a good illustration of the inadequacies of the ellipsoidal distribution: they quote surface densities of 19.8, 11.3 and 11.9 in their example of the method, which cannot possibly arise from an ellipsoidal distribution (it is too near the linear case), and use an anisotropy correction obtained from their computed values for the planar case.

Another type of non randomness arises if there is a density gradient in the root system. This is automatically accounted for in the isotropic

case, by the number of intersections per unit area of plane. Lang and Melhuish (1970) have shown that if the root distribution is uniformly anisotropic, but the density of the roots varies linearly with distance, averaging the counts on three mutually perpendicular planes gives the correct answer.

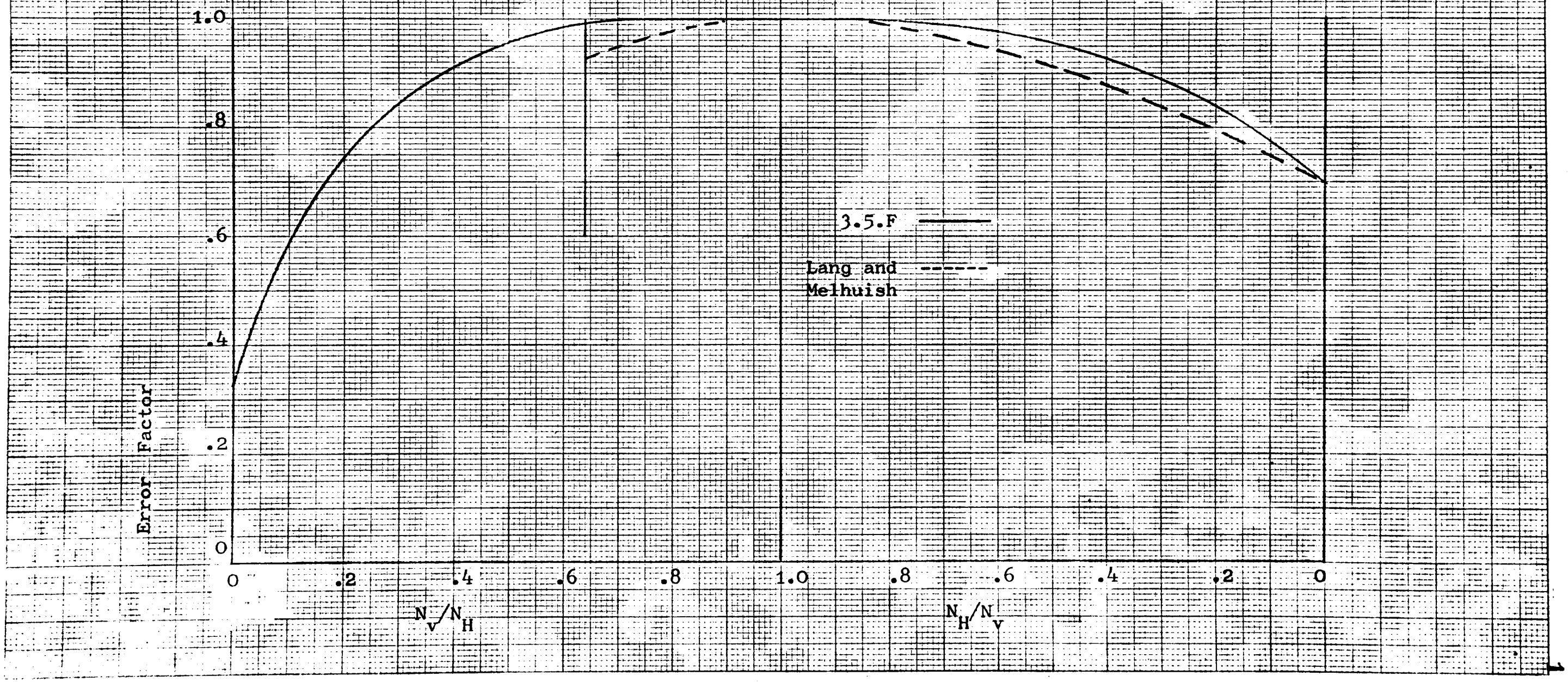
Fig 3.8 Field Site for Test of Autoradiographic Method for Measuring Root Length. The interrow distance is 25 cm.



Fig 3.9 Relative Positions of Films, for autoradiographing onion root system. The largest plate is 17 cm across.



Fig 3.11 A plot of the error factor against the preference ratio for the probability distribution used in section 3.5.F, and that used by Lang and Melhuish (1970).



3.5 a ii 2 <u>The isotopic injection method for estimating the length and spatial patterns of two interpenetrating root systems</u>

This section does not discuss a method which is essential for the experimental studies into the usefulness of the theoretical models suggested in chapter 2. However, it is appropriate to continue here as the technique involves isotopes for indirectly estimating root length. Readers not wishing to digress are advised to turn to section 3.6.

If plant roots labelled with different isotopes can be distinguished, the root length and pattern of two root systems may be measured simultaneously. This idea was developed for studying competition between root systems. Different plants are labelled with isotopes emitting β particles of differing maximum energies, so that the radiation from the roots of one plant can be screened out whilst that from the other plant roots is detected. Comparison with similar autoradiographs without screening distinguishes the roots from the two plants. I have successfully used S^{35} (β energy 0.17 MeV, $t_{\frac{1}{2}}$ = 89 days) or ^{33}P (β energy 0.25 MeV, $t_{\frac{1}{2}}$ = 25 days) in one plant with ^{32}P in the other. Melinex screens of density 25 mg cm^{-2} and 60 mg cm^{-2} respectively are adequate to absorb the less energetic radiation. Aluminium foil (density 4.5 mg cm^{-2}) was used to protect the X-ray film from light.

^{14}C (β energy = .155 MeV, $t_{\frac{1}{2}}$ = 5568y)-glucose was also tried. Although it labels root systems completely, there was some leakage of the ^{14}C out of the roots. There is a danger that the ^{14}C exuded from the roots of one plant may be assimilated by those of another. This isotope has been used by Litav and Harper (1967) for studying the spatial relationships between the root systems of different plants.

The size, shape and density of the spot on the autoradiograph caused by a root is a function of the energy of β emission of the isotope, the

radius of the root and its inclination to the surface, the activity per unit length of root, and the soil density. If the last 4 are constant, the number of β particles merging from a soil face will be in the ratio 25:1.39:1 for the ^{32}P, ^{33}P and ^{35}S labelled roots. On the other hand, both ^{33}P and ^{35}S are about twice as efficient as ^{32}P at blackening X-ray film (Herz loc. cit.). The only possibility of error in the method lies in the emission from the weaker isotope being so small that a root is not detected, or so high that it can be mistaken for a root containing small amounts of the stronger isotope. The latter is unlikely, since the size and appearance of the spots are quite different, and generous amounts of the weaker isotope should be used.

This procedure is more convenient in the laboratory than the alternative technique of using isotopes with different half lives (such as ^{42}K and ^{32}P with $t_{\frac{1}{2}}$ = 12 hours and 14.7 days respectively), and allowing one to decay before taking the second autoradiograph. For field use, this latter approach may be the more satisfactory, since the film holders described earlier require a strong plastic sheet to protect the film, which would absorb the weaker radiation. However, additional roots labelled with ^{32}P may grow against the film whilst the ^{42}K is decaying, which requires some 5 days with the level of activity required. The error caused by this may be serious if cutting the roots encourages branching. For the ^{32}P and ^{33}P or ^{35}S method to be of use in the field, the film holders require modification. Alternatively, a trench could be dug and the film pressed against the exposed face.

The method was tested with onions growing in association with Agropyron repens, Polygonum aviculare, Brassica napus or Lolium multiflorum.

3.5.a.ii.2.A. Isotope injection techniques for additional species.

1. Use of dyes to test injection methods.

Following Roach (1938) an attempt was made to test different injection methods by using a dye. This gives the type of distribution resulting from leaf injection in less than 1 hour. A 0.1% solution of a) acid fuchsin, which moves the fastest in plant tissue (Roach 1938), and b) fluorescein was injected into Agropyron repens in the suggested ways (Roach 1938), but no method resulted in any translocation of dye to the roots. A trial with onion plants was also unsuccessful.

2. Methods using labelled phosphate

Various methods were tested using ^{32}P with four week old plants growing in solution culture in special cells (fig. 3.3). The ^{32}P was injected at a rate of 5 μc/g plant in a solution of 5×10^{-6} M NaH_2PO_4. The specific activity was 150 μc/ml. When the isotope was injected in more than one place, the volume of solution was equally divided between each site. 24 hours after injection the roots were displayed on aluminium foil, and autoradiographed to test the completeness of labelling. This procedure also enables a qualitative assessment to be made of the uniformity of isotope distribution. In all cases, the culture solution was tested for ^{32}P by counting a 2 ml sample on a planchet. Where there was accidental contamination, the plants were rejected. For each species tested, a successful injection method was found and tested with six replicate plants.

2.1. Details of successful injection techniques

a) Agropyron repens: the junction of each leaf sheath and its blade was bruised, and isotope injected over the bruise between the sheath and the stem.

b) Lolium multiflorum: as with A. repens.

c) Brassica napus: the mid rib and upper surface of each leaf was bruised with a syringe needle. A droplet of isotope solution was spread over the bruised area.

d, Polygonum aviculare: two incisions at right angles were made with a scalpel along the stem of the two basal internodes. Isotope was injected into the damaged stem.

3. Methods using labelled sulphate

^{35}S is not as satisfactory as ^{33}phosphate for root length measurements as it usually has a fairly high diffusion coefficient in soil, and therefore may move away from a cut root, causing a large diffuse spot on the autoradiograph. However, it is cheap and readily available and injected sulphate is translocated to the same extent as phosphate (Buchovac and Wittwer 1957). The distribution of the label in 4 week old onions was tested by injecting .02 mls of $^{35}SO_4$ as K_2SO_4 into every leaf at an activity of 5 μc per g fresh weight of plant. All the roots were labelled with isotope after 18 hours.

3.5.a.ii.2.B. Levels of activity found on roots

For the double labelling technique to be successful, the roots from both plants must blacken the film in the same exposure time. In addition to the two factors discussed in section 3.5.a.iii, a knowledge of the % of injected isotope translocated, and the resulting activity per unit length of root is required. This was calculated by injecting a known activity of isotope into plants in solution culture. Roots were sampled for radioactivity by dissolving 2 cm lengths in nitric acid on a planchet, and counting 3 samples at once under a GM tube. The results are in table 3.5. The per cent of the injected isotope in the whole root system was calculated from the activity in the sample analysed, and the dry weight of the whole root system. Although the results are rather variable, they give an estimate of the activity per g dry weight of plant which gives rise to a particular count rate per cm of root.

3.5.a.ii.2.C. Test of method as a laboratory technique for estimating the lengths and spatial patterns of two interpenetrating root systems

The method was tested in an experiment designed to screen 5 plant species for use in competition experiments.

A 25cmx11cmx11cm box was packed with soil (B3L) sieved to 2 mm at a bulk density of 1.3 in four sections 6.25 cm long. The soil sections were separated by lens tissue coated in silicone grease, to prevent lateral movement of water and nutrients. After packing, the soil was leached on a tension table (Clements 1966) at 50 cm suction with three bed volumes of nutrient solution. The solution composition was $2.24X10^{-3}$ M N as NO_3^-, $1.0[illegible]X10^{-3}$ M Ca as $Ca(NO_3)_2$, $.1[illegible]X10^{-3}$ M Mg as $Mg(NO_3)_2$, $.363X10^{-4}$ M K as KNO_3 and $1.405X10^{-4}$ M Na as [illegible]. A row of onions (A.cepa var Mustang) was planted across the middle of the box either alone, or 2 cm away from a parallel row of A.repens, P. aviculare, L. napus, L. multiflorum or A. cepa. The aerial environment was kept constant in all cases by a reflective screen 1 cm from each row, and the plants were grown in an antitranspiration chamber (see section 3.3.B) to minimise water uptake, and hence competition for water. Fig. 3.12 is a diagram of the box in transverse section. The boxes with one row and two rows of A. cepa were harvested after 4 weeks, the others after 6 weeks. At harvest, all A. cepa plants were injected with ^{32}P, and the other species with ^{33}P, except in the A. cepa-A. cepa box, where plants in one row were injected with ^{35}S. After two days, the soil in the box was sliced horisontally 5 cm below the surface, and autoradiographs were taken of the two faces, one with and one without a screen. After reassembly, the box was sliced vertically, parallel to the row, at 5 intervals of 4.17 cm, and further autoradiographs taken. Fig. 3.12 shows the locations of the slices. The autoradiographs gave the density and pattern of roots from each row at different positions in the box. In all cases, A. cepa root and shoot growth were very much reduced by the presence of the other species. No quantitative

comparisons are possible, as different amounts of N, P, K, Ca and Mg were added uniformly to each box in an attempt to locate the nutrient limiting the onion growth. The attempt was unsuccessful; there was no response by the onion, and the dominant row must have taken all the added nutrient.

Fig. 3.13 shows the box containing A. cepa and L. multiflorum, and fig. 3.14 shows autoradiographs of the roots of L. multiflorum growing in association with A. cepa. It is clear that L. multiflorum established a much denser root system, (a mean of 8 cm/cm^3 compared with a maximum of .3 cm/cm^3 for A. cepa) and this is presumably the reason why it was such a successful competitor (Lee 1960).

The results from the box with A. cepa alone and that with two rows of A. cepa illustrate how the technique gives information on the probable mechanisms whereby root systems influence each other. Fig. 3.15 is a plot of the root densities of each row in the A. cepa-A. cepa box, A, (O and +), compared with the single row of A. cepa growing alone, B, (X). In A, both rows had a similar root system distribution, but the greatest density was well to the side of the row. Thus each row is limiting the volume of soil available for exploitation by the other row; a similar phenomenon has been observed with soybean root systems (Raper and Barber 1970). This suggests some root exclusion mechanism, either due to toxic root excretions or nutrient concentration gradients. In B, the roots are distributed symmetrically throughout the box.

Roots may be positioned in a random, regular or clumped manner. This may be expressed in terms of the nearest neighbour distance (Clark and Evans 1954). Any root exclusion mechanism depending on toxin excretions (Bonner 1950) would be expected to cause regularity in the rooting pattern, which can be tested for on the autoradiographs. No evidence was found in either A (with all the roots included) or B for

departure from randomness (P=0.05). Nutrient concentration differences (probably nitrate) appear more likely to be the cause of the changed distribution.

Although root individuals are unlikely to detect gradients of nitrate, root systems will branch most where there is greatest concentration of nitrate in the soil. Gradients around single roots are probably too small to have any effect, and it is major gradients only that cause measurable differences in root branching. This restriction of the available soil volume is an established mechanism of competition for water (Harris 1967), but quantitative data on the plant nutrients is still lacking.

Table 3.5.

The level of activity in root systems of different species, after plant injection with ^{32}P

Species	Top dry wt. gm	Root dry wt. gm	^{32}P injected	ρ cm^{-1} root	total ^{32}P in plant
B. napus	1100	30.4	10.8 μc	780	.61
	1022	40.0	3.6 μc	163	.49
P. aviculare	355	70.0	9.0	106	.19
	122	40.0	7.6	170	.88
	304	40.0	7.6	74	.12
L. multiflorum	361	150	9.0	845	.87
	512	65.0	9.0	837	.54
A. repens	565	160	9.0	3868	5.2
	482	100	9.0	833	.89
A. cepa	406	80.0	9.0	736	1.5
	483	90.0	9.0	523	1.2

Fig 3.10 Metal Jig, for inserting a nearly horizontal X-ray film into soil.



Fig 3.12 Transverse section of box used to test the double labelling injection method (natural size).

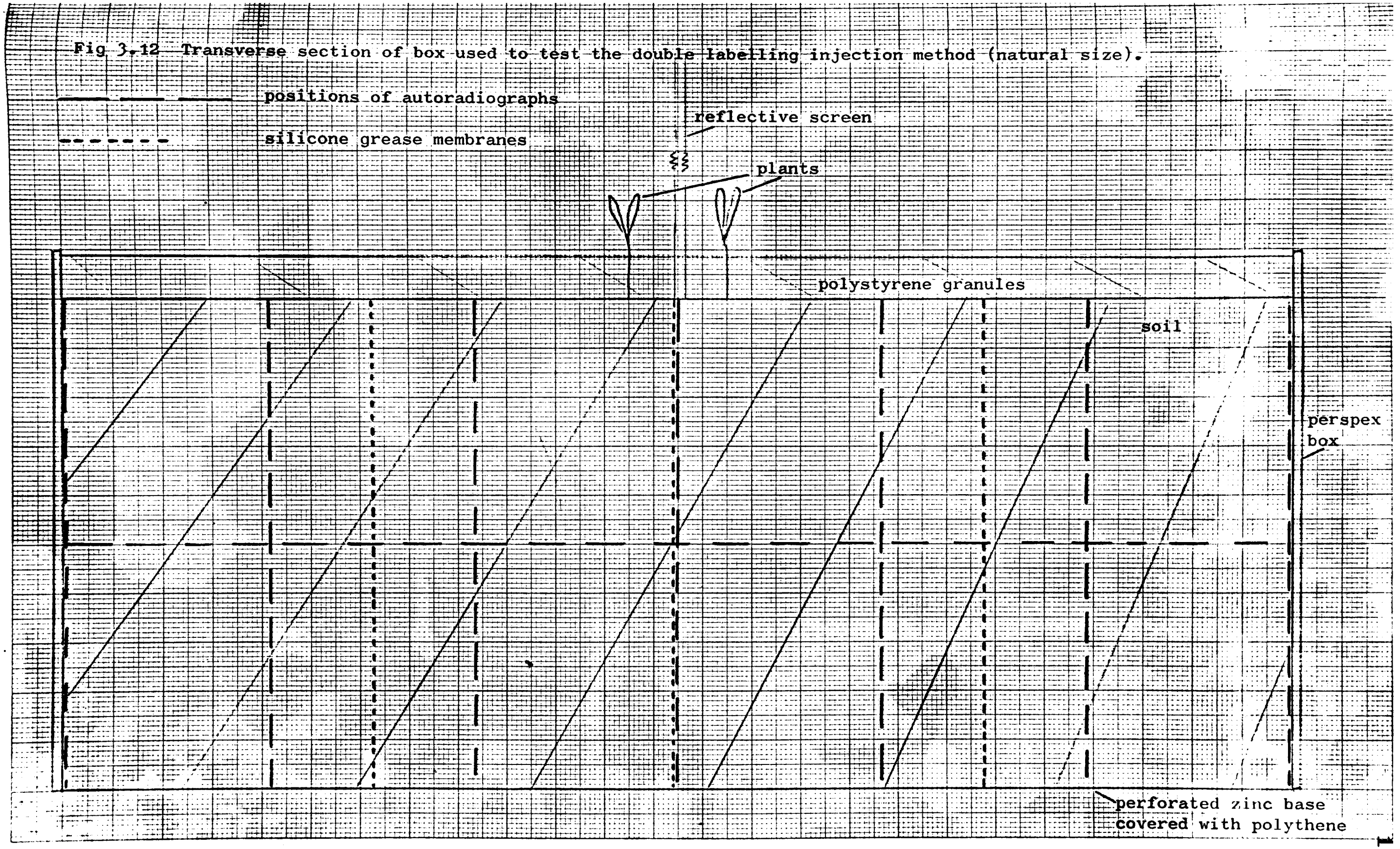


Fig 3.13 Experiment on Competition between A. cepa (right) and L. multiflorum, at harvest.

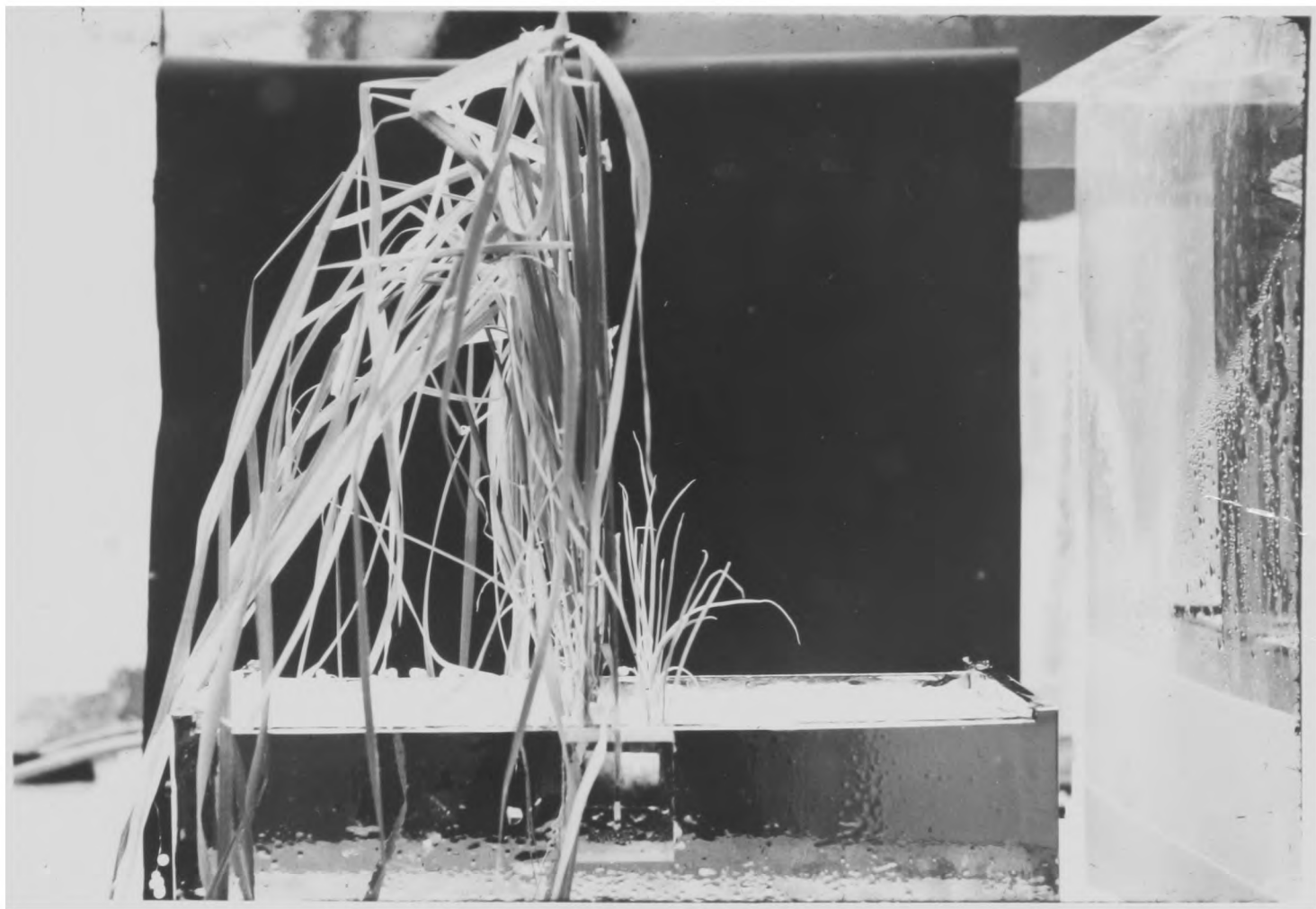


Fig 3.16

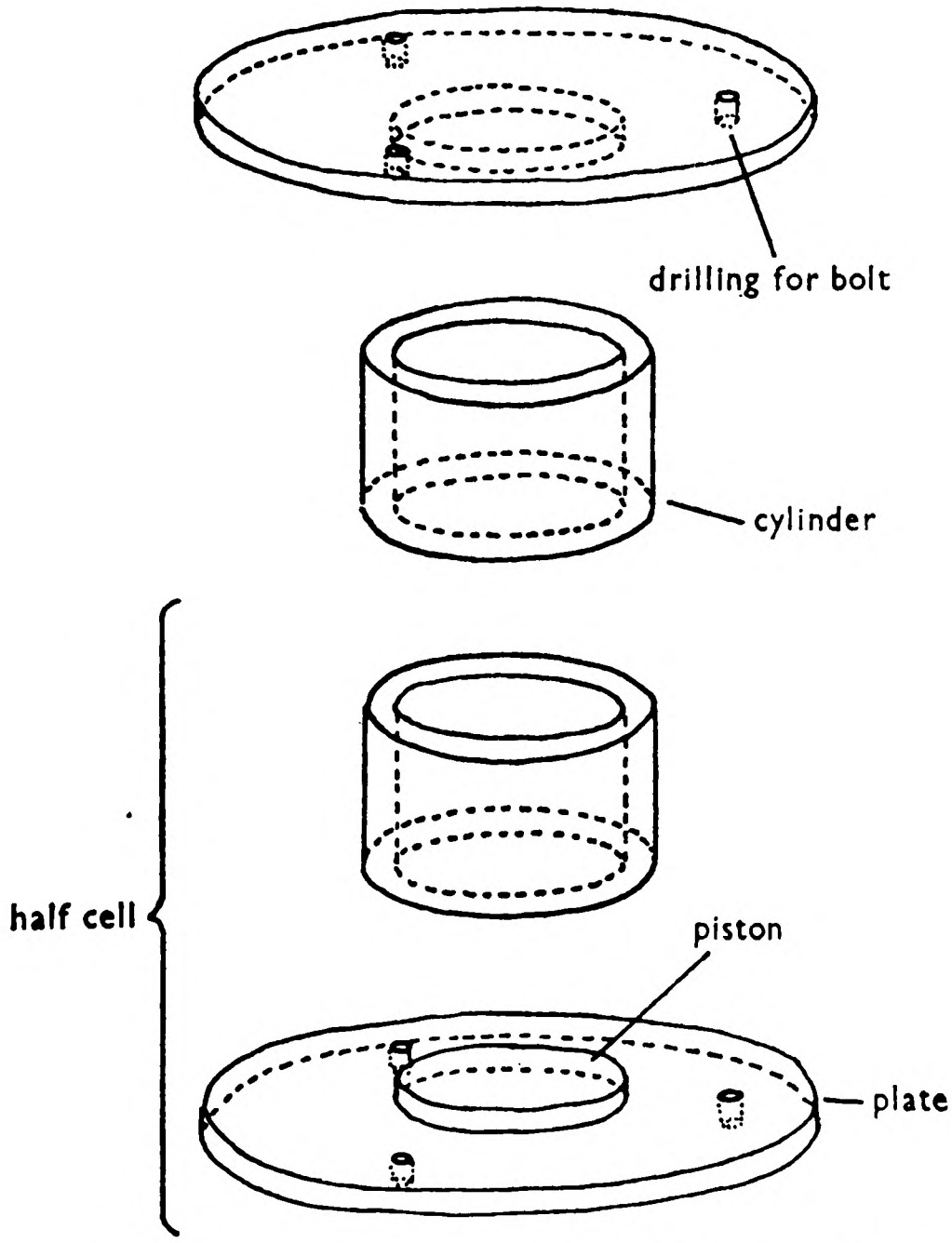
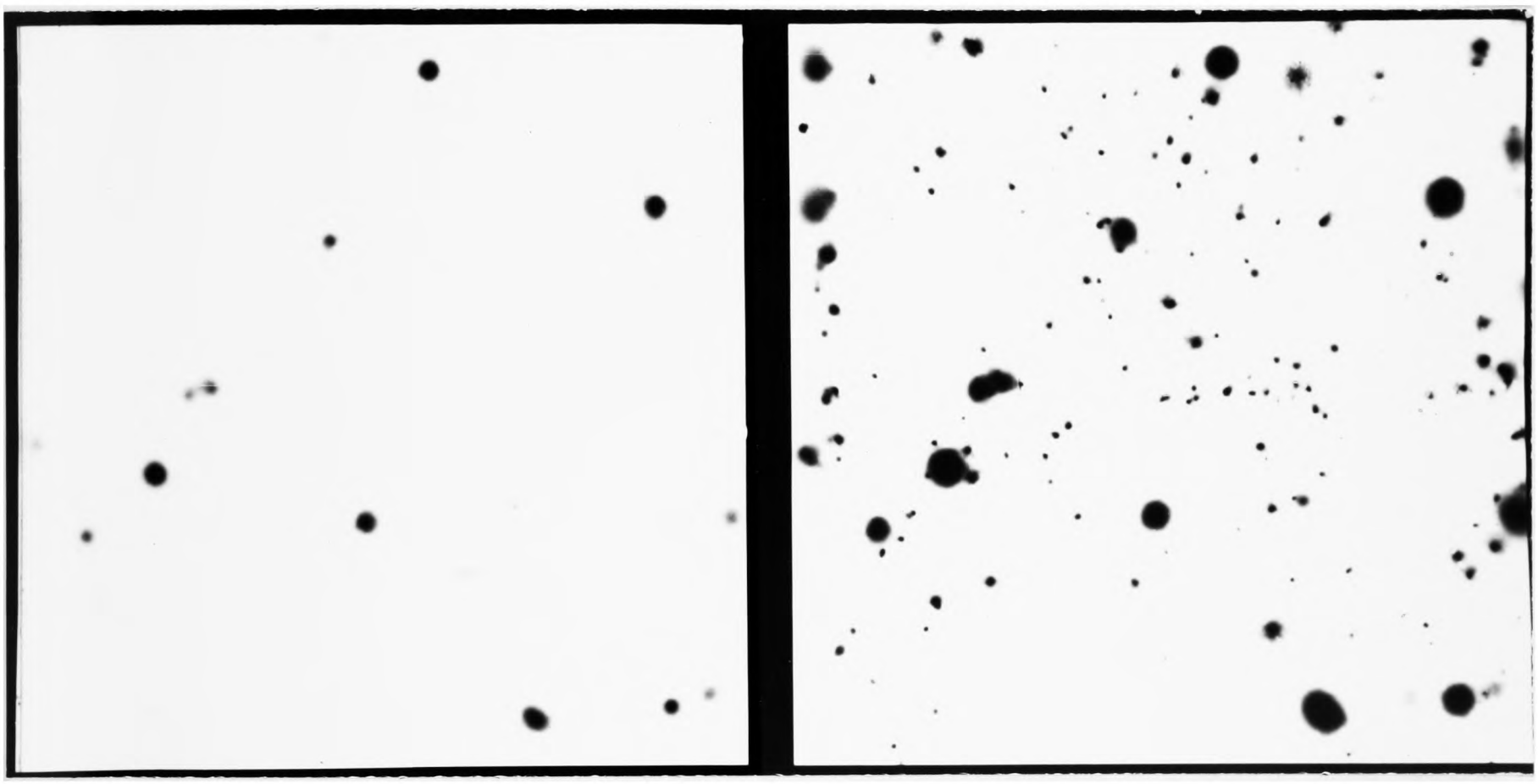


FIG. 1. Cells used to measure self-diffusion coefficients.

Fig 3.14 An autoradiograph obtained using the double labelling injection technique. The picture on the right shows the roots of L.multiflorum labelled with ^{33}P, and the roots of A. cepa labelled with ^{32}P. The other, on the left, shows the roots of A. cepa only. The root density of L. multiflorum is found by difference.



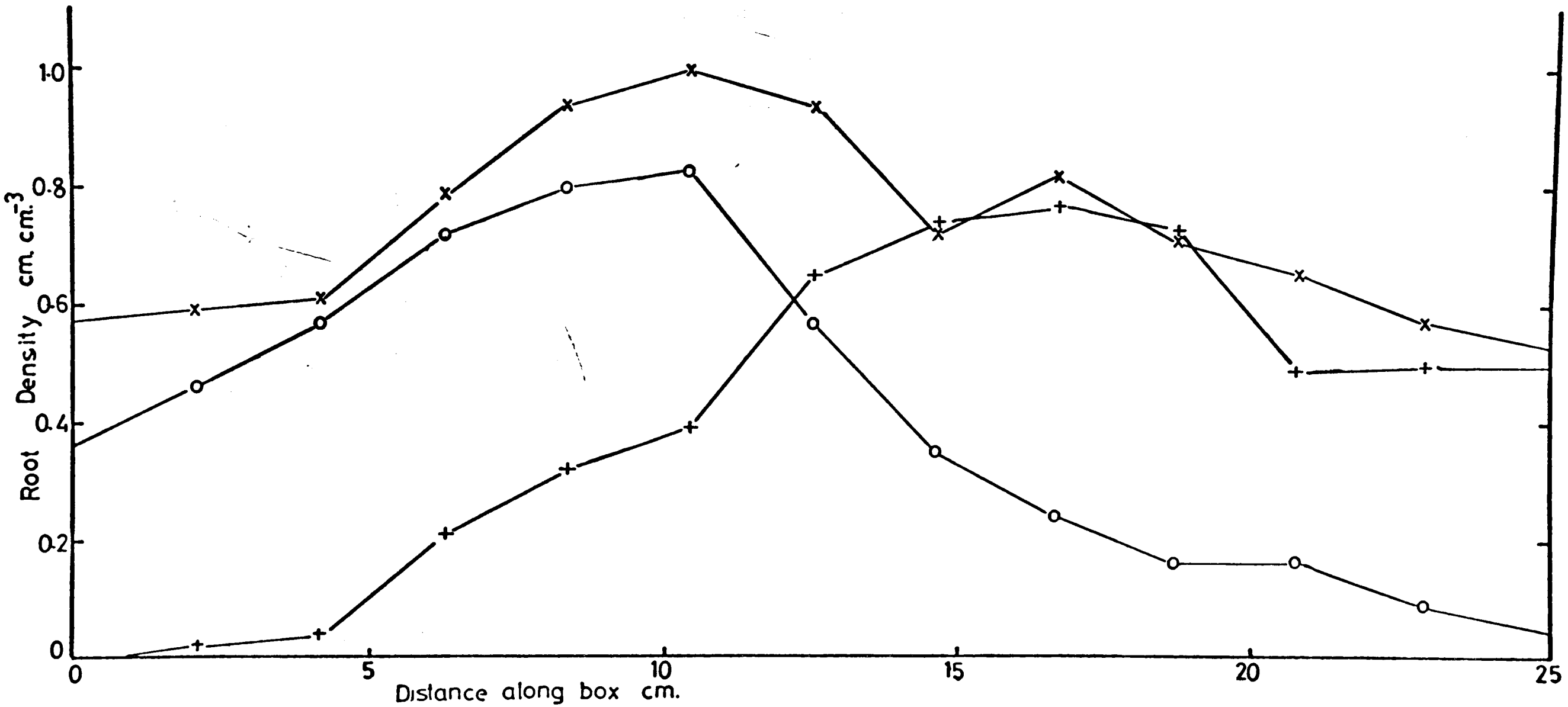


Fig. 3.15 Plot of root density against distance along the box for a row of A. cepa growing alone, X, and for two rows growing together; O injected with ^{32}P, + injected with ^{35}S. Root densities obtained by averaging results from vertical and horizontal autoradiographs.

3.6. Measurement of diffusion properties in soil

The diffusion coefficient D of an ionic species is defined by $F = -D \frac{dC}{dx}$, where F = ionic flux along the x axis and C = concentration of diffusible ions. The ionic flux of a particular ion A in a mixture of ions is the sum of the flux due to its own gradient and that due to the gradient of the diffusion potential which arises because of the different diffusion rates of cations and anions. Nye (1966b) and Olsen and Kemper (1968) have pointed out that diffusion potentials are unlikely to be significant in soils where the ion concentration is low.

The total diffusive flux in soil is approximately equal to the sum of the fluxes through the liquid and solid phases respectively (Nye 1966b), i.e. $F = F_l + F_s$, where subscripts l and s refer to liquid and solid phase respectively, and, therefore,

$$D \frac{dC}{dx} = D_l v_l f_l \frac{dC_l}{dx} + D_s v_s f_s \frac{dC_s}{dx}$$

where $\frac{dC_l}{dx}$ and $\frac{dC_s}{dx}$ are averaged over all pores, and f_l and f_s are introduced to account for the fact that the ion follows a devious pathway (Porter *et al* 1960). The values of f_l and f_s depend primarily on the soil moisture content. D_l and D_s are the diffusion coefficients in the free liquid and solid respectively, and v_l and v_s are the fraction of the soil volume occupied by the liquid and solid respectively. Hence,

$$D = D_l v_l f_l \frac{dC_l}{dC} + D_s v_s f_s \frac{dC_s}{dC} \qquad (3.6.1.)$$

$\frac{dC_l}{dC}$ and $\frac{dC_s}{dC}$ are deduced from the slope of the desorption isotherm measured at the same electrolyte concentration as the soil solution, by assuming that the diffusing ions equilibrate instantaneously between the solid and liquid in adjacent pores. Several workers (see Kelley 1948)

have shown that ion exchange is extremely rapid; in particular, Beckett and Craig (1964) demonstrated that K equilibrium between soil and solution takes place in 1 minute. If the isotherm is non linear, the average gradient over the concentration range is appropriate (Nye 1966b).

Equation 3.6.1. has been verified for K by Vaidyanathan et al. (1968) for both curved and linear isotherms; the concentration dependence of D was ascribed solely to the curvature of the isotherm. They went on to show that the solid contribution to the flux is negligible for K, and, hence, $D = D_1 v_1 f_1 \frac{dC_1}{dC}$. This has also been shown for Sr and P, and Na in moist soils (Rowell et al. 1967). For K, therefore, the diffusion coefficient can be estimated from the slope of the desorption isotherm, the diffusion coefficient in free liquid (obtainable from tables, Parsons 1959), and f_1, the tortuosity factor. The desorption isotherm is derived from the Q/I, the total electrolyte concentration, the bulk density and the v_1 of the soil.

For nitrate, with no ions in the exchangeable form, the solid contribution to the flux must be zero, and $D = D_1 v_1 f_1 \frac{dC_1}{dC} = D_1 f_1$.

Nitrate diffusion to plant roots is an example of salt diffusion, essentially $Ca(NO_3)_2$ and KNO_3. Thus, D_1 for NO_3^- is modified by the diffusion potential set up by the slower cation diffusion. An approximate average D_1 of 1.8×10^{-5} cm^2/sec has been used throughout in the present work.

The value of f_1 must be determined experimentally, but Porter et al. (1960), Rowell et al. (1967) and Vaidynathan et al. (1968) have found fair agreement between f_1 values determined for various ions in the same soil. The general conclusion from these workers is that f_1 is similar for the major nutrient ions in a single soil, and thus one measurement with a convenient ion can give results for all. Chloride is usually used as

it is non-absorbed and has a suitable isotope.

3.6.i. Measurement of f_l in BSL.

f_l over a range of v_l was calculated by measuring the self diffusion coefficient of chloride using the method of Rowell et al. (1967). The amount of ^{36}Cl which diffuses in a given time from one half cell of soil to another with the same chloride concentration but unlabelled is estimated, and if $Q_t/Q_\infty < .5$, then $f_l = \left(\frac{X}{2} \frac{Q_t}{Q_\infty}\right)^2 \frac{\pi}{t.D_l}$

(Schofield and Graham-Bryce 1960),

where X = length of one half cell cm.

Q_t = total chloride which transfers in time t

Q_∞ = chloride which would transfer in infinite time

t = time sec

D_l = self diffusion coefficient of chloride in free liquid

Method

BSL, sieved to < 2 mm, and at 16% moisture was packed into perspex cells of the type used by Rowell et al. (1967), but 3.5 cm deep, to a bulk density of 1.3. At 1 cm intervals during the packing, the soil was watered to 24% moisture in exactly the same way as in the plant experiments, with M/100 $CaCl_2$. A diagram of the cells is in fig. 3.16. Each half cell was packed to a depth of 3 cm. When the piston was pressed fully into the cylinder, the internal dimensions of the half-cell were 3 cm X 2.54 cm diameter. After packing, one half cell was leached with M/100 $CaCl_2$, and the other with M/100 $CaCl_2$ containing .01 μc/ml ^{36}Cl. The cells were leached at 50 cm suction on a tension table for 36 hours with 4 bed volumes of solution. At the end of the leaching period, the cells were allowed to equilibrate at a range of suctions which correspond with v_l values between .16 - .36. It is essential that any two half cells

which are joined are at the same suction. Otherwise, there is mass flow of soil solution and the estimate of total transfer by diffusion will be in error. After leaching, lens tissue was placed on the face of each half cell and allowed to equilibrate with the soil. The half cells were joined with the lens tissue in the middle, taking care to eliminate any air pockets, taped together, and placed in the jig shown in fig. 3.16. The pistons compress the soil slightly, giving good contact at the interface, and a precise knowledge of the path length. The whole cell was dipped in molten paraffin wax at 50°C for 1 sec. The wax, on solidifying, seals the cell against water loss. t was estimated for a Q_t/Q_∞ of .35 by assuming $f_1 = v_1$. After the diffusion period, the half cells plus their lens tissue were separated, and the soil was dried at 105°C to give v_{II}. The dry soil from each cell was extracted with N/100 $CaCl_2$ and the solution assayed for ^{36}Cl to give Q_t/Q_∞. A graph of f_1 against v_1 is shown in fig. 3.17. The form of the curve is similar to those given by Powell et al. (1967) and Porter et al. (1960). For many studies, it may be sufficiently accurate to obtain the v_1 f_1 relations from the soil type and a published curve.

3.7. Measurement of nutrient uptake from different zones of soil.

3.7.1. Nitrate.

An Orion specific ion electrode was used to measure nitrate concentrations in soil extracts. This has been shown to be as accurate and more precise than the phenoldisulphonic acid or steam distillation methods (Bremner et al. 1968, Mahendrappa 1969). The electrode responds to anions other than nitrate; the selectivity constants for interfering anions are in table 3.6. As an example, interference due to chloride in a solution of equal nitrate and chloride concentrations is given by the selectivity constant as 6×10^{-3}, or .6%. If there is 10x more chloride

than nitrate, the interference is 6%. There is no interference from cations.

The electrode is usable 2 days after assembly for a period of several months, and will measure concentrations of nitrate-N down to 10^{-5}M. The measurement is made by inserting the electrode in a magnetically stirred sample and comparing the potential with a calibration curve obtained using standards. The reading drifts with time, and so the time for any reading must be standardised. The results of a set of 6 replicates are in table 3.7. and indicate that one minute stirring is sufficient to give reproducibility. After 60 secs., 95% of all readings are within ± .4 mV, which is equivalent to ± 2% in the measurement of nitrate ion activity.

a) Method

All reagents were made up in distilled water containing 1 drop per l of Triton-X 100 wetting agent and 1 ml per l of phenylmercuric acetate, PMA, preservative. The PMA solution contained .1 g of PMA, 20 ml dioxane and 80 ml distilled water.

About 20 g of soil were extracted with 50 mls of M/200 $CaSO_4$ by shaking for 15 minutes and leaving for a further 45 minutes. The sample was centrifuged and 30 ml of the supernatant used for the analysis. Millivolt readings were taken on the expanded scale of a Beckman pH meter exactly one minute after the electrode was inserted, and then the electrode was washed in nitrate free M/200 $CaSO_4$ for one minute before the next reading. The electrode was blotted dry with tissue before transferring to a new solution. When the electrode was in a sample or wash, the solution was stirred continuously with a magnetic stirrer. The washing procedure was found necessary to prevent drift in the mV readings. The standard deviation of a set of 7 readings of 130 mV with and without washing was .20 and .64 respectively. The calibration curve was prepared using 4

standards and taking measurements in exactly the same way as the samples. The calibration curve was checked every four samples with one standard solution. Occasionally it had drifted by up to .5 mV, and in this case, the meter was reset to reproduce the original curve. This was possible as any drift was found to be due to a change in the electrode constant, and not the slope of the calibration line. (The mV reading is given by mV = electrode constant + $\frac{2.303\ RT}{F}$ log a_{NO_3}).

A typical calibration curve is reproduced in fig. 3.18. Notice that a change in potential of 1 mV is equivalent to a 4% change in the nitrate N activity. It is possible to read the Beckman mV scale to within .2 mV.

The method was tested by investigating the recovery of NO_3 added to soil. In duplicate, 20 g of soil were shaken with 50 ml of N/200 $CaSO_4$ containing three levels of N as nitrate. The results are in table 3.8. These results are satisfactory. The 3.45% increase in N content, in column 2, was measured to within 12 .

b) Nitrate transformations in BSL

An experiment was carried out to test the stability of the nitrate concentration in the soil solution during an experimental period. Two pots were prepared in exactly the same way as those described in section 3.9.1. They were left without plants but under the conditions of a growth experiment for 2 weeks, and then analysed for nitrate using the electrode. The nitrate concentration in the top 3 cm of the pot had increased by 5 . There was no change in the nitrate level in the 3-6, 6-9 and 9-12 cm regions of the pot. These results were considered satisfactory for a growth experiment in which uptake was to be measured by loss from the soil.

3.7.2. <u>Potassium</u>

The measurement of K loss from the soil is more difficult than for

nitrate, as the total present is usually higher. The soil used in experiment 1(section 3.9A) was analysed for K by extraction with neutral normal ammonium acetate (Metson 1956). The mean and standard deviation of 10 replicates was .210 mM K/100 g soil and.012 respectively. This level of precision is insufficient in plant experiments where the maximum expected uptake is approximately .08 mM K/100 g soil (see experimental section).

Mathews and Beckett (1962) have described a technique for measuring the quantity of K fixed or released by a soil when it is subject to K fertilisation or depletion, which does not involve a measurement of the total exchangeable K. This method assumes that the form of the "immediate" Q/I relations for labile K in soil is a characteristic of the soil. If this is so, fixation or release of K will cause only a vertical displacement in the Q/I curve. Mathews and Beckett (1962) reported that the shape of the curve is independent of the soil:solution ratio, the total electrolyte concentration (up to .06 M) and the fixation or release of K. Beckett (1964) has shown that changes in pH in the region pH 5-7, such as might occur around plant roots, have very little effect on the slope of the isotherm, although below pH 5.0, the effect was considerable (see also Tinker 1964). A moderate removal of K by plants has no effect on the form of the Q/I (Beckett et al. 1966, Moss et al. 1972, Moss 1967, Addiscott 1971), although exhaustive cropping may cause a change of slope. This latter is most likely to occur in soils which release large amounts of K to plants from non-exchangeable sources, particularly illitic clay minerals, and which, therefore, sustain plants at a low level of K nutrition for long periods (Moss et al. 1972).

In many conditions, the Q/I relation may be considered a soil characteristic. In order to estimate plant uptake of K, two further

conditions must be satisfied i) there is no K available to the crop that does not exist in solution as K^+. Fergus et al. (1972) in a study of exhaustive cropping on 10 soils and Beckett et al. (1966) measuring uptake from 6 soils, found nothing to suggest this may occur. ii) There is no natural release of fixed K during plant growth, which would lead to an underestimation of uptake. We can conclude from Mathews and Beckett's (1962) data that soils with relatively low equilibrium activity ratios, $< .007\ (M/l)^{\frac{1}{2}}$, fix large amounts of added K, but are able to release very little on depletion. On the other hand, soils of a high equilibrium activity ratio, $>.01\ (M/l)^{\frac{1}{2}}$, have a limited fixing capacity, but release large quantities on depletion.

The equilibrium AR of BIL was measured by repeatedly extracting soil with 50 ml of $CaCl_2$ solution until there was no change in the K concentration when extra soil was added. The final solution was analysed for K, Ca and Mg. The equilibrium AR was $.002\ (M/l)^{\frac{1}{2}}$, and further, more comprehensive tests were carried out to verify that the soil did not release K on depletion by M/100 $CaCl_2$ solution.

3.7.2.a. <u>The K releasing properties of BIL</u>

The K releasing capacity was investigated on both samples of soil. This was necessary as the equilibrium AR was different for each sample.

2.a.i. Experiments on sample 1

In duplicate, 5 g of soil were shaken with 50 ml of M/100 $CaCl_2$ solution containing the following range of concentrations: .00, .02, .06 .24, .30, mM K l^{-1}. After 1.5 hours at 19° C, the solutions were centrifuged and the supernatant analysed for K using emission spectrophotometry. The equilibrium AR for each solution was calculated, assuming the dibasic cations are M/100, and also Δ K, the amount of K which each sample of soil has gained or lost to the solution in order to come to equilibrium. Δ K is expressed as mM/100 g of oven dry soil.

This procedure gives the "immediate" C/I relations of the soil. After analysis, each solution was agitated, to mix the soil and solution, and left for 54 days at 19° C, with occasional shaking and aeration. The solutions were recentrifuged and reanalysed for K. A new C/I was calculated and compared with the first one to determine the release or fixation of K by the soil. There was no release of K from a depleted soil, but some fixation of added K.

To investigate the K release potential at very low values of the AR, in quadruplicate, 20 g of soil were successively extracted with 100 ml of M/100 $CaCl_2$ solution. Each extraction took 1.5 h and each was analysed for K, giving the C/I curve down to very low values of the solution AR. When the soil was completely depleted of K exchangeable to M/100 $CaCl_2$, the soil and solution were left for 14 days at 19°C and then reanalysed for K. In none of the 4 cases was there any release of K from the soil into the solution. It was concluded that sample 1 did not release K on depletion by M/100 $CaCl_2$ solution, and was, therefore, suitable for a plant uptake experiment.

2.a.ii. Experiment on sample 2

The ammonium acetate exchangeable K for this sample was .505 mM/100 g of soil.

The K release potential was investigated by depleting moist soil with $CaCl_2$, and storing it moist for 14 days. Any K release was measured by comparing the depletion calculated from a $CaCl_2$ extraction after storage, and the C/I, with that calculated by analysing the $CaCl_2$ used to deplete the soil.

Method

In triplicate, a $\frac{1}{2}$ cm layer of soil was weighed into the base of a Buchner funnel and moistened to give a v_1 of .35 (nearly saturated).

After a 45 minute equilibration time, the soil was leached with N/100 $CaCl_2$ solution to deplete the soil K. Next, the soil was sucked dry on the funnel to give a v_1 of approximately .28 (typical of a plant experiment). The leachate was analysed for K to give the total depletion. The Buchner was sealed, except for a pin hole to allow aeration, and stored at constant temperature for 14 days. After this period the soil was extracted with N/100 $CaCl_2$ and the depletion estimated from the Q/I. The results are in table 3.9. The Q/I for this sample is in fig. 3.19. The K fixation suggested in row 3 of table 3.9 is probably experimental error.

The conclusion from these experiments was that the Mathews and Beckett (1962) technique was suitable for estimating the loss of K from soil resulting from plant uptake.

3.8. Estimation of the nutrient content of the plants

a) nitrogen

Total plant N was estimated by the Kjeldahl method modified to include free nitrate (Bremner 1965). 3 ml of a solution containing 3.4 g salycylic acid in 100 ml conc. H_2SO_4 were added to about 100 g of dried, ground plant material in a 50 ml semi-micro Kjeldahl flask. After standing for 1 h, .5 g of powered sodium thiosulphate were added and the flask warmed. When frothing subsided and the flask cool, 1 tablet of Na_2SO_4/Se catalyst and 3 ml conc. H_2SO_4 were added. The plant material was digested until the solution was clear, and then for a further 20 minutes. This procedure reduces all the N to NH_4^+, which is liberated in a Markham still by NaOH. The free ammonia was collected in 1% boric acid and estimated by titration with .01 N HCl using screened methyl red as indicator.

Using this procedure, 99% and 101% of added $NaNO_3$ was recovered.

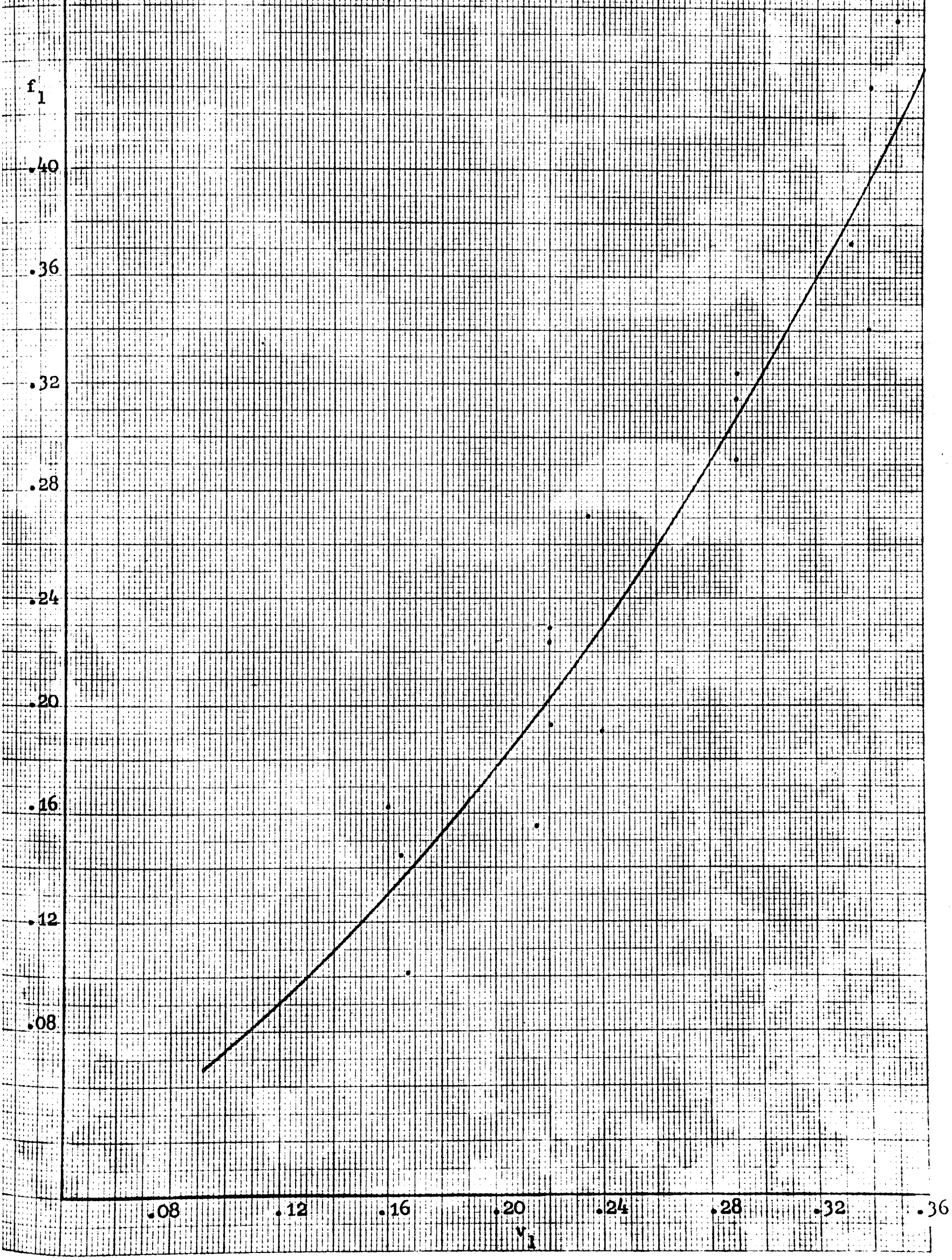
b) Cations and Phosphate

Dried, ground plant material was wet ashed according to Jackson's method (1958). 'bout .05 g of plant material were placed in a 100 ml flask and heated at 180° C with 5 ml of conc. HNO_3 until nearly dryness. 4 ml of a solution of conc. HNO_3, conc. H_2SO_4 and 60% $HClO_4$ in the ratio 10:1:4 were added and the solution was left overnight. The solution was heated at 180°C until clear, and the acid largely volatalised. There was a white precipitate of dehydrated silica. The solution was washed into a 50 ml volumetric flask with 5 ml of 6 N HCl, and made up to the mark with N/10 HCl. This extract was suitable for analysis of cations and P.

Na and K were determined using flame emission, and Ca and Mg with atomic absorption spectophotometry using a Unicam SP 90.

P was determined by reducing a phosphomolybdate complex with stannous chloride and analysing the solution colourimetrically (Watson 1956).

Fig 3.17 Relation between the tortuosity factor, f_l, and the volumetric moisture content v_l. Values obtained by measuring the self diffusion coefficient of chloride.



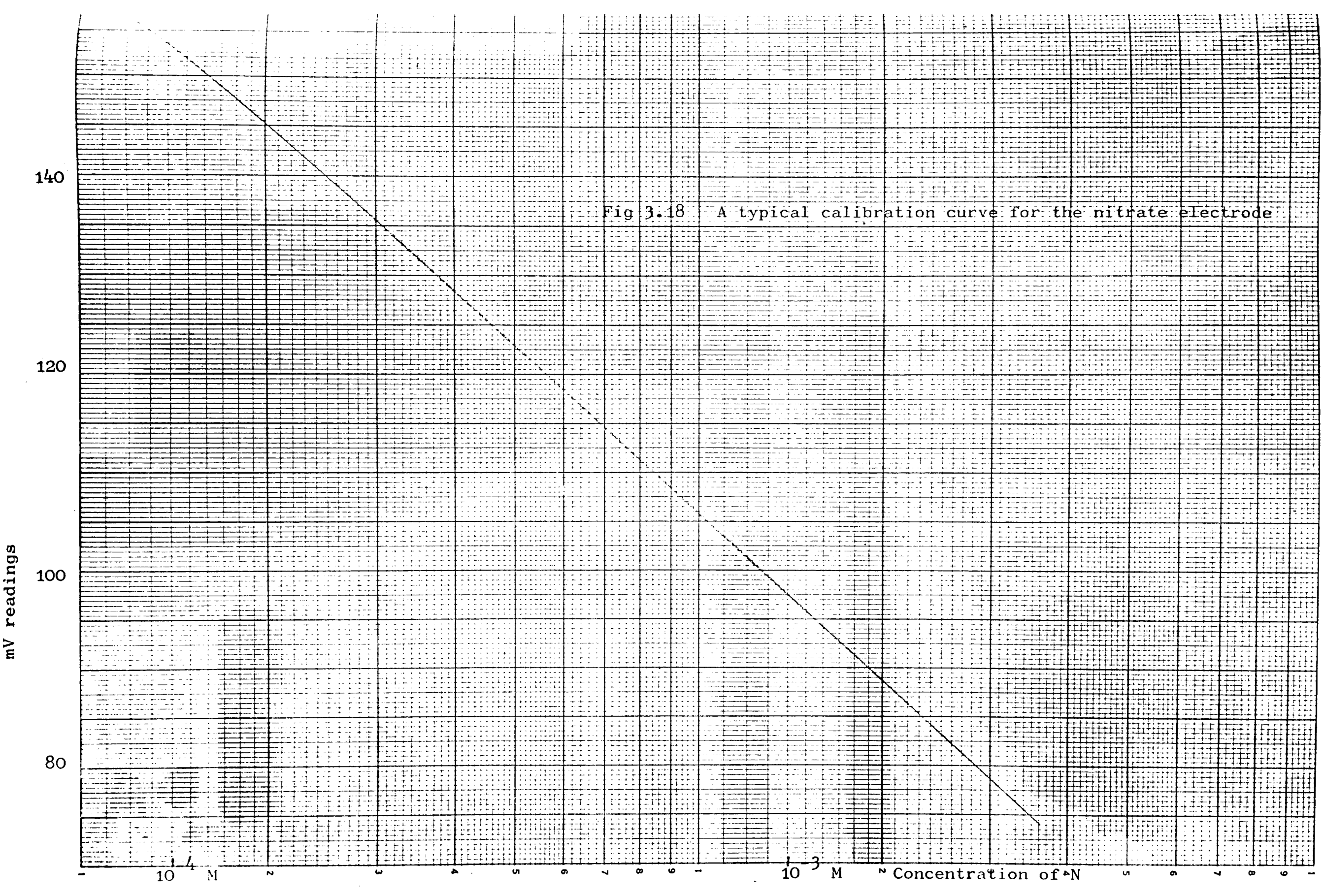


Fig 3.18 A typical calibration curve for the nitrate electrode

Table 3.7

'tability of the nitrate electrode

time elapsed before reading, sec	30	60	90	120	180	240	300
mean mV	132.0	131.8	131.6	131.4	130.9	130.4	129.9
standard deviation	.21	.20	.26	.31	.22	.38	.24
mean mV	95.2	95.6	95.5	95.5	95.4	95.3	95.2
standard deviation	.23	.22	.17	.17	.16	.11	.04

Table 3.

'ecov[illegible] of N using nitrate electrode

N added µg/g soil	N measured in soil µg/g soil	N recovered µg/g soil
0	33.6	0
2.8[illegible]	36.1	2.50
14.[illegible]	47.9	14.3

Table 3.6

selectivity constants of interfering anions

interfering anion	selectivity constant
ClO_4^-	10^3
I^-	20
ClO_3^-	2
Br^-	0.9
$S^=$	0.57
NO_2^-	6×10^{-2}
CN^-	2×10^{-2}
HCO_3^-	2×10^{-2}
Cl^-	6×10^{-3}
OAc^-	6×10^{-3}
$CO_3^=$	6×10^{-3}
$S_2O_3^-$	6×10^{-3}
$SO_3^=$	6×10^{-3}
F^-	9×10^{-4}
$SO_4^=$	6×10^{-4}
$H_2PO_4^-$	3×10^{-4}
PO_4^{-3}	3×10^{-4}
$HPO_4^=$	8×10^{-5}

Table 3.9

K release properties of BSL (sample 2)

A comparison of K eluted by M/100 $CaCl_2$ with the depletion estimated from the Q/I after 14 days storage.

	K eluted by M/100 $CaCl_2$ mM/100g soil	K depletion estimated using Q/I mM/100g soil
1	.236	.210
2	.222	.226
3	.140	.162

Table 3.10

The relation between U and L in period 1

(for definition of k, see text)

Nutrient	H_2O	N	P	K	Ca	Mg	Na
Value of k	.98	.99	.97	1.0	1.0	.98	.91

Fig 3.19 Desorption Isotherms for K and Na

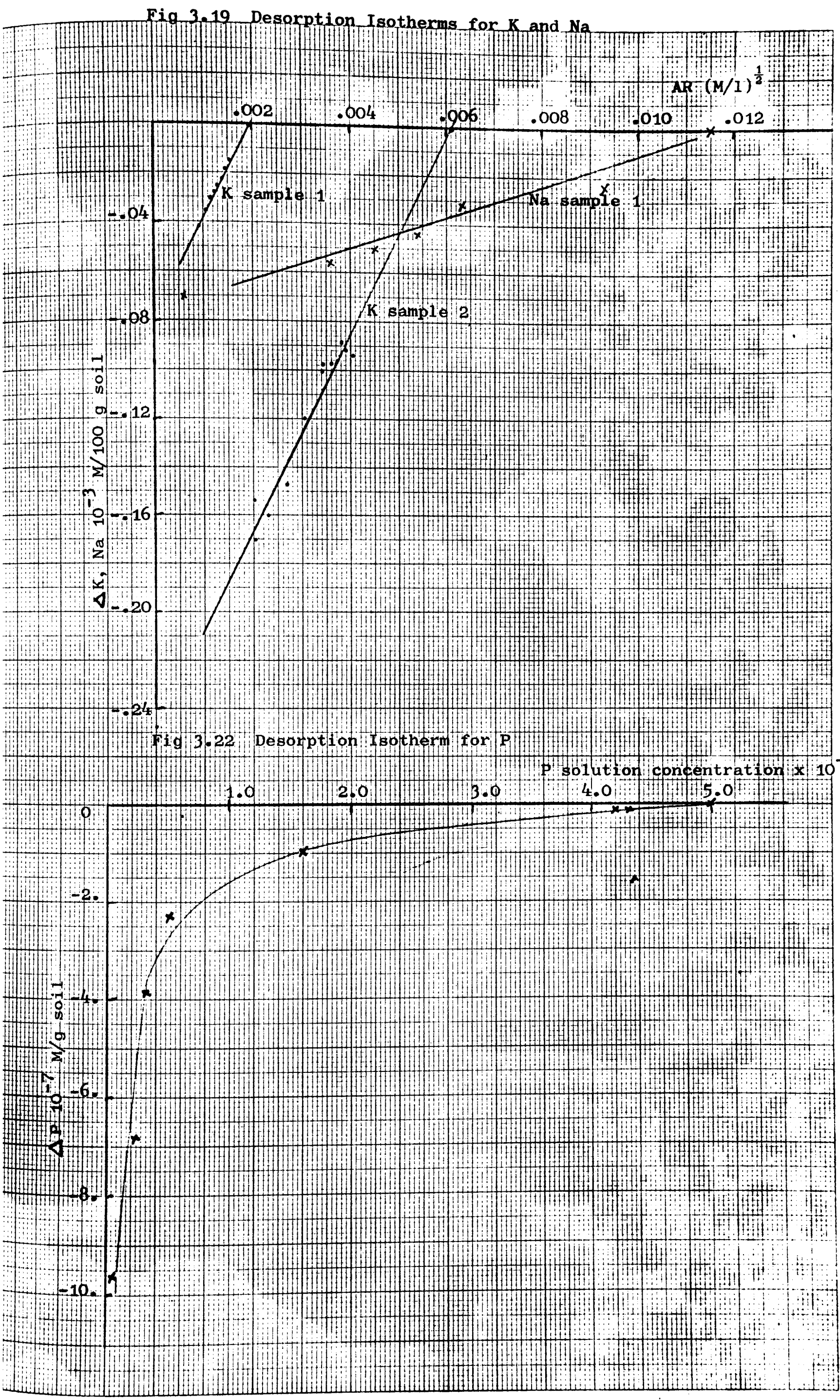


Fig 3.22 Desorption Isotherm for P

3.9 Details of plant experiments

The plant experiments were designed so that they may be interpreted by the model of nutrient flow to an absorbing root system. For the model to be satisfactory, two factors must obtain:

i) a purely physicochemical treatment of the transport phenomena is applicable to nutrient supply to a growing plant root system.

ii) the boundary condition at the root surface can be represented in some simple way.

The model was tested qualitatively, by investigating experimentally, the importance of the different parameters, and quantitatively, by considering the ability of the model to predict plant uptake, in particular the uptake of N and K. Of course, if anything less than total depletion at the root surface is sufficient to account for the nutrient supply to the roots, then the value of $\overline{\alpha a}$ can always be fiddled to give the observed uptake. The model can be considered useful only if $\overline{\alpha a}$ is constant, or simply related to other variables.

3.91 Experiment 1

In the first experiment, 19 onions were grown in a regular pattern in a cylindrical pot 45.5 cm^2 cross-sectional area and 13.5 cm deep. The pot was made up of sections 3 cm high with $\frac{1}{2}$ cm at the base, so that the soil and pot could be sliced horizontally, with a steel wire, prior to autoradiography of the root system. Soil (BSL, sample 1), at a moisture content of 12%, and sieved to < 2 mm, was added to the pot in 50 g aliquots to minimise heterogeneity of particle size distribution. At each cm depth of soil, the soil surface was levelled, and distilled water added to give the final v_1 of .31. Watering of a complete pot from the base was unsatisfactory due to the redistribution of nitrate as the soil wetted. After assembly, the soil was left at 19° C for 10 days to equilibrate. This is essentially to stabilise the nitrate level - it is well known that

sieving and moistening a soil causes a bacterial flush and changes in mineral nitrogen content. The initial nitrate concentration, under these conditions, was 18 X 10^{-6} moles/ml, which gives a K solution concentration of 0.185 x 10^{-6} M/ml. After the equilibration period, freshly germinated onion seedlings var Mustang, 1 cm long, were planted in preformed holes (1 cm deep) in a hexagonal pattern, and allowed to grow under the conditions detailed in section 3.3. There were 14 identical pots, which gave 4 harvests of three pots, and 2 blanks. This was intended as the first half of an experiment with 6 replicates at each harvest. However, modifications made to the second half made comparisons impossible, and experiment 1 will be considered alone. Two days before each harvest, the plants were injected with ^{32}P for root measurements, and at each harvest the pot was divided into 4 sections. The sections were analysed for moisture, nitrate and potassium, and root properties, and the plants for N, P, K, Mg, Ca and Na. Every 2 days during the course of the experiment, all the pots were weighed to measure the transpiration, and then replaced in the growth cabinet in a different place. The replacement positions in the cabinet were systematic, and designed to minimise the effects of any light or temperature gradients. Three pots were harvested on days 25, 34, 41 and 45 after sowing. Growth from harvest 3-4 was restricted due to water deficiency, and the results from this period are not presented. The first 3 periods will hereafter be referred to as periods 1, 2 and 3 respectively.

3.9.A.1 Results of Experiment 1

The intention was to relate the loss of nitrate and potassium from the soil to the plant uptake and root development in the 4 soil zones. For NO_3, the loss from the soil was within 10% of the measured plant uptake at each harvest, which was regarded as satisfactory. For K, however,

there was no correspondence between recovery from the soil and plant uptake. A mistake was made, in that the soil was air dried prior to K analysis. There are several reports that this treatment causes K release (e.g. Lahav et al. 1968) and, in fact, a sample of EEL depleted of K by elution with $CaCl_2$ was found to release K on air drying. This experimental artefact rendered impossible a comparison of the calculated uptake in each layer, with the loss from that layer.

Another unsatisfactory feature of the experiment was that it did not provide sufficient data for the construction of accurate curves of nutrient uptake and root length against time, which could be used for comparison with theoretical calculations of uptake rate. However, if there is a known integrable relation between nutrient uptake and root length, it is possible to derive the mean nutrient inflow during an interharvest period. Brewster and Tinker (1971) reported a linear relation between uptake and root length, i.e. $U = a+bL$, in leeks, and it is reasonable that onions will behave similarly.

The graphs of nutrient uptake, U, against time and root length, L, against time suggest that U and L are linearly related in periods 2 and 3, but this may not be the case in period 1. In period 1, an equation of the form $U = a+bL^k$, where k = constant, was assumed. a = zero, and k is given by $k = \log U_2/U_1 \Big/ \log \frac{L_2}{L_1}$ (Whitehead and Myerscough 1962).

Table 3.10 gives the value of k for each nutrient. k is approximately 1.0. Therefore, the mathematical error in using equation 1.vii to calculate mean inflow will be small (see section 1.4). Equation 1.vii was used throughout.

Fig. 3.20 presents the primary data on growth and transpiration, and volumetric moisture content of the soil, and figs. 3.21 a, b give

the nutrient uptake dat for N,P,K,Ca,Mg, and Na. The mean RGR over periods 1, 2 and 3, calculated by Fisher's (1920) method, was .050g/g/day, .037g/g/day and .016g/g/day. These values are rather low, typical values for an arable crop being .2 to .3 g/g/day (Warren Wilson 1966). In the presence of abundant light, CO_2 and moisture, they imply that nutrient supply was limiting growth.

The inflows calculated using equation 1.vii are in tables 3.12 a, b and c. In period 1, the N and P inflows are similar to, and the K inflow about .5 times, those Brewster and Tinker (1972) consider typical (10^{-12}, 10^{-13} and 10^{-12} moles/cm/sec respectively). There is insufficient data available in the literature to draw any firm conclusions from this, but it suggests that K is the nutrient limiting growth. An analysis of the transport properties of the soil will reveal whether this low K inflow is a consequence of the soil supplying power, or of some plant property.

The nutrient per cent in the tissue remained, in all cases, fairly constant throughout at 5.0, .36, 3.9, 2.2, .21 and .6% for N, P, K, Ca, Mg and Na respectively.

There was no evidence of root hairs in any pots, and the root radius was fairly constant at .023 cm.

The total anion and cation inflows over the 3 periods were 24.9, 6.9 and 4.8, and 16.8, 4.7 and 2.6 equivalents x 10^{-13}/cm/sec respectively (assuming nitrate was the only anion). This excess of anions over cations must have resulted in a net outflow of HCO_3^- or, less likely, OH^-. The diffusion away from the root of HCO_3^- cannot be treated exactly, in a simple way, as the reaction with H^+ to give CO_2 and H_2O is slow. At the mean pH (6.4) of this soil, the half time for the reaction is several hours, and it is likely that the pH at the root surface rose ½ a unit (Ramsan 1971). Under these conditions, there would be no

significant build up of HCO_3^- in the soil (Ramsan 1971), which would affect the potassium diffusion coefficient or solution concentration.

3.9.A 1.1 Theoretical analysis of the data

If there is no depletion at the root surface, or if there is no significant overlap of depletion zones, the calculated mean inflow, over a period, can be used in conjunction with the equation 1.vi, to compare the soil supplying power and plant demand.

For N, Ca, Mg and Na, mass flow supplied sufficient to maintain the root surface concentration approximately equal to the average solution concentration, and equation 1.vi, using a mean C_{li} corrected for total depletion, is appropriate.

For P, supply is mainly by diffusion, and since D was low, there would have been little overlap of depletion zones (the radial spread of a depletion zone is roughly equal to $\sqrt{Dt}$ cm). Again equation 1.vi is a good approximation, if the strict model of diffusion to roots is correct (see later for discussion of results).

Potassium falls in between these two stools. The value of $\sqrt{Dt}$ for K, for the mid time of each period, was .54cm, .70cm and .62cm, and the mean interroot distance assuming regularly dispersed roots was 1.3 cm, .90 cm and .83 cm. Interroot competition becomes important when the interroot distance is $< 2\sqrt{Dt}$ (see section 2.7), and so it may have been significant before the first harvest. For this reason, the K uptake data were analysed using the analogue model presented in section 2.13.

1.1. Data required for use in equation 1.vi

Equation 1.vi has the form

$$\bar{I} = 2\pi D_l w_l f_l (C_{li} - C_{la}) \bar{G} + M C_{li} = 2\pi \bar{\alpha} a C_{la}$$

a) D_l was obtained from tables (Parsons 1959). D_l for nitrate was taken as 1.8×10^{-5} cm^2/sec, a value adjusted for the diffusion potentials created by the Ca, K and NO_3 diffusion.

b) v_1 was the mean value of v_1 during an inter-harvest period.

c) f_1 was obtained from mean v_1 and fig. 3.17.

d) i. C_{1i} for nitrate was the mean nitrate concentration during a period.

ii. C_{1i} for P was taken as the initial soil solution concentration in a centrifuged extract.

iii. C_{1i} for Na was calculated from the nitrate content, the equilibrium activity ratio, $Na/\sqrt{Ca+Mg}$, the mean buffer power $\Delta C/\Delta C_l$, from t=0 to the end of a period, and the uptake during a period.

iv. C_{1i} for Ca and Mg was calculated from the mean NO_3 concentration, and the initial Ca:Mg ratio in solution, which was 9:1.

e) $\bar{G}$ was taken as the "average flux parameter" G (Nye 1966), at a time equal to half the total time up to any harvest. This assumes that the root system behaved as a static root system, which existed for half the time up to any harvest. It is probable that roots would, on average, have been younger than this, but there is insufficient data to divide the roots into classes, and use the mean Instantaneous flux parameter for each class, as Brewster (1971) has suggested. As γ and G are insensitive to time (fig. 1.1), little error will result from this approximation. Since G is a function of Dt/a^2, D for each ion is required.

$D = D_1 v_1 f_1 \frac{dC_1}{dC}$, and $\frac{dC_1}{dC}$ was calculated from the slope of the C/I in fig. 3.19 for K and Na, and from fig. 3.22 for P. For NO_3, $D = D_1 f_1$, and this formula may be used for Ca when the change in exchangeable Ca, for any reasonable change in liquid phase Ca, such as is likely to occur around plant roots growing in Ca dominated soils is small, (Tinker 1970). The buffer power for Mg was unknown, and a value of 10 assumed. As noted above, G is insensitive to D, and there should be little error in the Ca and Mg results from this source.

f) M is the mean water inflow, and was calculated from the weight loss by transpiration, and the root length, using equation 1.vii. All roots were assumed to be equally active in their absorption of water. Supporting evidence for this is given by Rosene (1937) who found that onion roots, aged 2-3 weeks and up to 22 cm long, absorbed water in all regions between the root tip and base. The results for all periods are in Table 3.11.

Table 3.11

Harvest period	1	2	3
mean water inflow mls/cm/sec	1.00×10^{-7}	6.76×10^{-8}	5.98×10^{-8}

These values give an indication of the gradients in v_1 and, therefore, D around roots which result from water uptake. Gardner (1960), using an inflow 10 times greater than the present values, predicted an almost negligible decrease in water content around plant roots in both clay and sandy loam soils at soil suctions of 5 bars. Suctions of this order only occurred in period 3 of experiment 1, and thus we may conclude that decreases in D due to local drying around roots would have been insignificant, even if water uptake was confined to only 1/10 of the root system.

The decrease in pot weight correlated well with the decrease in v_1 of the soil, as expected. However it is not possible to relate the water uptake from any layer with the root length in that layer, because of the incalculable magnitude of interlayer movement of water - the diffusivity of water is very sensitive to soil moisture content (see Gardner 1960). The v_1 in the 4 layers went down fairly uniformly, and it seems that at least some water was taken up from all layers.

The results obtained using equations 1.vii and 1.vi, and assuming all the roots were active, are in Tables 3.12 a,b.

1.2 Interpretation of results for P, N, Ca, Mg, Na

a) Phosphate

These results are discussed first because of their influence on the interpretation of other data.

The striking feature about the phosphate results is that the measured inflow was about 6 times greater than the maximum possible, according to the theoretical model of diffusion and mass flow. There seem to be two possible explanations for this.

A) the root is exuding substances which desorb exchangeable P, so increasing the P solution concentration in the rhizosphere. This may be a direct influence, or indirect through the action of micro-organisms. There is no conclusive evidence regarding the magnitude of such an effect. However, Brewster (pers comm) has found no increase in the solution concentration of P extracted from the rhizosphere of rape plants growing in BCL.

B) the plants formed a symbiotic relation with mycorrhiza. There are several examples of increased growth of crop plants as a result of mycorrhizal infection (see Harley 1969). More specifically, Sanders and Tinker (1971) have investigated the phosphate nutrition of infected and non infected onions growing in BCL, of the same P status as the present soil. For non infected plants, they found that the measured mean inflow could be accounted for on the assumption that all the roots were active, and maintaining a zero sink condition at the root surface. In contrast, the observed inflow into mycorrhizal roots was 3 to 14 times greater than possible due to diffusion and mass flow. They observed external hyphae extending into the soil around roots of the infected plants, and concluded that the hyphae were increasing the effective length of the sink to which nutrients may move by diffusion. A similar analysis has been made by Hayman and Mosse (1972).

A mycorrhizal infection of the type found by Sanders and Tinker (1971) is the simplest explanation of the present results. Supporting evidence has come from Brewster (pers comm), who found that onions growing in 3GL, sample 1, became mycorrhizal through natural infection after 14 days. Further circumstantial evidence is suggested in section 3.9.B.

If the plants were mycorrhizal, a discussion of the influence of the external hyphae on the uptake of other ions is appropriate; of particular interest is the effect of mycorrhiza on the inflow of other nutrients. The only data reasonably relevant to experiment 1 is that of Sanders (pers comm), who found the inflow of K, in the experiment described by Sanders and Tinker (1971), to be the same in the infected and non infected treatments. This does not answer the question completely, however, as his soil had been fertilised with K. Table 3.13 has been constructed from data given by Nosse (1957) and Gerdemann (1964), and was prepared assuming a linear relation between nutrient content and root weight. Comparisons of inflow are valid only if the specific root weight in mycorrhizal and non-mycorrhizal plants was the same. Nosse's data suggest mycorrhiza have no effect on the inflow of K and Ca, but Mg inflow was increased, whereas Gerdemann found no difference in the inflow of Ca and Mg, P was increased and K decreased.

In experiment 1 the supply of Ca, Mg and Na was entirely by mass flow, and the presence of mycorrhiza will have no influence on the conclusions regarding the transport process, although the actual values of the relative contributions of diffusion and mass flow may not be very useful.

i.e. no effect on conclusions that build upon depletion - probably.

The data on K is by no means conclusive. There seems no ready explanation for the decrease in K inflow reported by Gerdemann, unless the plants had reached different physiological ages. However, the fact

that there is no report of mycorrhiza increasing K influx allows us to proceed, but with caution..

b) Nitrate

Although nitrate measurements were made at 4 different depths in the pot, the possibility of interlayer bulk flow and diffusion was not eliminated. The diffusion term can easily be calculated, but there is uncertainty as to the extent of the interlayer water movement, and hence the interlayer bulk flow of nitrate. For this reason, the pot was treated as a whole, and no complex theoretical analysis was attempted. The results, however, are of some value. They are interpreted assuming water uptake was evenly distributed throughout the root system.

In periods 2 and 3, all the nutrient was supplied by mass flow and in period 1, 74% of the total. Note that an oversupply by mass flow does not result in large accumulations around roots as back diffusion is rapid. Marriot and Nye (1968) pointed out that equation 1.vi. underestimates C_{la}/C_{li} when $v > \alpha$, i.e. when there are accumulations around roots. Their data is for a dry soil and is not directly applicable. Passioura and Frere (1967) also have investigated the magnitude of build ups around roots. Their curves suggest the accumulations under the present experimental conditions would be very small.

Note also, that if there had been no mass flow, the drop in solution concentration at the root surface necessary to cause the required flux is only 10^{-6} moles/ml, which is small in comparison with solution concentrations in this and most arable soils. Thus, either mass flow or diffusion will supply nitrate to plant roots, depending on the value of the water inflow, and transport phenomena are unlikely to be rate limiting in nitrate nutrition.

$\bar{\alpha}_a$ for nitrate is lower than that concluded typical in 1.7 b. The high solution concentration of nitrate may account for this, but there

is no constant flux into the roots (which has been suggested to obtain when the solution concentration is $> 10^{-4}$ M (van den Honert and Hooymans 1955)), as the inflow decreases with time. From table 3.12 a, $\bar{C}_1$ is roughly constant, and $\overline{\alpha a}$ drops with the inflow. The percent N in the tissue is constant at a high value (5%), and the drop in $\overline{\alpha a}$ may be due to oversupply, the plant reducing $\overline{\alpha a}$ to maintain the internal N concentration as it grows.

c) Calcium, Magnesium and Sodium

These data were interpreted using equations 1.vi and 1.vii, on the assumption that nutrient and water inflows were distributed equally over the root system. The major points of interest are

i) supply by mass flow was sufficient to account for uptake, except for Na in period 1.

ii) an oversupply by mass flow caused no significant build ups at the root surface.

The mean water inflow was typical of that reported by others for field crops (Newman 1969), as too were the solution concentrations and diffusion coefficients of these ions. We may conclude from this that large build ups are unlikely to occur in moist field soils in this country.

iii) if there had been no supply by mass flow, a very small decrease in concentration at the root surface would have been sufficient to supply the observed inflow.

These general conclusions are in agreement with those of Brewster and Tinker (1970), who worked with leeks in the field.

1.3 Interpretation of K results

The results for K have been analysed using the analogue model described in section 2.13. The data required are the mean diffusion coefficient from t=0 to a harvest, and the root length and root pattern

against time relation. The mean diffusion coefficient was calculated from the C/I and the anion concentration. Since D decreases rapidly towards the end, a time averaged D was used. The root length against time relation was measured in 4 layers of the pot, and the pot is, therefore, analysed in 4 sub volumes. There is no problem due to water movement between layers as the solution concentration of K is low, and diffusion between layers may be neglected since D was low; the data does not warrant a too precise treatment. The root length v time relation in the 4 layers is in fig. 3.23. The time averaged root density was calculated assuming root length increased linearly with time during the interharvests. It was assumed that all layers started from day 0, which is clearly wrong for layers 3 and 4. However, onion roots were observed at the bottom of the pot after 6 days, and so any error will be small.

Autoradiographs taken in 3 mutually perpendicular directions in each layer indicated the root system was developing randomly in space. An example is in plate 13a, section 3.5.E. The mass flow contribution was calculated from the ml transpired and the average C_l values, derived from the mean NO_3 concentration and the buffer power. This product was added to the diffusion contribution to give the total possible supply.

The intermediate steps and the final results, calculated assuming all roots were absorbing as a zero sink, are given in table 3.12 c. The calculated maximum supply is remarkably close to the observed uptake. This is indicative that all roots are active, and that $\overline{\alpha a}$ is sufficiently high to reduce C_{ls}/C_{li} to $<.1$. This high value is in accord with Bhat's (unpublished) findings with onions in solution culture at concentrations below 10^{-4} M.

In view of the possible association between the roots and external mycorrhizal hyphae, we cannot be absolutely certain that the analysis is

correct. We can conclude that mycorrhiza did not enable the plant to take up more than could be supplied by the transport processes to non infected roots, which is a significant finding remembering that K was in short supply. The results also suggest that nutrient supply by mass flow is insignificant for K under these conditions.

A discussion of the close relation between the theoretical maximum supply and the observed uptake is in section 3.9.C.5.vi, which refers to more reliable data.

3.9.A.ii Conclusions from experiment 1

1. Competition between roots was not important in the uptake of N as the water flow in the transpiration stream was sufficient to maintain the root surface concentration approximately equal to the average solution concentration.

The root surface concentration was above the level at which α is usually constant. However the inflow decreased, indicating there was no constant flux into the roots. The N concentration in the plants was maintained at 5%, and presumably the NO_3 inflow decreased as plant growth was restricted by another nutrient. In these circumstances, the model, as it stands, is of little value for predicting N uptake.

N uptake is more likely to be limited by the total NO_3 present than the transport processes.

2. If the plants were mycorrhizal, the symbiosis did not increase the K inflow above that which could be supplied by physicochemical transport processes. If the mycorrhiza had no effect on K inflow, interroot competition was an important factor influencing the uptake rate of K.

K uptake was limited entirely by diffusion, and could have been predicted fairly accurately if the root length development with time had been known, on the assumption that all roots were absorbing at the maximum possible rate. This would have required an α a similar to

that found in solution culture by Bhat (unpublished). Agreement between theory and experiment was remarkably good.

The result illustrates the importance of root length when the rate limiting step in the uptake process is movement through the soil.

The K supply by mass flow in this experiment was insignificant.

3. The observed P inflow was several times greater than possible if the supply to the roots was a purely physical process. The presence of external mycelium of mycorrhiza is inferred, and if the inference is correct, the data demonstrate the great importance of mycorrhiza in P nutrition.

4. The transport processes were not rate limiting in the supply of Ca, Mg or Na. For these ions, the total quantity present is likely to be the limiting factor. If there is an oversupply due to mass flow, back diffusion is sufficiently rapid to prevent serious accumulations around roots which may cause salt damage, unless the soil is very dry.

5. For nutrients in short supply, the model may successfully predict which the nutrients are, and how much the plant will get of each. It can also be used to interpret the processes in the uptake of other ions.

6. The R.G.R. was low, considering the favourable environmental conditions. There was a plentiful supply of N, P, Ca, Mg and Na, but the physical supply of K through the soil was at all times maximal. This implies that the RGR was limited by K deficiency.

This conclusion illustrates how a deficiency of an immobile nutrient restricts all stages of growth. If the same quantity of K were used in stirred solution culture, the K would initially be adequate, and deficiency would be manifest only when the total quantity was depleted. This situation rarely obtains for K in soil, but is normal for nitrate, hence, the difference in behaviour of N and K in relation to discussions of nutrient availability.

Transpiration

120
80
40

v_1

.30
.20
.10
0

mean v_1 in whole pot

10 20 30 40

days after sowing

Plant dry weight

.4
.3
.2
.1

weight g

10 20 30 40

root length cm

Total root length

800
600
400
200

10 20 30 40

days after sowing

Fig 3.20 Primary Data from Experiment 1

Fig 3.21a Plant Uptake of N, P, Ca, K (Expt 1)

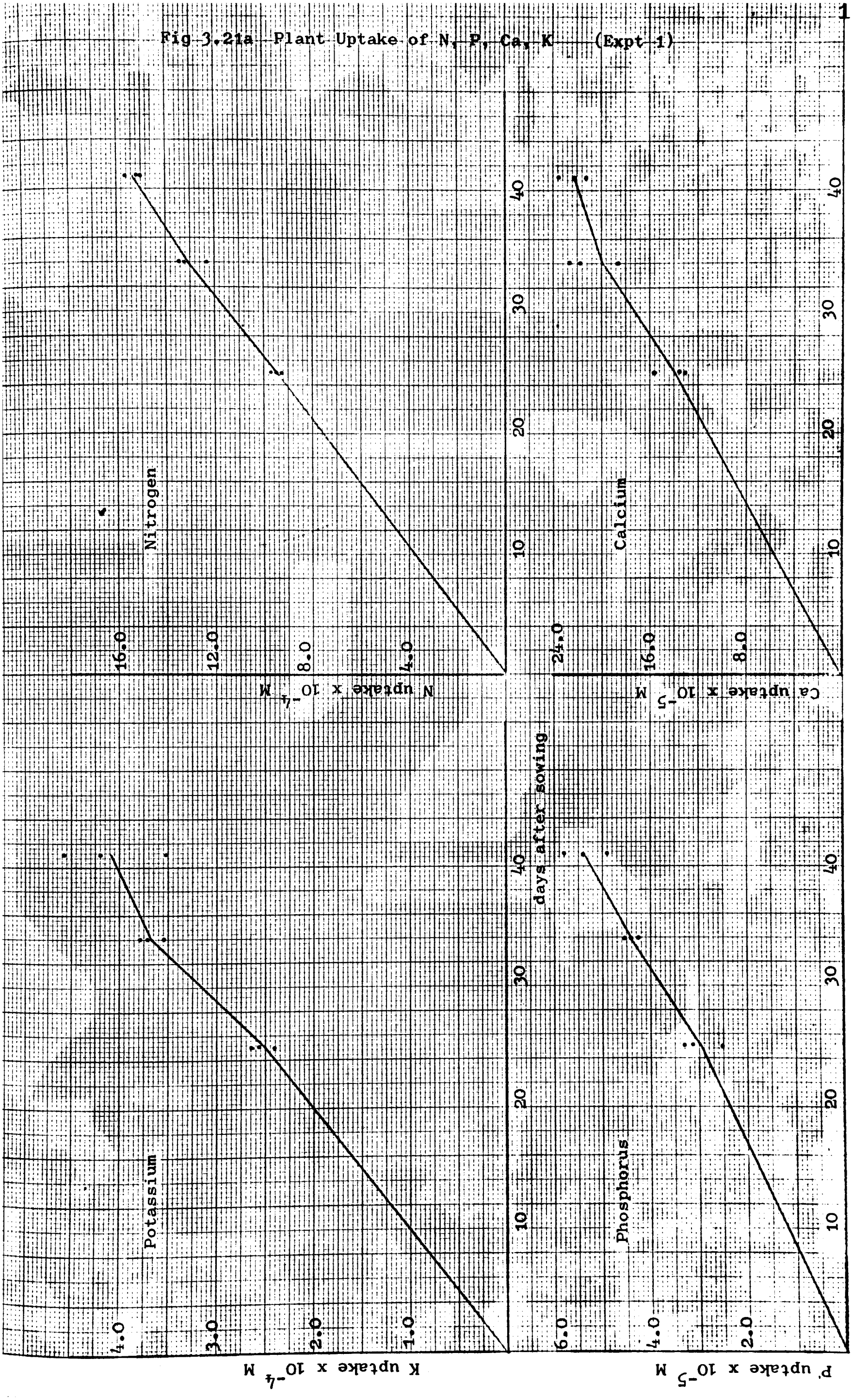


Fig 3.21b Plant Uptake of Mg and Na, plus behaviour of solution concentration of nitrate

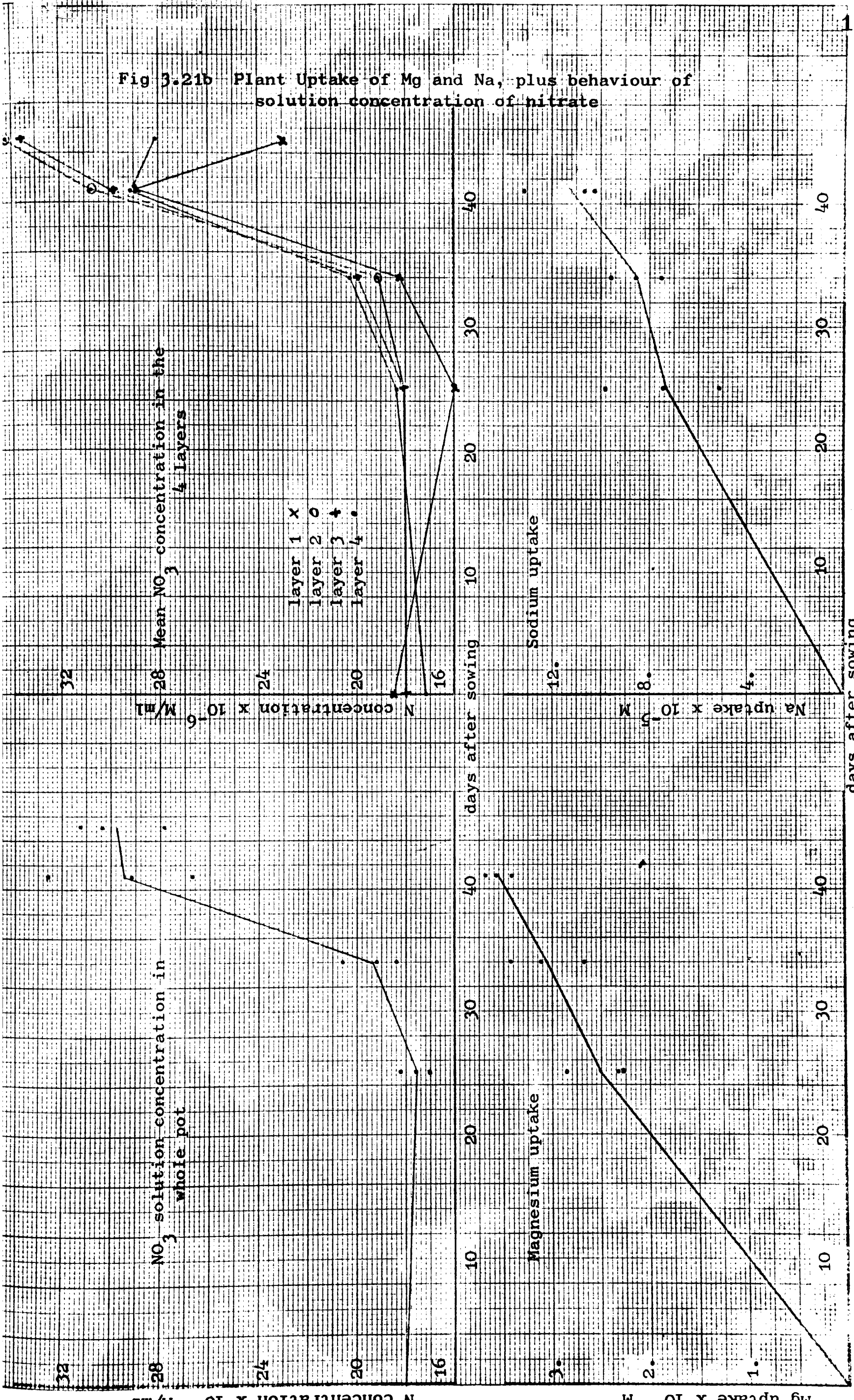


Fig 3.23 Root length in each layer (Expt 1)
mean and range

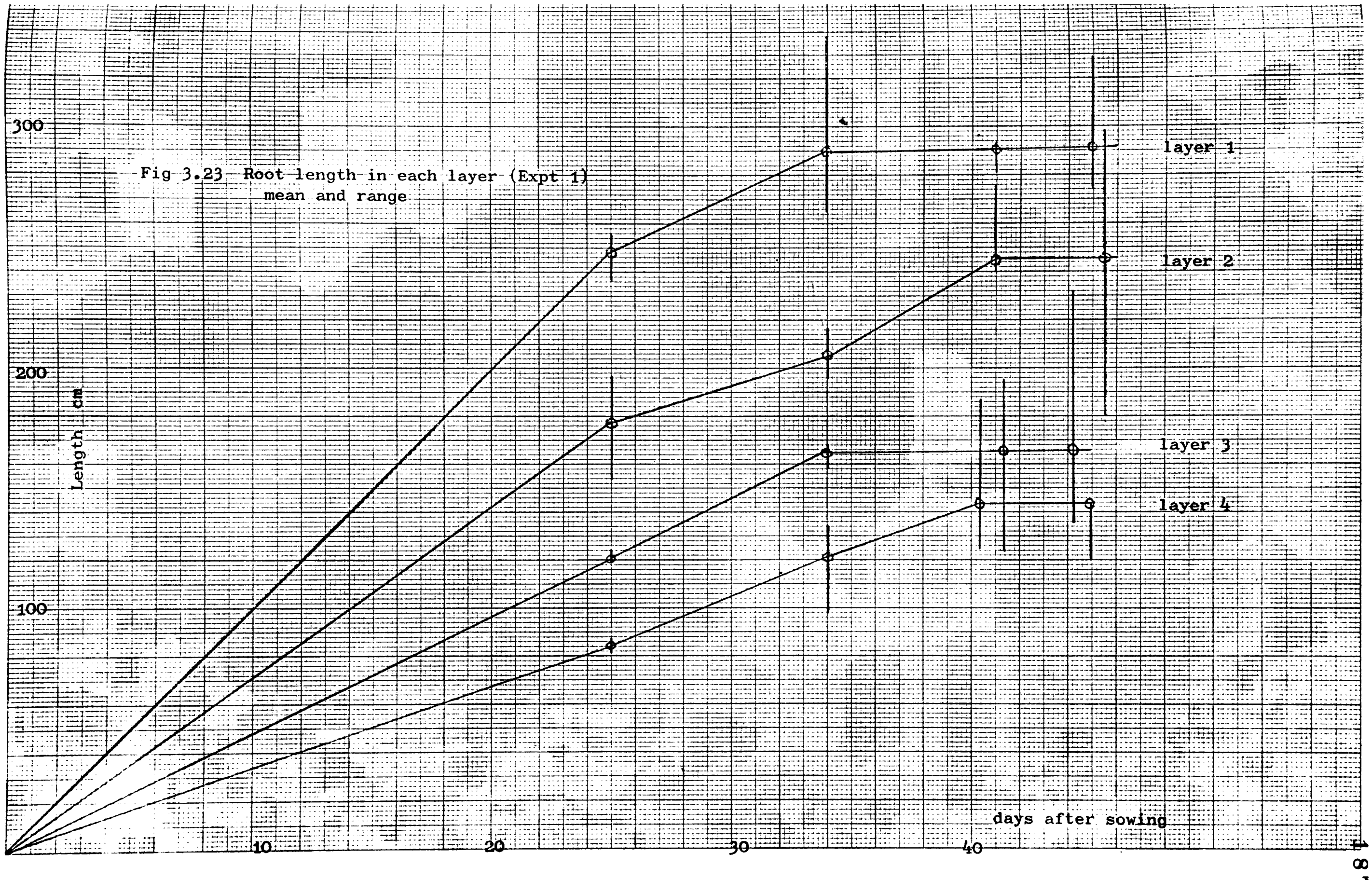


Table 3.12

Calculations of nutrient supply, Experiment 1

1) using Brewster and Tinker (1970) model.

3.12a Nitrate

Period	Observed Inflow moles/cm/sec	$\overline{C_1}$ M/ml	mean dC/dC_1 $0 \rightarrow t$	mean D cm^2/sec $t_1 \rightarrow t_2$	G	$\frac{C_{1a}}{C_{1i}}$	$\overline{\alpha^2}$ cm^2/sec	$\frac{M\ C_{1i}}{\text{Inflow}}$	C_{1a}/C_{1i} required if supply by diffusion only
1	2.41×10^{-12}	17.8×10^{-6}	.279	5×10^{-6}	.22	.98	2.2×10^{-8}	.74	.93
2	$.67\times10^{-12}$	18.5×10^{-6}	.249	3.6×10^{-6}	.20	1.04	$.55\times10^{-8}$	1.9	.96
3	$.46\times10^{-12}$	24.5×10^{-6}	.215	2.2×10^{-6}	.20	1.10	$.27\times10^{-8}$	3.2	.95

3.12a Phosphate

Period	Observed Inflow moles/cm/sec	$\overline{C_1}$	mean dC/dC_1 $0 \rightarrow t$	mean D cm^2/sec $t_1 \rightarrow t_2$	G	$\frac{C_{1a}}{C_{1i}}$	Maximum Inflow on Brewster and Tinker (1970) model moles/cm/sec	$\frac{\text{Observed Inflow}}{\text{Maximum Inflow}}$	$\frac{M\ C_{1i}}{\text{Observed Inflow}}$
1	7.61×10^{-14}	5×10^{-9}	38	1.9×10^{-8}	.51	< 0	1.2×10^{-14}	6.3	.0066
2	2.66×10^{-14}	5×10^{-9}	38	0.98×10^{-8}	.47	< 0	$.58\times10^{-14}$	4.6	.0127
3	1.91×10^{-14}	5×10^{-9}	38	0.42×10^{-8}	.46	< 0	$.26\times10^{-14}$	7.4	.0155

ii) Using Brewster and Tinker (1970) model

3.12b Calcium

Period	Observed Inflow moles/cm/sec	$\overline{C_1}$ M/ml	mean dC/dC_1 $0 \rightarrow t$	mean D cm^2/sec $t_1 \rightarrow t_2$	G	$\frac{C_{1a}}{C_{1i}}$	$\overline{\alpha}_a$ cm^2/sec	$\frac{V\ C_{1i}}{Inflow}$	$\frac{C_{1a}}{C_{1i}}$ required if supply by diffusion only
1	$3.59x10^{-13}$	$8.0x10^{-6}$	.279	$2.3x10^{-6}$	.25	1.06	$6.7x10^{-9}$	3.2	.95
2	$1.06x10^{-13}$	$8.3x10^{-6}$	.249	$1.5x10^{-6}$	.25	1.11	$1.8x10^{-9}$	5.3	.97
3	$.52x10^{-13}$	$11.0x10^{-6}$	.215	$.94x10^{-6}$	.25	1.25	$.59x10^{-9}$	12.8	.98

3.12b Magnesium

1	$6.4x10^{-14}$	$.89x10^{-6}$	10	$5.7x10^{-6}$	.4	1.02	$1.1x10^{-8}$	1.4	.96
2	$1.1x10^{-14}$	$.92x10^{-6}$	10	$2.9x10^{-6}$	.4	1.08	$.17x10^{-8}$	5.9	.98
3	$.99x10^{-14}$	$1.2x10^{-6}$	10	$1.3x10^{-6}$	.4	1.16	$.11x10^{-8}$	7.4	.97

3.12b Sodium

1	$1.9x10^{-13}$	$1.0x10^{-6}$	.90	$1.2x10^{-6}$	.27	.96	$3.1x10^{-8}$	.33	.90
2	$.20x10^{-13}$	$.93x10^{-6}$	1.0	$.55x10^{-6}$	.27	1.05	$.33x10^{-8}$	3.1	.98
3	$.66x10^{-13}$	$.93x10^{-6}$	1.4	$.17x10^{-6}$	.38	.98	$.98x10^{-8}$	.99	.89

iii) Using the analogue model in 2.13

3.12c Potassium

layer	mean dC/dC_1	mean D cm^2/sec	$Dt\tilde{\rho}$	$\frac{M_t}{M_\infty}$ random array, from fig.4	$\frac{M_t}{M_\infty}$ corrected for a-ρ relation	M_t moles $Kx10^{-4}$	Total supply by diffusion $x10^{-4}$ moles	Theoretical maximum supply $x10^{-4}$ moles	Observed Uptake $x10^{-4}$ moles	Observed Inflow moles/cm/sec
				period 0 - 1						
1	5.87	$2.73x10^{-7}$	.595	.68	.57	.84				
2	5.87	$2.73x10^{-7}$	.387	.56	.42	.62				
3	5.87	$2.73x10^{-7}$	.260	.48	.32	.48	2.30	2.36	2.49	$6.4x10^{-13}$
4	5.87	$2.73x10^{-7}$	.146	.35	.21	.36				
				period 0 - 2						
1	6.51	$2.34x10^{-7}$	.819	.73	.67	1.1				
2	6.51	$2.34x10^{-7}$	.678	.69	.58	.96				
3	6.51	$2.34x10^{-7}$	.416	.59	.45	.75	3.38	3.50	3.68	$2.2x10^{-13}$
4	6.51	$2.34x10^{-7}$	.260	.47	.30	.58				
				period 0 - 3						
1	6.85	$2.03x10^{-7}$	.970	.76	.69	1.2				
2	6.85	$2.03x10^{-7}$	.708	.70	.61	1.1				
3	6.85	$2.03x10^{-7}$	.507	.63	.51	.88	3.87	4.04	4.09	$.82x10^{-13}$
4	6.85	$2.03x10^{-7}$	.315	.53	.37	.74				

Table 3.13

Effect of a mycorrhizal association, M, on nutrient inflow

Author	Species	Nutrient	Weight M plants / Weight non M plants	Inflow into mycorrhizal roots / Inflow into non-mycorrhizal roots
Mosse (1957)	Apple seedlings	K	1.32	1.01
"	"	Ca	1.32	1.06
"	"	Mg	1.32	1.58
Gerdemann (1964)	Maize	P	3.6	1.51
"	"	K	3.6	0.74
"	"	Ca	3.6	1.03
"	"	Mg	3.6	0.95

3.9.B Experiment 2

The objectives of this experiment were the same as for experiment 1. There were several modifications in design in order to clarify the interpretation of the results.

3.9.B.i Details of experimental modifications

1. The initial nitrogen concentration / was fixed at the lowest acceptable level to increase the precision of the analysis of N uptake by loss from the soil, and to minimise the supply of N by mass flow. In addition, the calculation of the solution concentration and diffusion coefficient of K was simplified, by ensuring that NO_3 was the only anion present in significant amounts. To control the quantity of immediately available N, i.e. NO_3^-, the soil was leached with a solution of 1.87×10^{-3} M $Ca(NO_3)_2$, $.208 \times 10^{-3}$ M $Mg(NO_3)_2$, $.26 \times 10^{-3}$ N KNO_3, $.73 \times 10^{-3}$ N $NaNO_3$ and 10^{-5} M NaH_2PO_4. The pH of the solution was adjusted to 6.5 with $Ca(OH)_2$. The solutions were molar with respect to the cations. The NO_3 concentration was arranged to give 1.0×10^{-3} moles of N per pot, which is sufficient for roughly .3 g of plant material.

2. In order that N uptake from different zones of soil might be estimated, vertical movement of nitrate and water was prevented. The pot was divided horizontally into 4 3cm layers, and a membrane of lens tissue, coated with silicone grease, placed between the layers before reassembly. The membrane included a $\frac{1}{2}$ cm^2 hole to allow aeration of the pot. Preliminary experiments showed the membrane to be no impediment to root development, and there was no significant decomposition of the membrane during 6 weeks in a soil block.

3. To simplify the analysis of the root system, horizontal wedged shaped rings .3 cm wide were placed at 3 cm intervals down the pot, to divert roots away from the pot sides.

4. An increase in individual plant size, with respect to experiment 1, was required to allow measurements in the early stages of exploitation of the pot - the plants should have at least one leaf for the isotopic injection method of root analysis to be successful. The number of plants per pot, therefore, was reduced to 9.

Apart from these differences in detail, experiment 2 was a repeat of experiment 1. The experiment was unsuccessful as the plants almost stopped growing after two weeks, when the first leaf was about 4 cm long. Symptoms of a malady were manifest, as chlorosis of the cotyledon for 1 cm behind the seed, and chlorosis of the tip of the first leaf. This region of the cotyledon rapidly withered and died, and the chlorosis spread to the base. Meanwhile, a .5 cm chlorotic zone appeared about 1 cm from the tip of the first leaf. All plants were roughly similar.

Several months were spent trying to identify the cause of the complaint. The following possibilities were tested:

a) Nutrient deficiency: the addition of $.05 \times 10^{-3}$, $.15 \times 10^{-3}$ and 1×10^{-3} moles per 100 g of soil of N, P and K respectively, either alone or together resulted in no alleviation of the symptoms. Micronutrient additions were also ineffective, and nutrient deficiency was ruled out.

b) Growing conditions: the only difference between this and previous experiments was the inclusion of the silicone grease membrane, and the leaching. Silicone grease is claimed to be inert, and Drew (1966) successfully used it with his onion experiments. Roots which penetrated the membrane appeared normal in all respects. There appeared to be no reason why leaching might be deleterious to plant growth. However, trials with membranes and/or leaching, in exactly the same conditions as in experiment 2, indicated that both treatments could result in "sick" plants. Leaching was the more harmful, and the effects were additive. This suggests that leaching was influencing the chemical or biological

nature of the soil.

c) The uniformity of the malady throughout all the pots argues against any pest damage. However, the following tests were carried out:

i. nematodes: some nematodes were extracted from the soil around the base of the plants, but all were identified as rhabditids, non pathogenic saprophytes, by Rothamstead. There was no sign of nematode damage to the roots.

ii. fungi: the symptoms were not typical of any known fungus disease (Jones and Mann 1963), and the stem bases were in all cases healthy. There were no mycelia on the leaves.

iii. virus: the symptoms did not tally with described (Jones and Mann 1963) virus infections, and Glasshouse Crops Research Institute confirmed the absence of any virus.

iv. insects: several species of springtails and one of thrips were captured, but none were identified (by the Hope Department of Entomology) as pathogens. No puncture marks (evidence of feeding) were detected on the leaves.

No positive conclusions could be drawn from these investigations regarding the nature of the malady. Since that time, Brewster, in an experiment on the effect of the P concentration of BSL on onion growth, has noticed similar symptoms in soil, fertilised with N and K, but not P and in soil fertilised above $.15 \times 10^{-3}$ moles P/100 g of soil, the level I used in my test for deficiency. In his case, however, the plants in unfertilised soil recovered after about 2 weeks. At harvest these plants had developed a mycorrhizal infection with an Endogone species. There was no such recovery, nor any infection, in the fertilised pots. This supports the findings of Sanders (pers. comm., that unnatural disturbances in a soil reduce the incidence of mycorrhizal infection.

I am inclined to conclude from this work that the leaching treatment

was sufficient to kill the soil mycorrhiza, or reduce their tendency to infect onions. The fact that Brewster's onions became infected naturally supports the hypothesis that the onions in experiment 1 were mycorrhizal, and that this was the reason for the high P inflow recorded (see 3.9.A.i.1.2)

3.9.B.ii Conclusions from experiment 2

1. Onions are not suitable as an experimental crop when the soil is leached with the solution described in 3.9.B.i , and divided into layers by silicone grease membranes. The reason for this has not been unequivocally established, although it is inferred that the soil pre-treatment affects the viability of endotrophic mycorrhiza, and consequently the P nutrition of the plants.

2. Circumstantial evidence supporting the hypothesis that the onions in experiment 1 were mycorrhizal is presented.

3.9.C Experiment 3

Prior to the third experiment, several plant species were screened for their suitability as material for investigations into interroot interactions. These tests were the basis of the inter-plant competition experiment referred to in section 3.5.a.ii.2. Rape (Brassica napus var Emerald) was chosen for the experiments.

3.9.C.1 Advantages of rape as an experimental plant

i. a series of preliminary trials showed that rape grows well in the conditions used in experiments 1 and 2.

ii. the relative growth rate is much higher than in onions, which means a lower investment of time per experiment, and a lower transpiration ratio. In spite of the advances in the theoretical description of the transport processes detailed in section 2.15, it is still beneficial to minimise mass flow. In a restricted soil volume, water supply is limited, and the consequences of water additions, during an experiment, on the nutrient concentration profile cannot be estimated easily. Also, the water flux, v, to roots may have an effect on $\bar{\alpha}$a which is dependent on both the magnitude of v, the salt status of the plant and the external nutrient solution concentration (Brouwer 1965).

iii. the cruciferae, which includes rape, are not infected with endotrophic mycorrhiza (Harley 1969).

iv. the seed reserves are small.

3.9.C.2 Disadvantages of rape as an experimental plant

The root system morphology has three disadvantages:

a) roots have hairs. Root hairs complicate the analysis - their rate of development, final length and frequency are difficult to measure, and their function as absorbing surfaces is obscure. It is usual to consider root hairs to uniformly deplete the soil within a cylinder whose radius equals the modal root hair length plus the root radius, and calculate the

nutrient flux to the outer boundary of this cylinder (Nye 1966a, Passioura 1963). This approximation is satisfactory for NO_3 and K where D is high, as overlap of root hair depletion zones will rapidly lead to this "equivalent cylinder" state. In addition, the error may not be large even if root hairs are inactive, as i) the fraction of the total uptake which comes from within the root hair cylinder is small, and ii) since we calculate $\overline{\alpha}$a and not $\overline{\alpha}$, the value of a enters only in a logarithmic term (equation 2.v, section 2.19). Note that the importance of this term decreases with α a/Db. The problem of root hairs is more complex for phosphate, where D is low. Firstly, autoradiographs of P concentration in the root hair cylinder indicate that the "equivalent cylinder" concept is not always appropriate (Bhat, pers comm.). Secondly, the fraction of the total uptake which is taken directly from within the hair zone may be large. Since the buffer power $\Delta C/\Delta C_1$ is often very high at low P solution concentrations, the total quantity of P which is absorbed from within the root hair cylinder is very sensitive to the P solution concentration at the root surface, which is primarily determined by α a/Db, and $\frac{Dt}{a^2}$. Thirdly, we cannot dismiss a as appearing in a logarithmic term, as with K above, since Dt/a^2 may be < 10, and we may be in the situation outlined in the top curve of fig. 1, section 2.19, i.e. the root surface concentration is decreasing fairly rapidly with time. In this case, fig. 13 of Nye (1966a) is appropriate, and we see the influence of root hairs, in increasing a, may lead to a substantial increase in uptake.

b) unlike the onion, the rape root system produces a primary root and first and second order laterals during a 3 week experimental period. The radius of the second order is usually less than that of the first order laterals, but the radius of the equivalent cylinder is not substantially less. However, if α is a function of root volume (Russell and Sanderson

1967), $\overline{\alpha a}$ for the whole root system may decrease as the proportion of finer secondary laterals increases. This adds another complication to the story, although it will be significant only if there are shallow depletions around roots (i.e. where uptake rate is sensitive to $\overline{\alpha a}$).

e) The root system does not exploit the soil in a uniform way. Initially, the tap root grows vertically downwards, and then the primary laterals grow out horizontally from the tap root. The tap root plus laterals form, therefore, a slump in the centre of the slab of soil. Since the pot is finite, the size of this slump, with respect to the available soil volume, increases as the laterals grow, until the soil is thoroughly exploited. Whether or not this slumping is a serious factor will depend on the rate of root growth.

3.9.C.3. Experimental details

The pot was made up of 4 3 cm deep, 7.6 cm diameter PVC cylinders, which had 16 1 mm diameter holes in their side to aerate the soil at all depths. The base was 2mm perforated zinc. BSL (sample 2) at 16% moisture and fertilised with 100 μg P, as $Ca(H_2PO_4)_2H_2O$, per g of dry soil was packed in 1 cm layers to a bulk density of 1.3. Each layer was watered to 24% moisture during the packing. After the moist soil had been left to equilibrate for 7 days, each pot was leached over 3 days, with 4 bed volumes of a solution of 3.21×10^{-3} M $Ca(NO_3)_2$, $.357 \times 10^{-3}$ M $Mg(NO_3)_2$, $.382 \times 10^{-3}$ M KNO_3, $.251 \times 10^{-4}$ M Na_2SO_4, plus traces of the micro-nutrients except Fe. The soils were leached with batches of 50 ml of solution, at a tension of 50 cm water. The final measured N level in the soil solution was 7.4×10^{-6} M/ml, and there was sufficient N in the pot to produce ca..6 g dry plant material. After leaching, the soil was sliced horizontally with a steel wire at 3,6 and 9 cm depths, and a membrane of lens tissue coated with silicone grease inserted between the layers before

reassembly of the pot. One germinating rape seed was planted in the centre of each pot, the soil surface covered with a layer of black polypropylene granules plus a 1 cm layer of white polysterene granules, the pot base was covered with polythene to prevent water loss and the whole was placed in an antitranspiration chamber (fig. 3.2) in a growth cabinet where the light intensity was 1500 foot candles and the temperature inside the chambers was 20° C. In total, there were 24 pots with plants, and two blanks. Two of the seeds failed to grow properly, and only 22 pots plus the blanks were analysed. Throughout the growth period, the pot position in the growth cabinet was changed to minimise the effects of light and temperature gradients. Pots were weighed daily to record transpiration, and there were 11 harvests of 1 to 3 pots which were taken to span the complete growth curve. At harvest, the soil was analysed for N and P, and the plants for dry weight, root length, N, P, K, Ca, Mg and Na, as described previously.

3.9.C.4 Results of Experiment 3

The plant growth curve was in two phases, each being characterised by a constant RGR (relative growth rate) of .477 and .243 g/g/day respectively, as shown in fig. 3.25. Fig. 3.26 shows the total root length against time following a similar trend. Also on fig. 3.26 is the increase in mean age of roots as time progresses. Even at the end of the experiment the average age is 3.5 days only, and ½ the roots are younger than 2.3 days; no large decrease in root absorbing power due to age should be expected.

The stages of plant development were as follows, the times referring to days after planting.

day 2: both cotyledons were formed and the tap root extended vertically 7.3 cm down the pot.

day 4: primary laterals developed off the basal 3 cm of the tap root.

day 5: the tap root reached the bottom of the pot.

day 7: the first leaf was initiated. Primary laterals had developed all along the 12 cm of tap root, at uniform intervals of ~ 2 mm. They grew horizontally until the edge of the pot, and then down.

day 8.75: the first leaf reached $\frac{1}{2}$ maximum size, and the number of primary laterals reached the maximum; rudimentary secondary laterals were evident in the top 6 cm of the pot.

day 9.75: the first leaf reached $\frac{3}{4}$ maximum size, and the second leaf was initiated. Secondary laterals were growing all through the pot.

day 11.75: first and second leaf fully and $\frac{1}{4}$ mature respectively.

day 12.75: third leaf initiated.

day 14.75: third leaf mature.

day 16.75: fourth leaf initiated.

In terms of the plant development, the change in RGR, around the 9th or 10th day after planting, was associated with a change over from cotyledon to leaf as photosynthetic tissue, and the development of secondary laterals. The former change was more likely to be causal in the RGR change; if so, it would be interesting to know the physiological differences in cotyledon and leaf tissue which give rise to different net assimilation rates (the R:S ratio was constant throughout, as shown in fig. 3.27a).

Figs. 3.28 and 3.29 give the decrease in total anion (nitrate) concentration and mean v_1 with time respectively. The nutrient uptake v time curves are shown in figs. 3.30 - 3.36, and the inflow v time curves in figs. 3.37 - 3.43. Inflow = $\frac{1}{L} \cdot \frac{dU}{dt}$ was calculated from the fitted curves shown in figs. 3.30 - 3.36 and the mean $\frac{U}{L}$. It should be recognised here that the actual value of inflow is sensitive to the type of curve fitted to U v t, but since the fit is good, the trends are valid.

Several points arise from the inflow curves;

1. the inflow of all nutrients decreases with time; for no element would a constant flux boundary condition at the root surface be

appropriate. This is particularly interesting in the nitrate case, as it conflicts with some reports from work in solution culture (see section 1.2).

2. The inflow, and, therefore, $\bar{\alpha}a$ does not reflect the fairly sudden change in RGR. Since $\bar{\alpha}a\ C_{la} = Y.\frac{W}{L}\left(RGR + \frac{1}{Y} \cdot \frac{dY}{dt}\right)$ (Nye and Tinker 1969), other terms in the equation must vary to compensate the sudden change in RGR. W/L is shown in fig. 3.27b to decrease steadily with time, but $\frac{1}{Y}\ \frac{dY}{dt}$, which is the slope of the curves in fig. 3.44, increases markedly on day 10. Therefore, as the plant growth slows down, nutrients build up in the tissue. This confirms that the change in RGR is not related to the nutrient status of the plant. After the build, nutrient per cent returns to the previous value for P, K and Mg, but continues to drop for Ca and N.

3. Initially, the relative rate of decrease of N and Mg inflows are similar, and greater than that of P, K and Ca, which are also similar. Na inflow is rather erratic, but since it is not a major essential plant nutrient, it warrants no discussion.

As the N supply is depleted, N inflow decreases rapidly and is followed by Ca, but Mg follows K and P. A possible explanation is that N inflow is limiting growth throughout, and the P, K, Ca and Mg inflows are decreasing at roughly the same rate to maintain the optimum level in the tissue, implying that $\bar{\alpha}a$ for P, K, Ca and Mg may be changing in response to the internal concentration of N. This is an attractive hypothesis and is supported by the fact that the P, K and Mg per cents are constant, except for the increase when the RGR decreases. However, the decreases in P and K inflows may be a consequence of the diffusion characteristics of the system. For P, where diffusion zones will not be overlapping significantly, equation 1.vi (Passioura 1963) gives the decrease in inflow with time; G decreases by 30% as DT/a^2 increases from

1 to 3 from day 6 to 16, where T is the mean age of the roots. $v_1 f_1$ decreases by about 2. The observed decrease in P inflow, therefore, is of the same order as that predicted by diffusion theory with roots of constant $\overline{\alpha}a$. For K, inflow is decreasing due to a) a decrease in $v_1 f_1$, b) an overall decrease in the average solution concentration, which goes down by a factor of 3 over the period due to nitrate depletion, c) overlapping depletion zones; if the average root age T is 3.5 days, DT/a^2 is 20 and the reduction in uptake rate due to overlapping zones is obtained approximately from fig. 1a, section 2.6, using an estimated $\overline{\alpha}a/Db$ of 1.06 (see section 1.7.2.b) and a mean interroot distance of $2r$ (for $\rho = 4$ and regularly dispersed roots), as 40". Although factors a, b and c interact it seems that the observed decreases in K and P inflow may be explicable in terms of diffusion to sinks operating with the boundary condition $F = \alpha C_{1a}$. At a minimum, we may conclude that $\overline{\alpha}a$ for P, or K is not changing markedly in response to the uptake of other elements.

The rapid drop in N inflow after day 14 is a consequence of a limitation in total supply. The approximate ΔC_1 required to give an inflow of 2×10^{-12} moles/cm/sec is 10^{-6} moles/ml, the level which the average solution concentration drops to on day 14. Ca inflow shows a similar but less pronounced drop. This may be a result of the decreased solution concentration of Ca, which is directly proportional to that of NO_3^-, or of a decreased cation inflow to follow the anion decrease. Mg inflow does not follow a similar pattern, which it may be expected to, if the cause was the decrease in solution concentration. The ratio of Ca:Mg inflow and initial solution concentration are the same, although of course, their buffer powers may be different. K solution concentration decreases with the square root of the NO_3, and is, therefore, less sensitive to the total nitrate concentration. P

concentration is also insensitive to the NO_3 level .

3.9.C.5 Application of the theoretical model of nutrient flow to the experimental results

Soil measurements were made on the K and nitrate levels only. Ca and Mg have not been studied in detail, as no principles are involved which are not covered by the nitrate and potassium treatments. P has not been dealt with because of a) the problem of root hairs, and b) the fact that P diffusion is limited to mm from the root surface, means that the diffusion coefficient of P may be influenced by incalculable rhizosphere effects, and c) the distance which P diffuses may be insufficient to "smooth out" the micro-disequilibrium conditions (White and Beckett 1964) which are common in field soils.

Root measurements: the nature of the root system morphology, as described in section 3.9.C.4, was such that no additional information was obtainable by using the isotopic injection technique (see section 3.5.a.ii.1) for measuring root pattern. Consequently, root length in each layer was measured by extracting the roots from the soil by hand, and using a ruler until day 8.75, and the transect method (section 3.5.a.i) after that time. The root length with time plots for each layer are shown in fig. 3.45 a-d. Root growth was sufficiently rapid, that each layer may be considered to have been exploited by a randomly dispersed root system. Since root development radiated from a central axis, a more precise treatment involving concentric annular soil zones was possible, but was not deemed necessary. Measurements on the length and number of root hairs, and on root radius were made every other harvest. On average, there were 50 root hairs per mm of root, and the modal length was well defined at .4 cm. The mean root radius was .13 mm. These data are in accord with Brewster's (pers. comm.) more detailed observations of rape root hairs growing in BSL.

Water uptake: Total transpiration was monitored daily by weighing, and the loss from each layer was calculated from the soil moisture content at each harvest. Evaporative loss measured on the blanks was negligible. There was a difference between the water uptake obtained by the two methods, which rose steadily to a constant level of 5 mls after 6 days. It was found that the silicone grease membrane had absorbed water, and trials suggested that this probably accounted for the discrepancy. This 5 ml, however, was a significant proportion of the total plant water uptake, which reached 43 mls at the end of the experiment, to give a transpiration ratio of 70. As the water loss from each layer was not known accurately, the calculated water flux, v, into the roots of each layer may be approximate only. This is given in terms of inflow in fig. 3.46, and was calculated by dividing the apparent water loss between the layers, according to their relation to the membranes. Since the water inflow was low, the effect of water flow on nutrient supply was negligible, even for nitrate, which exists solely in the soil solution. A constant value of water inflow = 4.5×10^{-8} mls/cm/sec was used throughout for the computer calculations.

3.9.C.5.i Results and interpretations of the nitrate analyses

Fig. 3.47 compares the values of N uptake obtained from the plant and soil analyses. There is a 20% difference between the measured values in the middle of the experimental period, the soil analysis suggesting the greater plant uptake. The maximum difference was 12×10^{-5} moles of N per g soil. There was no denitrification in the two blank pots, and this was excluded as a cause for the nitrate loss, unless it was stimulated by the presence of roots. Possible biological phenomena which could account for this apparent loss are, a) microbial utilisation of nitrate. If we assume the microflora make up 2% of the organic matter (Russell 1961), since the C:N ratio of soil and microflora is 10:1 and 5:1 respectively,

the N content of the microbes is roughly 4% of the total, which was measured as 107×10^{-6} moles/g soil. Thus the microbial N in the bulk soil is 4.3×10^{-6} moles/g soil. A typical ratio of rhizosphere microflora: bulk soil microflora is 10:1 (Russell 1961), which leads to a rhizosphere microbial N of 43×10^{-6} moles/g soil, or an increase of 39×10^{-6} moles/g rhizosphere soil. There is 1 g of soil per 100 cm of root hair cylinder, and 400 cm of root + rhizosphere would be sufficient to account for the N discrepancy, if the increase in microbial N was at the expense of soil nitrate. Calculations based on the soil within the root hair cylinder only may be an underestimate; the rhizosphere can extend up to 1.8 cm from the root surface (Papavizas and Davey 1961). b) several workers (e.g. Rovira and McDougall 1967) have reported the exudation of organic N compounds from plant roots, and a value of $3\text{-}7 \times 10^{-6}$ moles N/g rhizosphere soil in 6 weeks may be a low figure (Harmsen and Jager 1962). It seems likely that both mechanisms were operative in the present experiments, and we can reasonably conclude from the evidence that the N discrepancy was of biological origin, resulting in an increased organic N level in the soil.

Since the disagreement between the two sets of data is small, the N uptake from each layer measured by loss from the soil has been used to compare actual uptakes with those calculated using a theoretical model of the transport processes, with the $F = \alpha C_{la}$ boundary condition at the root surface. Finally, the theoretical uptakes from each layer are summed, and compared with the observed total uptake measured by analysis of the soil and the plant. A constant flux boundary condition is also considered.

a. Computations of nitrate uptake.

We can make inferences as to the type of model required from the average interroot distance and the value of $\sqrt{Dt}$. If the interroot distance is $> 2\sqrt{Dt}$, overlap of depletion zones around roots would have

a small effect on uptake rate, and Brewster and Tinker's (1971) model describing nutrient flow to a root system composed of isolated roots is appropriate. If the interroot distance is $< 2\sqrt{Dt}$, competition between roots will reduce the flux to each root, and the model put forward in 2.21 may be suitable.

In the case of nitrate, on day 12 for example, L = 1.28 cm/cm^3 and, therefore, the average interroot distance is .34 cm (assuming a parallel population of roots whose "equivalent cylinder" radius is .053 cm, which are randomly dispersed on a plane (see Marriott 1972 for justification)), and $\sqrt{Dt}$ = 1.1cm for roots of mean age 2.7 days. Since .34 < 2x1.1, the model which allows for interroot competition is the most useful.

The time course of the depletion of nitrate from the soil was calculated using the procedure developed in section 2.21. This assumes that plant uptake equals the amount removed from the soil when randomly dispersed sinks are absorbing nutrients at a rate proportional to the solution concentration at the sink surface, and water at a specified rate. It assumes also that the nutrient concentration distance profile in the soil solution is controlled by the physical processes of diffusion and mass flow. The sink surface was assumed to be the outside boundary of the equivalent cylinder, which is defined by the modal root hair length and mean root radius.

The programme which calculates nitrate uptake is in appendix 4. The programmes for nitrogen and potassium were checked for any error introduced because of the extrapolar nature of the computing method, by varying the length of the individual time steps. Both were found satisfactory.

b. Input data

a) the root length with time relation

b) the v_1 with time relation. This was obtained from the measured

moisture content and the bulk density of the soil.

c) the v_1 f_1 relation, in fig. 3.17.

d) the modal root hair length and root radius

e) D_1 for nitrate was taken as 1.8 cm^2/sec, an average value to allow for the faster K^+ and slower Ca^{++} diffusion

f) the initial solution concentration of nitrate (measured)

g) a series of values of $\bar{\alpha}$, which were constant for any run.

h) the measured water inflow.

i) the volume of each layer.

j) the length of a time step in the computation was set at .1 days

e. Output

The programme prints out the average solution concentration, the nutrient uptake, $C_{1a}/\bar{C}_1$ and $\overline{\alpha a}$ at daily intervals. $C_{1a}/\bar{C}_1$ is a measure of the limitation on uptake imposed by the transport processes. $\overline{\alpha a}$ is equal to the calculated inflow divided by the average solution concentration in the root hair cylinder times 2π. Its relation to the input $\bar{\alpha}$ and the radius of the equivalent cylinder will depend on the contribution to total uptake supplied from within the root hair zone. For nitrate, this contribution is usually negligible.

The computations for 4 values of $\overline{\alpha a}$ and the four layers are in fig. 3.48 a-h together with the experimental points. Table 3.14 gives the average $C_{1a}/\bar{C}_1$, as it depends on the different $\overline{\alpha a}$ values.

3.9.C.5.ii Discussion of the results and computations of nitrate uptake.

1. Roots in all layers are absorbing nitrate.

2. The observed and calculated uptake v time relations have a similar form, suggesting that the uptake can be explained by the transport processes conducting nutrients to randomly disposed roots which are all absorbing at a rate proportional to C_{1a}.

t is conceivable that at any time, only a fraction of the root

system in each layer is absorbing. The size of this fraction is most likely to be a function of root age. Inspection of fig. 3.45 a-d shows that the mean root age in the 4 layers at any one time is different, and, thus, also is the fraction of the root system of any particular age. If roots of 1 age only were able to absorb, $\overline{\alpha}_a$ calculated assuming all the roots were active, might be expected to vary between the layers. We can estimate this variability from the sensitivity of uptake rate to $\overline{\alpha}_a$; since $C_{1s}/\overline{C}_1$ remains near unity, uptake rate is almost directly proportional to $\overline{\alpha}_a$, and we can say, roughly, that if L was decreased by $\frac{1}{4}$, $\overline{\alpha}_a$ would require to be increased by about 4 times (in fact, it must be greater than 4).

The simplest explanation of the results is that all the root length was absorbing at any one time. The fact that this hypothesis cannot be tested is one of the difficulties in this approach to the subject.

3. A value of $\overline{\alpha}_a$ of $1\text{-}2\times10^{-7}$ cm^2/sec and 2×10^{-7} cm^2/sec gives reasonable fit to the data in layers 1, and 2, 3 and 4 respectively. There is no obvious reason for the interlayer difference. The four theoretical curves show the sensitivity of nutrient uptake to the value of $\overline{\alpha}_a$.

The observed uptake rate decreases towards the end of the experimental period more rapidly than suggested by a model with $\overline{\alpha}_a$ constant in time. The fact that this difference is only noticeable at the end of the period argues against the second and first order laterals having different $\overline{\alpha}_a$. The decrease is not sufficient for it to be connected to other variables; it may be related to water stress (Dunham 1971), although the maximum tension in the soil was .3 bars.

The observed decrease in uptake rate may be an experimental artefact - the measured concentration in the soil solution was 10^{-3} M or less, and I) slicing and thoroughly mixing the soil whilst the roots were extracted may

have caused bacterial nitrification, although the process took about 1 hour only, or II) the result may be experimental error since the concentration of the solution after extraction was roughly $5x10^{-5}$ M, which is approaching the lower detection limit of the nitrate electrode. At these lower levels, the sulphate in the extracting solution begins to show marked interference (the selectivity constant for SO_4^{--} is $6x10^{-4}$, and a nitrate reading of $5x10^{-5}$ M will be overestimated by 6% when the sulphate concentration is $5x10^{-3}$ M).

4. Table 3.14 shows that there was a 20 to 30% reduction in the average solution concentration at the root surface. This is a measure of the limitation to uptake rate imposed by the physical conditions of the soil and the diffusion coefficient of nitrate in the liquid phase. We see that local depletions of nitrate around roots are small, in spite of the fact that nitrate supply was mainly by diffusion (the mass flow contribution would have been less than 15%, even if it had been calculated assuming the 40 ml brought, on average, a solution of $5x10^{-6}$ M/ml to the root surface).

5. The average $D_l v_l f_l$ is approximately $1.4x10^{-6}$ cm^2/sec, and, therefore, $\overline{\alpha}a/Db$ is ca. .14. Thus, fig. 2.5, section 2.12, gives a direct illustration of the effects pattern and density would have on nitrate uptake by rape plants. Since clumping can be important at this value of $\overline{\alpha}a/Db$, we may conclude that rape, which lays down a tap root and then produces horizontal laterals, may be less efficient at exploiting a volume of soil than a system which radiated roots from its base. However, it would be naive to extend this conclusion to a field situation, where it may be necessary to establish a root density deep in the profile in order to corner the N or water supply, or where the top soil may dry out.

The results for the four layers can be summarised by bulking the calculated values of uptake for each layer, for each value of $\overline{\alpha}a$, and

comparing them with the total observed plant uptake. The results for $\overline{\alpha}\,a = 10^{-7}$ and 2×10^{-7} cm^2/sec are in fig. 3.47, and are compared with the uptakes obtained by soil and plant analysis. The calculated and observed uptakes are in close agreement, one value fitting the soil data, and the other the plant data. The most appropriate $\overline{\alpha}\,a$ would depend on the reason for the discrepancy between the soil and plant figures.

3.9.C.5.iii Other boundary conditions.

Although fig. 3.37 shows that a constant flux boundary condition at the root surface is inappropriate, such has been used to illustrate the results obtainable.

For a constant flux, $I = 2\pi\,\overline{\alpha}\,a C_{1a} = \text{constant}$

Since $I = \frac{1}{L}\frac{dU}{dt}$, $\int_{U_1}^{U_2} dU = I \int_{t_1}^{t_2} L\,dt$

In the present case, $\ln L = a + bT$, and $\frac{1}{L}\frac{dL}{dt} = b$

$$\therefore U = I \int_{t_1}^{t_2} L \cdot \frac{dt}{dL} \cdot dL$$

$$= I \int_{L_1}^{L_2} \frac{L}{b} \cdot dL = \frac{I}{b}\left(L_2 - L_1\right) \qquad \ldots\ldots 3.9.i$$

Curves were fitted to the root length v time data, and the uptake v time relation calculated by equation 3.9.i, for $I = 2\times10^{-12}$ moles/cm/sec, is shown dotted in fig. 3.47. The shape of this curve does not conform to the experimental data as well as those calculated using the $F = \alpha C_{1a}$ boundary condition.

3.9.C.5.iv. Predictive value of the model.

Clearly, if we had chosen the values of $\overline{\alpha}\,a$ used to construct the curves in fig. 3.47, our predictions of total N uptake would have been very good. However, inspection of table 1.1b, shows that these are very

reasonable values at solution concentrations less than 5×10^{-3} M. From a review of the literature, Clarke and Barley (1967) found the value of $\overline{\alpha}_a$ to be of the order of 10^{-7} cm^2/sec, and they chose an $\overline{\alpha}_a$ of 2.5×10^{-7} cm^2/sec to interpret their data. Thus, we conclude that the model, as it was used, would have successfully predicted the N uptake, if we had taken a typical value of $\overline{\alpha}_a$ from table 1.1b.

If a constant flux boundary condition had been used, the predicted uptake curve would not have had the same trend as the observed experimental data.

We note that both methods of calculation are sensitive to the value of L. The model using an $F = \alpha C_{la}$ boundary condition is less sensitive to the estimated / term than the F = constant boundary condition, when uptake is directly proportional to the estimated flux.

3.9.C.5.v Results and interpretation of the potassium analyses.

plant and soil measurements of K uptake.

There was no systematic difference between the

We do a similar calculation to that in section 3.9.C.5.i.a in order to distinguish which model of nutrient supply is the most suitable. On day 12, where the mean interroot distance is .34 cm, $\sqrt{Dt}$ for K is, roughly, .24 cm. In such a situation, interroot competition will seriously affect uptake rate, and should be included in the theoretical treatment. Therefore, K uptake was calculated from the soil and plant root properties using the computer solution of equation 2.viii, which describes the transport processes to plant roots in soil.

a. Computations of K uptake.

The computer programme is basically the same as that used to calculate nitrate uptake. There is an important modification as K is an adsorbed ion, and the buffer power, and, therefore, the solution concentration in equilibrium with any total exchangeable concentration, depends on the total

anion concentration.

Initially, the nitrate ion was the dominant anion in the soil solution. During the experiment, the ratio of anion : cation inflows was approximately constant at 1.5 up to day 13, after which it decreased. On the 10th day, the net HCO_3^- outflow was 1.0×10^{-12} moles/cm/sec, but there would have been no significant build ups of HCO_3^- in the soil solution (Ramsan 1971). Thus it is reasonable to consider the nitrate concentration to equal the total anion concentration.

The solution concentration of K in equilibrium with any total concentration is governed by the divalent cation concentration according to the ratio law (Schofield 1947): $a_k / \sqrt{a_{Ca} + a_{Mg}} \simeq [k] / \sqrt{[Ca] + [Mg]}$ = constant, called the activity ratio, AR, where a refers to activity, and [ ] to concentration. When AR is $\ll 1$, it is possible to equate the divalent cation concentration to the total anion concentration. In this case, $[Ca] + [Mg] = \frac{1}{2}[NO_3]$, and $[K] = AR \sqrt{\frac{1}{2}[NO_3]}$.

As local depletions of nitrate around roots are small, the K buffer power does not vary significantly with position at any one time.

The programme to calculate K uptake assuming the plant uptake rate is proportional to the root surface solution concentration is in appendix 5.

The input is essentially the same as for the nitrate programme, D_1 is 1.98×10^{-5} cm^2/sec, and the variation in nitrate solution concentration with time was fed in as an equation.

3.9.C.5.vi <u>Discussion of the results and computations of K uptake.</u>

Figs. 30 a-d give the experimental points and calculated values of uptake for 4 values of $\overline{\alpha a}$ for the 4 layers, and table 3.15 gives the mean $C_{1a} / \bar{C}_1$ corresponding to the 4 values of $\overline{\alpha a}$.

The average K solution concentration in the pot decreased from 3.7×10^{-7} to $.9 \times 10^{-7}$ moles/ml, and the values of $\overline{\alpha a}$ chosen are in the range of those found by workers in solution culture (see table 1.1a).

If there had been no K uptake, the solution concentration would have been reduced to 1.66×10^{-7} M/ml, as the N concentration declined. This emphasises the importance of the inclusion of the behaviour of the anion concentration.

Mass flow contributed an insignificant amount of K to the total uptake - a rough estimation is given by ml transpired x $\bar{C}_1$, or 8×10^{-6} M K, less than 2% of the total.

The first thing to note regarding fig. 3.50 is that the experimental scatter is very great. This is a consequence of the method of measurement. The major difficulty follows from the fact that uptake is calculated from the difference between two large numbers, but in addition, the C/I measured on the blanks, in fig. 3.19, was more unstable than previous investigations had indicated. It is possible that the leaching treatment influenced the stability of the C/I. The experimental points determined from soil analysis are, therefore, a very rough check only of the appropriateness of the model. Experimental points obtained at later harvests should be more accurate.

In spite of the experimental scatter, it is clear that roots in all layers are absorbing K. It is also apparent that the theoretical curves roughly describe the experimental data in all 4 layers as time increases, implying that we are batting on the right wicket. Nothing precise can be said about the value of $\bar{\alpha}$a in each layer, except that it is higher than the value for nitrate. Note that the uptake rate is tailing off at the end as the N supply in the soil is depleted.

The analysis of the plants for K is a positive measure, and, therefore, should be more accurate. The experimentally determined values of total uptake of K are compared with theoretically derived curves for a constant $\bar{\alpha}$a, obtained by summing the calculations on each layer, in fig. 3.51. Also in fig. 3.51, is the curve calculated assuming a constant

flux boundary condition operated at the root surface, with $I = 0.8 \times 10^{-12}$ moles/cm/sec.

Points which arise from the curves

1. The complete growth curve is well described if we assume all the roots were absorbing at a rate proportional to their external solution concentration, the rate constant $\overline{\alpha}a$ being 2.6×10^{-6} cm^2/sec, and nutrient supply was by diffusion and mass flow.

2. A twenty fold increase in $\overline{\alpha}a$ results in a 20% increase in uptake, i.e. uptake rate is insensitive to the plant demand coefficient, and is almost entirely limited by transport processes in the soil. This is reflected in the average $C_{1a}/\bar{C}_1$ in table 3.15. As the plants were absorbing throughout at the maximum possible rate, the observed decrease in K inflow discussed in 3.9.C.4.3 was a consequence of the soil supplying power.

3. All the roots must have been absorbing all along their length all the time. A consequence of the model calculating the observed uptake only when $\overline{\alpha}a$ is high, with all roots absorbing, is that the plant would not have been supplied with sufficient K, if all the roots had not been absorbing. Within the physio-chemical framework of diffusion and mass flow outlined in the introduction, there is no way that a plant root can absorb nutrients from the soil solution more rapidly than by instantly depleting the root surface concentration to zero, and then absorbing all the nutrient which moves in due to the gradient in potential.

4. The total plant inflow = $2\pi \overline{\alpha} a C_{1a} L$, and since $\overline{\alpha} a C_{1a}$ is independent of $\overline{\alpha}a$, the plant uptake rate of K is directly proportional to L. This emphasises the importance of root density to the uptake of relatively immobile nutrients.

5. The constant flux boundary condition is inappropriate as the theoretical and observed curves are differently shaped.

6. The function of root hairs as absorbing organs can be inferred from this data. The dotted curve shown in fig. 3.51 was calculated assuming all roots were absorbing with an $\bar{\alpha}a = 5.3 \times 10^{-5}$ cm^2/sec, similar to the upper full curve, but the root surface formed the inner boundary for the nutrient flux calculation. This curve represents the maximum uptake the plant could achieve if root hairs were not absorbing. It lies below all the experimental points, from which we deduce that root hairs were functioning as absorbers. The fraction of the total uptake which originates within the root hair zone when $C_{1a}/\bar{C}_1$ is less than .1, is, in this system, less than 5%, and the influence of root hairs is essentially due to an increase in effective root radius.

If root hairs were able to absorb all the ammonium acetate exchangeable K within the root hair zone, the root hair cylinder would have contributed about 28% of the total plant K. This is an unreal system, in that it implies there is no K diffusion in response to the depletion.

7. The experimental points may not be following a smooth curve, one curve fitting the data to day 12, and another, similar shaped one, being appropriate after that day. There is insufficient data to support this "twin curve" suggestion, but it remains a possibility. The change is associated with the build up of K in the tissue which follows the change in RGR (see fig. 3.25), and could be associated with a feedback mechanism, i.e. the K build up signals that no more is required, and as plant growth dilutes the K, there is a lag before uptake recommences. If the roots were absorbing at the maximum rate until day 12, and then continued to do so after the lag, the theoretical curve would fit the experimental data. More observations on the true shape of the growth curve would establish this point.

3.9.C.5.vii Predictive value of the model

If we had assumed from the outset that plant roots + root hairs were able to decrease the solution concentration of K at the root surface to below .1 of the average concentration, which itself was a function of the anion concentration, and calculated the nutrient flux to the root system as it increased in density, we would have given a very good estimate of the total plant uptake at all times in the growth period. A similar condition at the root surface was required in experiment 1. The root demand coefficient required would have been similar to that reported by workers in solution culture, where the root surface solution concentration was less than 5×10^{-7} M/ml.

The model appears highly satisfactory for predicting K uptake, as the only data required are measurements on the diffusion characteristics of the soil, the anion concentration in the soil solution, and the root characteristics of length and radius and root hair length, as they develop in time.

A constant flux boundary condition at the root surface would not have been as satisfactory, although, if the inflow used in fig. 3.51 had been chosen, a reasonable estimate of uptake would have been obtained. The major disadvantage of this boundary condition in predicting K uptake, is that it takes no account of the supplying power of the soil; it is shown inadequate at the end of the period, as it predicts a greater uptake rate than theoretically possible, within the accepted framework of diffusion and mass flow through the soil solution. The other disadvantage is that the predicted uptake is linearly related to the chosen value of inflow, whereas uptake rate is insensitive to α, if $F = \alpha C_{la}$, with α constant.

3.9.C.6 Conclusions from experiment 3

1. 17 days of growth of rape plants from seedlings is characterised by two periods of constant RGR. Nutrient inflow (moles/cm/sec) does not reflect the change in RGR. The consequence is that nutrient % in the

tissue increases as growth rate slows down. The fairly sudden decline in RGR is possibly associated with a change in the photosynthetic tissue, from cotyledon to leaf.

2. Inflow of all nutrients decreases with time, the relative rate of change being constant, except for Ca and N towards the end of the period when the inflow drops rapidly as the total quantity of N limits uptake. A boundary condition for the transport processes which assumes a constant rate of uptake into the roots would in no case be appropriate.

3. Mass flow contributed less than 15% of the total N, and less than 2% of the total K absorbed by each plant over the growing period. The actual significance of mass flow is probably much less than the figures quoted, since a large proportion of the water was transpired when the nutrient concentration in the soil solution was low. This may be typical of the situation of crops in the field, i.e. nutrient uptake is most rapid in the early stages of growth when the total leaf area and temperature and, therefore, transpiration rate is low.

4. The supply of both nitrate and potassium to the plant roots was reduced by interroot competition. Competition in this sense is manifest as a reduction in nutrient uptake rate, and follows from the depletion in the soil solution when there is absorption into another root.

5. Using a constant value of $\overline{\alpha}a$ and assuming the roots were developing in the soil in the way the measurements suggested, the experimental uptake curve was adequately reproduced by the theoretical model of nutrient supply by diffusion and mass flow to all the roots which were absorbing at a rate proportional to the external solution concentration, C_{1a}.

6. If the boundary condition defined by $I = 2\pi\overline{\alpha}aC_{1a}$ = constant had been used, the form of the experimental uptake time relation would not have been determined.

7. $\overline{\alpha}a = 1\times10^{-7}$ cm^2/sec and 2×10^{-7} cm^2/sec represented the behaviour

of the roots with respect to nitrogen uptake, as measured by analysis of the plants and soil respectively, (there was a discrepancy between the N uptake estimated from soil and plant which reached a maximum of 20%). These values of $\overline{\alpha}a$ are similar to those reported by other workers, although they appear to obtain at higher solution concentrations than some would suggest (see 1.2). The reason for these conflicting observations is not apparent. Clarke and Barley (1967) also drew attention to it, when they reported N to be linearly related to soil solution concentrations of nitrate up to 70 mM. Their suggestion that the nitrate concentration at the root surface was reduced from 70 mM to .70 mM appears unrealistic (for their single roots, and their $\alpha a/Db$ of 1.4, $C_{1a}/\overline{C}_1$ is .3-.4).

8. The transport processes through the soil reduced the uptake rate of nitrate by 20 - 30%, at any given average concentration in the soil.

9. If we assumed that an $F = \alpha C_{1a}$ boundary condition was operating up to 7×10^{-3} M NO_3, and used the constant value of $\overline{\alpha}a$ found appropriate by other workers (Clarke and Barley 1967), the model described in 2.15 would have predicted uptake reasonably well.

10. Potassium uptake could have been explained on the assumption that all roots were absorbing at a near maximal rate. In these circumstances, uptake rate is insensitive to the root demand coefficient, as it is inversely related to C_{1a}. K uptake rate, therefore, was governed entirely by the factors which control the movement of potassium in the soil. A consequence of this is that plant uptake rate of K is directly proportional to the length of root.

11. The observed uptake could not have been attained if the root hairs had not been actively absorbing. Root hairs may be considered to create a zone around the root through which diffusion is rapid; the actual contribution from within the root hair cylinder is small.

12. Since uptake rate is insensitive to the value of $\overline{\alpha}a$, the uptake could have been predicted from a knowledge of the diffusion characteristics of the soil with respect to K, the anion concentration, and the root length development with time. The results emphasise the need to include changes in anion concentration in considerations of the K solution concentration, buffer power or diffusion coefficient.

13. A constant flux boundary condition would have been less satisfactory than one assuming $F = \alpha C_{la}$, with α constant as a) the shape of the theoretical and experimental curves are dissimilar, and b) the calculated uptake is directly proportional to the chosen value of inflow.

14. The experiment afforded an example of the differences between N and K with respect to concepts of nutrient availability and soil supplying power. Throughout the experiment, the soil was just able to supply the plant roots with sufficient K to maintain the nutrient % in the tissue, and it appears that it would have continued to do so, since M_t/M_∞ was less than .2 at day 17. In contrast, nitrogen was in plentiful supply in the early stages of growth, and the plant absorbed its requirement with a lower value of $\overline{\alpha}a$ than for K. Local depletions at the root surface were small, and the soil could have supported a higher plant demand. Toward the end of the experiment, however, the total quantity of N in the soil was reduced to a lower level than required to maintain the N% in the tissue. Although growth rate did not decline, it would have done if the experiment had continued, and the cause would have been N deficiency. If K had been deficient, the symptoms would have been evident throughout the growth period.

Limitation would have been ... although this is a symptom

Fig 3.25 Plant Weight against Time

Fig 3.26 Total Root Length against Time

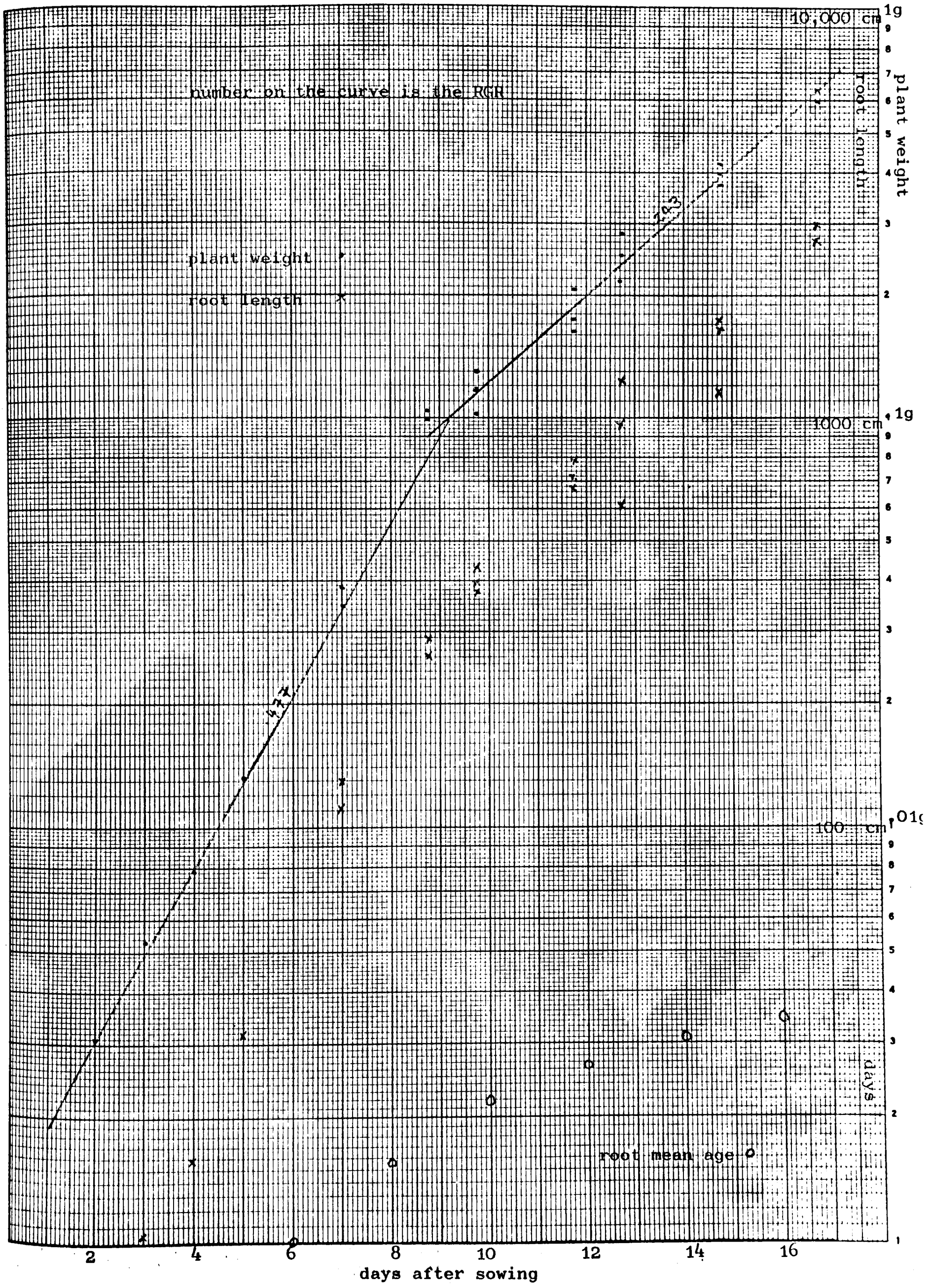


Fig 3.27a Root:Shoot ratio against time

b Plant weight per unit length against time

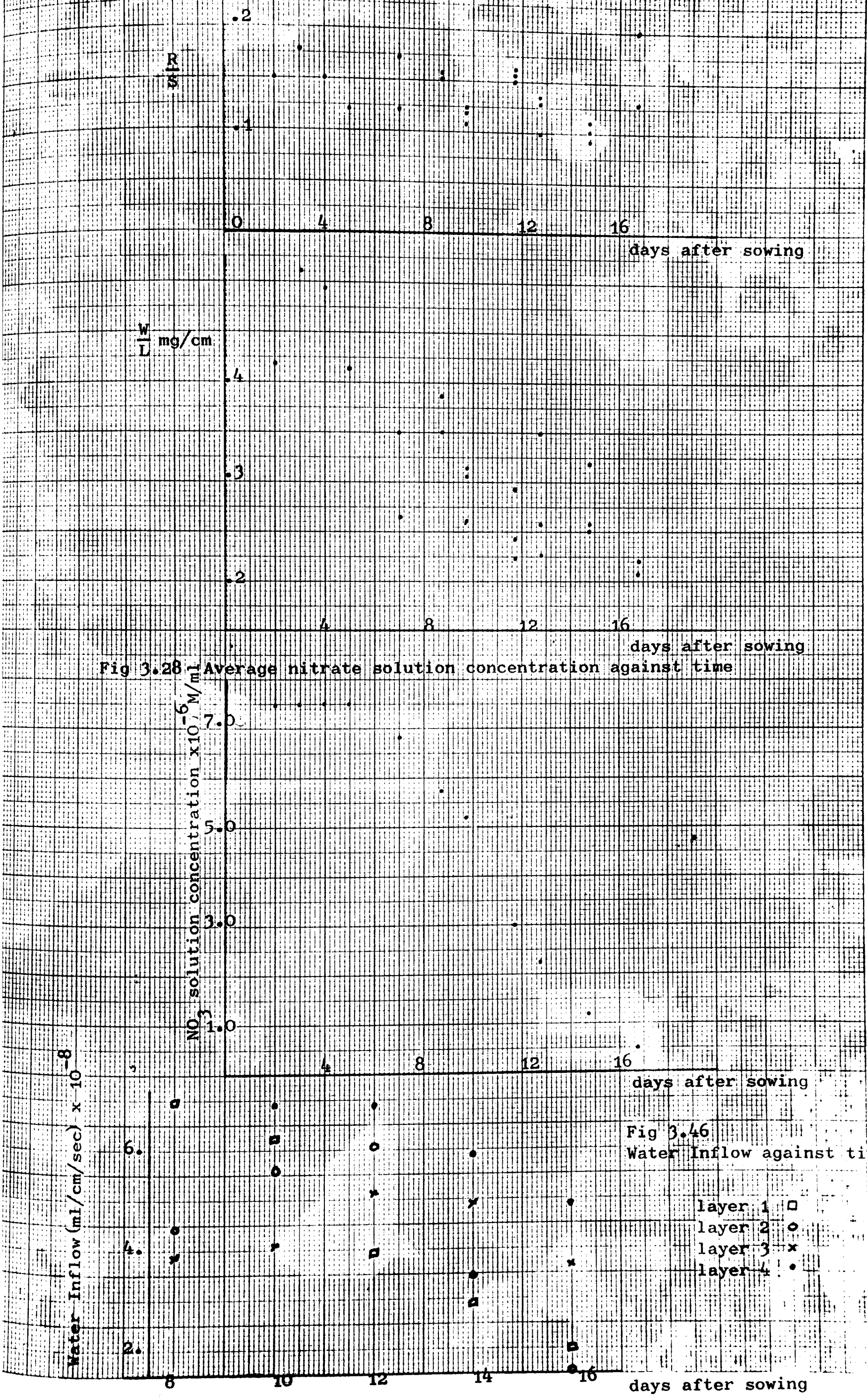


Fig 3.28 Average nitrate solution concentration against time

Fig 3.46
Water Inflow against time

Fig 3.29 Mean v_1 in the 4 layers

(Lines used in the computations)

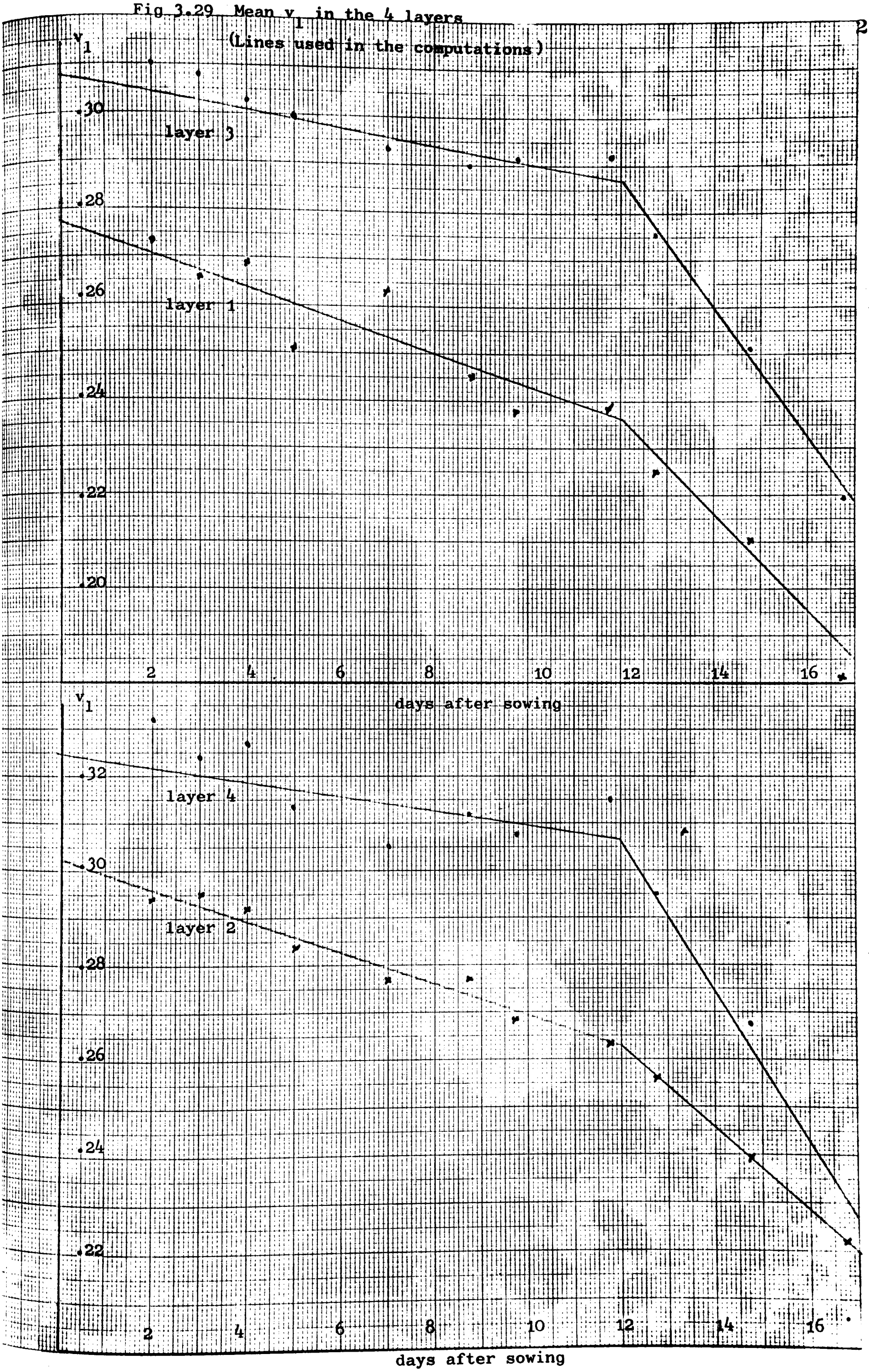


Fig 3.30 Total uptake of potassium

Fig 3.31 Total uptake of nitrogen

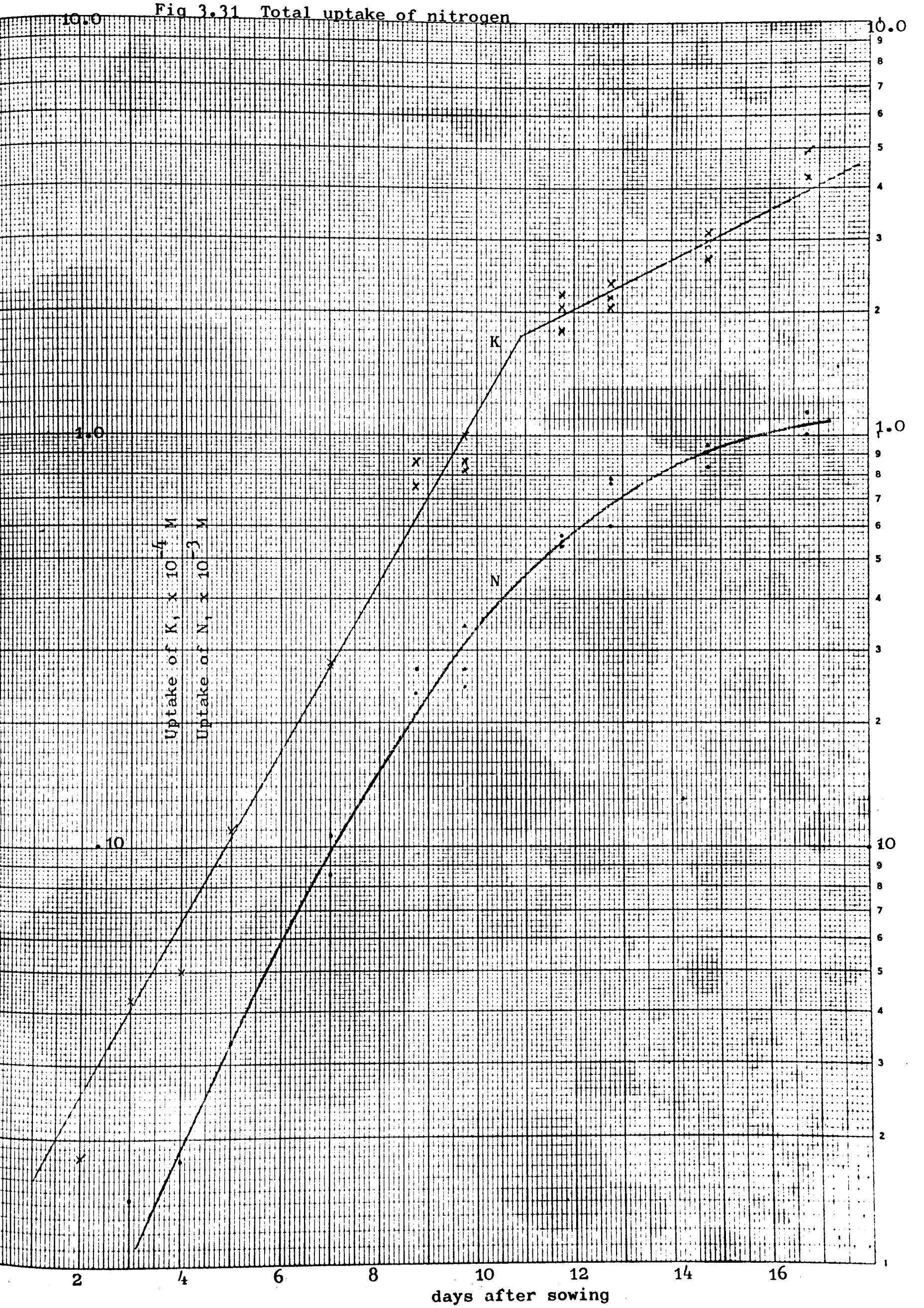


Fig 3.32 Total uptake of phosphorus

10. Fig 3.33 Total uptake of sodium

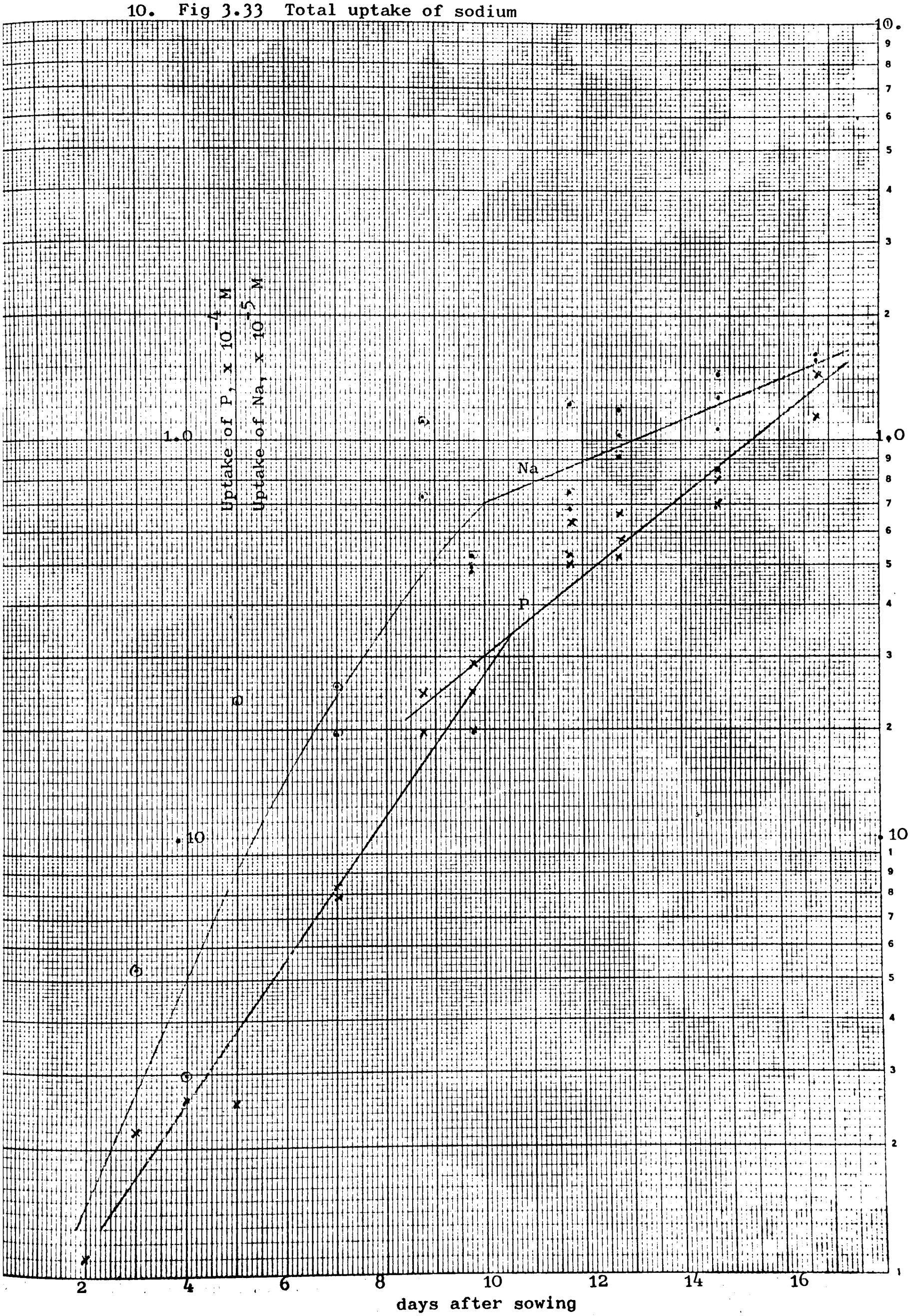


Fig 3.34 Total uptake of Calcium

Fig 3.35 Total uptake of Magnesium

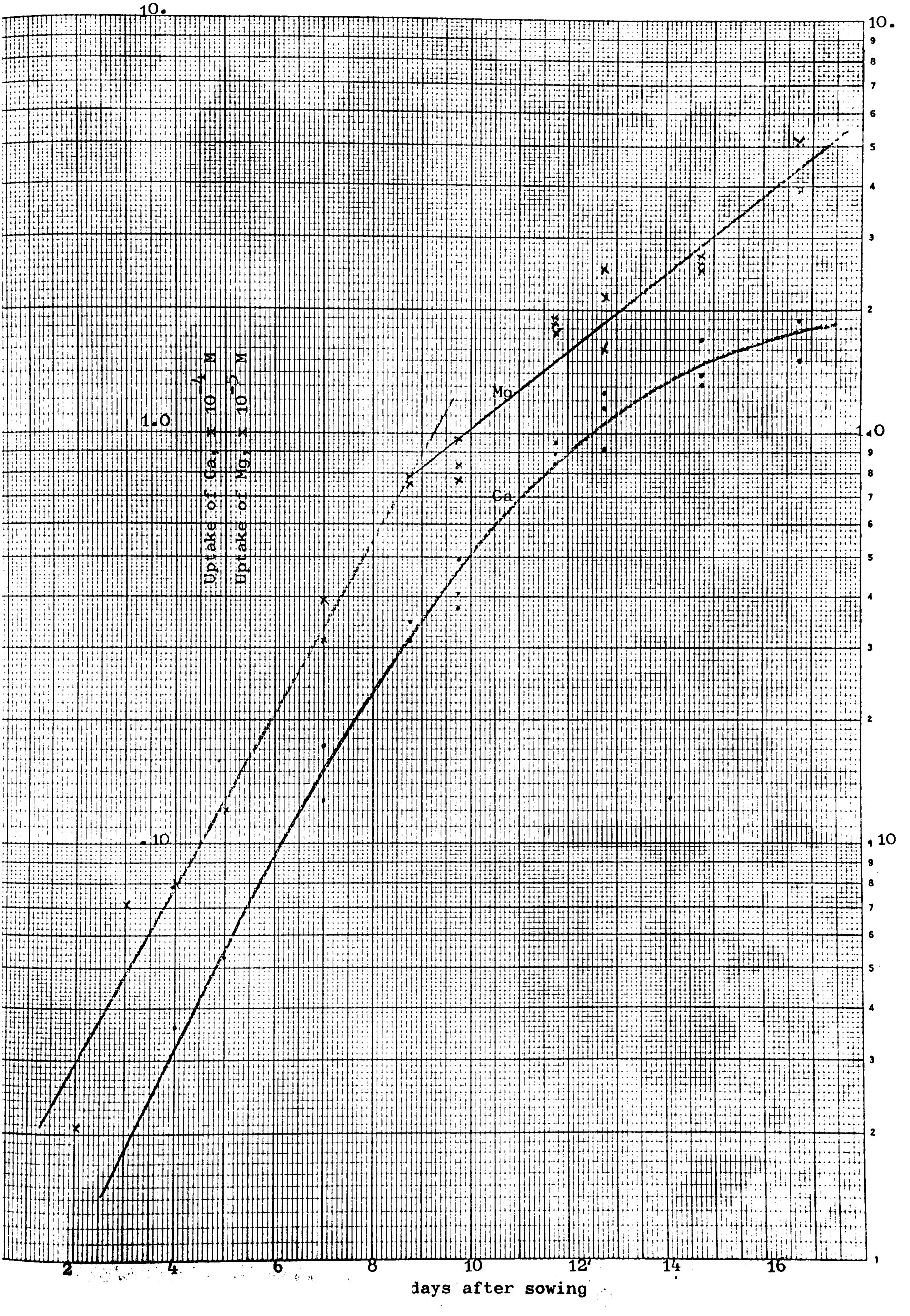


Fig 3.37,38,39 Nutrient Inflow against Time (Expt 3)

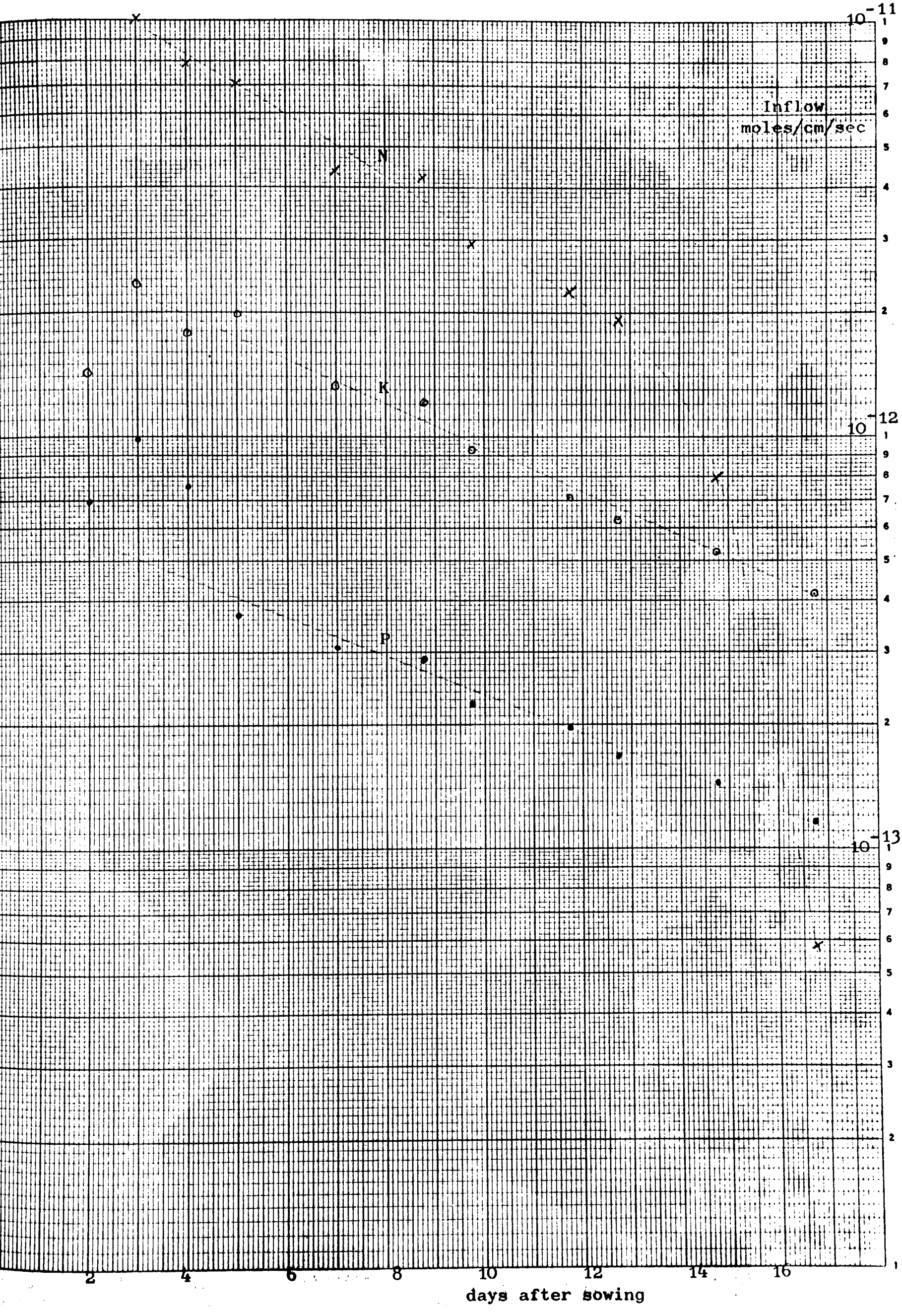


Fig 3.40,41,42 Nutrient Inflow against Time (Expt 3)

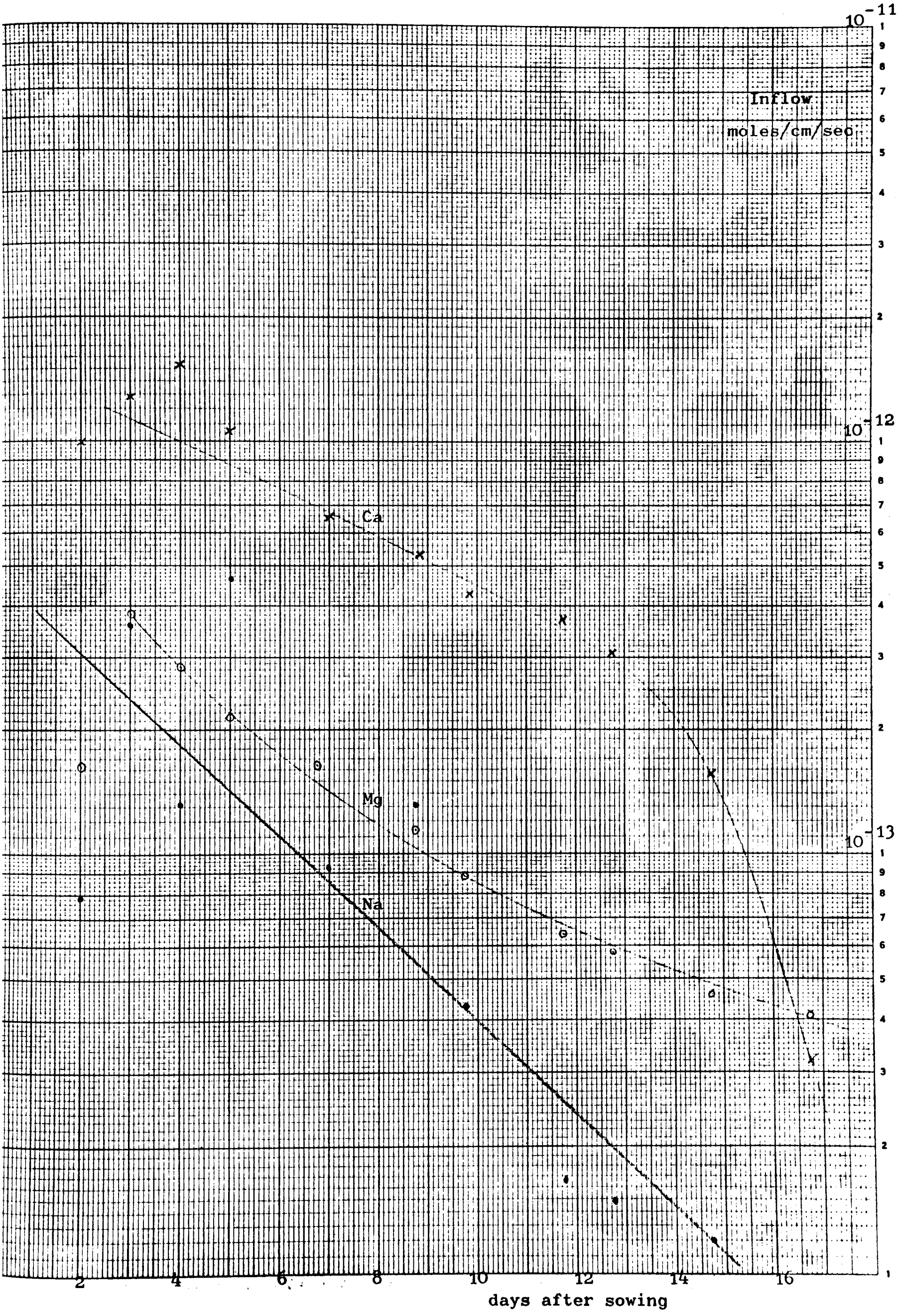


Fig 3.44 Nutrient percent in the tissue

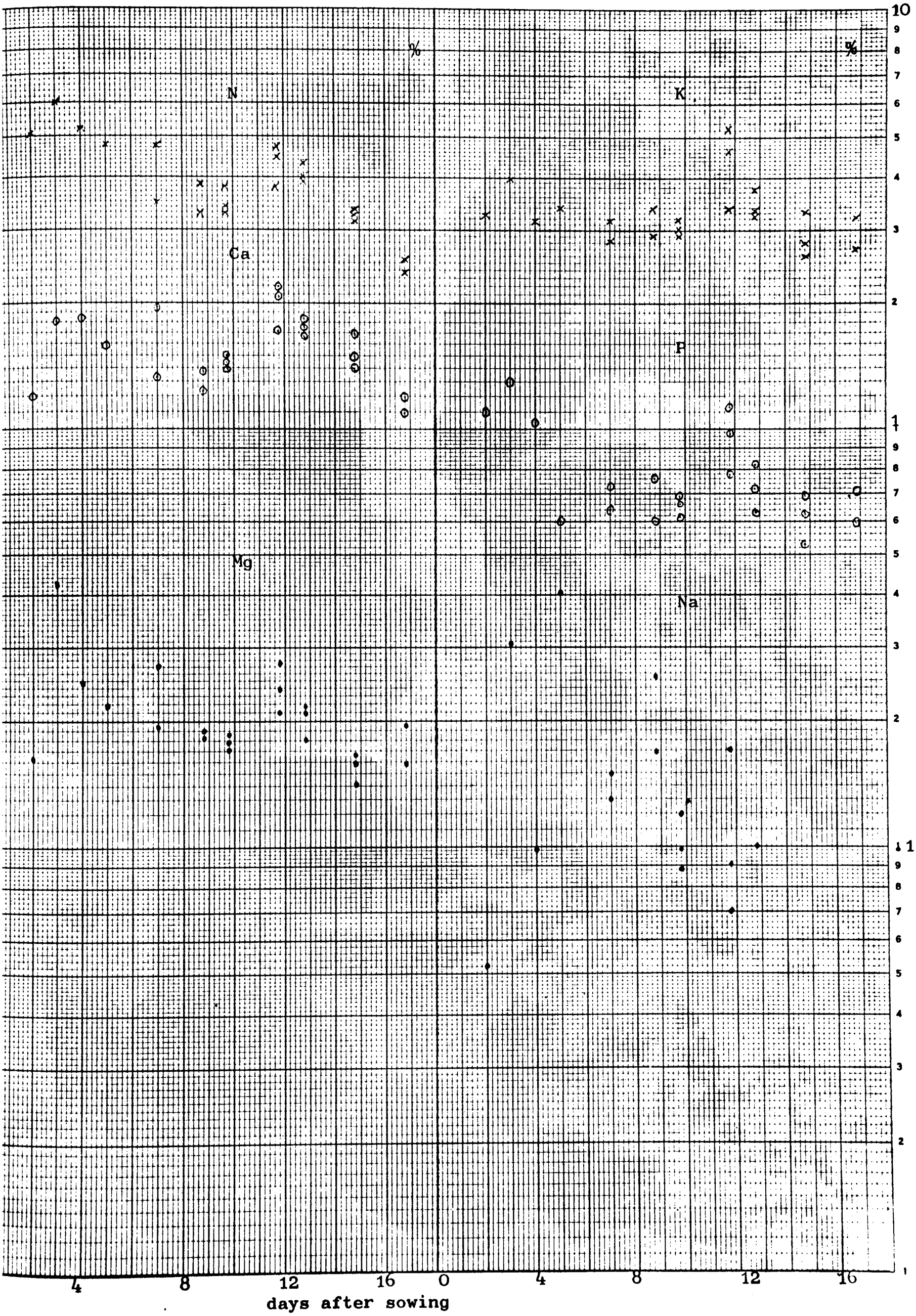


Fig 3.45 Root length in each layer against time

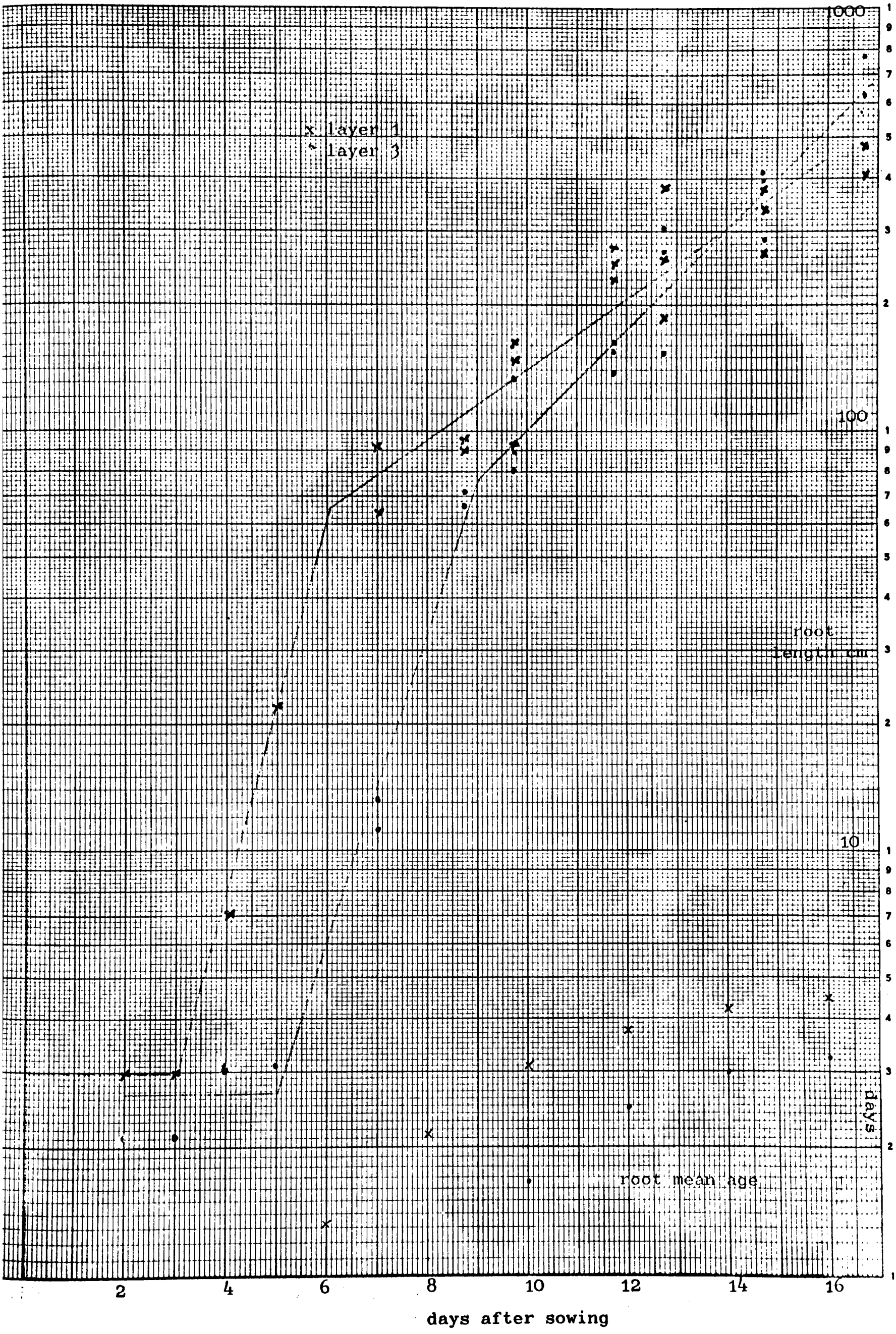


Fig 3.45c,d

o layer 2
x layer 4

root length cm

root mean age days

days after sowing

Fig 3.47 N uptake in each layer determined by soil analysis, and curves calculated by equation 2.viii.
Numbers on the curves are $\overline{da}$ cm^2/sec

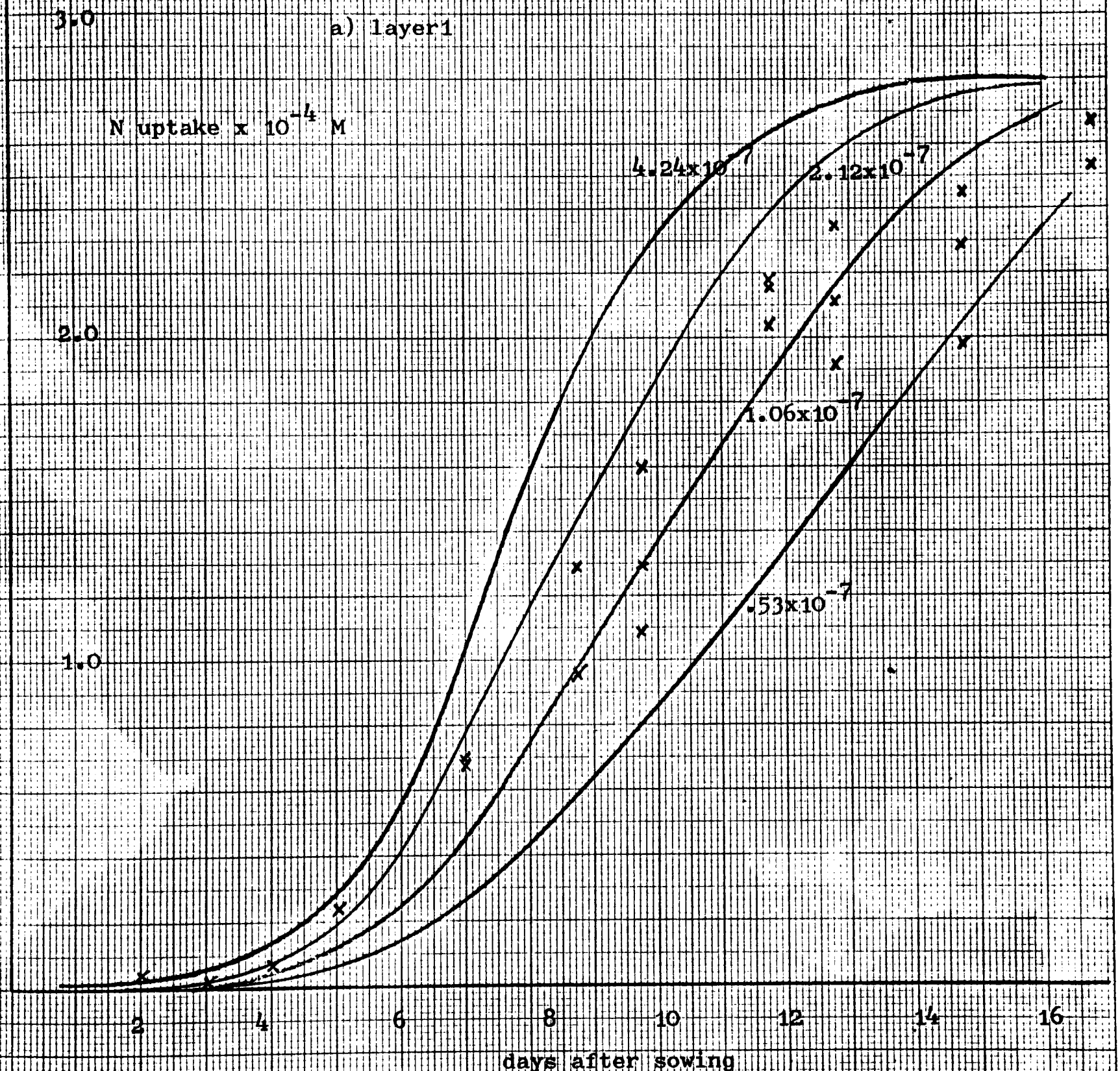


Fig 3.47b

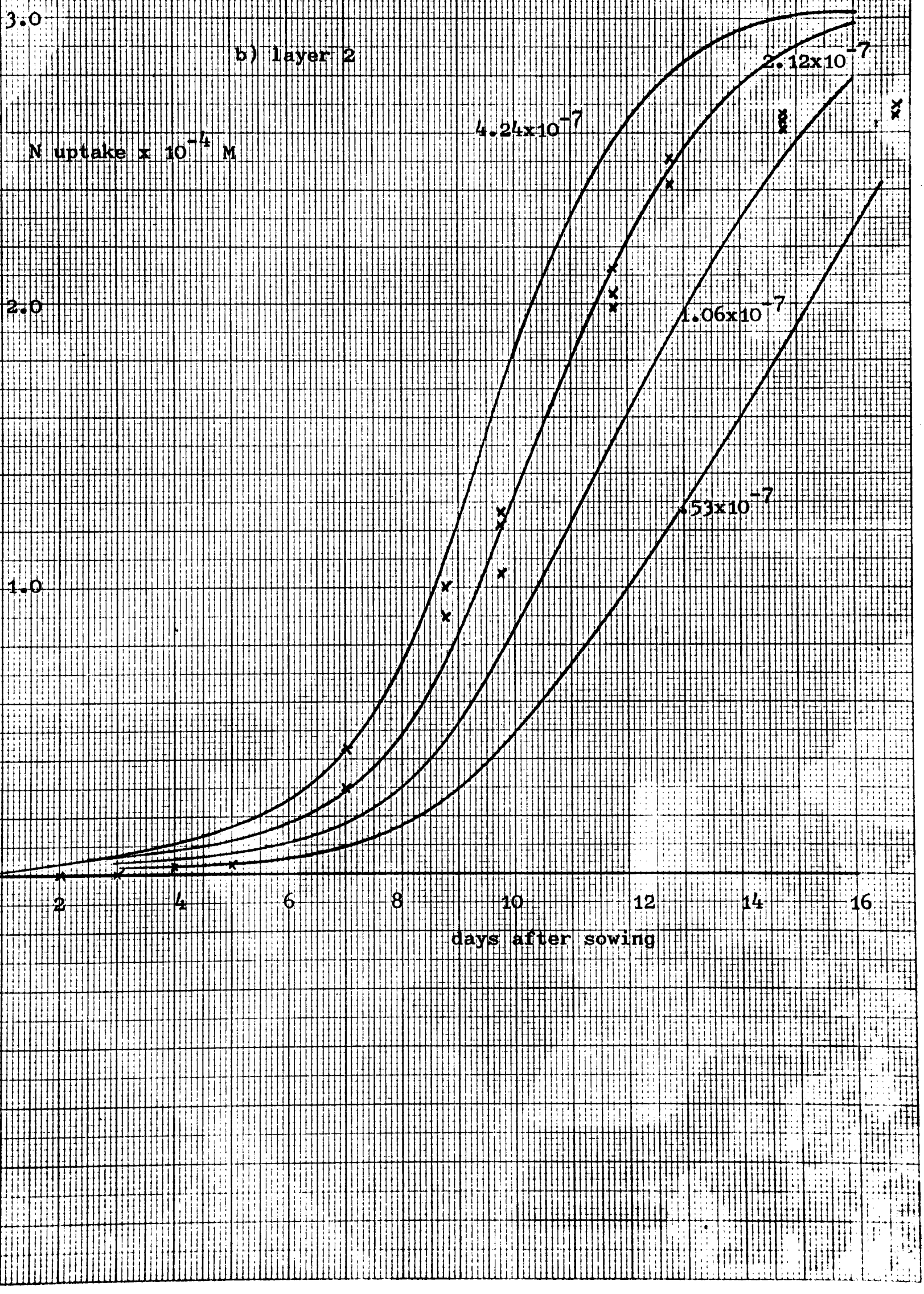

3.0
b) layer 2
N uptake x 10^{-4} M
2.0
1.0
$4.24x10^{-7}$
$2.12x10^{-7}$
$1.06x10^{-7}$
$.53x10^{-7}$
2
4
6
8
10
12
14
16
days after sowing

Fig 3.47c

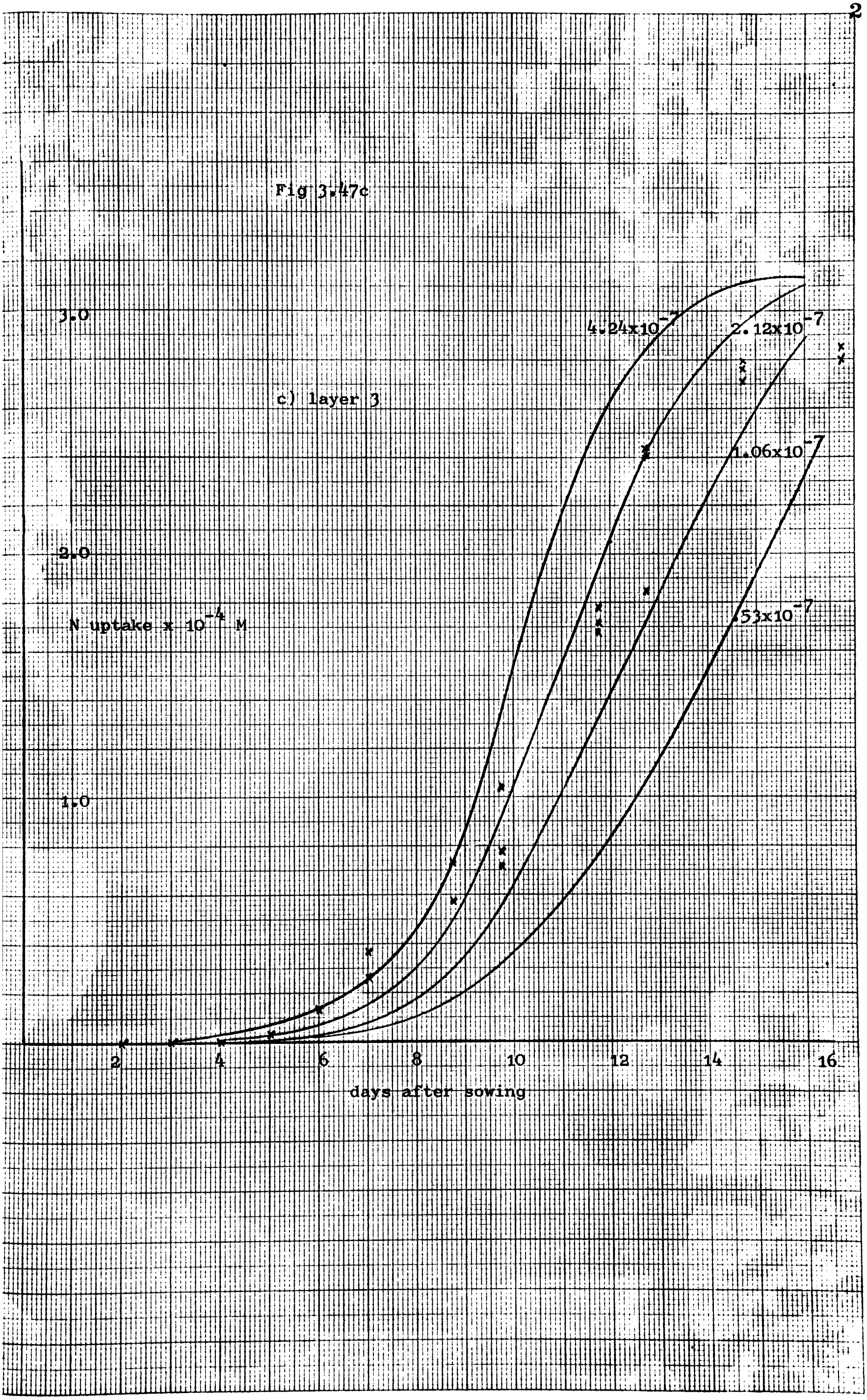

3.0
2.0
1.0
N uptake x 10^{-4} M
c) layer 3
4.24×10^{-7}
2.12×10^{-7}
1.06×10^{-7}
$.53 \times 10^{-7}$
2
4
6
8
10
12
14
16
days after sowing

Fig 3.47d

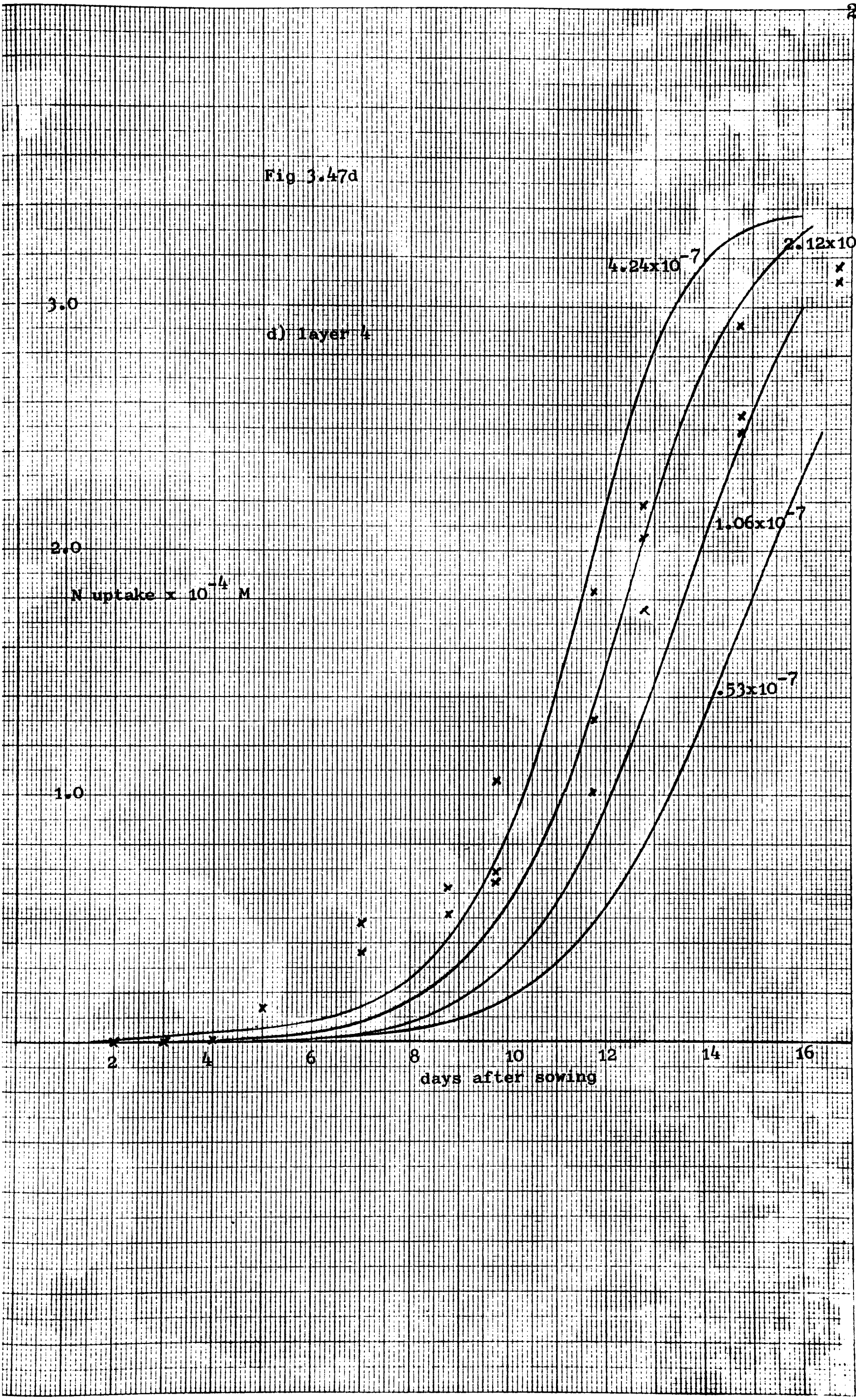

4.24x10-7
2.12x10-7
1.06x10-7
.53x10-7
d) layer 4
3.0
2.0
1.0
N uptake x 10-4 M
2
4
6
8
10
12
14
16
days after sowing

Fig 3.48 Whole plant uptake of nitrogen (Expt 3)

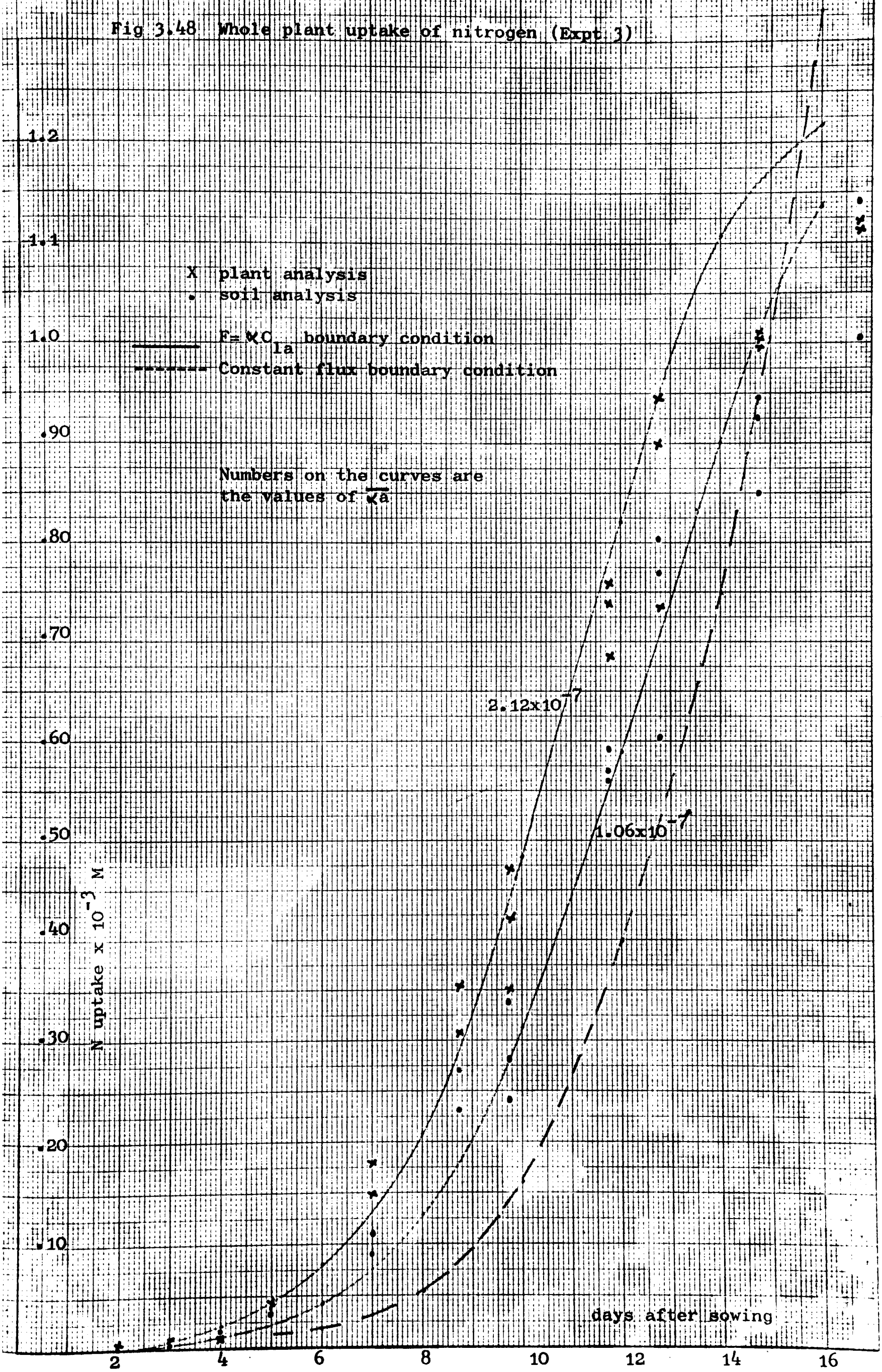


Fig 3.50 K uptake in each layer determined by soil analysis, and curves calculated by equation 2.viii. Numbers on the curves are $\overline{\alpha a}$ cm^2/sec

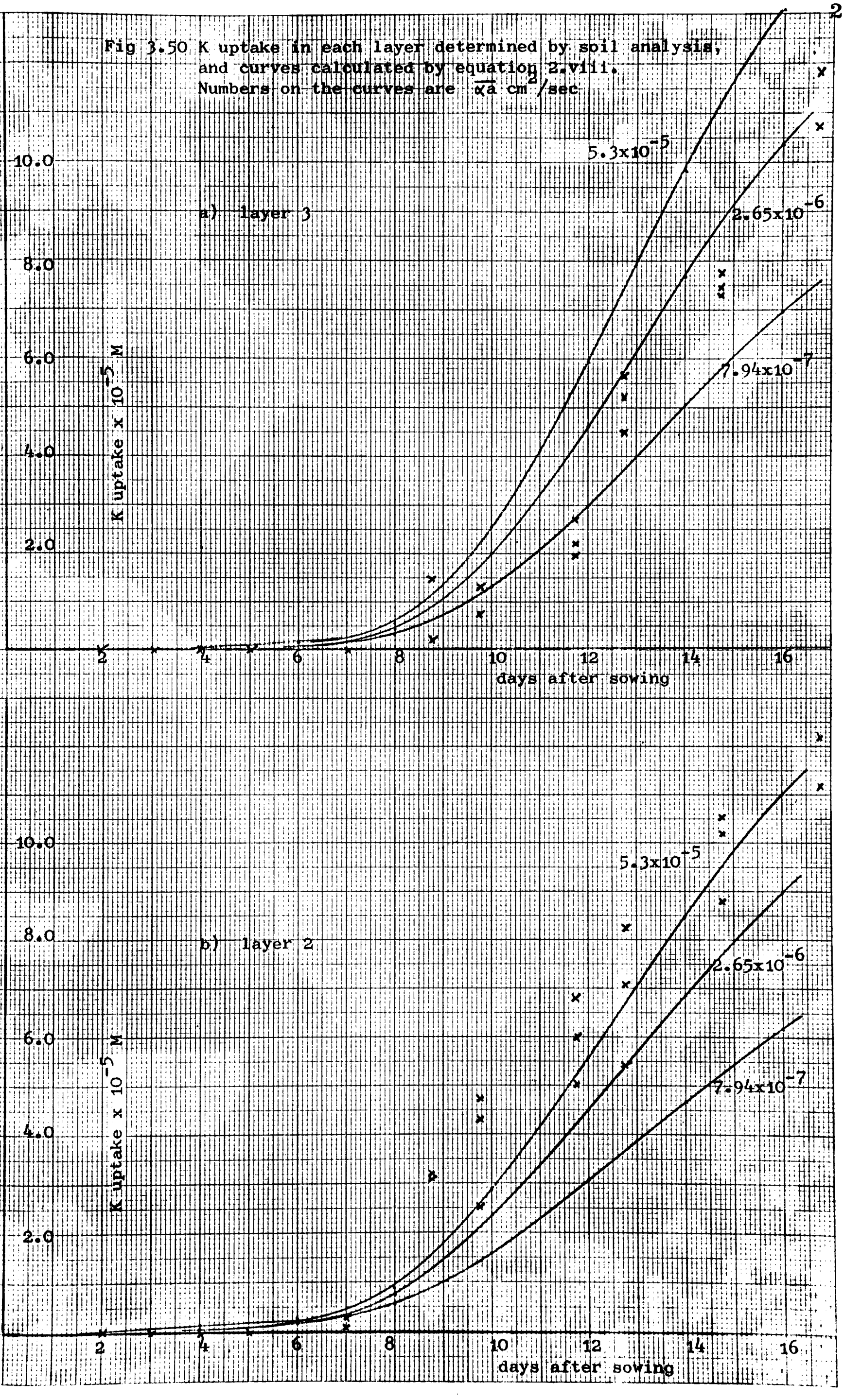
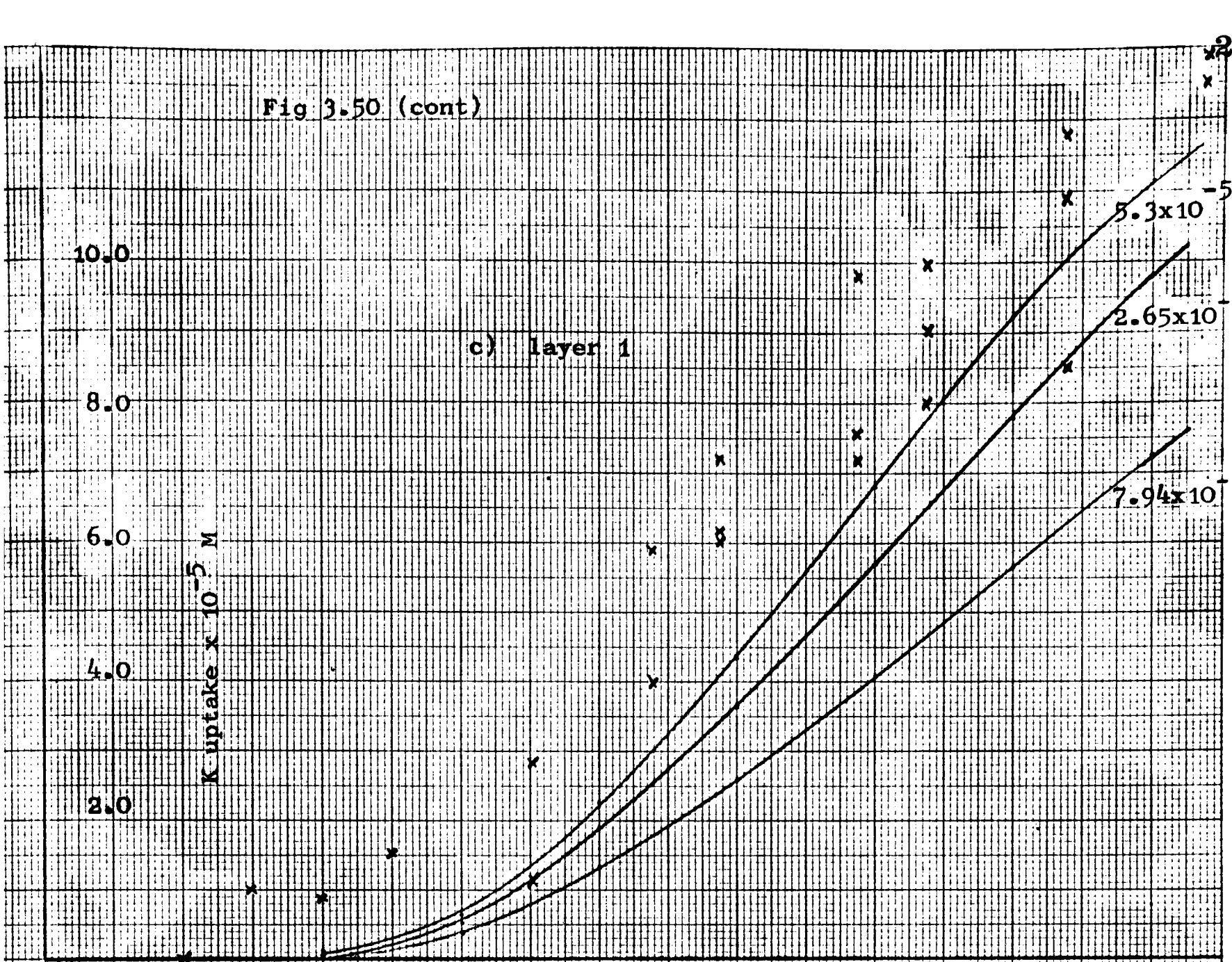


Fig 3.50 (cont)

c) layer 1



d) layer 4

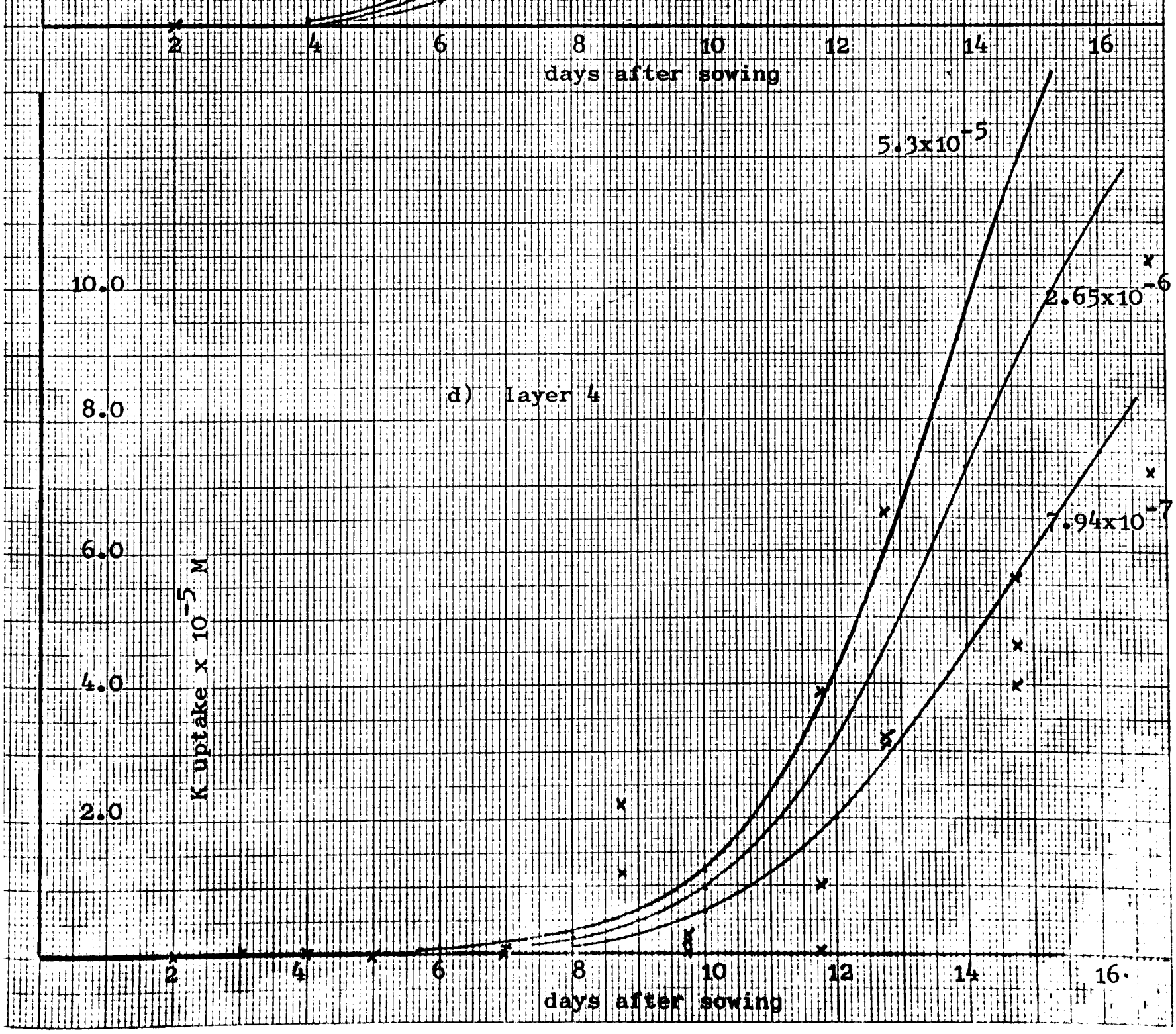


Fig 3.51 Whole plant uptake of potassium (Expt 3)

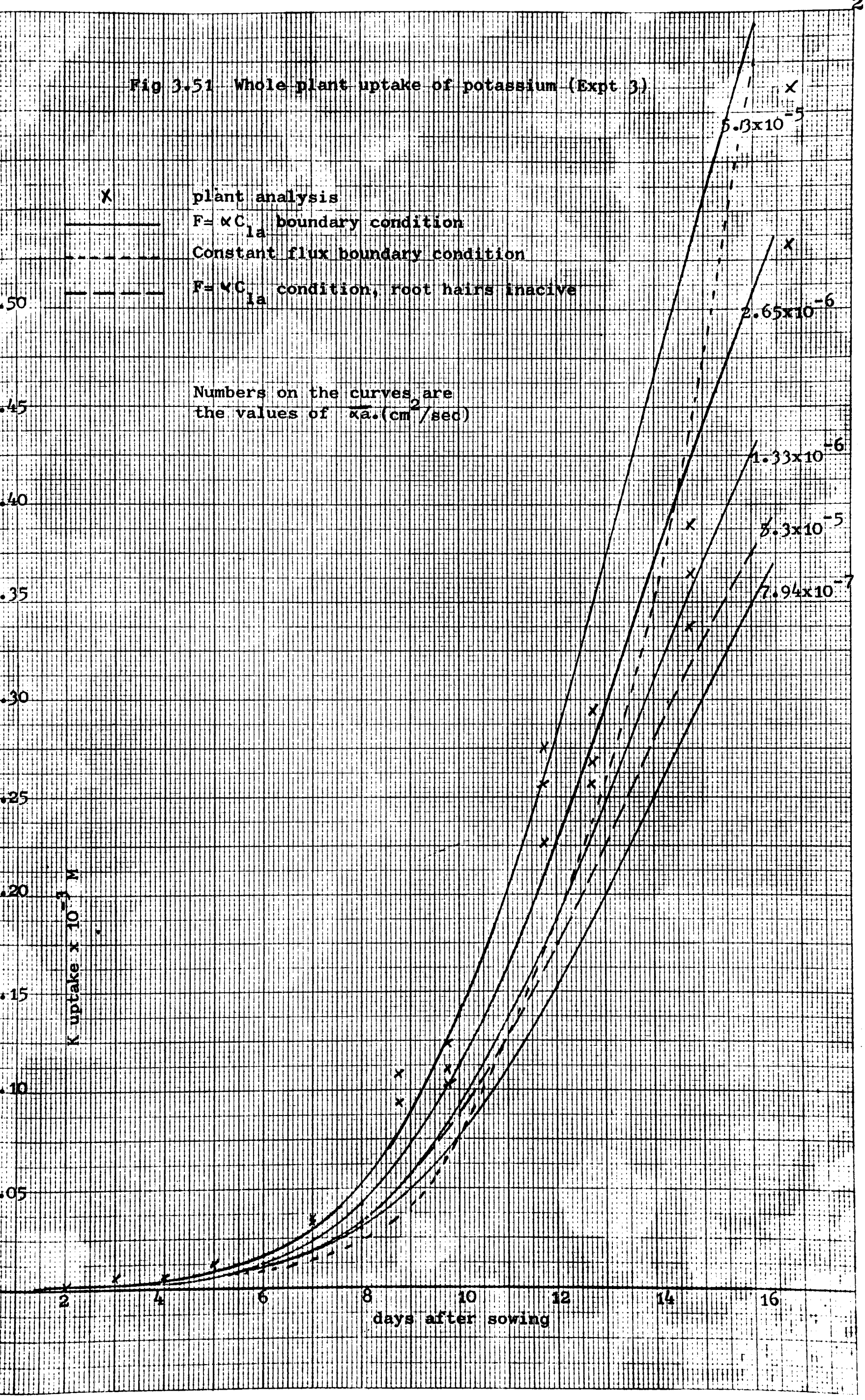


Table 3.14

Average Nitrate concentration ratio, $C_{1a}/\overline{C_1}$, for values of the root demand coefficient used to calculate N uptake

$\overline{\alpha a}$ cm^2/sec	$\frac{\overline{C_{1a}}}{\overline{C_1}}$
$.53 \times 10^{-7}$	.91
1.06×10^{-7}	.85
2.12×10^{-7}	.73
4.24×10^{-7}	.60

Table 3.15

Average potassium concentration ratio, $C_{1a}/\overline{C_1}$, for values of the root demand coefficient used to calculate K uptake

$\overline{\alpha a}$	$\frac{\overline{C_{1a}}}{\overline{C_1}}$
$.79 \times 10^{-6}$	.45
1.3×10^{-6}	.35
2.6×10^{-6}	.20
53×10^{-6}	.012

Chapter 4

Conclusions

Methods of assaying nutrient availability must be incomplete unless there is consideration of the plant's role as the nutrient absorber. The influence of the soil on the mobility of a nutrient, and the length and distribution of the roots needs to be related to the plant demand.

In this work, the effects of the pattern, density, radius and demand coefficient of roots on their efficiency as absorbers of the major plant nutrients, in a range of soil conditions, were considered. A model was developed to calculate the uptake by a root system when nutrient supply is restricted to the physical processes of diffusion and mass flow, and the plant roots are absorbing in a known way. The aim was to investigate whether this, together with previous knowledge, would allow predictions of the uptake of nutrients from soil, if the relevant root and soil properties were given. This may lead to a wider appreciation of the significance of the various factors affecting nutrient availability.

The next step towards an understanding of the nutrient supplying power of a soil would seem to be the inclusion in the model, in a quantitative manner, of the effects of the soil properties on root development. This was beyond the scope of the present work, and appears much more difficult. Root development depends on such diverse properties as soil structure, in particular, the effects of mechanical heterogeneity on a macroscale (Gracoen et al 1968), texture, moisture content, nutrient solution concentration (which seems especially important in the first 2-3 weeks of growth, when the quantitative pattern of root growth is established (May et al 1965), although any heterogeneity in supply e.g. due to a fertiliser granule, has a strong influence on root distribution, particularly the local abundance of laterals, (e.g. Duncan and Ohlrogge 1958)), deficiency or presence of a single nutrient (Viersum 1958), and the presence or absence of other plants (e.g. section 3.5.a.ii.2.C).

However, for many crop species and grasses growing in monoculture, a good indication of their likely and comparative root density can be obtained from published accounts (e.g. Weaver 1926, Weaver and Bruner 1927, Kutschera 1960). As an example, rape plants will usually have a much denser rooting system than onions. If the structure and texture of the soil do not create a good rooting environment, root density is usually below optimum, and the individual roots are often clumped (e.g. in soil cracks). Some progress may be possible if we can assume all root systems will react similarly to unfavourable soil conditions, but this takes no account of different adaptive qualities of plants.

The object of the present study was to investigate whether the nutrient supply to a root system could be calculated from soil properties and a simple relation expressing plant demand, if its development was known. For a discussion of any steps made towards this goal, we return to and consider the items in the plan outlined in 1.8.

An electrical analogue of the soil-root system, which can simulate solute diffusion to groups of absorbing roots, formed the basis of the first model of nutrient flow within multiple root systems. Using the analogue, and assuming plant roots absorbed at a rate proportional to their external solution concentration, the effects of root demand coefficient, α, rooting density and pattern, and root radius on the time course of uptake of solutes of varying degrees of mobility were investigated, and quantitative interrelations established.

All the conclusions which were drawn from work with the analogue are subject to boundary condition $F = \alpha C_{la}$ obtaining at the root surface. There was no way of testing the usefulness of this as a working hypothesis until a model to describe nutrient flow within a multiple root system was devised. Studies with single roots (see 1.3) suggested that the $F = \alpha C_{la}$

condition holds under some circumstances.

The graphs which were constructed to discover the above mentioned interrelations can be used to calculate diffusive supply of solute to a developing root system absorbing at a rate proportional to C_{la}. Mass flow may be included by adding an 'apparent' mass flow contribution, defined by Brewster and Tinker (1970), to the diffusive flux.

The electrical analogue of diffusion to roots illustrated, in a general way, the importance to plant uptake of individual soil and plant properties. However, it is tedious to perform exact simulations of increasing root densities, and a more versatile, but less accurate, representation of the root-soil system was developed. This assumes that the form of the concentration distance profile in a multiple root system approximates to one in a steady state. The model computes uptake in small time steps. This allows considerable flexibility. In each step a steady state condition exists which is defined by the average concentration of solute in the soil block, the rate of uptake of solute into the plant, and the root density. Any time variable property which affects the soil uniformly can be included, and any function relating plant uptake rate to loss from the soil can be investigated.

The model was tested for a) nutrient supply by diffusion and mass flow to a regular array of roots of constant density, and b) nutrient supply by diffusion alone to a randomly dispersed developing root density. In both cases uptake was calculated satisfactorily. We may conclude that diffusive and convective flow of solutes to randomly dispersed sinks, whose density may be changing, is described sufficiently accurately for interpretations of the behaviour of plant roots in soil. There seems to be unlimited scope for investigating the boundary conditions that operate when roots grow in soil, and using appropriate boundary conditions to predict the consequences of a wide variety of environmental conditions.

The model can be generally useful only if the underlying assumptions are sound. The more important ones are listed below:

1. Simple diffusion theory applies in the vicinity of plant roots.

This is a reasonable assumption for N and K where the diffusion distances are usually much greater than the width of the region strongly influenced by the presence of living plant roots. In addition, it seems unlikely that root exudates will affect the solution concentration of K or N directly, although the concomitant microbial activity may. Accumulations or depletions of the divalent cations or nitrate around roots will not usually affect the K buffer power significantly (K solution concentration varies as the square root of solution concentration of the divalent cations).

For P, the assumption is more open to question as i) the radius of the diffusion zones is often of the order of that of the rhizosphere, and b) roots exude organic anions, e.g. citrate, which may affect P solubility by ion exchange, and sugars, which may be active in the chelation of Fe or Al. There is little convincing evidence of the participation of exudates in P nutrition. Sanders and Tinker (1971) reported that non-mycorrhizal onion roots were absorbing exactly as much P as the soil could supply according to diffusion theory, which seems an unlikely coincidence if other mechanisms were operative to increase the P supply. However, there is some evidence (Brewster, pers comm) that roots with root hairs can absorb more than the soil can theoretically supply (but note that the contribution to uptake from the root hair zone is very sensitive to the solution concentration at the root surface, which is difficult to determine when the buffer power is high), and the P story is by no means complete.

There is some evidence that transport in fungal hyphae may represent a third mechanism of nutrient flow to roots. For example, Sanders and

Tinker (1971) have suggested that external mycelium of endotrophic fungi can increase the P supply to roots. Many species are naturally mycorrhizal in the field (Harley 1969), and the influence of these fungal hyphae on the supply of other nutrients is a problem urgently requiring attention, (see section 3.9.A.i.1.2.a.).

2. The diffusion coefficient is constant in space. For many ions in soil, $D = D_l \theta f_l \frac{dC_l}{dC}$, and we can use this equation to consider the possible changes in D which may occur around roots.

The problem of decreases in θ, and also f_l, due to water uptake was discussed in section 3.9.A.i.1.1e. It was concluded, from Gardner's (1960) calculations, that gradients in water potential were unlikely in soils below 5 bars suction. Since D for nitrate $= D_l f_l$, spatial variation in D seems unlikely. For K and P, the term $\frac{dC_l}{dC}$ must be considered, and if the desorption isotherm is non linear, D will vary accordingly within the depletion zone. Brewster (1971) compared the diffusive flux when D varied with concentration, and therefore position, with that obtained when a constant, average D was used. He reported that averaging gave results within 10% of the exact ones. In many circumstances, an assumption of constant D for N, P and K will not introduce any significant error when the flux is to roots without root hairs. The presence of root hairs complicates the issue only when there is a significant contribution from within the root hair zone. This is likely to be the case for P, but not N or K.

3. Solute flux is at all times radial. This is reasonable in a plant root system where there is a long length of root for each tip.

4. There is no release of solute from non-exchangeable sources. Any such release will cause no difficulty if it is uniform throughout the soil, and the rate is known. If release is a function of the degree of

depletion, it cannot be treated easily. It is likely that microbial release of N is not a function of the local nitrate concentration. Such a simplifying assumption may be misleading for K, although the rate of release may be slow on the time scale of the diffusion process.

There appeared to be no serious theoretical limitations which might detract from the success of the model in an ideal soil environment.

Experiments were carried out in laboratory conditions to test the usefulness of the model and gain insight into the boundary conditions operating when plant roots deplete soil. Conclusions on the effects of $\overline{\alpha}$ a, root density and root pattern would hardly be acceptable if the model were unable to sensibly calculate plant uptake in carefully controlled conditions.

Experimental data on root system morphology are difficult and laborious to gather, and an indirect method for measuring root length per unit volume and rooting pattern was devised. The method was used successfully in the laboratory, and a small field trial yielded very encouraging results. The method may be of most value in the field, where data on the rooting habits of individual plants or species within a community are desired. The technique enables the interrelations of two plant root systems to be followed, and inferences can be drawn from the data on possible mechanisms of inter-plant competition. A qualitative demonstration of the competitive advantage of a high root density was given. For two plants of a similar rooting density, the results obtained with the method suggested that the root distribution of each plant was modified by bulk nutrient gradients in the profile, probably of nitrate (if the total quantity of an unbuffered nutrient is insufficient to support the demand of both plants, there may be an effect on root growth before the density is high enough for interroot competition to reduce the uptake rate of a buffered ion e.g.K).

This technique, together with others developed elsewhere (Racz et al. 1964, Russell and Ellis 1967, Newman 1966, the automatic transect method in 3.5.D.b) should have brought to a close the era when biologists could ignore root systems because of their inaccessibility. I am inclined to the view of Brewster and Tinker (1972), who wrote "Future work (on plant nutrient uptake from soil or solutions) which omits root dimension data can only be regarded as incomplete."

The new method and the transect method were used in experiments designed so that they may be simulated with a theoretical model of the nutrient depletion which follows plant uptake. The experiments illustrated the difficulties of obtaining all the data which are required for adequate testing of the model. An important conclusion from the first experiment was that precise measurements of root length throughout a complete growth period are essential before any confidence can be placed on theoretical calculations. The significance of root length increases as the concentration in solution at the root surface decreases below that in the bulk; when $C_{1s}/\bar{C}_1$ is $<.1$, as may be the case for P and K, total nutrient uptake rate is limited by the length of root.

The conclusions from experiment 1 on the mechanism of nutrient supply were not unequivocal, as endotrophic fungi may have infected the plants. This was suggested by the fact that the observed P inflow was 7 times greater than probable if supply to roots had been by physico-chemical processes only.

In the presence or absence of mycorrhiza, there would have been little build up or depletion of NO_3, Ca, Mg or Na at the root surface.

The K story was interesting; if mycorrhizal hyphae had no effect on K supply, the observed inflow could have been explained assuming all roots were absorbing at the maximum rate, with $\bar{\alpha}$a values typical of those

reported in solution culture. If, on the other hand, mycorrhiza were transporting K to the plant, they did not increase the uptake over that which could have been supplied in their absence. This is especially significant in view of the fact that plant growth rate appeared to be limited by K deficiency. Any mycorrhiza would seem to have little effect on K inflow.

Although not definitely established that mycorrhizas increased P but not K inflow, the results may be sufficiently convincing to stimulate further work on this topic. It raises questions on the uptake processes into fungal hyphae, and the mechanisms involved in the transfer of nutrients from fungi to host.

The third experiment offered more reliable data on the behaviour of plant nutrients in soil, and a computer model of the soil-root system was used to aid the interpretation of the plant uptake of N and K.

The simple physical model of diffusion and mass flow accounted for the time course of uptake of both N and K when it was assumed that roots were absorbing at a rate proportional to C_{la}, with αa equal to 2×10^{-7} cm^2/sec and $> 2.5\times10^{-6}$ cm^2/sec respectively. The calculated and observed uptake with time relations were similar, which is good evidence that the model is useful for describing plant uptake. An alternative boundary condition, which assumes a constant flux at the root surface, gave a less satisfactory prediction of uptake.

If the relation between nutrient depletion and plant uptake was simulated by the computer model, the uptake rate of both N and K was seriously reduced by interroot competition. This factor establishes the advantages offered by the more complex treatment given here, over Brewster and Tinker's (1970) model for calculating uptake by whole plant root systems.

Note that it is not possible to check each assumption in the model

independently, as the variables cannot be isolated. This is an obvious limitation to the approach, but some value remains if we can correctly determine plant uptake. If the model is consistently successful, we may be led to believe that it is offering a reasonable description of the actual process.

The results from the third experiment indicate that useful progress can be made toward understanding the interrelations between roots and soil by assuming plant roots absorb at a rate proportional to their external nutrient solution concentration. We can take some steps in this direction by considering the results obtained from the electrical analogue.

The following deductions were made by varying the input parameters on the analogue:

1. For any set of circumstances, the lower the root demand coefficient, the slower the rate of uptake, and the less the reduction in uptake rate due to competition between roots.

2. The solute supplied by diffusion to a root system of any absorbing strength, expressed as a fraction of the total labile pool, is roughly determined by the product of the diffusion coefficient of the solute in the soil, the root density and the absorption time, the three terms being approximately inversely related, and the rooting pattern.

3. There are relatively small differences between the uptake rate of random and regular patterns.

4. The effect of root pattern on the uptake by any root system depends on the product $Dt\rho$, being greatest at intermediate values where uptake may be reduced by a factor of 5. At low values, either D, t or ρ is so low that the uptake rate per root is already very much reduced by the time there is significant overlap of depletion zones. At high values, either D, t or ρ is sufficiently high that all the available

nutrient is supplied to the most inefficiently dispersed root system. The actual value of high, intermediate and low depends, essentially, on the root demand coefficient and the rooting pattern.

These ideas may be translated into qualitative concepts of nutrient mobility; if $Dt\rho$ is low, the nutrient is immobile, if it is high, the nutrient is mobile. Since D for N, P and K is usually in the ratio 100:1:10, $Dt\rho$ for the three ions is widely separated; the scale of interest is usually in the range $Dt\rho$ = 0-4. As an example of why P is often regarded as immobile in this context, the value of $Dt\rho$ for a root density of 10 cm/cm^3 absorbing for 10^6 sec is approximately 0.1; for nitrate it would be 10. Potassium will most frequently fall in the 'intermediate' range of $Dt\rho$.

Can we say anything more in the light of the present study about the availability of nutrients in soil? It certainly should be clear that no estimate of the availability can be satisfactory unless account is taken of the soil as a rooting environment, the plant's root system as an absorber of nutrients, and the plant demand for the particular nutrient.

Experiment 3 demonstrated the importance of quantity, mobility and root length in the uptake of N and K - the potentially deficient N level in the soil was more than adequate in the early stages of growth, and became limiting only when the total quantity was depleted, whereas K supply was maximal throughout, and if D had been lower, uptake would have been restricted in all stages of growth.

The graphs prepared from the analogue enable the importance of any soil or plant property to be assessed in any particular context. If $\alpha a/Db$ is > 10 or < 0.1, equations 2.xv and 2.xviii are a fairly exact statement of the interrelations of quantity, intensity, buffer power, nutrient mobility and root density. In more specific terms,

equations 2.xvi and 2.xix may be applicable to K and NO_3 respectively, when supply is by diffusion. If we accept that α a/Db for K will in soil often be high, we can see how the K absorbing power of a root system is limited by the length of root; the contrasting performances of different crops on the same soil may well be explicable in terms of different root system morphology.

It is not always desirable to have a high root density; Passioura (priv. comm.) has shown that a low root density in the early part of a season may be vital to the success of cereals in Australia - plants with dense root systems quickly use the available water, and then suffer drought conditions at earing. This point illustrates that a study of nutrient flow in soil can tell only part of the story of plant behaviour in soils.

If we consider communities instead of monocultures, the model suggests the competitive advantages of root systems of the greatest density which are transpiring at the highest rate. A mycorrhizal association may compensate for a low root density. However, there are two essential differences between inter- and intra-root system competition:

i. when two root systems are growing together, the outcome of the competition at any one point in time influences the competitive ability of the plant at the next point in time, i.e. a successful plant gets bigger and so becomes more successful - plants are not unlike capitalists.

ii. there may be intra-root system competition, manifest in a restriction of the soil volume available for exploitation, in addition to the interroot competition due to overlap of depletion zones.

The consequence of a limitation in soil volume is a decrease in quantity of total nutrient for supplying the plant. This decrease is more significant for the mobile than immobile nutrients, and competition is

most likely to be for nitrate or water. If the total root length is decreased, P and K supply will also be reduced.

There have been several qualitative demonstrations of inter-root system competition. For example, Donald (1958) and Aspinall (1960) concluded that a more rapid root development and consequent prior occupation of soil was the major factor determining the successful plant out of a mixture of two. Harris (1967) reported that the earlier root development by Bromus tectorum (cheat grass), which was a result of root growth at a lower temperature, and the consequent capture of soil water supplies, led to its success and domination over Agropyron spicatum (blue bunch wheatgrass). King (1971) illustrated the importance of time of germination, when he manipulated the succession in an association by varying the relative sowing dates.

Root systems of similar vigour and potential influence each other's spatial distribution also. This follows the observation that roots from rows of a single species often do not interpenetrate. Radke and Burrows (1970), for example, noted the absence of root interpenetration between two adjacent rows of soybean or corn; when corn and soybean were grown contiguously, there was interpenetration and the soybean suffered as a result. Similar observations have been reported between the root systems of cotton (Basset et al. 1970), and some trees (Rogers and Head 1968).

A quantitative interpretation of competition in multiroot systems is logically the next step in nutrient flow analysis. If the root density of each species is given, there should be little difficulty in extending the model in 2.15. If the root development is not given, we shall have to predict the effects of 1 root system on the rate of development and subsequent spatial distribution of the other. This is a difficult one; an additional complication to those mentioned at the beginning of this

chapter is introduced. It seems that any effects will stem from organic exudates (with the accompanying microbial activity), the solution concentration of nutrient in the soil, or the life forces in the individual plants. This remains to be seen.

APPENDIX 1

Computer programme of equation 2.viii

```
 20 COMPUTING 45 SECONDS
 30 STORE 80/130 BLOCKS
 40 INPUT 1 TABLE
 50 OUTPUT 0 FILE JUMBO
 60 OUTPUT 1 FILE RESULT
 70 USE HARTRAN
 80 *FORTRAN
 90 C        UPTAKE FROM VOLUME WITH CONSTANT ROOT LENGTH,STEADY STATE
100 C       DIFFUSION AND MASS FLOW
110        REAL L,LL,LLL
120        INTEGER Q
130        DIMENSION T(100),L(100),DELC(100),TUPT(100),FU(100),
140       1CL(100),VL(100),FL(100),VEL(5),B(100),G(100)
150        READ (1,1000) ALPHA,DL,VL(1),FL(1),R,Z,DELT
160  1000  FORMAT (7E10.2)
161        READ (1,1001) X,VEL(1),VEL(2),VEL(3),VEL(4),VEL(5),CL(1)
162  1001  FORMAT (7E10.2)
170        WRITE (1,2000) ALPHA,DL,VL(1),FL(1),R,Z,DELT,X
180  2000  FORMAT (50H      ALPHA          DL          VL          FL          R
190       130H           Z        DELT          X/8E10.2)
200 C        STARTING CONDITIONS
201        DO 200 N=1,5
202        WRITE (1,6000) VEL(N)
203  6000  FORMAT (4HVEL=,E10.2)
210        T(1)=0
215        FU(1)=0
220        DELC(1)=0
230        TUPT(1)=0
235        V=3.142*(X**2-R**2)
236        L(1)=1./V
238        TOTUPT=V*VL(1)*CL(1)
240 C        SET TIME STEPS
245        Y=X/R
250        DO 10 I=2,100
260        T(I)=T(I-1)+DELT
265        VL(I)=VL(1)-2.*3.142*R*VEL(N)*T(I)/V
266
267        FL(I)=VL(I)
270     10 CONTINUE
280 C        READ L
290        B(1)=R*ALPHA/(DL*VL(1)*FL(1))
300        G(1)=R*VEL(N)/(DL*VL(1)*FL(1))
540 C        READ CL,CALC UPT,UPDATE TUPT,CALC DELC
550        DO 110 I=2,100
555        B(I)=R*ALPHA/(DL*VL(I)*FL(I))
560        L(I)=1./V
565        G(I)=R*VEL(N)/(DL*VL(I)*FL(I))
570        IF (VL(I)-.1) 110,110,150
580    150 IF (G(I)) 120,120,160
590    160 UPT=2.*3.142*ALPHA*R*Z*L(I)*V*CL(I-1)*(T(I)-T(I-1))/
595       1(B(I)/(G(I))+(1.-B(I)/G(I))*(2./(2.-G(I)))*((Y**(2.-G(I))
605       1-1.)/(Y**2-1.)))
610        GO TO 20
615    120 UPT=2.*3.142*ALPHA*R*Z*L(I)*V*CL(I-1)*(T(I)-T(I-1))/
620       1(1.+B(I)*((Y*.Y* LOG(Y)/(Y*Y-1.))-.5))
```

```
660      20  TUPT(I)=TUPT(I-1) +UPT
665          FU(I)=TUPT(I)/TOTUPT
670          DELC(I)=TUPT(I)/V
675          CL(I)=(CL(I)*VL(I)-DELC(I))/VL(I)
680     110  CONTINUE
690          WRITE (1,5000) (T(I),L(I),CL(I),TUPT(I),DELC(I),VL(I),
695         1FU(I),I=1,91,10)
700    5000  FORMAT (/50H     T(SEC) L(CM)E-2 CL(MOL/ML)  TUPT(M) DELC(M/ML)
710         120H      VL        FU      ,/(7E10.2))
715     200  CONTINUE
728          STOP
730          END
740  *ENTER
```

APPENDIX 2

Computer programme of Nye and Marriott's (1969) solution for the distribution of solutes around roots in a finite soil volume.

(Programme written by P.H.Nye)

```
 5 *FORTRAN
10 C       DIFFUSION WITH REACTION, VARIABLE D, ALPHA, WATER LIMITED
30        DIMENSION CL(101,152),T(101),G(101),R(152),TUPT(101),UPRT(101),
40
50       1E(152),F(152),A(152),B(152),C(152),D(152),VL(101),FL(101),Z(101),
55       1RV(5,152)
60        INTEGER S,P
70        READ (1,1000) ALPHA,CL(1,1),DELT,DELR,DL,VL(1),FL(1)
80  1000  FORMAT (E8.2,E8.2,F8.2,F8.4,E8.2,F8.4,F8.4)
90        READ (1,1100) S,N,K
100 1100  FORMAT (3I8)
110       WRITE (1,2000) ALPHA,CL(1,1),DELT,DELR,DL,VL(1),FL(1),S,N,K
120 2000  FORMAT (40H      ALPHA    CL(1,1)       DELT        DELR/
130      1E10.2,E10.2,F10.4,F10.4,/
140      140H          DL       VL(1)       FL(1)          S,
150      120H           N             K,/
160      1E10.2,F10.4,F10.4,3I10)
170 C       STARTING CONDITIONS
180       T(1)=0
190       DO 10 M=2,S+N+1
200       CL(1,M)=CL(1,1)
210    10 CONTINUE
220 C       SET TIME STEP
230       G(1)=.5*DELT
235       DO 20 I=2,10
240       G(I)=2.*G(I-1)
250       T(I)=T(I-1)+G(I)
260    20 CONTINUE
270       G(11)=489*DELT
280       T(11)=T(10)+G(11)
350       DO 36 I=12,K
360       G(I)=1000.*DELT
370       T(I)=T(I-1)+G(I)
380    36 CONTINUE
390 C       SET DISTANCE STEP
400       H=DELR
410       DO 80 M=1,S+N+1
420       R(M)=FLOAT(M)*H
430    80 CONTINUE
431       RV(1,S)=5.E-7*R(S)
432       RV(2,S)=1.E-6*R(S)
433       RV(3,S)=2.5E-6*R(S)
434       RV(4,S)=5.E-6*R(S)
440 C       START ITERATION
441       DO 25 P=1,4
442       WRITE (1,4000) RV(P,S)
443  4000 FORMAT (/10HRAD X VEL=,E10.4)
450       DO 40 I=2,K
451       VL(I)=VL(1)-2.*RV(P,S)*T(I)/(R(S+N)**2-R(S)**2)
452       FL(I)=VL(I)
455       IF (VL(I)-.1) 45,45,90
460    90 BP=VL(I)
470       GCL=ALPHA*CL(I-1,S)
480       DGCL=ALPHA
```

```
      FCL=0.
      DFCL=0.
      Z(I)=DL*VL(I)*FL(I)
      XM=-2.*Z(I)/(H**2)
      XL=(-Z(I)/FLOAT(2*S)+Z(I)-RV(P,S)/FLOAT(2*S))/(H**2)

      Y=-XM-XL*(-(2.*H/Z(I))*(DGCL-RV(P,S)/R(S)))+2.*BP/G(I)-DFCL
      E(S)=(2.*Z(I)/H**2)/Y
      F(S)=((2.*Z(I)/H**2.)/Y)*CL(I-1,S+1)+((XM+XL*2.*H*RV(P,S)/(Z(I)*
     1R(S))
     1+XL*2.*H*DGCL/Z(I)+2.*BP/G(I)-DFCL)/Y)*CL(I-1,S)
     1+(-(2.*H/Z(I))*GCL*XL+2.*FCL-(2.*H/Z(I))*GCL*XL)/Y
      DO 50 M=S+1,S+N
      FCL=0.
      DFCL=0.
      Z(I)=DL*VL(I)*FL(I)
      RV(P,M)=RV(P,S)*(R(S+N)**2-R(M)**2)/(R(S+N)**2-R(S)**2)
      XU=(Z(I)/FLOAT(2*M)+Z(I)+RV(P,M)/FLOAT(2*M))/(H**2)
      XM=-2.*Z(I)/(H**2)
      XL=(-Z(I)/FLOAT(2*M)+Z(I)-RV(P,M)/FLOAT(2*M))/(H**2)
      A(M)=XU
      B(M)=-XM-DFCL+2.*BP/G(I)
      C(M)=XL
      D(M)=XU*CL(I-1,M+1)+(XM-DFCL+2.*BP/G(I))*CL(I-1,M)+XL*CL(I-1,M-1)
     1+2.*FCL
      E(M)=A(M)/(B(M)-C(M)*E(M-1))
      F(M)=(D(M)+C(M)*F(M-1))/(B(M)-C(M)*E(M-1))
   50 CONTINUE
C        ZERO GRADIENT AT BOUNDARY
      CL(I,S+N+1)=F(S+N)/(1.-E(S+N))
      DO 55 L=1,N+1
      M=S+N+1-L
      CL(I,M)=E(M)*CL(I,M+1)+F(M)
   55 CONTINUE
      IF (I-13) 6,6,16
    6 WRITE (1,2300) CL(I,S)
 2300 FORMAT (E12.4)
   16 CONTINUE
   40 CONTINUE
   45 TUPT(1)=0
      DO 91 I=2,K
      UPT=ALPHA*0.5*(CL(I-1,S)+CL(I,S))*6.284*R(S)*G(I)
      TUPT(I)=TUPT(I-1)+UPT
      UPRT(I)=CL(I,S)*ALPHA*6.284*R(S)
   91 CONTINUE
      WRITE (1,3000) (R(M),M=S,S+10,5),(R(M),M=S+20,S+40,10),
     1(T(I),TUPT(I),VL(I),(CL(I,M),M=S,S+10,5),(CL(I,M),
     1M=S+20,S+40,10),I=10,100,10)
 3000 FORMAT (//6F10.4/(/F12.2,23HSEC   TOT UPT (MOL/CM)=,E12.4,
     113HVL=,E12.4,/(6E10.3)))
   25 CONTINUE
      STOP
      END
* ENTER
```

APPENDIX 3

Computer programme of equation 2.xiv

```
20 COMPUTING 45 SECONDS
30 STORE 80/130 BLOCKS
40 INPUT 1 TABLE
50 OUTPUT 0 FILE JUMBO
60 OUTPUT 1 FILE RESULT
70 USE HARTRAN
80 *FORTRAN
90 C        UPTAKE FROM VOLUME WITH CONSTANT ROOT LENGTH,STEADY STATE
100 C       DIFFUSION AND MASS FLOW
110        REAL L,LL,LLL
120        INTEGER Q
130        DIMENSION T(100),L(100),DELC(100),TUPT(100),FU(100),
140       1CL(100),VL(100),FL(100),VEL(5)
150        READ (1,1000) ALPHA,DL,VL(1),FL(1),R,Z,DELT
160  1000  FORMAT (7E10.2)
161        READ (1,1001) X,VEL(1),VEL(2),VEL(3),VEL(4),VEL(5),CL(1)
162  1001  FORMAT (7E10.2)
170        WRITE (1,2000) ALPHA,DL,VL(1),FL(1),R,Z,DELT,X
180  2000  FORMAT (50H      ALPHA          DL           VL           FL          R
190       130H           Z        DELT          X/8E10.2)
200 C       STARTING CONDITIONS
201        DO 200 N=1,5
202        WRITE (1,6000) VEL(N)
203  6000  FORMAT (4HVEL=,E10.2)
210        T(1)=0
215        FU(1)=0
220        DELC(1)=0
230        TUPT(1)=0
235        V=3.142*(X**2-R**2)
236        L(1)=1./V
238        TOTUPT=V*VL(1)*CL(1)
240 C        SET TIME STEPS
245        G=R/X
250        DO 10 I=2,100
260        T(I)=T(I-1)+DELT
265        VL(I)=VL(1)-2.*3.142*R*VEL(N)*T(I)/V
266
267        FL(I)=VL(I)
270     10 CONTINUE
280 C        READ L
540 C        READ CL,CALC UPT,UPDATE TUPT,CALC DELC
550        DO 110 I=2,100
560        L(I)=1./V
570        IF (VL(I)-.1) 110,110,160
590    160 UPT=2.*3.142*ALPHA*R*Z*L(I)*V*CL(I-1)*(T(I)-T(I-1))*
600       1(1.+VEL(N)*R/(DL*VL(I)*FL(I))*((LOG(1./G)/(1.-G**2))-.5))/
610       1(1.+ALPHA*R/(DL*VL(I)*FL(I))*((LOG(1./G)/(1.-G**2))-.5))
660        TUPT(I)=TUPT(I-1) +UPT
665        FU(I)=TUPT(I)/TOTUPT
670        DELC(I)=TUPT(I)/V
675        CL(I)=(CL(1)*VL(1)-DELC(I))/VL(I)
680    110 CONTINUE
690        WRITE (1,5000) (T(I),L(I),CL(I),TUPT(I),DELC(I),VL(I),
695       1FU(I),I=1,91,10)
700  5000  FORMAT (/50H    T(SEC) L(CM)E-2 CL(MOL/ML)  TUPT(M) DELC(M/ML)
```

```
710        120H      VL        FU      ,/(7E10.2))
715    200 CONTINUE
728         STOP
730         END
740 *ENTER
```

APPENDIX 4

Computer programme of equation 2.viii, for NO_3 uptake by a developing root system (with root hairs).

```
 20 COMPUTING 10 SECONDS
 30 STORE 80/160 BLOCKS
 40 INPUT 1 FANCY1
 50 OUTPUT 0 FILE MUMBO1
 60 OUTPUT 1 FILE FACT1
 70 USE HARTRAN
 80 *FORTRAN
 90 C        UPTAKE FROM VOLUME WITH  ROOT LENGTH CHANGING,  STEADY STATE
100 C       DIFFUSION AND MASS FLOW.  M F REQUIRED. RV/BD NEQ 2
110         REAL L,N,LIM
120         INTEGER Q
130         DIMENSION T(180),L(180),DELC(180),TUPT(180),FU(180),B(180),
140        1CL(180),VL(180),FL(180),ALPHA(4),CLA(180),ALPHAR(180),G(180),
150        1N(180),C(180),CA(180),LIM(180)
160         READ (1,1000) VEL,DL,RA,RH,DELT
170  1000   FORMAT (5E10.2)
180         READ (1,1001) V,ALPHA(1),ALPHA(2),ALPHA(3),ALPHA(4),CL(1)
190  1001   FORMAT (6E10.2)
200         WRITE (1,2000) VEL,DL,RA,RH,DELT,V
210  2000   FORMAT (30H      VEL            DL         RA
220        130H        RH         DELT         V  /6E10.2)
230 C         STARTING CONDITIONS
240         DO 200 M=1,4
250         WRITE (1,6000) ALPHA(M)
260  6000   FORMAT (6HALPHA=,E10.2)
270 C          STARTING CONDITIONS
280         ALPHAR(1)=ALPHA(M)*RA
290         VL(1)=0.285
300         FL(1)=.0198+.3236*VL(1)+2.3208*VL(1)**2
350         CLA(1)=CL(1)
360         C(1)=CL(1)*VL(1)
370         CA(1)=C(1)
380         T(1)=0
390         FU(1)=0
400         DELC(1)=0
410         L(1)=EXP(-6.1094)
420         TUPT(1)=0
430         TOTUPT=V*C(1)
435         LIM(1)=1.
460 C         SET TIME STEPS
470         DO 10 I=2,180
480         T(I)=T(I-1)+DELT
```

```
490
500      10 CONTINUE
510  C          L (LENGTH PER UNIT VOLUME)
520           DO 110 I=2,180
530           IF (T(I).LE.518400.) 25, 35
531      25   IF (T(I).LE.259200.) 71, 72
533      71   L(I)=3./136.5
534           GO TO 37
536      72   L(I)=EXP(-7.01536+1.0403*T(I)/86400.)
537           GO TO 37
560      35   L(I)=EXP(-1.87406+.19086*T(I)/86400.)
570      37   IF (T(I).LE.1036800.) 9, 15
580       9   VL(I)=.277-.0034*T(I)/86400.
590           GO TO 23
600      15   VL(I)=.359-.01025*T(I)/86400.
610      23   FL(I)=.01908+.3236*VL(I)+2.3208*VL(I)**2
650      70   B(I)=RH*ALPHA(M)/(DL*VL(I)*FL(I))
660           G(I)=RH*VEL/(DL*VL(I)*FL(I))
670           CLA(I)=CL(I-1)/(B(I)/G(I)+(1.-B(I)/G(I))*2./(2.-G(I))*
680          1((1./(SQRT(3.142*L(I))*RH))**(2.-G(I))-1.)/
690          1((1./(RH*SQRT(3.142*L(I))))**2-1.))
700           CA(I)=CLA(I)*VL(I)
710           UPT=3.142*.5*(L(I)+L(I-1))*V*(2.*ALPHA(M)*RH*(T(I)-T(I-1))*CLA(I)
720          1+(CA(I-1)-CA(I))*(RH**2-RA**2))
730           TUPT(I)=TUPT(I-1) +UPT
740           FU(I)=TUPT(I)/TOTUPT
750           DELC(I)=UPT/V
755           C(I)=C(I-1)-DELC(I)
759           CL(I)=C(I)/VL(I)
770           ALPHAR(I)=UPT/(3.142*CLA(I)*(L(I)+L(I-1))*V*(T(I)-T(I-1)))
775           LIM(I)=CLA(I)/CL(I-1)
780       110 CONTINUE
790           WRITE (1,5000) (T(I),L(I),CL(I),TUPT(I),ALPHAR(I),LIM(I),
800          1 FU(I),I=1,161,20)
810    5000  FORMAT (/50H     T(SEC)  L(CM)E-2 CL(MOL/ML)   TUPT(M)   ALPHA X R
820          120H    CLA/CL      FU       ,/(7E10.2))
830     200  CONTINUE
840           STOP
850           END
860  *ENTER
870
880
890
900
```

APPENDIX 5

Computer programme of equation 2.viii, for K uptake by a developing root system (with root hairs).

```
20 COMPUTING 10 SECONDS
30 STORE 80/160 BLOCKS
40 INPUT 1 FANCY1
50 OUTPUT 0 FILE MUMBO1
60 OUTPUT 1 FILE FACT1
70 USE HARTRAN
80 *FORTRAN
90 C      UPTAKE FROM VOLUME WITH  ROOT LENGTH CHANGING,  STEADY STATE
100 C      DIFFUSION AND MASS FLOW.  M F REQUIRED. RV/BD NEQ 2
110       REAL L,N,LIM
120       INTEGER Q
130       DIMENSION T(180),L(180),DELC(180),TUPT(180),FU(180),B(180),
140      1CL(180),VL(180),FL(180),ALPHA(4),CLA(180),ALPHAR(180),G(180),
150      1 N(180),C(180),CA(180),LIM(180)
160       READ (1,1000) VEL,DL,RA,RH,DELT
170  1000 FORMAT (5E10.2)
180       READ (1,1001) V,ALPHA(1),ALPHA(2),ALPHA(3),ALPHA(4),CL(1)
190  1001 FORMAT (6E10.2)
200       WRITE (1,2000) VEL,DL,RA,RH,DELT,V
210  2000 FORMAT (30H      VEL              DL          RA
220      130H        RH        DELT         V  /6E10.2)
230 C       STARTING CONDITIONS
240       DO 200 M=1,4
250       WRITE (1,6000) ALPHA(M)
260  6000 FORMAT (6HALPHA=,E10.2)
270 C       STARTING CONDITIONS
280       ALPHAR(1)=ALPHA(M)*RA
290       VL(1)=0.298
300       FL(1)=.0198+.3236*VL(1)+2.3208*VL(1)**2
310       ARO=.193E-3
320       GR=1.665E-2
330       N(1)=7.50E-6
340       CL(1)=ARO*SQRT(.5*N(1))
350       CLA(1)=CL(1)
360       C(1)=CL(1)*(GR/SQRT(.5*N(1))+VL(1))
370       CA(1)=C(1)
380       T(1)=0
400       DELC(1)=0
410       L(1)=EXP(-7.0774)
420       TUPT(1)=0
435       LIM(1)=1.
460 C       SET TIME STEPS
470       DO 10 I=2,180
480       T(I)=T(I-1)+DELT
490
500    10 CONTINUE
```

```
C          L (LENGTH PER UNIT VOLUME)
      DO 110 I=2,180
      IF (T(I).LE.8.75*86400.) 91, 92
   91 IF (T(I).LE.4.8*86400.) 93, 94
   93 IF (T(I).LE.86400.) 95, 96
   95 L(I)=.5/136.5

      GO TO 37
   96 L(I)=5./136.5
      GO TO 37
   94 L(I)= EXP(-6.70282+.71015* T(I)/86400.)
      GO TO 37
   92 L(I)= EXP(-2.4917+.23107* T(I)/86400.)
   37 IF (T(I).LE.1036800.) 9, 15
    9 VL(I)=.3022-.0033* T(I)/86400.
      GO TO 23
   15 VL(I)=.367-.00867* T(I)/86400.
   23 FL(I)=.01908+.3236*VL(I)+2.3208*VL(I)**2
      N(I)=(12.6712-.8441* T(I)/86400.)*1.0E-6
      IF (N(I).GT. N(1)) 6,7
    6 N(I)= N(1)
    7 IF (N(I).LT.0.60E-6) 60,70
   60 N(I)=.60E-6
   70 B(I)=RH*ALPHA(M)/(DL*VL(I)*FL(I))
      G(I)=RH* VEL/(DL*VL(I)*FL(I))
      CLA(I)=CL(I-1)/(B(I)/G(I)+(1.-B(I)/G(I))*2./(2.- G(I))*
     1((1./(SQRT(3.142* L(I))*RH) )**(2.- G(I))-1.)/
     1((1./(RH* SQRT(3.142* L(I))))**2-1.))
      CA(I)=CLA(I)*(GR/SQRT(.5*N(I))+VL(I))
      UPT=3.142*.5*(L(I)+ L(I-1))* V*(2.*ALPHA(M)*RH*(T(I)- T(I-1))*CLA(I)
     1+(CA(I-1)-CA(I))*(RH**2-RA**2))
      TUPT(I)= TUPT(I-1) + UPT
      DELC(I)= UPT/ V
      C(I)=C(I-1)- DELC(I)
      CL(I)=C(I)/(VL(I)+GR/ SQRT(.5* N(I)))
      ALPHAR(I)= UPT/(3.142*CLA(I)*(L(I)+L(I-1))* V*(T(I)- T(I-1)))
      LIM(I)=CLA(I)/CL(I-1)
  110 CONTINUE
      WRITE (1,5000) (T(I),L(I),CL(I),TUPT(I),ALPHAR(I),LIM(I),
     1 N(I),I=1,161,20)
 5000 FORMAT (/50H     T(SEC)  L(CM)E-2 CL(MOL/ML)   TUPT(M)   ALPHA X R
     120H    CLA/CL   N(MOL/ML),/(7E10.2))
  200 CONTINUE
      STOP
      END
* ENTER
```

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