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SOME FACTORS AFFECTING THE UPTAKE OF PLANT NUTRIENTS FROM THE SOIL

A Thesis submitted for the Degree of
Doctor of Philosophy

by

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Oxford,1971.

ABSTRACT

The thesis is primarily concerned with the rate of uptake of nutrients by plant roots in relation to the ability of soil to supply nutrients to roots by diffusion and by mass flow. In Chapter One, some current concepts of the chemistry and availability of plant nutrients in soil are briefly discussed. Particular attention is paid to work that stresses the role of the dynamic processes of diffusion, and the mass flow of dissolved nutrients in the transpiration stream, in supplying nutrients to roots. In Chapter Two, diffusion coefficients of nutrients in soil are discussed. In Chapter Three, the mathematical description of nutrient flow to a root system in soil is discussed. An equation is developed which relates the mean nutrient inflow into a root system to the concentration of nutrients initially present in the soil solution, to the mean concentration of nutrients in the soil solution at the surface of the root system, to the mean rate of flow of water to the roots, to the diffusion coefficient of the nutrient in the soil and to the age of the roots. The mean nutrient inflow into a root system is defined as the mean rate of flow of nutrients into unit length of root.

In Chapter Four, an experiment is described in which all the terms in the above mentioned equation were measured apart from the mean root surface concentration of nutrients. In the experiment, the growth and nutrient uptake of leek plants growing outdoors in a moist, fertilised, silty loam soil was followed. The plants were grown in large pots containing an ample reservoir of soil water, so that watering was unnecessary during growth. The growing period was from early May to mid-July. The nutrient uptake rate was followed by harvesting, and analysing for nutrients, samples of ten plants taken at approximately ten day intervals. Root length was measured at each harvest after washing the roots free from the soil. The pots were weighed every few days to determine the water lost by transpiration. At intervals during the growing period

soil samples were taken from the pots, and the soil solution was extracted and analysed. From separate experiments, diffusion coefficients for nutrients in the soil were calculated. The data from the experiments yielded all the terms in the above mentioned equation except maan root surface concentration which could be calculated. The nutrients considered were N, P, K, Ca, Na, Mg, S and Cl. It was found that mass flow supplied on average more of all nutrients to the roots than/apart they absorbed, from K and P, which were supplied mainly by diffusion. For those nutrients that were found to be supplied by mass flow in excess of uptake, calculations indicated that the resultant mean accumulations at the root surface did not give rise to a solution concentration at the root surface greater than 120% of the initial concentration in the soil. In contrast it was calculated that the root surface concentration of K was less than half its initial level in the soil. P had a concentration dependent diffusion coefficient which meant that the quantity of P diffusing to a root had to be calculated numerically using a computer. The results of such a calculation are given in Chapter Five. It was found that even if the roots acted a zero sink for phosphate, the theoretical mean inflow of phosphate was somewhat less than the observed mean inflow. In Chapter Seven an experimental investigation is described into the accumulation of sulphate at the surface of a root in conditions of high mass flow. Autoradiography using S^{35} was the technique used. In accordance with theory, accumulations became large only when the soil was fairly dry.

One of the difficulties in the mathematical analysis of nutrient flow to roots is the uncertainty about the inherent absorbing power of roots of different ages. In Section Three, experiments are described in which the uptake of short segments of leek root of different ages was measured. The leeks for these experiments were grown in solution culture and the mean inflow into the roots was measured by sampling and analysis as described for the pot experiment in soil. Some plants from solution were then selected and short segments of the roots of different ages were sealed into tubes containing two radioactively labelled nutrients, the rest of the root system being grown in unlabelled nutrient

solution. ^{32}P, and either ^{42}K or ^{85}Sr, ^{85}Sr being taken as a label for Ca, were the labelled nutrients used. The plants were harvested after twenty four hours of exposure to labelled nutrients and the quantity of label absorbed was measured. There were no significant differences in the mean absorption of different aged roots, but different root segments varied very widely in their uptake in a way that could not be connected with their age. The possibility of such variation in absorbing power in roots in soil and its consequences in soil are discussed at the end of Chapter Eleven.

In Chapter Twelve values for the mean inflow of nutrients into roots from a wide range of published experiments are tabulated. The rates are also given as specific absorption rates, this term meaning the rate of flow of nutrient into unit fresh weight of root. Similar values of mean inflow and specific absorption rate have been measured in widely different conditions, ranging from a few minutes uptake from solution to several weeks uptake from soil. Plant factors which affect mean nutrient inflows are discussed and possible future developments along the lines suggested by the experiment in Chapter Four are considered. In the final Chapter the evidence is stated on which is based current theory of nutrient flow to roots by mass flow and diffusion. In conclusion the insight the theory provides into the concept of nutrient availability in soil, into root competition for nutrients and into ideas about root system efficiency is considered.

ACKNOWLEDGEMENTS

The writer would like to thank the following,

1) Dr.P.B.Tinker for supervision and guidance.

2) Mr.P.H.Nye for the computer results in Chapter five.

3) Professor G.E.Blackman for laboratory facilities.

4) Dr.R.S.Russell for facilities at Letcombe Laboratory for the experimental work in Section 3.

5) Dr.D.T.Clarkson for advice and guidance with the experimental work of Section 3.

6) The Ministry of Agriculture, Fisheries and Food for a postgraduate studentship.

7) The numerous colleagues in the Soil Science Laboratory, Oxford, whose comments and discussion have been helpful throughout the work.

IMPORTANT ABBREVIATIONS IN THE TEXT

Abbreviation	Meaning	See Chapter
D.F.S.	Donnan Free Space of plant tissues	8.1.
O.V.	Osmotic Volume of plant tissues	8.1.
W.F.S.	Water Free Space of plant tissues	8.1.
Q/I	The immediate Quantity/Intensity relation of a nutrient in the soil	1.1 and 4.5.b.
P_E	The isotopically exchangeable phosphorus in a soil	4.5.b.2.

The chemical symbols for the different nutrient elements have been used in the text interchangeably with their full names.

TABLE OF SYMBOLS USED IN THE TEXT

Symbol	Meaning	See Equation	See Chapter	Units used
a	Radial distance from the central axis of the root (sometimes also used in text to stand for the activity of an ion in solution)		3.2	cm
α	The root absorbing power of an element of root surface.		3.4	cm/sec.
$\overline{\alpha}$	The mean root absorbing power of a whole root system		3.4	cm/sec.
b	The buffer power of a soil for nutrients		2	dimensionless
C	The concentration of exchangeable nutrient per unit volume of soil		3.2	Mols/cc
C_i	The initial concentration of exchangeable nutrient per unit volume of soil		3,2	Mols/cc
C_R	The concentration of exchangeable nutrient in the soil at the root surface		3.2	Mols/cc
C_L	The concentration of nutrient in the soil solution		3.2	Mols/cc
C_{Li}	The concentration of nutrient initially present in the soil solution.		3.2	Mols/cc
C_{LR}	The concentration of nutrient in the soil solution at the root surface.		3.2	Mols/cc
$\overline{C_{LR}}$	The "mean" concentration of nutrient in the soil solution at the root surface.		3.3	Mols/cc
ΔC_L	$C_{Li} - C_{LR}$		3.2	Mols/cc
$\overline{\Delta C_L}$	$C_{Li} - \overline{C_{LR}}$		3.3 and 3.4	Mols/cc
D	The diffusion coefficient of a nutrient in soil		2	cm^2/sec
D_L	The diffusion coefficient of a nutrient ion in dilute solution at 25°C.		2	$cm^2/sec.$
D'	$D_L V_L f_L$		2	$cm^2/sec.$
f_L	The tortuosity factor for the diffusion of nutrients through soil.		2	dimensionless

Symbol	Meaning	See Equation	See Chapter	Units used
F	The nutrient flux at an element of root surface.		3.3	Mols/cm^2/sec
$\bar{F}$	The mean nutrient flux at the surfaces of a root system	3.X	3.4	Mols/cm^2/sec
g	The cylindrical flux parameter. This describes the time dependency of the diffusive flux into a cylindrical sink.		3.2	dimensionless
G	The average flux parameter for an element of root length		3.3	dimensionless
$\bar{g}$	The mean flux parameter. The "mean" value of g for all the different aged elements of root length in a root system.		3.3 and 4.6.c.	dimensionless
I	The inflow of nutrients into a root. The rate of uptake of nutrient per unit length of root.		3.2	Mols/cm/sec.
$\bar{I}$	The mean inflow into a root system.		3,3	Mols/cm/sec
L	The total root length of a plant.		3.3	cm
M	The rate of nutrient supply per centimetre of root length by apparent mass flow.		3.3	Mols/cm/sec
r	The radius of a root		3.2	cm
$\bar{r}$	The mean radius of the roots in a root system.		3.3	cm
$\overline{SAR}$	The mean Specific Absorption Rate of a root system. The mean rate of uptake of nutrients per gram of root fresh weight.		12.1	Mols/g/sec
t	time			secs.
T	The total quantity of water transpired by a plant		4.9.a.	g
U	The total quantity of nutrients absorbed by a plant			Moles or strictly gram atoms
V	The velocity of water into a root surface		3.2	cm/sec
V_L	The volumetric water content of a soil. The cc of water per cc of soil.		2	dimensionless
W	The total dry weight of a plant			g.
X	The mean proportion by weight of a specified nutrient element in a plant dry matter.		12.2	dimensionless

The above list gives the symbols that recur widely in the thesis. Other symbols, or occasionally some of the above symbols, with a clearly defined but purely local meaning can be found in the text.

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2.I. $$D \simeq D_L v_L f_L \frac{dC_L}{dC} = D' \frac{1}{b}$$

2.II. $$(D) = \frac{D' \Delta C_L}{\Delta C}$$

2.III. $$F_A = D_{LA} \left(\frac{dC_A}{dx} + z_A C_A f \frac{d\psi}{dx} \right)$$

2.IV. $$D_{AB} = D_A D_B \frac{(C_A + C_B)}{(C_A D_A + C_B D_B)}$$

3.I. $$\frac{dC_L}{dt} = \frac{1}{a} \frac{d}{da} \left(aD \frac{dC_L}{da} + \frac{v\ r\ C_L}{b} \right)$$

3.II. $$F = \frac{(C_{Li} - C_{LR})\ D\ g}{r} + v\ C_{Li}$$

3.III. $$F = \frac{(C_i - C_R)\ D\ g}{r} + v\ C_{Li}$$

3.IV. $$I = 2\pi\ r\ F = 2\pi (C_{Li} - C_{LR})\ D' g + 2\pi\ r\ v\ C_{Li}$$

3.V. $$\bar{g} = \frac{\int_0^T 1\ g\ dt}{L}$$

3.VI. $$\bar{g} = \frac{1}{L} \left(\int_0^{t_1} 1\ dt\ G + t_1 \int_{t_1}^{t_2} 1\ dt\ \frac{t_1 \int_{t_1}^{t_2} g\ dt}{t_2 - t_1} + t_2 \int_{t_2}^{t_3} 1\ dt\ \frac{t_2 \int_{t_2}^{t_3} g\ dt}{t_3 - t_2} \ldots \right)$$

3.VII. $$\overline{\Delta C_L} = \frac{\bar{I} - M}{2\pi \bar{r}\ D' \bar{g}} = C_{Li} - \overline{C_{LR}}$$

3.VIII. $$F = \frac{k\ C_{LR}}{1 + \frac{k C_{LR}}{F_{MAX}}} = \alpha r$$

3.IX. $$\bar{F} = \frac{\bar{I}}{2\pi \bar{r}} = \alpha \overline{C_{LR}}$$

3.X. $$\bar{I} = 2\pi D' \bar{g} (C_{Li} - \overline{C_{LR}}) + M = 2\pi \alpha \bar{r} \overline{C_{LR}}$$

EQUATION NUMBER

3.XI. $$r \simeq \frac{1}{L} \int_0^L \alpha r \, dL$$

3.XII. $$\overline{I}_{MAX} = 2\pi \bar{r} \, C_{Li} D' \bar{g} + M$$

3.XIII. $$L_{MIN} = \frac{dU / dt}{\overline{I}_{MAX}}$$

12.I. $$\bar{I} = \frac{dU/dt}{L} = \frac{W}{L} X \left(\frac{1}{W} dW/dt + \frac{1}{X} dX/dt \right) = 2\pi \bar{\alpha} \bar{r} \overline{C_{LR}}$$

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Section One

INTRODUCTORY CHAPTERS

Chapter One

GENERAL INTRODUCTION

1.1 An Introductory Discussion of Certain Aspects of the Chemistry and Availability of Nutrients in Soil

The subject of plant nutrition now ranges from the study of the role of nutrients in cell physiology to the study of the cycling of nutrients through the biosphere. Nutrient uptake from the soil has long been an important, and in some ways, a central area of investigation in this field. A principal objective of soil chemists has been to gain the ability to characterise a soil in the laboratory, and from this to predict both its ability to supply nutrients to crops and the responses to fertilizer of crops in the soil. However, the complexity of the soil/plant system is such that even now, no certain prediction can be made of the ability of the soil to supply nutrients to a crop. Fertilizer application rates are still largely determined by costly empirical field trials on different crops under varying conditions, and using a range of fertilizer levels. The large expenditure on fertilizers has long given economic significance to these studies, whilst today more and more emphasis is also being placed upon aspects of ecological concern. Thus, the need to conserve natural resources and to avoid pollution has led to increased interest in the more efficient use of fertilisers, in order to maximise their utilisation by crops, and minimise their leaching into natural waters.

Plants require C, O, H, N,P,K,S,Ca, Mg, Na, Si, Cl, Fe, Mn, Zn, Cu, Mo and B for growth (Russell,1961, Chapter 3). Of these, N, P and K are widely applied as fertilizers and are frequently termed the macronutrients. Considerable quantities of Ca, Mg, S and Fe are also absorbed byt only relatively trace amounts of the other elements are required.

Nutrients present in different chemical forms in the soil are not all equally available for plant uptake. Soil chemists have devised numerous chemical tests to measure the quantity of available nutrients in soils.(See Hesse,1971).

They have sought to understand soil fertility in terms of the quantities of available nutrients present in different soils (Bray,1945). Nye (1968a) discussed the development of such studies and distinguished a first phase in which numerous different solutions were used to extract the "available" nutrients. The quantities of nutrients extracted were correlated with field trials, in order to calibrate the chemical tests in terms of crop yields. In general, such tests have proved predictive over only a fairly restricted range of circumstances, where similar crops growing in similar climates and in similar soils have been compared (see Hesse, 1971, p.9). Nye (1968a) delineated a second phase in the study of soil fertility, in which the intensity of supply in the soil, and its relation to plant availability were studied. Schofield (1955) wrote, "It is not the amount of available phosphate in a soil that primarily controls the uptake of phosphate by plants, but the work needed to withdraw it from the labile pool". This concept was re-inforced by the extensive plant physiological evidence, that nutrient uptake from dilute solutions was proportional to the concentration in solution (Epstein,1956); but it now seems to be an oversimplification.

Subsequent work has combined the above two approaches and has investigated both the quantity and intensity of available nutrients in soil. The relation between the nutrient intensity in a soil and the quantity present can be expressed by the quantity/intensity, Q/I, curve. (Beckett,1964b). This measures the ability of soils to maintain nutrient intensity against depletion. Mattingley (1965) showed that the early growth of ryegrass in a range of soils was well correlated with the initial phosphate potential of the soils (a measure of phosphate intensity). However, over a longer period, growth correlated with the total quantity of isotopically exchangeable P in the soils. Mattingley's conclusions here indicate that the appropriate measure of nutrient availability depends on the circumstances, and as a generalisation, it is now clear that no one soil chemical test is appropriate to predict plant uptake in all circumstances.

The transfer of nutrients from soils to plants involves a series of processes which interact in a complicated way. Nevertheless, as Nye (1968a) indicated, if we understand the system, and have a quantitative model connecting the different processes involved, we should be able to predict how much nutrient the soil can potentially supply to root systems of specified geometry. The need for this more thorough analysis was emphasised by Nye (1963) when he wrote "the future of soil testing will consist of an endless series of fertilizer trials designed for correlation with an ever increasing number of hit or miss extractions". The only alternative to such a state of affairs must come from a more fundamental understanding of the transfer of nutrients from soils to plants.

Having considered the need for a fuller model of the nutrient uptake process, we must return and consider what the basis of such a model must be. It is now generally accepted that plants absorb their nutrients from the soil solution (Kasenwha, 1971, Lagerwerff, 1960). It follows that only those nutrients that can enter the soil solution are available. Furthermore, the rate of nutrient uptake by roots from dilute solutions increases with the nutrient concentration of the solution. (Epstein, 1956). Consequently, an understanding of how nutrients reach plants requires a clear picture of how nutrients enter the soil solution.

Two types of process release nutrients to the soil solution, firstly the microbial mineralisation of organic solids, and secondly , the purely physical reactions of ion exchange and dissolution. Nitrate forms the bulk of the anions in a typical soil solution (Burd and Martin 1923). Significant quantities of chloride and sulphate were found in Californian soil solutions (Burgess, 1921, Burd and Martin, 1923), but lesser amounts of these ions are to be expected in more humid areas such as Britain, where irrigation is less common and leaching is more intense. Bicarbonate may be present in significant amounts above a pH of about 7 or with high levels of CO_2 in the soil atmosphere (Adams, 1971). However it is a reasonable assumption that in a

typical British agricultural soil, the nitrate level in the soil along with its water content determines the electrolyte concentration of the soil solution. Nitrate remains in the soil solution as such, since it is not adsorbed, it does not precipitate and does not form complex ions(Adams,1971). In nature nitrate is released to the solution by the mineralisation of organic nitrogen (Russell 1961). In agricultural practice, soluble nitrates or ammonium compounds, which are rapidly converted to nitrates by microbial action, may be applied to soils.

To maintain the electroneutrality of the soil solution, anions must be balanced by an equivalent number of cations. Hence the cation concentration of the soil solution is determined by the anion content, which, as we have seen, may often be equated with the nitrate content of the soil. Of the cations, calcium, magnesium and potassium are required in considerable quantities by plants, but typically there are much greater quantities of exchangeable calcium and magnesium in soil than of potassium. The relative quantities of exchangeable Ca, Mg and K are typically about 100:10:1. Hence ,K the cation required in greatest quantity, is normally present in the immediately available form in soil in relatively low amounts.

An equilibrium is rapidly established between exchangeable cations and the soil solution (Malcolm and Kennedy,1969). The equilibrium can be described by the Donnan equations (see Briggs, Hope and Robertson,1960). One consequence of this is the Ratio Law of Schofield (1947) which states that, as the concentration of electrolyte in the solution in equilibrium with a given soil changes, then the concentration of cations in the solution will vary in such a way that the ratio [monovalent ion] : $\sqrt{}$[divalent ion]: $\sqrt[3]{}$[trivalent ion], where the brackets stand for activity, will remain constant. The Ratio Law does not apply to soils with a substantial proportion of anion exchange sites (Schofield 1947) or when a large fraction of the exchangeable nutrients is in solution as opposed to adsorbed on the exchange surfaces. However, Beckett (1964a) showed that the law applied with a Greensand soil

up to a solution concentration of 0.12 g ions/L. of Cl, which is three to ten times the anion concentration of a typical field soil.

The activity ratio $K/\sqrt{Ca + Mg}$ in the soil solution is a useful measure of the K intensity, and is independent of the anion concentration in the soil solution. Schofield (1947) suggested that this would be a good measure of the K availability in a soil. However, soils differ in their ability to maintain their initial K activity ratio in the soil solution whilst K is being removed. Hence, the Q/I graph, (Beckett, 1964b) is a more complete description of a soil's K status. It is the plot of the $K/\sqrt{Ca + Mg}$ activity ratio, or K intensity, I, that is present in solution in equilibrium with Q, a given quantity of K adsorbed or desorbed by the soil. The slope of this plot, $\Delta Q/\Delta I$, measures the amount of K that can be removed before I decreases by a certain amount. $\Delta Q/\Delta I$ has been termed the potential buffering capacity of a soil (Beckett, 1964b).

A knowledge of the chemistry of exchangeable K does not constitute a complete picture of the plant available K. There are slower reactions which can release or remove rapidly exchangeable K. A number of investigations indicate that these reactions tend to maintain the exchangeable K potential of a soil at a characteristic level despite K addition or removal. It appears that K is normally released and fixed by reactions involving the transformation of one type of clay mineral to another. Thus ultimately K in the soil solution will be in equilibrium with a pool of rapidly exchangeable K on the cation exchange surfaces and a pool of slowly exchangeable K in the clay fraction of the soil (see Addiscott and Talibudeen, 1969). Non-exchangeable K can be extracted from soils by exhaustive cropping for several months and it seems likely that non exchangeable K will be released to the exchangeable pool during the course of a growing season.

Phosphate is released to the soil solution by both the mineralisation of organic phosphorus and by the dissolution of the sparingly soluble phos-

phates which occur primarily in the clay fraction of soils either as mineral particles or surface films (Larsen 1967). In slightly acid, neutral and alkaline soils, calcium phosphates exist. Hydroxyapatite is the stable precipitate of calcium phosphate in solutions of pH from about 6 to 14, and this is thought to be the dominant phosphate mineral permanently present in neutral and calcareous soils (Larsen 1967). However, less stable precipitates may form after the addition of phosphate fertilisers, and these may be converted to hydroxyapatite rather slowly so that they may often be present in agricultural soils. In acid soils, the evidence to date suggests that phosphate solubility is controlled by surface complexes of hydroxyaluminium phosphates and iron phosphates (Larsen, 1967). In slightly acid soils iron and aluminium phosphates will coexist with calcium phosphates.

Although there may be present in soils a range of solids which give rise to a complex series of interrelated equilibria between the soil and the solution, it is possible to predict the equilibrium composition of the soil solution given a knowledge of the equilibrium constants for all the reactions involved (Adams 1971). Such principles, embodied in solubility products, have been extensively applied to soil phosphate reactions (Lindsay and Moreno, 1960; Larsen, 1967), but they can at present give only a qualitative insight into the effect of various changes in soil solution composition on phosphate solubility. Among the difficulties are, firstly, an as yet incomplete knowledge of the complex solubility product of hydroxyapatite (Larsen, 1967); secondly, equilibrium between phosphate in solution and phosphate on solid surfaces may be only slowly established in soil (Bache, 1965); and thirdly, equilibrium constants for the dissolution of the amorphous phosphates and surface film of phosphates which often occur in soil cannot be precisely enumerated (Larsen, 1967). Thus, reactions of dissolution, precipitation and hydrolysis involving phosphate will undoubtedly be affected by the electrolyte concentration and composition of the soil

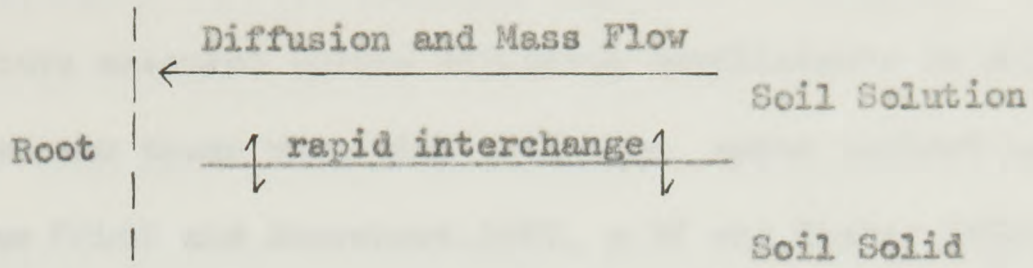
solution but it is not yet possible to make any simple general rules to describe such effects on phosphate solubility.

The concentration of phosphate in the soil solution and the amount of phosphate desorbed from a soil can be related by a desorption isotherm (Nye, 1968b). The above discussion indicates the complex nature of soil phosphate reactions, and for this reason Nye (1968b) stressed that such isotherms should be determined, as nearly as possible, under the exact conditions to which they are to be applied. Thus, if such an isotherm is to be used in an investigation of the depletion of soil phosphate by plant uptake, the aeration and the ionic strength and composition when determining the isotherm should be those of the natural soil solution.

It is clear that the soil solution concentration of the three major fertiliser elements is determined by widely different processes. Thus, for nitrate, microbial mineralisation is of overriding significance; for potassium, ion exchange and slow dissolution and fixation reactions are predominant; for phosphorus, dissolution and precipitation reactions are normally the most significant. Only the elements N, P, K, Ca, Mg, Na, S and Cl were considered in experimental work described in this thesis. The behaviour of Ca, Mg, and Na in soil can be understood in terms of cation exchange, and Q/I curves, similar to those for K described above, can be derived for Mg and Na. Cl, like NO_3, normally exists solely in the soil solution. SO_4 is adsorbed to a considerable extent by some soils (Aylmore, Karim, Mesbahul and Quirk, 1967) but in the present experiments it was almost totally in the soil solution.

The soil solution composition, Q/I curves and desorption isotherms are incorporated within the model of nutrient supply to roots discussed by Nye (1968a). When an adsorbing root extends into an initially uniform soil, nutrients will be absorbed from the solution at the root surface. This will lead to a decrease in the concentration at root surface and nutrient ions will diffuse from a distance to compensate for the depletion. The situation

is described in the diagram below.



Interchange between solution and solid surfaces is sufficiently rapid to maintain local equilibrium between solution and adsorbed ions in the way predicted by desorption isotherms, so that the depletion of both dissolved and adsorbed nutrients will occur round roots. The rate which ions can diffuse to the root surface sets an upper limit to the possible root uptake rate. The emphasis on rates and on the kinetic process of diffusion characterises this latest phase in plant nutrition studies. There has been a shift of emphasis from a static view of the soil as containing a quantity of available nutrients to a dynamic view of soil-plant systems, in which nutrients move according to the laws of diffusion and of water flow towards roots of defined dimensions, distribution, growth rate and nutrient demand. The origins of this approach can be seen in a number of papers; these, together with a brief survey of whole plant experiments in this field are discussed in the next section.

1.2 The Development of the Dynamic View of Plant Nutrient Uptake

Bray (1954) was one of the first authors to call attention to the importance of the mobility of a nutrient in soil in determining its availability. He also recognised the importance of root distribution and density in combination with nutrient distribution, in determining availability in a given situation, and suggested that the rate at which nutrients can move through soil to roots, and the mean distance they have to move in order to reach root absorbing surfaces, are important factors in determining the rate of nutrient flow in a soil/plant system.

Schofield and Graham Bryce (1960) pioneered the physico-chemical investigation of ionic mobility in soil with their study of rubidium diffusion.

They pointed out that a knowledge of the mobility of ions was essential to an understanding of soil transport procesees generally. Since then, other workers have measured solute diffusion coefficients in soil, and have investigated how these vary with soil type, water content and exchange capacity. (see Fried and Broeshart,1967, p.57 and Tinker,1970).

Another important component of the root/soil system was emphasized by Barber (1962), who drew attention to the significance in supplying ions to the root surface, of water movement to roots. In calculations based on the mean nutrient content of maize in the midwestern U.S.A., the mean concentrations of soil solution, and the mean transpiration ratios there, he showed that on average the mass flow of dissolved nutrients in the transpirational water entering the roots could account for the supply to root surfaces of Ca, Mg, Na, N and S.

More recently, these mobility concepts have been stated more precisely in mathematical terms. Amongothers,Passioura (1963) and Nye (1966a) have published models for the nutrient flow around single cylindrical roots based on equations describing the diffusive flux around a cylindrical sink or source (Crank,1956, p.62). Passioura considered the effects of both mass flow and diffusion in a simple way, whilst Nye considered solely the diffusion of ions depleted by uptake at the root surface. These models are discussed in detail in Chapter Three.

In parallel with the growing interest of soil scientists in the rates of nutrient movement in soil, plant physiologists have been measuring rates of nutrient flow into roots. The well-known kinetic invesitgations using excised roots (Epstein,1956) have shown the general dependency of root uptake rate on nutrient concentration in solution. An interest in measuring the efficiency of root tissue in absorbing nutrients led Williams (1948) to investigate the rate of nutrient flow into the roots of whole plants. More recently the research school in Western Australia has broadened this approach and has investigated the relation between nutrient flows into whole plants and the concentration of nutrients around their roots. (Asher and

Ozanne 1967, Asher and Loneragan 1967 a and b, Loneragan and Snowball,1969a and b, Carroll and Loneragan 1968 and 1969). As a consequence we now have a knowledge of the requirements of a wide range of species for a number of nutrients. From such data it is possible to calculate the nutrient demand of root surfaces (Nye and Tinker,1969) and to match this with the ability of soils to supply the surfaces. Thus developments in soil science and plant physiology are converging and providing data that can be incorporated in models of the nutrient flow to roots such as those of Passioura (1963) and Nye (1966) mentioned above.

The general conclusion of Barber (1962) on the importance of mass flow in supplying nutrients to roots were based on averages of quantities that may vary considerably, namely, plant nutrient content (Whitehead,1966, Goodall and Gregory,1947), soil solution concentrations (Barber,1962) and transpiration ratios. However, in several experiments, Barber and his collaborators have measured transpiration ratios, nutrient uptakes, soil solution concentrations and root volumes (Al Abbas and Barber,1964, Oliver and Barber,1966). Their results confirmed that mass flow could supply roots with Ca, Na, Mg and B but not with sufficient K, P, Mn, Fe or Zn. Diffusion was clearly important for supplying K and P. They also calculated what proportion of the uptake could be accounted for by "root interception", on the assumption that roots absorb all the exchangeable nutrients from a volume of soil equal to their own volume. However, roots do not engulf soil as they grow but force their way between soil particles. It seems therefore that root interception is a misconception. The rate of root growth determines the age distribution of a plant's roots, and, as will be apparent later, the diffusive flow to a root will diminish with age. Hence, root growth rate can be an important determinant of plant uptake rate from soil, but it is properly considered within calculations of diffusive supply to roots, not by the concept of root interception.

The conclusions of Al Abbas and Barber (1964) and Oliver and Barber (1966)

concerning the relative importance of mass flow and diffusion were based on nutrient uptakes and cumulative transpiration between sowing and a single final harvest. Furthermore, root lengths were not given. Hence, it was not possible to calculate the rate of nutrient uptake at any one time or the mean rate of nutrient flow into unit length of root or, as we term it, "inflow" (Brewster and Tinker, 1970). It is quite possible that the mean inflow of water and nutrients into roots changes with plant age, but single harvest experiments offer no evidence on this point. It was therefore decided to initiate an experiment to measure the nutrient and water inflows into the roots of a crop growing in soil under as near as possible field conditions. Along with a number of soil measurements, the data so obtained were sufficiently complete to be analysed in terms of the equation of Passioura (1963) mentioned above. A description and the results of the experiment comprise the bulk of section two of the thesis. This is preceded by two chapters in which the theory of nutrient flow to roots is discussed in more detail.

Chapter Two

DIFFUSION COEFFICIENTS IN SOIL

A fairly comprehensive body of theory has been developed to account for diffusion coefficients of both adsorbed and non-adsorbed ions in soil. Nye (1966a) proposed that the total diffusive flux of adsorbed ions could be regarded as made up of two additive components, a flux through the liquid phase or soil solution and a flux of "solid associated" ions along solid surfaces. Experiments have since shown that in moist, calcium dominated soils, the flux along solid surfaces is small (Mott and Nye, 1968, Nye, 1968b, Tinker, 1970). Nye (1966a) proposed that, if ions in solution are in equilibrium with those on adsorbed surfaces, which is a reasonable assumption in the light of the very rapid exchange between adsorbed and solution cations (Malcolm and Kennedy, 1969) and between adsorbed and solution phosphorus (Olsen and Kemper, 1968, p.105), then the diffusion coefficient, D, of an ion in soil can be described by the equation,

$$2.I \qquad D \triangleq D_L v_L f_L \frac{dC_L}{dC} = D' \cdot \frac{1}{b}$$

where, D_L = diffusion coefficient of the ion in free solution

v_L = volumetric water content of the soil

f_L = tortuosity factor for diffusion in the soil at this v_L

$\frac{dC_L}{dC}$ = slope of the desorption isotherm of the ion in the soil.

$D' = D_L v_L f_L$

b = the buffer power of the soil for the ion $\left(= \frac{dC}{dC_L}\right)$

Nye (1966a) went on to show that, in the case of the bulk diffusion of an ion species of initial concentration C_1 from the soil to a planar sink with surface concentration C_2, the effective diffusion coefficient, (D), is given by,

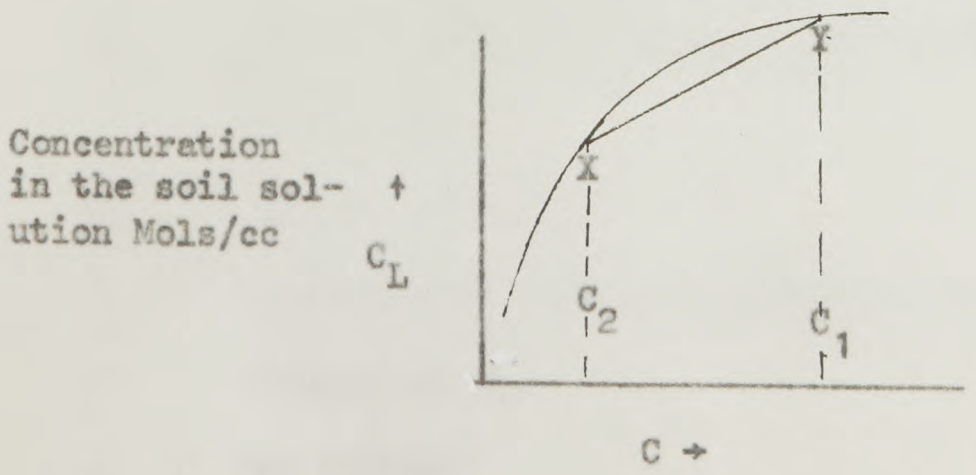
$$(D) = \frac{1}{C_1 - C_2} \int_{C_1}^{C_2} D.dC = \frac{D^1}{C_1 - C_2} \int_{C_1}^{C_2} C_L.dC$$

$$= \frac{D^1 (C_{L1} - C_{L2})}{C_1 - C_2}$$

Hence,

$$2.II. \quad (D) = D^1 \frac{\Delta C_L}{\Delta C}$$

where C_L = concentration of the ion in the soil solution $\frac{\Delta C_L}{\Delta C}$ has been termed the mean buffer power between C_1 and C_2. If the relation between C_L abd C, the desorption isotherm for the nutrient ion in the soil, is found experimentally, then, as illustrated in the diagram below, $\frac{\Delta C_L}{\Delta C}$ is the slope of the line joining the points X and Y.



Total concentration in the soil Mols/cc

It follows that variations in (D) should be linearly related to variations in $\frac{\Delta C_L}{\Delta C}$ for a given soil at a constant water content.

Considering in detail each of the terms in equations 2.I and 2.II;

(1) V_L the volumetric water content of the soil, will be the same for all ions and can easily be calculated from the bulk density and water content of the soil.

(2) D_L, the diffusion coefficient of the ion in free soil solution, is normally taken from tables (Parsons, 1959) and is the limiting diffusion coefficient for self-diffusion of the ion in question through a solution at infinite dilution at 25°C. This is termed here the liberated diffusion coefficient or liberated D_L following Vinograd and McBain (1941). In fact D_L will be only slightly less than this for self-diffusion through solutions of the order of 0.01 Molar such as the soil solution.

The flux of a single ion diffusing through a dilute electrolyte solution can be approximately described by the equation.

$$2.III. \qquad F_A = -D_{LA}\left(\frac{dC_A}{dx} + \frac{Z_A C_A f}{RT}\frac{d\psi}{dx}\right)$$

i.e. Flux = Diffusion Coefficient x (Gradient in chemical potential + Gradient in electrical potential x valency x concentration x constant)

where F_A = Flux of the ion A

D_{LA} = Limiting Diffusion Coefficient at infinite dilution in sllution of the ion A

Z_A = Valency of ion A

C_A = Concentration in the solution of the ion A

F = Faraday number

R = Gas constant

T = Absolute temperature

$\frac{dC_A}{dx}$ = Gradient in chemical potential of the ion A

$\frac{d\psi}{dx}$ = Gradient in electrical potential in the solution.

(see Robinson and Stokes (1959 p. 286) for a more precise treatment).

For both co-diffusion and counter-diffusion of just two ion species A and B, equation 2 III and the electroneutrality condition, which states, $\Sigma z_i F_i = 0$, where Z_i = valency of ions and F_i = Flux of ions, can be combined to derive the mutual diffusion coefficient

2.IV $$D_{AB} = \frac{D_A D_B (C_A + C_B)}{C_A D_A + C_B D_B}$$

D_{AB} = Diffusion coefficient describing the mobility of both ions in the system.

Where more than two ionic species are present, the situation is more complex. There is an infinite number of ways of satisfying the electrical neutrality condition in such cases. General equations can be derived but not necessarily solved (Robinson and Stokes, 1959 p.286); Vinograd and McBain (1941) have however, applied equation 3.III and the electroneutrality condition to solve diffusion problems in systems containing three ions in solution. Their calculations show good accord with experimental results. The diffusion potential created in such systems sometimes greatly changed the mobility of some ions away from that predicted by their D_L value.

Turning to the importance of diffusion potentials in modifying D_L values in soil, Olsen and Kemper (1968 p.109) suggested that the many adsorbed ions held by the fixed charges in soil will readily shift to buffer, and consequently to minimise diffusion potentials. Further, Nye (1966 has pointed out that where an ion of low concentration is diffusing through an atmosphere of

other ions that are present in greater concentration, then the potential term in equation 2.III will be insignificant. Such a situation is likely to occur when K and P diffuse to roots. Hence, D_L values for K and P should not normally be greatly modified by diffusion potentials round plant roots. The latter argument will not hold for the co-diffusion of anions and cations that are present in high concentration in the soil solution. In such cases equation 3.IV may be applicable. Such a situation is likely to arise when salts accumulated by mass flow at the root surface diffuse away from the root.

(3) f_L What has been termed the tortuosity factor, f_L, is a complex term to include all factors impeding the diffusion of a solute through soil as opposed to its diffusion through free solution. The geometrically greater mean path length in soil is envisaged as the main cause of the difference. f_L varies with water content, soil bulk density, soil texture and soil structure and its value must be determined experimentally. Equation 2.I implies that f_L is the same for all ions. It may be objected that, in soil, with its predominance of negatively charged surfaces which are surrounded by electrical double layers, f_L is unlikely to be the same for anions, which are excluded from the double layers, as for cations which can penetrate the double layers. Further, divalent anions are subject to a greater degree of negative adsorption than are monovalent anions (Olsen and Kemper,1968) and some experiments have shown sulphate to produce an apparently low value for f_L in a given soil. (Tinker,1970). However, recent experiments, using soil moistened to a v_L of about 0.4 with 0.01M. $Ca\,Cl_2$ solution, have shown no differentes in f_L between Cl and SO_4 (Bhat pers.comm.). Rowell, Martin and Nye (1967) found f_L to be independent of ion species for a number of cations and anions. There seems good reason to suppose that in a moist soil with the typical calcium concentration of 0.01M in solution, the double layers will be compact in comparison to the width of capillary water films and f_L will be the same for all ions. This being the case, f_L can be determined for one ion alone and applied to others. In the present

experiments f_L was masured for the self diffusion of chloride by the method of Rowell et al (1967).

(4) $\frac{dC_L}{dC}$ the reciprocal of the buffer capacity, really describes the partition of exchangeable ions between the soil solution and the solid surfaces as they diffuse in a concentration gradient in the soil. For non-adsorbed ions, for example, Cl and NO_3, $\frac{dC_L}{dC}$ equals $\frac{1}{V_L}$ and $D = D_L f_L$. These ions are the most mobile and have the highest D values in soil. $\frac{dC_L}{dC}$ is the slope of the isotherm for the desorption of the ion from the soil solid into solution. If these isotherms are determined, $\frac{dC_L}{dC}$ can be measured and D calculated for adsorbed ions at any concentrations, thus avoiding the need for tedious direct determinations of D. Vaidyanathan, Drew and Nye (1968) showed that the effective diffusion coefficient for the inter-diffusion of potassium and hydrogen between aCoral rag clay soil, with a markedly curved potassium desorption isotherm, and a hydrogen loaded cation exchange resin, varied linearly with the mean value of $\frac{dC_L}{dC}$ in different concentration ranges. This is in accord with the causal relation between (D) and $\frac{\Delta C_L}{\Delta C}$ implied by the equation 2.II. Vaidyanathan and Nye (1971) have published a convincing demonstration that variations in the effective diffusion coefficients of phosphate diffusing from a loam soil to sinks of various phosphate concentrations, can be totally accounted for by variations in the value of $\frac{\Delta C_L}{\Delta C}$.

Chapter Three

THE MATHEMATICAL DESCRIPTION OF NUTRIENT FLOW TO ROOTS IN SOIL

3.1 Introduction

We can formulate a mathematical description of a root system absorbing nutrients from the soil if we make certain simplifying assumptions. As a first model of root activity, we can assume that roots do no more than (1) absorb water and ions that are carried towards them by mass flow and by diffusion, and (2) balance any charge discrepancy arising from ion uptake by excreting H^+, OH^- or HCO_3^- ions. The flows around a short segment of root acting as such a simple sink can be described by the cylindrical case of the diffusion equation (Crank, 1956). A whole root system can be regarded as the sum of a large number of such short segments of root of different ages. This is the basis of the model which is described more fully below.

3.2 The Flow of Nutrients into a Single Short Length of Root

If we first consider the uptake of a single root growing and absorbing in isolation, we can ignore questions of root and nutrient distribution in the soil profile. If such roots are regarded as straight cylinders acting simply as sinks for water and nutrients, then it becomes possible to apply a precise mathematical approach to the transport of solutes around them. Equations have been developed to describe the flow rates round cylindrical sinks in infinite media (Carslaw and Jaeger, 1959) and these can be applied to the transport of nutrients towards roots (Bouldin, 1961, Olsen, Kemper and Jackson, 1962, Youngs and Gardner, 1963, Passioura, 1963, Nye, 1966b, Lewis and Quirk, 1967, Kautsky, Barley and Fiddaman, 1968, Olsen and Kemper, 1968). All such equations incorporate a boundary condition which relates root uptake to nutrient concentration in the adjacent solution. Several different boundary conditions have been used by different workers (Olsen and Kemper 1968).

The concentration changes brought about by the simultaneous flux of water and solute towards a uniform cylindrical root are correctly described by the differential equation below. (Nye and Marriott, 1969, Marriott and Nye, 1968, Passioura and Frere, 1967).

$$3.I \qquad \frac{dC_L}{dt} = \frac{1}{a}\frac{d}{da}\left(aD\frac{dC_L}{da} + \frac{VrC_L}{b}\right)$$

Where

C_L = solute concentration in the soil solution.

D = diffusion coefficient of the solute in soil

V = the water velocity at the root surface, or the flux of water across the root surface.

r = root radius

b = buffer power of soil for the solute

a = radial distance from the central axis of the root

t = time

3.I assumes that D is independent of V, which seems reasonable for the low water velocities that occur around roots (Nye and Marriott, 1969, Nielsen and Biggar, 1962). Published solutions for 3.I include those for boundary conditions 1, 2 and 3 below.

(1) $t = 0 \quad a \geq r \quad C_L = C_{Li}$

$t > 0 \quad a = r \quad F = \alpha C_{LR}$

$t > 0 \quad a \to \infty \quad C_L \to C_{Li}$

2) $t = 0 \quad a \geq r \quad C_L = C_{Li}$

$t > 0 \quad a = r \quad F = Db \frac{dC_L}{dr} + V C_{LR} = \frac{KC_{LR}}{1 + \frac{KC_{LR}}{F_{max}}}$

$t \geq 0 \quad a \to \infty \quad C_L \to C_{Li}$

3) $t = 0 \quad a \geq r \quad C_L = C_{Li}$

$t > 0 \quad a = r \quad D\frac{dC_L}{dr} + VC_L = 0$

$t > 0 \quad a \to \infty \quad C_L \to C_{Li}$

Where

C_{Li} = initial solute concentration in the soil solution

C_{LR} = solute concentration in solution at the root surface

α = a constant relating the flux of solute into roots to the solute concentration. It is known as the root absorbing power (Nye, 1966b).

K = a constant relating the flux of solute into roots to the solute concentration as found appropriate by Epstein and Hagen (1952).

F = Flux of solute into the root.

F_{max} = the maximum flux of solute into roots.

(1) (Nye and Spiers, (1964) published an analytical solution for the case where a steady state is reached and Marriott and Nye (1968) published a numerical solution for the transient state. (2) (Nye and Marriott, (1969) and (3) (Passioura and Frere, (1967) were both numerical solutions of the equation for the transient state. Most situations round roots will be transient state cases (i.e. concentration gradients will be changing with time). Nye and Spiers (1964) showed that a steady state can be

reached only when $\frac{rv}{bD} > 2$, which is, in effect, where there is high transpiration from a moderately dry soil with low diffusion coefficients. Geering (1967) has developed an analytical solution for 3.I with boundary condition (1), but it involves complex Bessel functions. However, by using the approximate equation of Passioura (1963), we can more easily gain some idea of the ionic environment at the root surface. In moist soil the calculations are not sensitive to small errors and we can safely derive approximate results.

Equation 3 of Passioura 1963 states,

$$3.II \qquad F = \frac{(C_{Li} - C_{LR})\, Dg}{r} + VC_{Li}$$

where, g = "the instantaneous flux parameter", a function of $\frac{Dt}{r^2}$, where t is the time for which the root has been absorbing. g is derived from the expression that describes diffusion around a cylindrical sink with a constant surface concentration and it accounts for the time dependency of the flux at the surface of such a sink. Values of g have been given by Jaeger and Clark (1942) and Carslaw and Jaeger (1947 p.335).

As originally presented, 3.II applied only to those ions that existed solely in the soil solution. However, for an adsorbed nutrient we can write,

$$3.III \qquad F = \frac{(C_i - C_R)\, Dg}{r} + V\, C_{Li}$$

where, C_i = initial concentration of exchangeable nutrient in the soil.

C_R = concentration of exchangeable nutrient in the soil at the root surface.

Now, by equation 2.I if $\frac{dC_L}{dC}$, the reciprocal of buffer power, b, is constant between C_i and C_R, $D = D' \frac{C_{Li} - C_{LR}}{C_i - C_R}$. If we substitute this for D in equation 3.III we find that,

$$F = \frac{(C_{Li} - C_{LR})\ D'g}{r} + V\,C_{Li}$$

Thus, both for those nutrients that exist solely in the soil solution and for those that are also adsorbed on soil solids, we can, provided b is constand, write an equation in terms of concentrations in the liquid phase alone. The value of g, however, depends on D rather than D', and hence the effect of buffering on the diffusion of exchangeable ions is incorporated in this term.

The rate of flow of nutrient into one centimetre of root, the inflow, is given by,

3.IV. $$I = 2\Pi\, r\, F = 2\Pi(C_{Li} - C_{LR})\, D'\, g + 2\Pi\, r\, VC_{Li}$$

Equations 3,II, 3,III and 3.IV. imply that solute flows due to mass flow and diffusion are separable and independent, but strictly, the two flows can be considered separately only in a differential equation, i.e. equation 3.I, since the flowing solution contains the concentration gradients that are driving diffusion. In view of this, the use of equation 3.IV needs some justification. Marriott and Nye (1968) compared the values of C_{LR} given by equation 3.IV with those given by their numerical solution of 3.I using boundary condition 2 above. They gave results for a range of values of D, α, r, b and V. They found that;

1) Where $V/\alpha = \frac{1}{2}$, that is, where the solute uptake rate was twice the mass flow supply rate, values of the root surface concentration depletions given by equation 3.IV were less than 10% greater than the more accurately computed values for roots aged between about three and thirty days.

2) Where $V/\alpha > 1$, equation 3.IV gave too low an estimate of the concentration increase at the root surface, the degree of error being larger the larger V/α became. If we take a value of V equal to the mean V found in the experiment described in Chapter 4, the numerical solution predicts a root surface concentration after thirty days of 4.7 C_{Li}, whereas equation 3.IV predicts one of 3 C_{Li}. Actually, these comparisons were based on a D value more

than a hundred times lower than that of the accumulating ions in the soil used in Chapter 4's experiment. Now, the lower the value of D for an ion wiich is being oversupplied by mass flow, the slower will be its back diffusion, and hence the greater its increase in root surface concentration. Thus, estimates made by using equation 3.IV, using such low values of D, predict much greater accumulations at the root surface than those expected in moist soil for mobile ions with high D values. Further, the lower the concentration increase, the less is the proportional error in using the approximate equation 3.IV.

Hence, although equation 3.IV is not theoretically strictly correct, we considered it sufficiently accurate in its results to be applied to the calculation of concentrations at the surface of roots in moist soil. However, we call the term $2\pi r V C_{Li}$ and terms derived from it in subsequent equations the "apparent mass flow" contribution to inflow (Brewster and Tinker, 1970), to emphasize that the mass flow and diffusive contributions to inflow cannot strictly be regarded as separate entities.

3.3 The Flow of Nutrients into a Root System

If we turn from considering a single cylindrical element of root to the root systems of whole plants, or plant stands, where several roots are absorbing from a finite volume of soil, then three complications may arise.

They are:-

1) Both available nutrients and roots may be unevenly distributed in the soil profile. Even in fairly homogeneous soil, leaching is likely to lead to uneven nutrient spread.

A considerable amount of experimental work on the uptake of nutrients from different parts of the soil profile has been published (Newbould, 1968).

2) Different roots may differ in their ability to absorb nutrients.

3) The soil is a finite volume and zones of depletion due to the activities of adjacent roots may overlap resulting in a diminished mean inflow compared with that into a single root in the same soil.

However, if for simplicity, we consider a sparse root system with uni-

form root absorbing power, extending into an initially homogeneous soil, then a complete root system can be considered to consist of a number of single root elements of different ages, and the uptake rate of the whole system can be analysed as the sum of the flows into such elements. Ignoring mass flow, equation 3.IV shows that the diffusive inflow to a root with a constant surface is given by,

$$I = 2\Pi\, r\, D'\, g\, \Delta C_L$$

where, $\Delta C_L = C_{Li} - C_{Lr}$, or the difference in solute concentration between the undepleted soil and that at the root surface.

A whole root system consists of many such short elements of root or different ages, where each age has a different value of the Instantaneous Flux Parameter g. For a whole root system we can define a "Mean Flux Parameter" $\bar{g}$ as:

3.V
$$\bar{g} = \frac{\int_0^T 1.g.dt.}{L}$$

Where l = length of the element of root produced in unit time

g = the value of the instantaneous flux parameter after a given time.

L = the total root length

T = total age of root system

Hence
$$\bar{g} \simeq \frac{1}{L}\left(\int_0^{t_1} 1\,dt\ \frac{\int_0^{t_1} g\,dt}{t_1} + \int_{t_1}^{t_2} 1\,dt\ \frac{\int_{t_1}^{t_2} g\,dt}{t_2 - t_1} + \int_{t_2}^{t_3} 1\,dt\ \frac{\int_{t_2}^{t_3} g\,dt}{t_3 - t_2} \cdots\right)$$

Therefore

$$3.VI. \qquad \bar{g} \simeq \frac{1}{L}\left(\int_{o}^{t_1} 1 \, dt \; G + \int_{t_1}^{t_2} 1 \, dt \; \frac{\int_{t_1}^{t_2} g \, dt}{t_2 - t_1} + \int_{t_2}^{t_3} 1 \, dt \; \frac{\int_{t_2}^{t_3} g \, dt}{t_3 - t_2} \cdots \right)$$

where G = The "Average Flux Parameter" of Nye (1966 b)

and

$$\frac{\int_{t_1}^{t_2} g}{t_2 - t_1} \simeq$$ the value of g, the Instantaneous Flux parameter at the average age of the roots lying between t_2 and t_1.

$\int_{t_1}^{t_2} 1 \, dt$ is simply the root length aged between t_2 and t and this can be read off from a curve of root length against time if no roots die.

Thus $\bar{I}$, the mean inflow into a root system will be given by,

$$\bar{I} = 2\Pi \, \bar{r} \, D' \bar{g} \, \overline{\Delta C_L}$$

where, $\bar{r}$ = the mean root radius.

$\overline{\Delta C_L}$ = "mean" concentration difference between the root surfaces and the undepleted soil as predicted by this equation.

Therefore, rearranging the terms,

$$\overline{\Delta C_L} = \frac{\bar{I}}{2\Pi \, \bar{r} \, D' \bar{g}}$$

If there is mass flow, from equation 3.IV.,

3.VII. $$\overline{\Delta C_L} = \frac{\overline{I} - M}{2\pi \overline{r} D' \overline{g}} = C_{Li} - \overline{C_{LR}}$$

Where $\overline{C_{LR}}$ = "mean" concentration of solute at the root surface as predicted by equation 3.VII.

M = mean mass flow contribution to inflow which we define as

$2\Pi \bar{r} \overline{V} C_{Li}$, $\overline{V}$ being the mean water velocity at the root surface.

For a whole plant M can be simply calculated as

$$\frac{\text{Transpiration Rate} \times C_{Li}}{\text{Root Length}}$$

All the terms in equation 3.VII can be determined from experiments except $\overline{C_{LR}}$; it is possible therefore to use the equation to analyse the nutrient flow around roots in a suitable experiment and hence to calculate the unknown $\overline{C_{LR}}$. Strictly, in using equation 3.VII, we are saying that, if the root surface solute concentration changes by $\overline{\Delta C_L}$ on the arrival of a root element in the soil, and thereafter ΔC_L remains constant, then this is sufficient to drive a measured total diffusive flow around the roots of a root system of measured age distribution. In other words, ΔC_L is a measure of the depletion or accumulation necessary if diffusion to or from a constant boundary concentration at the root surface drives the nutrient flow towards or away from the roots. Diffusion to a constant surface concentration sounds a rather unlikely model for root behaviour since roots cannot suddenly arrive at a point in the soil and deplete it instantly to a constant concentration at their surface. In dilute solution cultures the uptake root of roots has often been found proportional to the concentration of nutrients. This proportionality breaks down in more concentrated solu-

tions and the uptake rate is well described by the equation,

3.VIII $$F = \frac{k\ C_{LR}}{1 + \frac{kC_{LR}}{F_{MAX}}} = \alpha r$$ (Epstein and Hagen 1952, Kautsky, Barley and Fiddaman, 1968)

Where C_{LR} is low, $F \triangleq k\ C_{LR}$.

However, as Marriott and Nye (1968) point out, where $F = kC_{LR}$, then a rapid initial decrease in C_{LR} occurs, followed by a much slower decrease in C_{LR}, so that in fact C_{LR} becomes almost constant after some time. A detailed comparison of the two boundary conditions was made by Drew (1966 p.157) illustrating the same point. This, and also the accord between the accurate and approximate values of C_{LR} found by Marriott and Nye (1968) and discussed in 3.2, vindicates the use of an equation involving a constant surface concentration boundary condition for the calculation of C_{LR}.

3.4 The Mean Root Absorbing Power

Having calculated $\overline{C_{LR}}$ it is possible to invoke equation 3.VIII and say by analogy;

3.IX $$\bar{F} = \frac{\bar{I}}{2\pi r} = \bar{\alpha}\ \overline{C_{LR}}$$

Where, $\bar{F}$ = mean flux across the surfaces of a root system

$\bar{\alpha}$ = the constant relating $\bar{F}$ to $\overline{C_{LR}}$

The series of equations developed for flow to a root system thus reads,

3.X $$\bar{I} = 2\pi\ D'\ \bar{g}\ (C_{Li} - \overline{C_{LR}}) + M = 2\pi\ \bar{\alpha}\ \bar{r}\ \overline{C_{LR}}$$

Here it is important to recall that, if for all root elements $F=\alpha C_{LR}$,

then C_{LR} is not a constant over the whole root system. The calculation of an $\bar{\alpha}$ value based on equation 3.X, is therefore something of a logical contradiction and appears to be using two different boundary conditions in the same equation. (see also Passioura 1965). However, we wish to stress that $\bar{\alpha}$ is a "mean α" in the sense defined by equation 3.X. (Nye and Tinker, 1969). In fact, as was pointed out at the end of 3.3. above, C_{LR} is nearly constant around all but the youngest roots in a root system, and the value of $\bar{\alpha}$ can be taken as a rough estimate of a true α value as defined by equation 3.VIII, provided root absorbing power α does not vary with root age.

The value of $\bar{\alpha}\bar{r}$ is a concise expression of the average demand for nutrients of a root system (Nye and Tinker, 1969). If nutrients are supplied to roots by diffusion, and the inflow is equal to $2\pi \alpha r C_{LR}$, then the relative depletion in solution concentration at the root surface, C_{LR}/C_{Li}, at a particular value of dimensionless time, Dt/r^2, depends on the value of $\alpha r/Db$ (Nye, 1966). A value of $\alpha r/Db$ of 0.2 means that C_{LR}/C_{Li} will remain close to 1 and that plant uptake rate will not be limited by diffusion to the root surface. In contrast, if $\alpha r/Db$ is 10, C_{LR}/C_{Li} rapidly decreases towards 0, and plant uptake rate is largely controlled by diffusion to the root surface. In a given soil Db is similar for all ions, hence C_{LR}/C_{Li} will depend on the value of αr. A value of Db of 10^{-6} is typical of a moist soil (Rowell, Martin and Nye, 1967). Hence, in such a soil, if αr is $0.2 \times 10^{-6} cm^2/sec$. there will be little depletion round the roots, whereas if αr is $10^{-5} cm^2/sec$ there will be rapid depletion. If we take roots as having a radius of 0.025 cm, these values of αr correspond to values of α of 0.8×10^{-5} cm/sec and 4×10^{-4} cm/sec respectively. In a drier soil where Db is lower, diffusion in soil will limit plant uptake at lower values of α.

The mean root absorbing power of a root system can be thought of as the sum of local αr values for small elements of the root system, i.e.

3.XI $$\overline{\alpha r} \triangleq \frac{1}{L}\int_0^L \alpha r \, dL$$

Given that a root system has a certain $\overline{\alpha r}$, then the actual αr values of the active absorbing elements of the root system will be a minimum if all the roots are equally active. If some roots are not absorbing nutrients then to maintain the mean absorbing power, $\overline{\alpha r}$, for the root system, the actual value αr of the absorbing roots must be correspondingly greater. As we have seen above, if nutrients are supplied by diffusion, C_{LR}/C_{Li} diminishes as αr increases. It follows that, when only a part of the root system absorbs nutrients, the value of C_{LR}/C_{Li} at the surface of the absorbing roots will be smaller than is the case when all the roots are absorbing and in fact, C_{LR}/C_{Li} at the surface of the absorbing roots will have the maximum possible value when all the roots are absorbing. In other words, the least root surface nutrient depletion is required to supply a given mean inflow to a root system when all its roots have an equal absorbing power.

If, in applying equation 3.X., we find that $\overline{C_{LR}}/C_{Li} > 0$, then it follows that, if only a part of the root system were in fact absorbing nutrients, then, for those roots which were absorbing, C_{LR}/C_{Li} would be less than $\overline{C_{LR}}/C_{Li}$, and αr would be greater than $\overline{\alpha r}$. However, at high values of αr (where $\frac{\alpha r}{Db} > 10$, see above), $C_{LR}/C_{Li} \to 0$. In other words at high values of αr the root becomes a zero sink for nutrients and further increases in αr cannot increase nutrient inflow, since this is totally determined by diffusion to the root surface. It follows that, in order to maintain a certain mean inflow into a root system, there must be a certain minimum proportion of the root system that is active in nutrient absorption; i.e. that proportion of the root system that could maintain the mean inflow if it were a zero sink for nutrients. Hence, if equation 3.X yields a value of $C_{LR}/C_{Li} > 0$, it means that diffusion and mass flow could supply the mean inflow considered, and that if all the roots were absorbing then, in reality, $C_{LR}/C_{Li} \triangleq \overline{C_{LR}} / C_{Li}$. Alternatively we could calculate a certain minimum fraction of the root length that must be absorbing if the absorbing roots were a zero sink for nutrients. The maximum

possible inflow into absorbing root elements, $\bar{I}_{MAX\ 1}$ is given by,

3.XII $$\bar{I}_{MAX} = 2\Pi\ r\ C_{Li}\ D'g + M$$

Therefore, the minimum absorbing root length, L_{MIN}, required to supply a particular plant uptake rate is given by,

3.XIII $$L_{MIN} = \frac{dU/dt}{\bar{I}_{MAX}}$$

where U = plant nutrient content

and hence, dU/dt = plant nutrient uptake rate.

(It should be noted that the value of $\bar{g}$ in equation 3.XII depends on the length of <u>active</u> root and would have to be recalculated to determine $\bar{I}_{MAX}$ accurately if $L_{MIN} < L$ (see 3.3 above). Hence, a series of successive approximations would be needed to calculate L_{MIN} accurately. However, $\bar{g}$ does not vary rapidly with Dt/r^2 (see Fig. 4.3) and one or two iterations would probably be sufficient).

If we assume that αr does not differ for different roots of a plant, then the mean value, $\overline{\alpha r}$, of the plant's root system is a guide to the importance, in governing uptake rate, of diffusion in soil. It should be interesting to compare values of $\overline{\alpha r}$ for different species in the same soil and the same species in different soils. Values of $\overline{\alpha r}$ can also be calculated from uptake rates measured in solution culture. The effect of concentration in solution on uptake rate has been measured for a wide range of species and nutrients (Asher and Ozanne, 1967, Asher and Loneragan, 1967a and b, Carroll and Loneragan 1969, Loneragan and Snowball, 1969, Lastuvka and Minar, 1970). By calculating values of $\overline{\alpha r}$ we can connect such results with the theory of diffusive supply to roots in soil. Thus, if we have a soil with a given value of C_L and a known value of Db, and if we know from

experiments in solution the relation between $\overline{\alpha r}$ and C_L, we can calculate $\overline{\alpha r}/Db$ and determine the likely importance of diffusion in limiting the nutrient supply to roots in the soil. Such calculations assume that αr is constant over the whole root system and hence equal to the mean value $\overline{\alpha r}$. However, if αr were to vary in a definable way with root age, similar calculations taking account of this would be possible.

3.5 The Application of Equation 3.X

It is possible using equation 3.X to calculate values of C_{LR} and $\overline{\alpha r}$ for plants growing in soil. The relation between time, plant nutrient content, transpiration and also root length must be known. From this, nutrient uptake rates can be calculated and inflows of nutrients and water determined. Such data on plant growth and uptake can be obtained by the sequential sampling of replicate plants. In addition, soil solution concentrations and values of diffusion coefficients in soil must be known. Soil solutions can be extracted from soil samples, and diffusion coefficients can be determined from a measurement of the tortuosity factor and from desorption isotherms.

In applying equation 3.X to plant uptake a number of assumptions must be made, namely that;

1) The flow of nutrients can be described by an appropriate form of the diffusion equation with suitable boundary conditions.

2) The root is a simple sink for water and certain ions.

3) The soil is initially homogeneous with solutes uniformly distributed through the soil volume.

4) The roots are cylindrical with constant dimensions.

5) All flow is radial.

6) Diffusion coefficients remain constant in the soil round roots.

7) The soil around roots is infinite in extent.

8) There is no supply of nutrients from alternative sources.

9) Water inflow is constant.

10) The root demand coefficient, α, is constant along the root.

These assumptions are discussed in a general way below. In Chapter 6 they are further discussed in the light of the experimental work to be described.

1) That nutrient flow to roots can be described by the diffusion equation is now considered as almost axiomatic, nevertheless, we should consider the possibility that the rate of supply of nutrients to roots is governed by the rate of a desorption reaction or a mineralisation process rather than by diffusion alone. The validity of equation 3.X depends on the assumption that the rate of transfer of adsorbed nutrients from the solid phase to the solution is rapid in comparison with the rate of diffusion. Cation exchange is a very rapid process (Malcolm and Kennedy, 1969), and Olsen, Kemper and Van Schaik (1965) showed that the desorption of exchangeable phosphate was also rapid in comparison to diffusion.

2) To assume that the root is a simple sink seems reasonable for a first model. However, there is considerable evidence that roots exude a range of organic molecules (Rovira, 1969). These may form soluble complexes with certain nutrients, thus increasing their fraction in solution and their mobility in the rhizosphere soil (Hodgson, 1969).

3) For experimental purposes soil can be sieved, mixed and equilibrated to ensure its homogeneity. Although such soil is micro-heterogeneous, the scale of variation is taken as sufficiently small for overall diffusion coefficients to be appropriate in describing nutrient flow to roots.

4) and 5) Assumptions 4) and 5) indicate that care must be exercised in applying equation 3.X to much branched roots with numerous root hairs.

6) The assumption that diffusion coefficients are constant overlooks a number of possible causes of variation. A moderate error in D (see equation 2.I) is not crucial, since it affects only the value of the rather insensitive term $\bar{g}$ in equation 3.X. Hence, small errors in the buffer power, b, will not be important. On the other hand, D' (or $D_L v_L f_L$, see chapter 2), enters equation 3.X directly, and it is more important to have accurate values of

D_L, v_L and f_L. Changes in the soil around roots brought about by root activity could affect all the terms in equation 2.I.

Let us consider the terms in turn D_L. The uptake by roots of water and solutes in different proportion to their concentrations in the undisturbed soil will lead to the diffusion of mixtures of ion species and diffusion potentials will modify values of D_L somewhat.

$V_L f_L$ and $\frac{dC_L}{dC}$ Values of V_L, with which f_L is correlated, may be increased by compaction of the soil around roots. This may also increase $\frac{dC}{dC_L}$, the buffer power, in the rhizosphere. However, roots tend to follow existing fissures in the soil (Graecen, Barley and Farrell,1969). Roots may also exude mucigel (Jenny and Grossenbacher, 1963) which may increase V_L and f_L in the rhizosphere. In order forwater to move to roots there must be a gradient in matric suction towards the root. A gradient in matric suction implies a gradient in soil water content, V_L near the root, which will decrease $V_L f_L$ near the root. However, only in dry soils are there likely to be significant gradients of suction between the bulk soil and the the root surface (Gardner,1960).

7) One of the boundary conditions of equation 3.I is $a \to \infty$, $C_L \to C_{Li}$. This implies that changes in nutrient concentration in the soil due to the activities of adjacent roots do not overlap to an important extent.

8) The possibility of the release of initially non-exchangeable nutrients such as fixed potassium, or organically bound elements, particularly N and P, by mineralisation, should be borne in mind.

9) It is clearly an oversimplification to consider water inflow as the same into all roots of a plant, since it ignores the effect of diurnal variations in transpiration and assumes that water flow is the same into roots of all ages and in all positions in the soil. The transpiration rates of mesophytes in moist soils fall to almost zero at night and rise to a maximum around the middle of the day (Kramer,1969, p.332). Lag periods of continued water

flow into roots, after transpiration has ceased at night, are unlikely to last more than an hour or two in moist soil (Cowan,1955, Slatyer, 1967, p.281). Passioura and Frere (1967) have considered the effect of diurnal variations in water inflow on the accumulation of solutes at the root surface, and in Chapter 6 their results are considered in the light of our experimental results. The permeability to water of the root is not a constant characteristic of a plant species. Permeability is generally higher in rapidly growing roots (Kramer,1969). It can be increased by water stress and by metabolic inhibitors at high concentrations (Brouwer,1954). It can be reduced by increasing the bicarbonate ion concentration and by low concentrations of metabolic inhibitors (Slatyer, 1967, p.182).

10) The constancy or otherwise of the local or short term values of the root absorbing power, α , within a given root system, has been investigated in relation to a number of factors, including:

i) Variations in water inflow. Numerous experiments showing both a correlation (e.g.Rylmo, 1953, 1955) and no correlation. between water and ion uptake (e.g.Brouwer, 1954a, Russell and Shorrocks,1959) have been published, but as Marriott and Nye (1968) point out, the balance of evidence suggests that, in low salt plants growing in dilute nutrient solutions akin to soil solutions, transpiration rate has little effect on ion uptake.

ii) Changes in the concentration of other ions. Diurnal fluctuations in water inflow, root absorption and root respiration may cause the ionic environment round roots to fluctuate somewhat, though probably not massively in moist soil. (see chapter 6). The value of α for one ion may be changed by changes in the concentration of other ions in the soil solution of the rhizosphere. For example Robson, Edwards and Loneragan (1970) showed that the phosphate uptake rate of plants can be affected by the concentration of calcium in the solution bathing their roots.

iii) The diurnal variation of α independently of any water flux effects. Honert, Hooyman and Volkers (1955) showed that the rate of

P, NO_3, NH_4 and K uptake did not vary significantly between day and night. However, Huck, Hageman and Hansen (1962) found that the K uptake rate of the roots of whole corn plants decreased at night to about half the daytime value.

iv) Root Age. A number of investigations have tackled the experimentally difficult problem of the variation in solute uptake with root age or position along the root. A knowledge of the relation between α and root age was considered particularly important for an analysis of uptake using equation 3.X. Experimental work into this relation is reported in Section 3 and other published work is also reviewed there.

We must recognise, however, that we do not yet have a clear and comprehensive picture of whether or not α varies within a root system. Assumption 10 represents the simplest possible case for mathematical study, and it also represents the least stringent condition, from the point of view of a soil's ability to supply nutrients by diffusion to a root system (see 3.4 above). It is therefore, logical to use assumption 10 in applying equation 3.X., since the result will indicate whether or not it is theoretically at all possible to account for the uptake of a root system in soil in terms of the model of root activity outlined in 3.1 above.

There may appear to be a rather formidable list of assumptions involved in applying equation 3.X to whole plants. However, many of them can be tested in experimental situations. Even if some of the assumptions prove false, equation 3.X can still form the basis of a mathematical analysis of uptake. For example, if α were found to vary with root diameter, the equation could still be applied to separate fractions of the root system of different diameter, and the uptake of the whole system could be found by summing that of the different fractions.

Section Two

EXPERIMENTAL STUDIES OF NUTRIENT FLOW TO ROOTS IN SOIL

Chapter Four

AN EXPERIMENT TO MEASURE MEAN NUTRIENT INFLOWS INTO ROOTS IN SOIL AND TO RELATE THEM TO THE SOIL'S ABILITY TO SUPPLY NUTRIENTS BY MASS FLOW AND BY DIFFUSION.

4.1 Aims of the Experiment

The mathematical model describing nutrient flow into root system given in Chapter 3 was the basis of an experiment seeking to answer the following two specific questions.

1) Using equation 3.X can we account for the observed mean inflow of nutrients into the roots of an experimental crop?

2) If so, what value of mean nutrient concentration at the root surface are predicted by equation 3.X?

The most appropriate first experiment seemed to be to investigate in these terms, the uptake of a crop growing without nutrient stress in a fertile mineral soil and with, as far as possible, typical British outdoor growing conditions.

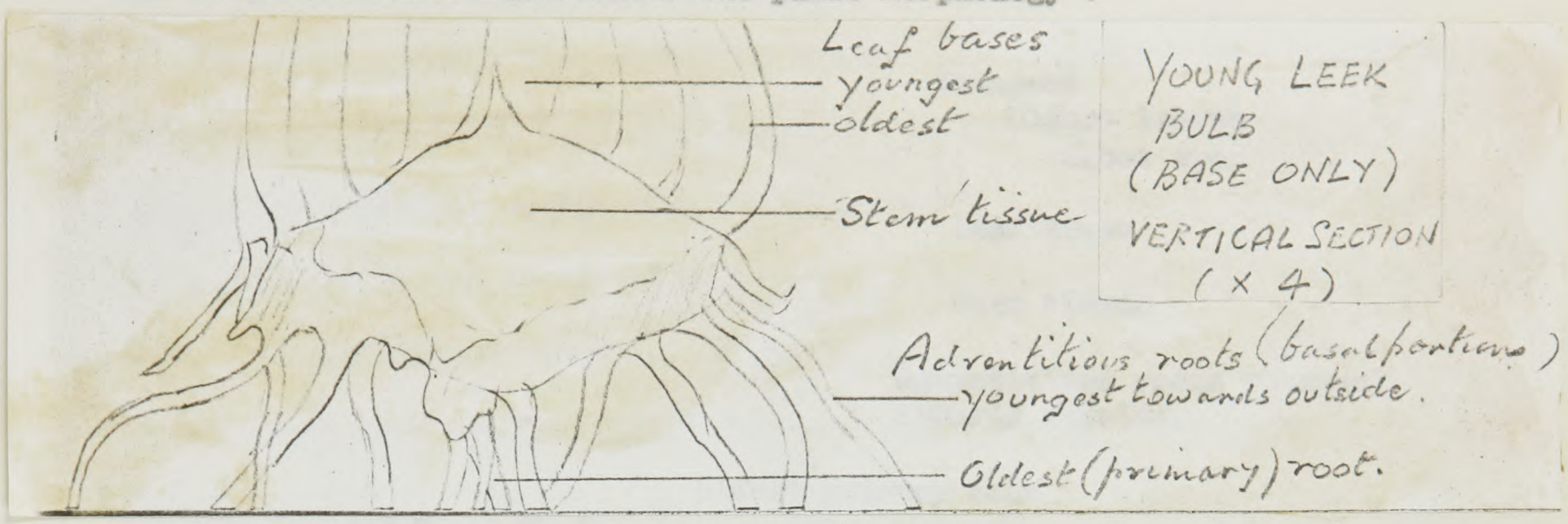
4.2 The Choice of an Experimental Plant

Leek Plants Allium porrum var. Musselburgh were used because their straight, robust and sparsely branched roots are easily extracted from the soil and measured.

The morphology and pattern of growth of leeks has been described by Hector (1946 Vol.II, p.481). The plants are biennials and form a narrow bulb from which the leaf blades emerge. The stem is reduced to a flattened disc at the base of the bulb. There is a central apex around which successive leaves are produced, the youngest leaves being closest to the apex. The root system develops at first as a primary root, which typically, stops growing when only 5 to 10 cm long. This is followed by a succession of adventitious roots, which emerge from the base of the bulb, the youngest towards the outside. This pattern is flexible; for example if adventitious roots are prevented from developing, then the primary root will continue to grow and will produce numerous

laterals.

The sketch below illustrates the plant morphology :-



In the pot experiment the roots were observed to range from 1.5 to 0.2 mm in diameter. The basal regions of the youngest adventitious roots were the thickest and diameter diminished somewhat towards the extremities. Lateral roots were markedly narrower than their parent roots. The basal regions of the adventitious roots were contractile. All roots remained white and alive during the period of the experiment. The adventitious roots tended to grow laterally, or obliquely downwards. Fine laterals became more conspicuous in the older plants. In the field Weaver and Bruner (1927) observed a horizontal root spread of up to 21 inches and penetration to a maximum depth of 30 inches. Weaver and Bruner found the majority of roots in the upper 25 cm of soil. They observed that the root density was greater than that of the onion crop in similar conditions.

Microtome sections of the roots of water culture grown leeks were cut from different root regions and a detailed analysis of the relative area of cortex, stele and vessels was made. The relative areas of the different regions was found to be similar in roots of all ages. Another noteworthy feature was the absence of any U shaped thickening in the walls of the endodermal cells of old roots. These roots still had the thickened band only in the radial walls of the endodermal cells, a feature normally regarded as typical of young roots. (Esau, 1953, p.480). This suggests that in the leek old roots remain similar to young roots in their uptake activity.

4.3 Growing and Sampling the Crop

4.3a Preparation of the Soil

The soil, a silty loam overlying gravel, was collected in late March 1967 from the trial field of the Oxford University Field Station at Wytham. Fairly dry handleable crumbs were scraped from the top three inches, broken down mechanically and passed through a 1 cm sieve to remove large stones and clods. A dressing of 35 ppm N, 30 ppm P and 75 ppm K, about equivalent to the NAAS feriliser recommendation for leeks, was added to the soil as a solution of $Ca(NO_3)_2$, KH_2PO_4 and KCl laboratory grade chemicals. The soil was then mechanically mixed and left moist in a bin to equilibrate for nearly a month.

Four sizes of container or pot were used for holding the soil and the plants. Polyethylene pots of 2.9 and 6.3L., glazed pot containers of 11.5 L. and polyethylene lined painted wooden boxes containing 28.5L of soil were used. The plants for the later harvests were grown in the larger containers and hence were provided with a greater reservoir of soil water than the plants harvested earlier. Therefore, watering was unnecessary during the experiment. Each pot was filled with four increments of soil. A calculated volume of water was added through a fine sprinkler after each addition of soil so as to avoid a large final watering and consequent heavy leaching from the top downwards. Water was added to bring the water in the pots to a suction of -0.05 bars, which corresponded to 33 g of water per 100 g of soil dried in the 105°C oven. This was determined from a previously obtained moisture characteristic for the soil (see 4.7a). Pots were filled to within 5 cm of the top, after which a layer of white expanded polystyrene granules was spread over the surface of the soil to minimise surface evaporation. The moistened pots were left in the cool greenhouse to equilibrate for a month. There were twelve each of the three larger sizes of container and sixteen of the smallest pots. Ten of each size were to contain plants and the remainder were to act as controls and give estimates of the water loss due to direct evaporation from the soil. A previous greenhouse test had shown the effective-

ness of the granules in reducing evaporation, and that they were not phytotoxic.

4.3.b. Growing and Harvesting the Plants

Carters selected leek seeds var. Musselburgh were sown in trays of sieved field soil on April 27 1967 and germinated in a greenhouse with a minimum temperature of 20°C. The seeds germinated in about two weeks and grew very slowly initially. Two seedlings per pot were transplanted on May 31. Growth was clearly accelerating ten days later and the pots were moved outside on June 10.

After planting, the pots were covered with a sheet of silver sprayed polyethylene rising to a small central aperture through which the plants emerged. This was to prevent the entry of rain splash, to reflect radiation and so minimise absorption of heat by the pot surface, and to prevent polystyrene granules from being blown away.

The pots were sunk with their rims at ground level in prepared holes laid out according to the ground plan in Fig.4.1. The pots were sunk in soil in order to simulate the field environment more closely and to minimise fluctuations in soil temperature, which could drive water and ion fluxes in the soil. The uniformity of measured soil temperatures in the system confirmed the success of these precautions (see section 4.8.). A light metal framework covered with clear polyethylene but open to the sides was placed over the pots to prevent the direct rainfall hitting the plants, with subsequent stem flow of water into the pots and the possible leaching of ions from the leaves. The ground plan, pot and pot line cross section are illustrated in fig.4.1.

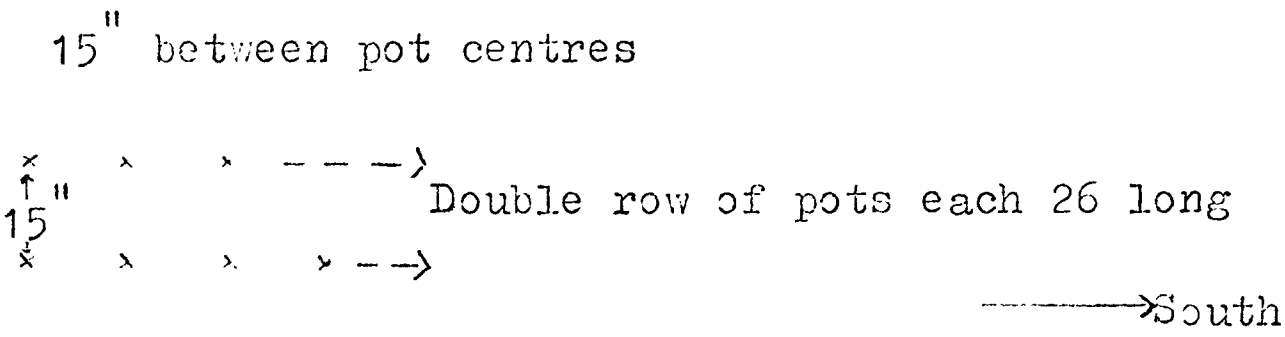
All pots were weighed twice a week the smaller two sizes to the nearest 1 g and the two largest ones to the nearest 8 g. Thus, cumulative water losses were measured, and by deducting plantless control pot losses, the water transpired was estimated. The greatest control losses amounting to 6% of the planted pot losses, occurred soon after planting out. This dropped to less than 1% later, so that we had an accurate measure of transpiration.

Successive samples of ten pairs of plants were harvested on the 16 and 29 June and the 7 and 18 July. The criterion for harvesting was that the pots

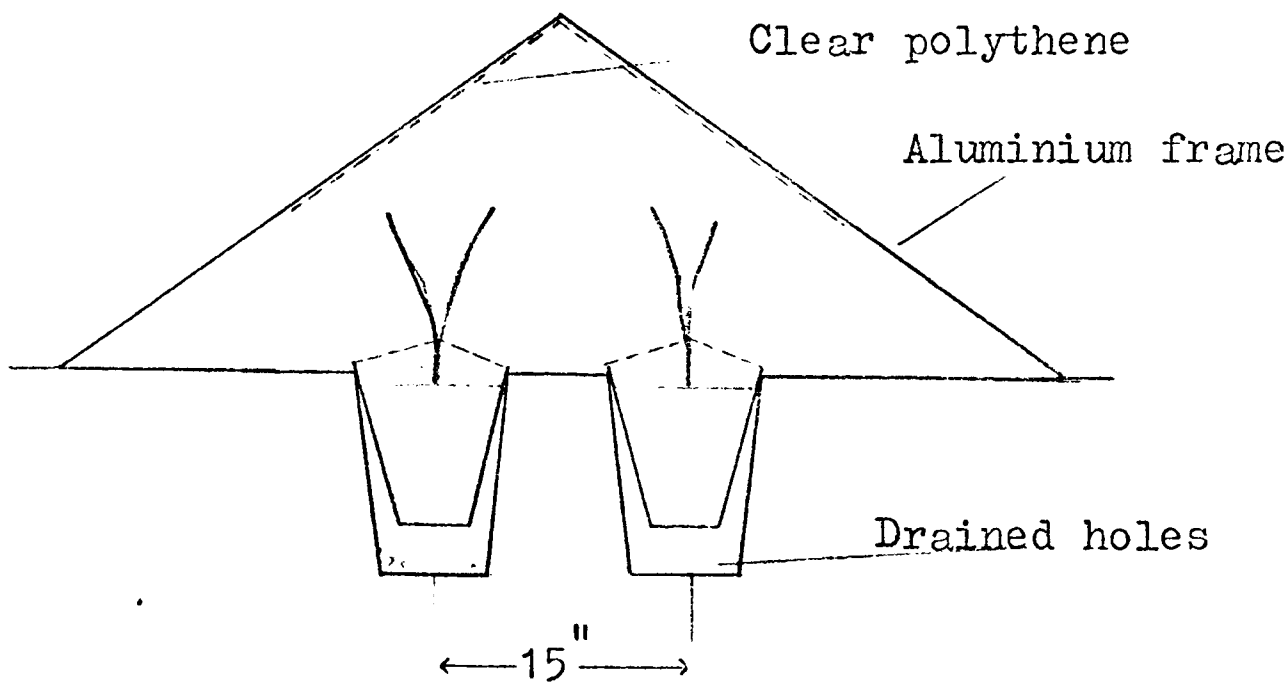
should have lost an average of 5% of their original weight by evapotranspiration.

STRUCTURE AND LAYOUT OF THE POTS

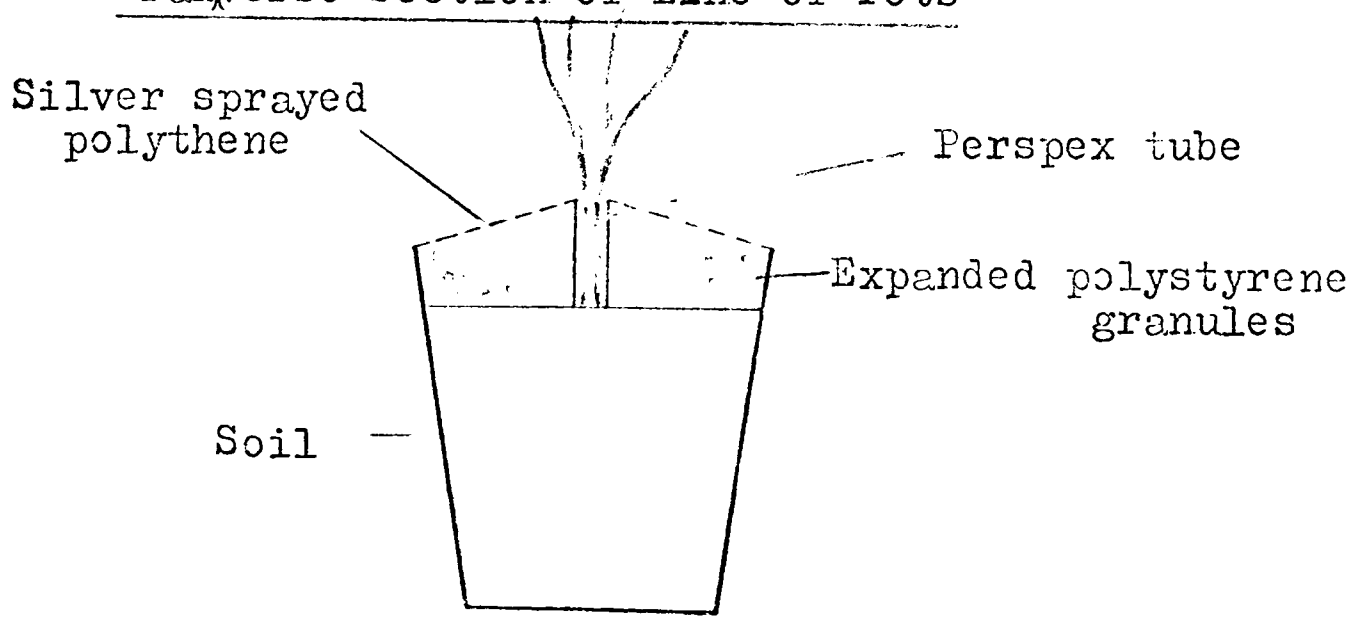
Fig.4.1.



Ground Plan of Pot Layout in the Field



Transverse Section of Line of Pots



Transverse Section of a Pot

should have lost an average of 5% of their original weight by evapotranspiration. This meant a loss of about 25% of their initial water and corresponded to a final mean water potential of 0.28 bars in the soil.

At harvesting the shoots were removed, sponged with cotton wool and weighed fresh, then dried at 70°C overnight before weighing dry. The dried material was stored in a dessicator and later ground and stored in polythene bags ready for chemical analysis.

The roots were separated from the soil by washing and sieving. Washed roots were centrifuged at 750 rpm in centrifuge cups lined with absorbent tissue to remove surface water evenly. They were then weighed fresh, and where there were more than about 3g of roots to a pot, a 3g subsample was taken. The root length of the sample was measured using a ruler. A full size photographic print of the roots was also made, suitable for alternative methods of measuring the root length (see 4.7 g). Subsamples were then returned to the rest of the roots for oven drying, weighing, grinding and storage in the dessicator ready for chemical analysis.

4.3c. Sampling the soil solution

Evenly spaced cores from the full depth of the soil were taken from all pots during the growth period. The sampling dates for the different pots are given in Table 4.6. The cores were obtained using a polished brass tube of 1 cm internal diameter with a sharp cutting base. The outside of this sampling tube was silicon greased to prevent soil sticking to its surface. About 100g of moist soil was extracted from each pot in each sample. This disturbed a negligible fraction of the soil and root system. Samples were stored in polythene bags at 0°C until the same evening when the solution was extracted.

The soil samples were rapidly hand mixed with 150g of pure coarse ground silica. The resulting mixture was packed evenly in 2.5 cm diameter glass tubes. A piece of Watman No. 42 filter paper was taped to the base of each tube. Ethyl alcohol was added to the top of the column. After rapid initial channelling the alcohol formed a continuous solvent front and moved

downwards displacing the equilibrium soil solution. The soil solution was collected in a polythene vial as it dripped from the filter paper. Drops of the displaced solution were tested with pernitrator ceric acid (10g in 50 ml of 1N. HNO_3) which forms a red compound with, and is a sensitive indicator for, alcohol. This test enabled us to stop collecting the solution as soon as alcohol began to dilute the displaced soil solution (Moss, 1963) The vials were sealed and the displaced solution was stored at -15°C until analysed.

4.4 Chemical Analysis of the Plants and Soil Solutions

4.4a. Preparation of the Plants and Soil Solutions for Analysis

About 0.3g of powdered plant material was weighed out into 50 ml conical flasks, 5 ml of fuming "Analar" HNO_3 was added and small sealed funnels were placed in the mouths of the flasks. The flasks were heated for 12 to 24 hrs on a sand bath, maintaining the HNO_3 just boiling and condensing in the funnel, until only a clear pale yellow liquid remained. Then the flasks were gently evaporated to dryness and 4 ml. of 6N.HCl was added to each and evaporated to dryness. The residue was dissolved and made up to 100 ml in N/10 HCl and stored in polythene bottles for analysis.

Before digesting all samples the above wet ashing procedure was compared with dry ashing. Plant material was dry ashed by heating about 0.3g at 450°C for 4 hours in a muffle furnace. The ash was dissolved in 100 ml of N/10 HCl. Ca, Mg, K and P were analysed in the solutions from both ashing procedures. The results from a sample of shoot from the final harvest are shown below. There were five replicates of each treatment.

Element	Ca		Mg		K		P	
Method of Digestion	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
% of Dry Weight	1.33	1.33	0.22	0.22	2.22	2.34	1.92	1.98
Coefficient of Variation(%)	2.1	3.2	all identical		5.9	4.1	1.3	1.2

Since there were no significant differences between the amounts extracted by the two procedures, the wet ashing was accepted as satisfactory.

1 ml of the extracted soil solution was diluted with 25 ml of N./5 HCl for K, Na, Mg and Ca analysis. For the other elements 1 ml. samples of the undiluted solutions were used with the exception of nitrate, for which the solution was diluted to ten times its volume before analysis.

Shoot and root digests and soil solutions from all the pots were analysed separately for each element apart from S. Thus, a picture of the variability in the contents of the different elements in both plants and soil solutions was obtained.

4.4b Analytical Methods

1)Cations. Cation concentrations were determined directly in the extracts using a Unicam S.P. 900. flame spectrophotometer. Standard solutions were prepared in HCl. K, Na and Ca were determined by emission, and Mg by absorption spectrophotometry. The wavelengths used were K-766.5mμ, Na-598 mμ, Ca-422.7 mμ and Mg 285.2 mμ. (Unicam Users Manual 1963).

2)Nitrogen in the Plants. The total N content of 0.1g samples of plant material was determined by a conventional microkeldjahl technique (Bremner 1965). The nitrogen in the plant material was reduced to the ammonium form by digestion in concentrated sulphuric acid containing selenium and K_2SO_4. Digest were transferred to a Markham apparatus and made alkaline by the addition of Na OH. The nitrogen was then driven off by steam distillation as ammonium which was collected in boric acid solution. The quantity of ammonia collected was determined by back titration with standard HCl. The procedure was checked by similarly digesting and volatilising known amounts of NH_4Cl.

3) Nitrate in the Soil Solutions. The Nitrate content of the soil solutions was determined by the phenol disulphonic acid method (Bremner 1965).

Special Reagents: Phenol Disulphonic Acid Reagent. 25 g of pure white phenol dissolved in 225 ml of concentrated H_2SO_4 and heated in a flask over boiling water for six hours.

The soil solution was diluted to ten times its volume with distilled water, and 1 ml of the resultant solution was gently evaporated at 100°C to

dryness. 2 ml of the phenol disulphonic acid reagent was added. The solution was made just alkaline with NH_4OH solution and made up to 50 ml with water. The colour intensity was determined using the Eel absorptiometer. A calibration curve was prepared using a calcium nitrate solution to which K, Na and Mg chlorides were added to the same mean concentrations as found in the soil solutions. The calibration graph was linear.

4) Chloride, The method of Tarnoky (1958) was used.

Chloride ions form a solution of the virtually undissociated mercuric chloride when added to a solution containing mercuric ions. If a solution containing a known concentration of mercuric ions is titrated into a solution containing an unknown quantity of chloride ions, when all the chloride ions have combined to form mercuric chloride free mercuric ions will remain in solution and their presence can be detected by the indicator diphenyl carbazone with which they form a blue complex. Thus the chloride content of the unknown can be determined by titration.

Special Reagents: 10% Sodium tungstate solution.

Chloride exists as the free ion in plant cells and is easily extracted by dilute acids. 0.1 g. samples of dry ground plant material were shaken with 10 ml of 0.1 N HNO_3 in stoppered tubes. The extract was filtered and 5 ml of the filtrate was added to a mixture of 1 ml of 0.66 N H_2SO_4, 1 ml of the 10% sodium tungstate and 0.1 ml of diphenyl carbazone indicator. The same mixed solutions were added to 1 ml samples of the soil solutions. Then mercuric nitrate (0.7×10^{-2} N) was added from a burette until a permanent pale violet colour remained in the flask. The titration was standardised using 10^{-2} M sodium chloride solution.

5)Sulphur. The microdetermination of sulphur is difficult. Several procedures were examined including the turbidimetric method (Bardsley and Lancaster, 1965) which gave reasonable results for soil solutions but required careful repetition of the same conditions in every analysis. Finally, the rather tedious procedure of Johnson and Nishita (1952) was used. Because of the time involved one shoot and one root digest from one pot from each harvest

was analysed and the soil solutions from all the pots sampled at each date were bulked before taking a subsample for S analysis.

Special Reagents: 1) Reducing Mixture - 300 ml of Hydriodic acid HI (sp.gr. 1.57 + 75 ml. of 50% hypophosphorus acid + 150 ml of 90% formic acid. Mixture boiled for 10 minutes at 115°C with a stream of N_2 passing.

2) 50g. of Zinc Acetate + 12.5 g of sodium acetate trihydrate mixed in distilled water and made to 1 L.

3) 2 g. of p.amino dimethyl aniline dissolved in 1500 ml distilled water. 400 ml of conc.H_2SO_4 added. Made to 2L.

4) 10g Sodium dihydrogen phosphate and 10 g of pyrogallic acid dissolved in 100 ml of distilled water.

5) 25 g of Ferric ammonium sulphate $Fe_2(SO_4)(NH_4)_2\ SO_4 2H_2O$ with 5 ml.conc H_2SO_4 and 195 ml of distilled water.

In this procedure sulphate is reduced to hydrogen sulphide by heating with the very strong reducing mixture. The hydrogen sulphide produced is blown by a stream of nitrogen into the zinc acetate solution where it is absorbed to form zinc sulphide. The sulphu is then converted to H_2S by the addition of ferric ammonium sulphate, and the H_2S reacts with p.amino dimethyl aniline to form methylene blue. The intensity of the blue colour can be determined colorimetrically. By running standards the absorption of the final blue solution can measure the amount of sulphur initially added.

0.5 ml samples of plant digests, soil solutions or standard K_2SO_4 solutions containing between 0 and 50 ug. of S were placed in a flask, 4 ml of the reducing mixture was quickly added and a stream of N_2 was connected to pass over the solution. The mixture was gently boiled under reflux for two hours. The stream of nitrogen carried off the H_2S evolved and the gas stream was washed in ten times diluted reagent 4 before passing into 50 ml of the acetate solution (reagent 2) where the sulphur was dissolved. The collecting flask was then disconnected and 10 ml of the ferric ammonium sulphate reagent (5) was added. The flask was swirled and 2 ml of the p. amino dimethyl aniline was added; the flask was again swirled and made up to

100 ml with water. After 10 minutes the intensity of the blue colour was determined on the Eel colorimeter using filter 608.

6) Phosphorus. Plant P content and soil solution phosphate concentration were determined by the method of Truog and Meyer (1929).

Special Reagents: 1) Ammonium molybdate, $(NH_4)_6 Mo_7O_{24}. 4H_2O.$, 24g was dissolved in 300 ml of distilled water. Then 560 ml of N/10 HCl was added slowly to the mixture and made up to 1L. with distilled water.

2) Stannous chloride, $SnCl_2.2H_2O.$, 40 g was dissolved in 100 ml of conc. HCl solution and added to 400 ml of distilled water.

1 ml of the unknown or standard KH_2PO_4 was mixed with 2 ml of the ammonium molybdate reagent and made up to 50 ml with distilled water. 25 ml of this solution was pipetted into the absorption cell of an Eel absorptiometer. The absorbance was recorded in comparison with a reagent blank. Then 0.1 ml of the stannous chloride reducing mixture was added and the absorbance of the blue solution was determined four minutes later.

7) Recovery Tests on the Analytical Methods.

In order to test the reliability of the analytical procedures for K, Na, Ca, Mg and P, known amounts of pure solutions of appropriate "Analar" salts were added to weighed samples of the shoot material from the final harvest. Increments of these elements equal to about 50% of that already in the plant material were added. The samples were dried and then wet ashed in parallel with untreated samples of the same plant material. A minimum of three replicates for each ion were so treated. The extracts were analysed in the ways described and the correspondence between the expected increases for each element and the analytical results was within ±2% for all elements except Na, which was consistently 10% higher than expected, indicating some enhancement effect in the flame photometer, or uniform contamination. No correction has been made in the results given for sodium to allow for this.

In the case of sulphur a known increment of K_2SO_4 was added to one of the plant digests and 100% recovery of S in the analysis was found. Known incre-

ments were similarly added to soil solution samples in all the analyses and the expected recovery was obtained.

These tests were taken as sufficient confirmation of the reliability of the methods used although the values given for the sodium content of the plants may be about 10% too high.

4.5 Measurements Needed to Calculate Diffusion Coefficients

The diffusion coefficients of the nutrients in the soil were determined indirectly using the approach described in Chapter 2. Equation 2.I reads,

$$D \triangleq D_L \quad v_L \quad f_L \quad \frac{dC_L}{dC}$$

D_L was obtained from tables (Parsons, 1959) and v_L was calculable from the known bulk density and water content of the soil. In order to calculate $\frac{dC_L}{dC}$ the bulk density and slope of the desorption isotherm were required hence isotherms for the exchangeable nutrients were determined experimentally f_L at the bulk density and water content of the pot soil was also measured experimentally.

4.5a The Tortuosity Factor f_L

f_L was measured by the method of Rowell, Martin and Nye (1967). Half cells of soil packed to a uniform bulk density were moistened with 0.01 M.$CaCl_2$ solution to a known V_L. In half of the cells Cl^{36} was incorporated in the solution. After equilibration the soil surfaces of the labelled and unlabelled cells were placed together, so that chloride self diffusion would occur between cells. In such a system the total amount of chloride that crosses the interface in time t, as a result of self-diffusion, is given by the equation,

$$\frac{Qt}{Q\infty} = \frac{2}{W}\sqrt{\frac{Dt}{\pi}} \quad , \text{ provided that } Qt/Q\infty < 0.5.$$

where, Q_t = amount that diffuses across the interface in time t.

Q_∞ = amount that diffuses across the interface in infinite time. This is equal to half the Cl^{36} initially added to the radioactively labelled half cell.

W = depth of one half cell.

Assuming $D = D_L f_l$ for chloride, f_L can be calculated from the derived formula,

$$f_L = (Q_t W / 2Q_\infty)^2 . (\pi/(D_L t))$$

In the experiment 2 mm. sieved soil was packed to the mean pot soil bulk density of 1.18 g. oven dry soil per cc. in six perspex half cells of measured dimensions. 0.01 M. $CaCl_2$ was added gently to bring V_L up to 0.39, same as that initially in the pot soil. Half of the cells contained 0.01µc/ml of ^{36}Cl. The moistened cells were sealed with polythene tape and silicon grease and stored in the dark in a humid atmosphere to equilibrate for four weeks. Then the cells were unsealed and the exposed faces of unlabelled and labelled cells were pressed together with a layer of lens tissue between, for later ease of separation, and left for four hours. After this time the halves were separated and the ^{36}Cl from each soil was extracted by shaking with 10 ml of 0.01M $CaCl_2$. Samples of the extract were counted and Q_t was determined

4.5b. Desorption Isotherms

4.5b.1 The Cations Potassium, Sodium and Magnesium.

Desorption isotherms for K, Mg and Na were calculated from experimentally determined Q/I curves for these elements (Beckett, 1964 b). Q/I curves were determined by equilibrating weighed quantities of soil with measured volumes of pure 0.01 M. $CaCl_2$ solution, or with $CaCl_2$ solution containing an initial amount of K, Na or Mg chloride. For example, in determining the K Q/I, solutions of 0.01 M $CaCl_2$ containing a range of initial KCl concentrations were equilibrated with samples of the soil. After equilibration, the K concentration in solution was measured. The amount of K that the soil had adsorbed from or desorbed into each solution, ΔK, was then calculated. The concentration of Ca and Mg in the equilibrated solutions was also measured

from which the activity ratio $a_K/\sqrt{a_{(Ca + Mg)}}$ was calculable . Thus, the Q/I curve for potassium, which is the plot of $a_K/\sqrt{a_{(Ca+Mg)}}$ against ΔK, could be drawn. Analogous procedures yield the Na Q/I, the plot of ΔNa against $a_{Na}/\sqrt{a_{(Ca+Mg)}}$ and the Mg Q/I, ΔMg against $a_{Mg}/\ a_{(Mg + Ca)}$. (Actually activity corrections, which are small in 0.01 M $CaCl_2$ solution, were not calculated and the curves presented and used were in terms of the concentration ratios

$$[K]\ /\sqrt{[Ca + Mg]}\ ,\quad [Na]\ /\sqrt{[Ca + Mg]}\quad \text{and}\quad [Mg]\ /\ [Mg + Ca]\ .)$$

As is predicted by the Ratio Law (Schofield, 1947, Schofield and Taylor, 1955), it has been shown that $a_K/\sqrt{a\ (Ca + Mg)}$ can be taken as constant in most soils over a range of total electrolyte concentration from 0.002 to 0.4 Equi s/L. (Beckett, 1964a, Tinker, 1964, Mathews and Beckett, 1963). Given that the Ratio Law applies, it is possible to derive the cation exchange isotherm of a soil for any concentration of Ca and Mg in the soil solution from the Q/I curve. Ca and Mg concentrations can be measured in soil solution samples as was done here. Alternatively, in a calcium dominated soil like Wytham silt loam, Ca and Mg comprise nearly all the cations in the soil solution (see Table 4.6) It follows that the combined concentration of these two ions almost equals the total electrolyte concentration of the soil solution and in such a case $\sqrt{a_{(Ca+Mg)}}$ can be approximately calculated from the total electrolyte concentration.

The exchange isotherm of a cation is the plot of its concentration in solution, usually in Moles/cc, against the total concentration of the exchangeable cation in the soil, again in Moles/cc. Again taking K as an example, if we know $\sqrt{a_{(Ca+Mg)}}$ in solution we can determine a_K in solution for different values of ΔK from the Q/I curve. Using the appropriate activity correction we can then calculate K concentrations in solution in equilibrium with different values of ΔK. ΔK in the Q/I curve is expressed as milliequivalents per 100g of oven dry soil, therefore it is necessary to know the bulk

density and water content of a soil in order to calculate an isotherm from the Q/I curve. Thus, if we have a soil bulk density of x g of oven dry soil /cc, a volumetric water content of V_L cc/cc, an initial equilibrium K concentration in the soil solution of K_{L1} Moles/cc, and from Q/I curve, a K concentration in solution of K_{L2} Moles/cc in equilibrium with a ΔK value of y m.e./100g of oven dry soil, the value of ΔK in moles/cc of soil will be given by

$$\Delta_K \text{ (moles/cc)} = \frac{y}{100} .x + V_L . (K_{L1} - K_{L2})$$

Hence, the ΔK axis of the Q/I can be converted to units of moles/cc of soil. Again, the same can be done for Na and Mg Q/I curves. The right hand term in the above expression is small for a strongly adsorbed cation like K, but for a weakly adsorbed ion, for example Na, it makes a considerable contribution to the values of Δ Cation/cc of moist soil.

Using this procedure the desorption isotherms of K, Na and Mg were derived from experimentally determined Q/I curves. The slopes of the isothemrs gave the values of dC_L/dC required to calculate diffusion coefficients for the cations (see Chapter 2).

It should be clear from the above that the cation desorption isotherm of a soil is unique to a particular total electrolyte concentration of the soil solution and that the diffusion coefficient of cations will vary with the total electrolyte cnncentration of the soil solution for this reason (Nye 1968b).

To determine the Q/I curve for potassium, 4g or 2 g samples of 1.2 mm sieved air dry soil were added to 40 cc of solutions of 0.01 M $CaCl_2$ containing KCl in some cases. KCl was added to 0.01M $CaCl_2$ to make a range of initial $K/\sqrt{Ca}$ concentration ratios from 0 to 0.008. The suspensions were shaken in open tubes, to allow aeration, for twenty four hours in the laboratory, where the temperature was about 15°C. The tubes were then centrifuged and the concentrations of K and Ca in the supernatant solution were measured.

Mg concentrations were rather small in this soil and Mg was not measured in determining the K or Na Q/I curves. From the analyses, ΔK and equilibrium $K/\sqrt{Ca}$ concentration ratios were calculated and the Q/I curve was drawn.

The sodium Q/I was determined in a similar fashion using a range of initial $Na/\sqrt{Ca}$ concentration ratios from 0 to 0.025. To obtain the magnesium Q/I, solutions of $MgCl_2$ and $CaCl_2$ were mixed together to give a total concentration in solution of 0.02 Equivs/L. and initial Mg/(Mg+Ca) concentration ratios from 0 to 0.08. These solutions were similarly shaken with soil and the final Mg/(Ca + Mg) and ΔMg values were determined.

4.5 b.2 Phosphate

It is known that the desorption of phosphate from soil into solution is affected by numerous conditions in the solution (White and Bekcett, 1964). For this reason, when determining desorption isotherms from which to calculate diffusion coefficients, every attempt was made to simulate the soil solution. The desorption solutions were maintained at the same total electrolyte concentration and pH as the mean values found in the soil solutions (see Table 4.6 and part 4.7b below) Previous workers in the laboratory had found that phosphate desorption was slow to reach a final equilibrium however a 24 hour desorption period was considered sufficient to establish equilibrium.

Some soil was labelled with P^{32} by adding 8 ml of a solution of 50μCi/ml P^{32} in 2×10^{-5} M. KH_2PO_4 carrier to 100 g. of air dry soil. The solution was added as very small drops using a syringe and the soil was mixed after each addition. The soil was mixed in a Kenwood mixer for two hours and distilled water was added to make a final water content of 33 g of water/100 g of dry soil. The soil was stored moist for six weeks to allow the added P^{32} to equilibrate with the labile P^{31} in the soil. The soil was stored in an insulated cupboard at 15°C and was kept aerated by opening the container and mixing by hand every five days. Two standards of the added

P^{32} solution were diluted 100 times and 1000 times respectively with 10^{-2} M.KH_2PO_4 and stored at -15°C.

After equilibration, samples of the labelled moist soil were weighed into small polythene vials. Five ml of a 1.65×10^{-2} M. $CaCl_2$ solution was added to each sample, and each was shaken vigorously on a wrist action shaker to break up the soil aggregates. Suspensions were then transferred to larger polythene bottles and volumes of 1.65×10^{-2} M.$CaCl_2$ ranging from 50 to 5000 cc were added. The 1.65×10^{-2} M.$CaCl_2$ solution was adjusted to pH 7 with $Ca(OH)_2$ solution before it was added to the soil. Most samples contained 1 g of soil but up to 4 g of soil were added to 50 ml of solution. Some solutions contained added KH_2PO_4 so that the upper regions of the isotherm above the equilibrium soil solution concentration could be obtained, in the normal way for a Q/I curve. The suspensions were aerated and agitated for 24 hours by a stream of moist air. The suspensions were then centrifuged at 4000 r.p.m., the pH of the supernatant was measured, and 5 ml samples were pipetted into polythene vials for counting. The phosphate concentration of the stronger solutions was determined by the method of Truog and Meyer (see4.4.b.6) from which it was possible to calculate the specific activity of the P^{32} in solution and determine the phosphate concentration in the more dilute solutions from their counts. The stored standards were counted at the same time and the counts initially added to the soil were determined. From this the counts adsorbed by the soil were calculated and, knowing the specific activity, the total exchangeable phosphate in the soil was calculated.

P^{32} was assayed by Cerenkov counting in a liquid scintillation counter (Turner 1967). Known amounts of P^{32} were added to all unknowns after they had been counted to check that the expected increase in counts occurred, and hence to ensure that no quenching effects were distorting the results. Quenching did not occur in the Ca Cl_2 extracts but previous erratic effects in perchloric acid digests of soil emphasized the need for this precaution.

The cation-anion balance of the experimental plants indicated that a net flow of negative ions, probably bicarbonate ions, had left the roots. This may have raised the pH in the rhizosphere. Previous work on an Upper Greensand soil of equilibrium pH about 6.5 had shown increased phosphate desorption when pH was either increased or decreased from 6.3 (Nye and Bagshaw pers. comm.). Hence the possibility that a different isotherm with greater phosphate solubility existed at higher pH values was investigated. The procedure was essentially the same as at pH 7, except that the 1.65×10^{-2} M $CaCl_2$ solutions were initially adjusted to pH 8 using calcium hydroxide solution. It is difficult to maintain constant high pH in aerated soil suspensions probably because of the formation of carbonic acid. After 18 hours the pH had decreased to 7.3 and at this time more calcium hydroxide was added to return the pH to 8. In more recent works, thedifficulty has been overcome by aerating the suspensions with $C0_2$ free air.

4.6 Methods of Calculation

4.6.a. Statistical Treatment of the Raw Data

Wherever a range of independent values was used to calculate a mean value the variability of the data was considered. Calculations of standard errors were made in the normal way. In the tables of data, coefficients of variations, expressed as percentages, are presented in brackets below such means, as for example in table 4.3.a.

4.6.b Calculation of Mean Nutrient Inflows

The mean inflows of nutrients over the three interharvest periods were calculated by an analogue of the equation for Net Assimilation Rate used in plant growth analysis (Gregory 1926, Williams, 1948, Loneragan 1968, Brewster and Tinker, 1970).

$$\bar{I} = \left[(\bar{U}_2 - \bar{U}_1)/(t_2 - t_1)\right] \quad \left[\ln.(\bar{L}_2/\bar{L}_1) \; /\bar{L}_2 - \bar{L}_1)\right]$$

Where $\bar{I}$ = Mean inflow of nutrient in Moles/cm/sec over the period between two harvests.

$\bar{U}$ = Mean plant nutrient content in Moles

t = time (secs)

$\bar{L}$ = Mean root length (cm)

Suffixes 1 and 2 stand for these values at two harvests at times 1 and 2 respectively.

As was emphasized by Radford (1967), this equation is valid only as long as the ratio of plant nutrient content to root length remains constant, i.e. only if $\bar{U}/\bar{L}$ is constant. This was the case for most nutrients here, since both uptake and root growth showed a parallel increase with time; but for sodium there was a decrease in $\bar{U}/\bar{L}$ over the growth period so that the calculated mean Na inflows may be slightly inaccurate.

Since plants harvested at successive times were not paired, there was no way of calculating individual plant inflow rates, from a set of which, standard errors and coefficients of variation for the mean inflow values could have been calculated in the routine way. Estimates of the error of the mean inflow values were nevertheless calculated from a formula which incorporated the variance of plant uptake and root length at each harvest. The formula is

$$\text{var.}\bar{I} = 1/(t_2-t_1)^2((\text{var.}\bar{U}_2-\text{var.}\bar{U}_1)(\ln.(\bar{L}_2/\bar{L}_1))^2/(L_2-L_1) +$$

$$2(K_2.\text{cov.}\bar{U}_2\bar{L}_2+K_1.\text{cov.}\bar{U}_1\bar{L}_1)(((\bar{U}_2-\bar{U}_1).\ln.(\bar{L}_2/\bar{L}_1))/(\bar{L}_2-\bar{L}_1)^3) +$$

$$(K_2^2.\text{var.}\bar{L}_2+K_1^2.\text{var.}\bar{L}_1)((U_2-U_1)^2/(\bar{L}_2-\bar{L}_1)^4))$$

where , I = nutrient inflow, U = plant nutrient content, L = root length. $\bar{I}$, $\bar{U}$, and $\bar{L}$ refer to the mean values for the ten plants from each harvest. var. stands for variance. cov. stands for covariance, thus cov.$\overline{UL}$ means the covariance of the values of U and L from a particular harvest. Suffixes 1 and 2 refer to values from harvests one and two respectively. ln. means $\log_e$.

$K_1 = (\bar{L}_2/\bar{L}_1)-1-\ln.(\bar{L}_2/\bar{L}_1)$ and $K_2 = 1-(\bar{L}_1/\bar{L}_2)-\ln.(\bar{L}_2/\bar{L}_1)$

$\text{var.}\bar{L} = (\Sigma(L-\bar{L}))^2/(n(n-1))$ and similarly for var.$\bar{U}$.

$\text{cov.}\overline{UL} = (\Sigma(L-\bar{L})\ (U-\bar{U}))/(n(n-1)$

n is the number of plants per harvest.

The estimate of the variance of mean inflow calculated in this way has n-1 degrees of freedom. The standard deviation of mean inflow is of course given by the square root of the variance.

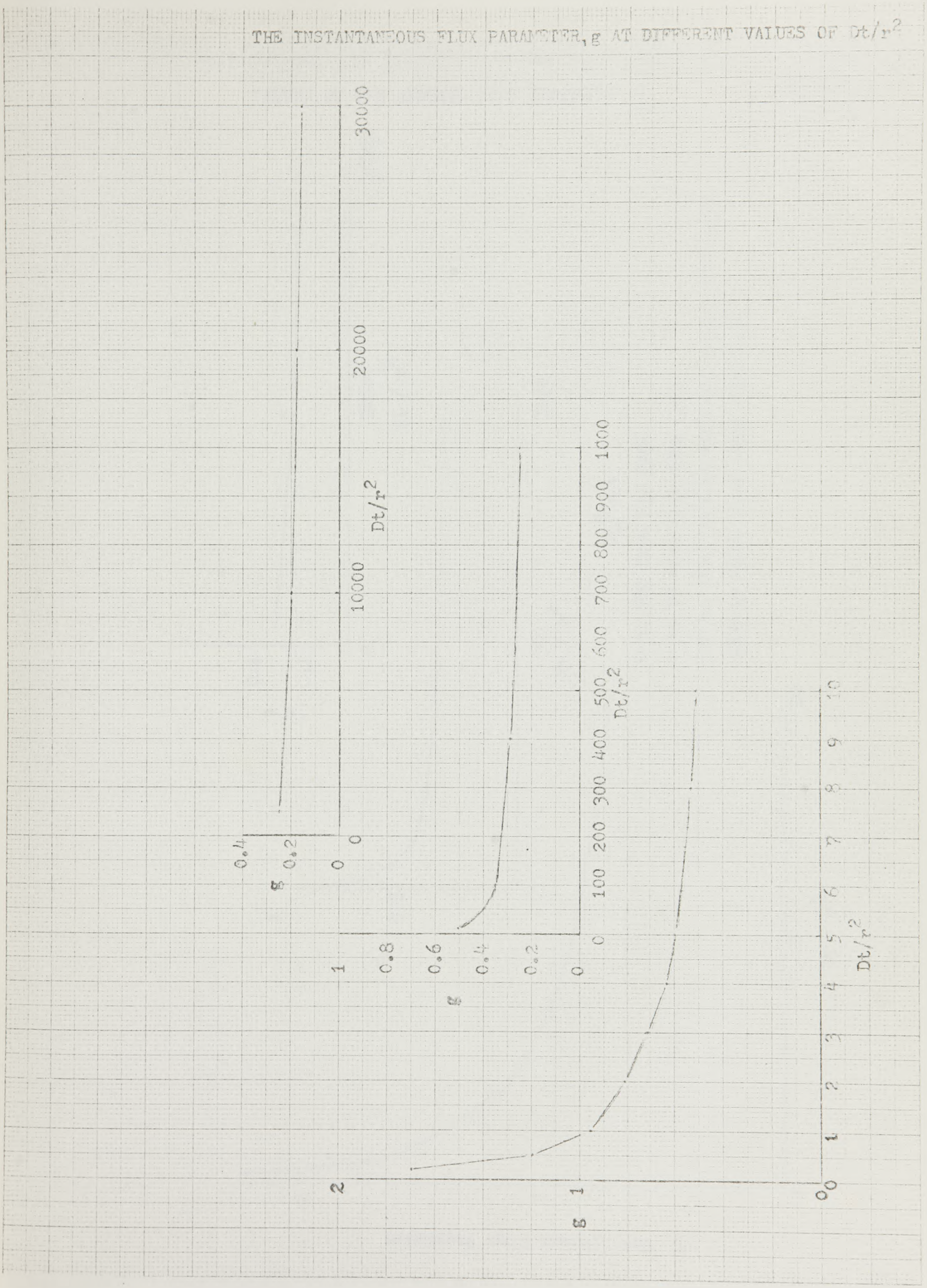
The formula was derived by the method of Kendall and Stuart (1968 vol.1 p.231).

4.6.c. Calculation of the Mean Flux Parameter, $\bar{g}$

The value of $\bar{g}$, the mean flux parameter for each interharvest period, was calculated for each ion in turn using the graphs shown in Figs.4.2,4.3 and 4.4 of the instantaneous flux parameter, g, and the average flux parameter, G, against Dt/r^2. $\bar{g}$ was calculated by dividing the root system into three age classes 0-1, 1-10 and greater than 10 days old. From the root growth curve (Fig.4.7) the fraction of the total root length in the three age classes, p_1, p_2 and p_3, and the mean age of the roots in each, t_1, t_2 and t_3, were calculated. Values of D for each nutrient had been calculated by equation 2.1; the mean root radius $\bar{r}$ was known and values of $Dt_1/\bar{r}^2$, $Dt_2/\bar{r}^2$ and $Dt_3/\bar{r}^2$ were calculated. The value of G at $Dt_1/\bar{r}^2$ was multiplied by p_1 and values of g at $Dt_2/\bar{r}^2$ and $Dt_3/\bar{r}^2$ were multiplied by p_2 and p_3 respectively. The sum of these products was the estimate of $\bar{g}$. The calculation of $\bar{g}$ for potassium is set out in full in Table 4.1.

The fraction of the total root length of each age remained constant up to the third harvest since the relative growth rate of root length (cm. of root produced/cm. of root/day) was constant during this period. Between harvests 3 and 4, however, the relative root growth rate diminished, and the proportion of roots of each age changed. The value of $\bar{r}$ also de-

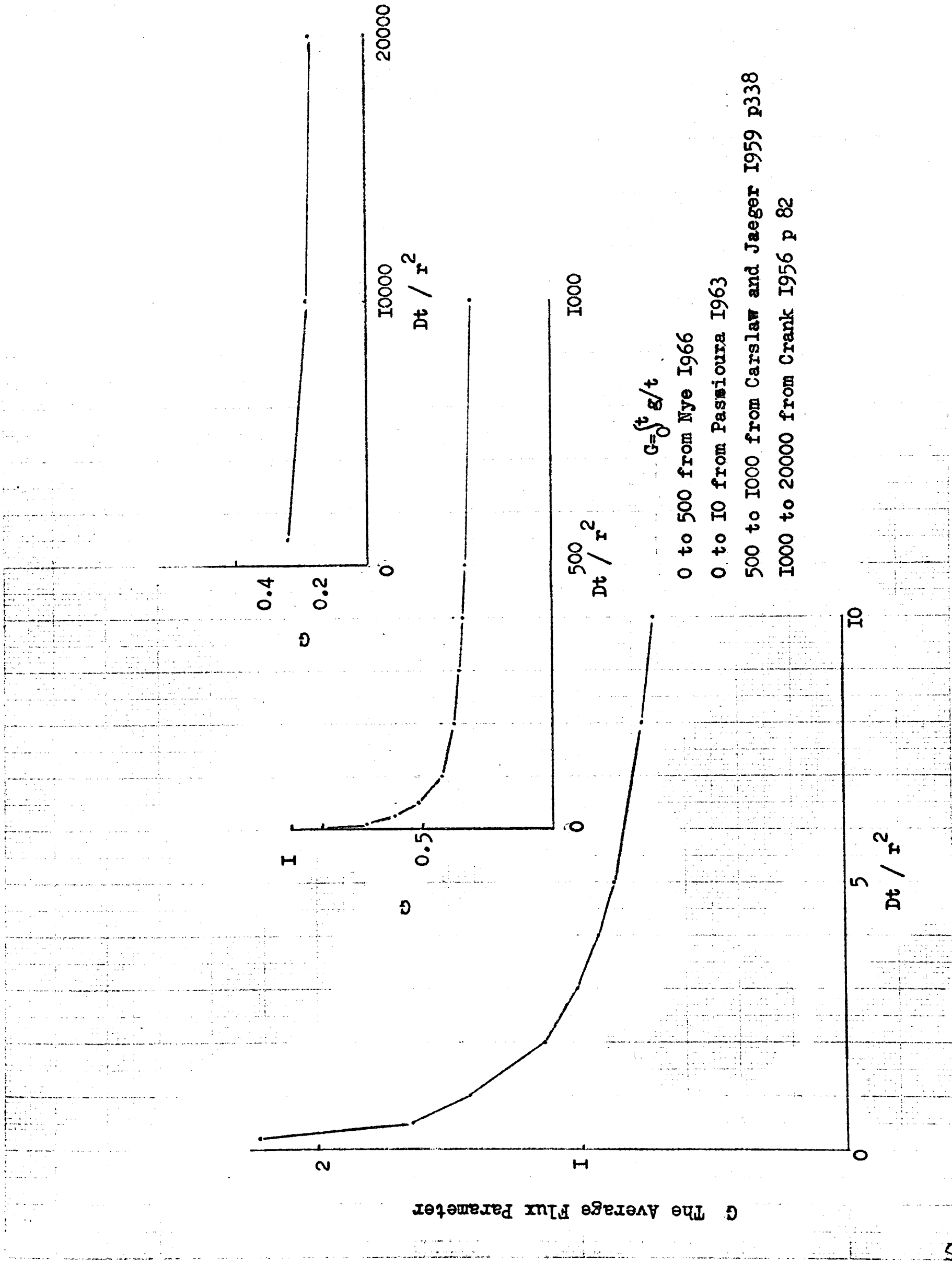
THE INSTANTANEOUS FLUX PARAMETER, g AT DIFFERENT VALUES OF Dt/r^2



CYLINDRICAL FLUX PARAMETERS AT LOW VALUES OF Dt/r^2

Fig.4.3.

VALUES OF THE AVERAGE FLUX PARAMETER G



CYLINDRICAL FLUX PARAMETERS AT LOW VALUES OF Dt/r^2

The Average Flux Parameter G
(by graphical integration of g)

The Instantaneous Flux Parameter g
from Jaeger and Clark(1942)

g=18.33 at Dt/r^2=0.001

G

g

Dt/r^2

0 0.1 0.2 0.3 0.4 0.5

0 2 4 6 8 10 12 14

THE CALCULATION OF THE MEAN FLUX PARAMETER $\bar{g}$ FOR POTASSIUM

Interharvest period	1 and 2			3		
Root age class (days)	0-1	1-10	10	0-1	1-10	>10
Mean root age (days)	0.5	4	16	0.5	5	17
Proportion of root this age p	0.11	0.53	0.36	0.08	0.50	0.42
Mean root radius $\bar{r}$		0.03			0.026	
$Dt/\bar{r}^2$	9	83	305	12	120	410
G or g (from fig 4.2, 4.3 or 4.4)	0.74	0.36	0.31	0.68	0.34	0.29
p X G or g	0.081	0.19	0.11	0.054	0.17	0.12
$\bar{g}$		0.38			0.35	

Table 4.1

VALUES OF THE MEAN FLUX PARAMETER $\bar{g}$

Nutrient	K	Na	Mg	Ca	NO_3	Cl	SO_4
Interharvest period							
1 and 2 (unbuffered)	0.38	0.28 (0.24)	0.46 (0.26)	0.27	0.24	0.24	0.26
3 (unbuffered)	0.35	0.26 (0.22)	0.41 (0.24)	0.25	0.23	0.22	0.24

Table 4.2

creased between harvests 3 and 4. Thus the same value of $\bar{g}$ for each nutrient applied to interharvest periods 1 and 2 and a different value of $\bar{g}$ was calculated for interharvest period 3.

4.7 Ancillary Experimental Work

A certain amount of experimental work was performed uyielding information not directly used to calculate values of the parameters in equation 3.X. This work is summarised in 4.7 along with its results.

4.7.a. Soil Moisture Characteristic

A water characteristic was needed to determine the water content at -0.05 bars water potential, the field capacity. It was also of interest to know the water stress imposed on the plants by the drying of the soil until the pots had lost 5% of their initial weight.

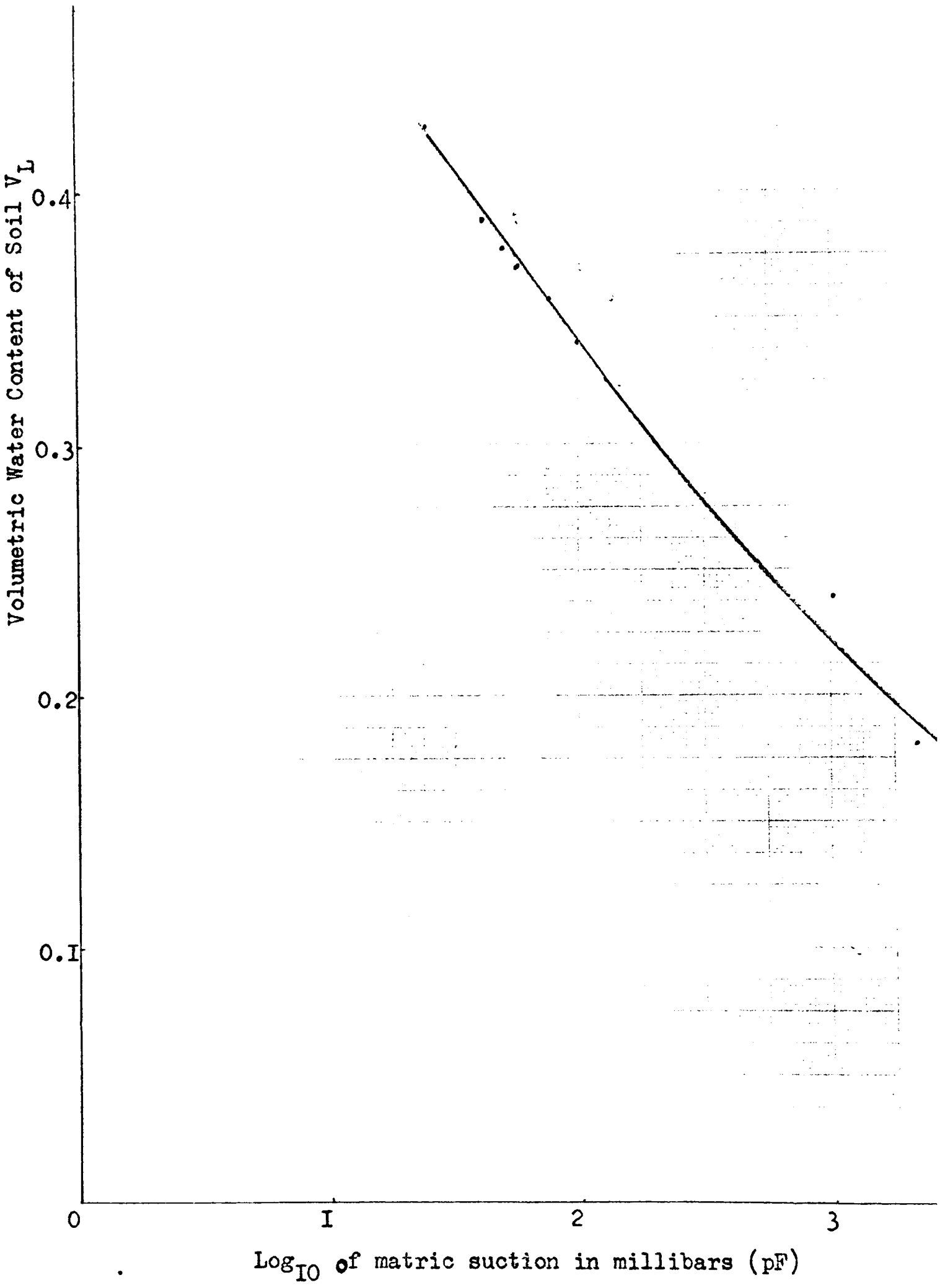
The water characteristic from 0 to-0.1 bars was determined by measuring the water content of 20g. of the structured pot soil on a sintered glass suction table at successively higher suctions. The water content at greater suctions was determined using the pressure membrane apparatus (Soil Moisture Inc). Samples of soil were weighed after they had reached equilibrium with a range of external gas pressures up to 2 atmospheres. The soil water content V_L is plotted against matric suction in fig.4.5. In the pot experiment the mean value of V_L at harvest was 0.30 which corresponded to a soil water potential of -0.28 bars.

4.7.b. Soil pH

The pH of the soil was measured in several ways and all indicated a pH around 7. The pH of bulked samples of displaced soil solution from each sample date ranged from 6.7 to 7.3. 10g of air dry soil shaken for one hour with 20g. of 1.65×10^{-2} M $CaCl_2$ gave a supernatant pH of 6.9 but the reading was not stable and drifted slowly upwards. Forty eight hours later it read pH 7.5. A shaking of 10g. of soil for one hour with 20g. of distilled water gave a pH of 7.2; this had drifted up to 7.7 after forty-eight hours. Drift is common in soil pH determination (Ramzan 1970). This soil may have been

WATER CHARACTERISTIC OF WYTHAM SILT LOAM

Fig.4.5.



drifting towards pH 8.2, the equilibrium pH for calcite in water with CO_2 at the atmospheric partial pressure, since it contained particles of calcite.

4.7.c. Cations Exchangeable to Ammonium Acetate

Exchangeable K, Na and Mg were determined in an ammonium acetate extract of pH 7. The soil contained free calcium carbonate so that the calcium content of an extract at pH 7 could not be used to determine exchangeable Ca. The total exchange capacity was estimated by subsequent displacement and determination of the adsorbed ammonium ions. Exchangeable Ca was estimated as the difference between the total exchange capacity and the K,Na and Mg desorbed, which is probably a fair assumption in a calcium dominated soil with pH normally around 7.

The cation exchange capacity was 25.5 m.e./100 g. of oven dry soil and the quantities of exchangeable K, Na, Mg and Ca were 0.91, 0.16, 1.0 and 23.3 me/100g of oven dry soil respectively.

4.7.d. Slow Release of Potassium from the Soil Solids

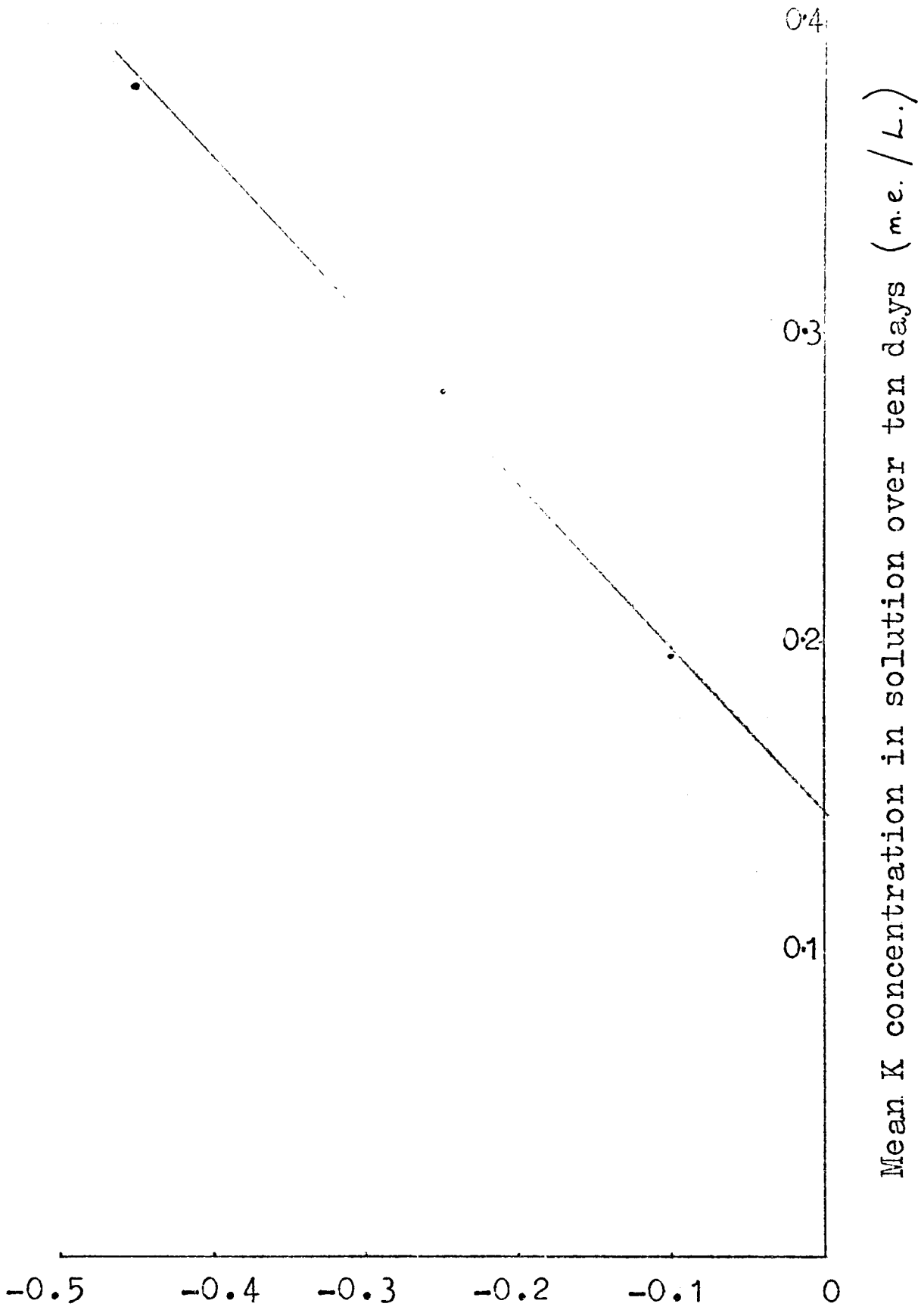
The fixation and slow release by soil of non-exchangeable potassium has often been reported. (Addiscott and Talibudeen,1969). If depletions are maintained for long around plant roots, then slow release could contribute significantly to the flow to roots. A failure to estimate this and deduct the K supply to roots due to such slow release could lead to an overestimate of the supply attributable to the diffusion of exchangeable K. Therefore, long term K release and fixation were studied using the approach of Mathews and Beckett (1962).

4g. samples of sieved air-dry soil were shaken with 40 ml. of various solutions of 0.01 M. $CaCl_2$ with KCl added to make initial $K/\sqrt{Ca}$ concentration ratios ranging from zero to 0.006. The $K/\sqrt{Ca}$ concentration ratio was determined after twenty four hours shaking and again after eleven days. To follow the effects of extreme K depletion, the solution was decanted and a further 40 ml. of pure 0.01 M.$CaCl_2$ solution was added, and the same procedure was repeated on the already depleted soil.

Fig.4.6 shows the change in $K/\sqrt{Ca}$ concentration ratio in solu-

Fig.4.6.

SLOW FIXATION OF POTASSIUM BY WYTHAM SILT LOAM.



Change in solution activity ratio $K/\sqrt{Ca}$ in ten days of shaking 4g of soil in 40ml of 0.01M $CaCl_2$ containing a range of KCl concentrations.

(X 10^3)

tion plotted against the mean $K/\sqrt{Ca}$ ratio in the solution over the ten days of shaking. Above a $K/\sqrt{Ca}$ of 0.0015 K was fixed by the soil at a rate proportioned to the concentration above this level. Suspensions with an initial $K/\sqrt{Ca}$ concentration ratio of 0.00016 had a ratio of 0.00033 after thirty three days of shaking, indicating that a very slow release could occur into solutions of very low K concentration.

Thus it appears that the soil was slowly fixing K at solution concentrations down to about 40% of that initially in the fertilised soil. It follows that before slow release could contribute to plant supply a 40% diffusion depletion at the root surface would be necessary.

Interestingly, from the Q/I plot a decrease in Activity ratio from 0.004 to 0.0015 is equivalent to a decrease of 0.2 me of K/100g of oven dry soil and the initial rate of fertilisation of 75 ppm K is about equal to 0.2 me K/100g soil, suggesting that in the fertilised soil the K concentration in solution was slowly diminishing towards the unfertilised level.

4.7e. Slow Desopption of Phosphate from the Soil Solids

Phosphate desorption from soil into solution has not necessarily reached equilibrium after 24 hours. In the pot experiment the roots had a mean age of about 6 days and slow release could have contributed to the phosphate flow to the roots. The possibility of such significant slow release was investigated by leaving aerated suspensions containing 1g of P^{32} labelled soil in 2400 and 5000 ml of 1.65 M $Ca\,Cl_2$ solution for ten days. The pH was 6.9 initially and fell to 6.7 after ten days. Phosphate concentration in solution was determined by p^{32} after 24 hours and after 10 days.

There was no release of phosphate into the extremely dilute solutions between one and ten days, and in fact, the concentration of phosphate in solution decreased about 20% in both cases. Hence, slow release seems unlikely to occur and slow adsorption appeared to be continuing even from solutions as dilute as 5×10^{-7}M.

4.7.f. Adsorption of Sulphate by the Soil

Two replicates of 10 g. of moist soil were shaken for an hour and a half with 20 ml of a solution containing 10^{-3} Moles/L $CaSO_4$, 1.8 x 10^{-2} µCi/ml of $S^{35}O_4$ and 1.65 x 10^{-2} Moles/L $CaCl_2$. The suspensions were then centrifuged and three 1 ml samples of the supernatant from both replicates plus three similar samples of the original solution were dried on planchettes and the β^- emission was counted. The water content of the soil was also determined by drying to 105°C. An allowance was made in calculation for the dilution of $S^{35}O_4$ by the solution initially present in the soil.

Both replicates showed a 15.5% decrease in counts below the level that would have been expected if there had been no SO_4 exchange or adsorption. Hence, 15.5% of the SO_4 initially added, either exchanged with native soil SO_4 or was adsorbed from solution on to the soil solid. There was therefore a little sulphate adsorption or exchange in the soil and strictly the calculation of a sulphate diffusion coefficient required a sulphate desorption isotherm.

4.7.g. Methods of Measuring Root Length

The measurement of root length can be difficult and tedious, and various methods for measuring length were tested prior to measuring all the samples. The four methods tested were,

1) Direct measurement by laying roots along a ruler.
2) Running a map measuring wheel along full sized photographs of roots.
3) On such a photograph, relating to the root length the number of intersections between roots and random lines traversing the photograph using Newman's (1966) formula.
4) Measuring the frequency distribution of diameter on a sample of roots and estimating the length by assuming the roots to be cylindrical with a specific gravity of 1g/cc.

In order to make the full sized photographs used in methods 2 and 3, washed roots were laid on a sheet of glass and pressed flat by superimposing a further sheet. This transparent "sandwich" was taken to a dark room and placed on a sheet of Kodak bromide paper. The paper was exposed for two seconds to tungsten

bulb light, developed, fixed and dried.

In method 3 the root photographs were placed under a sheet of glass. The sides of the glass were marked with numbered half centimetre divisions like the x and y coordinates of a graph. Random points in the sheet were obtained by using random number tables to derive random coordinates. A 10 cm long piece of celluloid upon which a line was scratched was spun with its centre on the random point. When this line came to rest the number of intersections it made with roots was counted. A random angle for the line could have been chosen from tables to be strictly statistically correct, but spinning was considered unlikely to be biassed. According to Newman (1966) $L = \pi NA/2H$ where, L = total root length on the print, N = number of intersections between random lines and roots, A = area of the print, and H = total length of the random lines. Since publication, and since my tests, Newman (pers comm.) has pointed out that an "edge area" around the edge of the print half as wide as the length of the random line should be included within the coordinates for choosing the random points on which to centre the random lines. If this is not done then the roots at the edge of the print have slightly less chance of intersecting a random line than those in the middle, and if for any reason the roots are clustered near to or away from the edge, the formula will yield a biassed estimate of L.

To test this method three 800 cm lengths of cotton thread were cut into 100 cm, 3 cm and 1 cm pieces respectively. A full sized photoprint was made of each batch. The mean length was estimated from the mean of 10 sets of 80 random 10 cm lines scattered over the 1600 sq.cm. of each print. The results were,

True Length cm.	Approximate Length of units cm.	Estimated Length cm.	95% Confidence Limits of the mean
800	100	850	813-884
800	3	820	788-852
800	1	807	763-851

Clearly, the variability was considerable and there was an unexplained tendency to overestimate the total length of the 100 cm threads. The omission of the "edge area" mentioned above, coupled with a tendency of the longer threads to cluster away from the edge of the prints may have been the cause of the overestimate.

To test method 4 the diameters of the roots intersected by a random transect crossing one of the prints were measured using a microscope with a scale in the eyepiece. The fresh weight of the sample had been determined immediately after harvest. Surface water was removed from washed root samples before weighing, by centrifuging them on adsorbent tissue for 2 minutes at 700 r.p.m. If the density of fresh roots is 1g/cc, then,

$$L = W.N./ (\Pi/4) (\Sigma d^2)$$

where L = root length, cm., W = root fresh weight, g., N = number of root diameters measured and d = root diameter, cm. From a sample of forty diameters the root length of the test sample was estimated to be 465 cm. The same sample was found to be 485 cm.long when measured by ruler.

In another trial, using the same sample of roots throughout, the times required to perform repeated measurements as well as the results obtained from them were recorded. The results were,

Method	Time (hrs.)	Length (cm)
1) Ruler	2.75	1155
	1.9	1164
	1.9	1161
2) Map Wheel	2.75	1005
	2.5	1043
3) Random Transects	1	1160
	0.8	1297

On balance it was decided to use a ruler and measure roots directly for these experiments. In general, the most satisfactory method will depend on the type of roots to be measured and the accuracy required. Methods 1 and 2 were possible with large fairly straight roots like those of leeks,

but for the majority of roots, methods 3 and 4 are probably the only practicable techniques. The knowledge of root diameter derived from method 4 could be incorporated into a model of diffusive nutrient supply to roots which could make some allowance for the effect of the different diameters of roots that are present in a root system. Root diameter might also be related to root absorbing power (α). Clarkson, D.T. and Sanderson, J. (1970).

4.8 The Climate during the Growth Period

The experimental plants were growing and transpiring rapidly between June 10 and July 17, 1967. The mean daily maximum air temperature during this period was 22°C and the mean daily minimum 12°C. Soil temperatures 7.5 cm below the surface were measured around 5.30 p.m. every third day. Values ranged between 18 and 24°C on different days and the temperatures in pots of different sizes were very similar at any one time. In Oxford, the yearly maximum mean potential evapotranspiration of 3.70"/month occurs in June and July (Meterrological Office, London, 1960). Records from a nearby reservoir showed large differences in the evaporation rate of surface water on different days during this period (Oxford and District Water Board, pers.comm.).

The values are tabulated below.

Tank evaporation inches/day	0-0.5	0.5-1.0	1.0-1.5	1.5-2.0	2.0-2.5	2.5-3.0	3.0-3.5
Number of days between June 12 and July 18 with evaporation in this class	4	9	10	6	4	0	4

In the pot experiment, the mean water velocity at the root surface, $\bar{v}$, during the first two interharvest periods was calculated as 1.25×10^{-6} cm/sec (see 4.9.a.below). If daily mean water velocities varied in parallel to open evaporation, the extreme values would have been 0.22×10^{-6} and 2.9×10^{-6} cm.sec. Weighing was not frequent enough to detect daily changes in transpiration rate and in fact, transpiration rates vary less drastically than surface water evaporation

from day to day (Geiger, 1965 p.278).

4.9 Results and Discussion of the Main Experiment

4.9.a. Plant Growth, Nutrient Uptake and Transpiration

The results are tabulated in detail in Table 4.3a, b, c, d and e.

The increase in plant dry weight with time is shown in Fig.4.7. Growth was exponential up to harvest three Over the whole period the average relative growth rate was 0.13 g./g./day. This is a rather low rate for an arable crop where typical values of 0.2 to 0.3 g./g./day have been found at 20°C. (Warren Wilson 1966).

The growth of root length is also shown in fig.4.7. This too followed an exponential curve until harvest three. There was an average of one centimetre of root length per milligram of plant dry matter. Mean root diameters for harvests one to four respectively were 0.56, 0.64, 0.53 and 0.44 mm. Mean radii of 0.03 cm for interharvest periods one and two, and of 0.026 cm for interharvest period three, were used in calculating $\bar{g}$ values. The measurements of root diameter are presented as histograms in Fig.4.8. In respect of root length, a similar pattern was found in all those pots where the distribution of root length was measured. The mean percentages of the total length in each region were; against the side of the pot, 23%, within the top quarter of the soil volume 35%, within the upper middle quarter 24%, within the lower middle quarter 11% and within the bottom quarter 7%.

Nutrient uptake is shown in Figs. 4.9 and 4.10. The curves for most nutrients were very similar to those for plant weight. Sodium had an atypical uptake curve and the percentages of sodium in the shoot tissue diminished markedly with plant age. The percentage nutrient contents of the dry matter (Table 4.3.c.d. and e) were rather high. The National Vegetable Research Station (pers. comm). gave typical values for the nutrient percentages of leek shoot dry matter as K 1.5 to 4, Mg 0.37 to 0.45, Ca 1.2 to 2.3, N 3.8 to 6.1 and P about 0.3. The fractions of the exchangeable nutrients initially present in the soil that had been absorbed by the plants at harvest are given

DRY WEIGHT AND ROOT LENGTH OF LEEKS IN POTS

Fig.4.7.

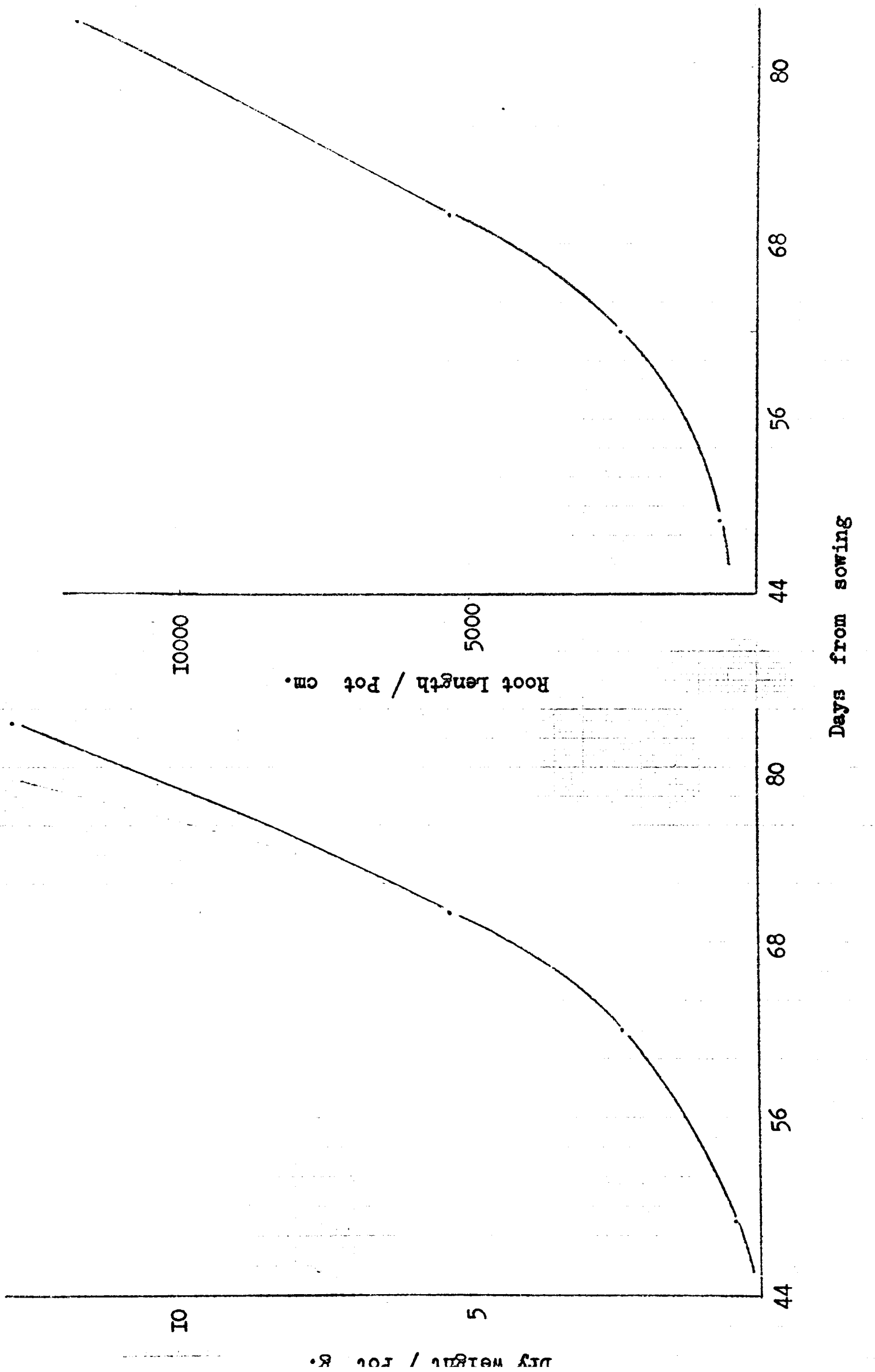
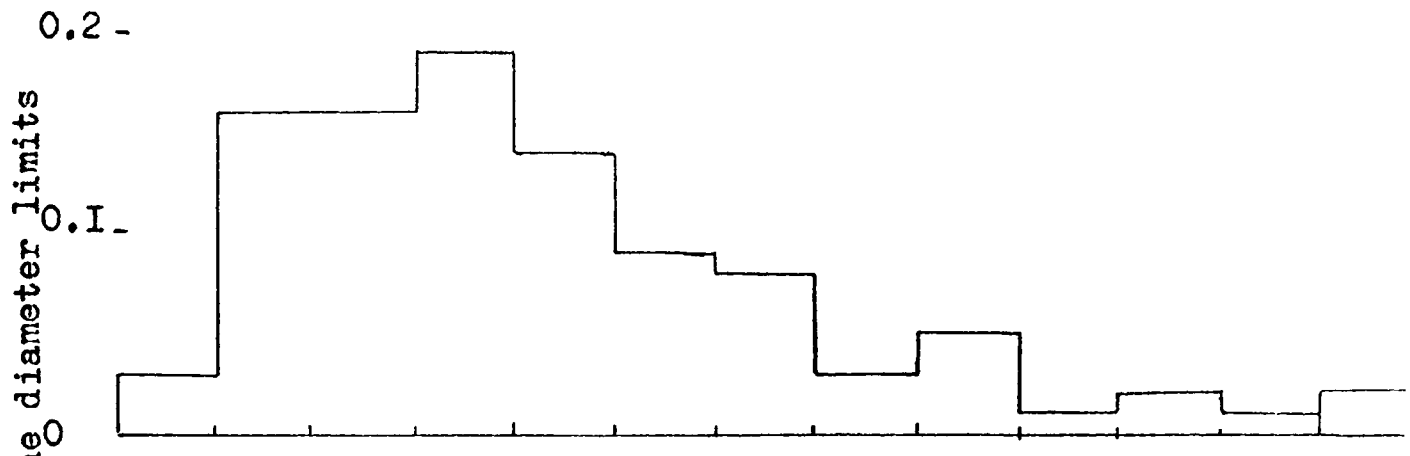


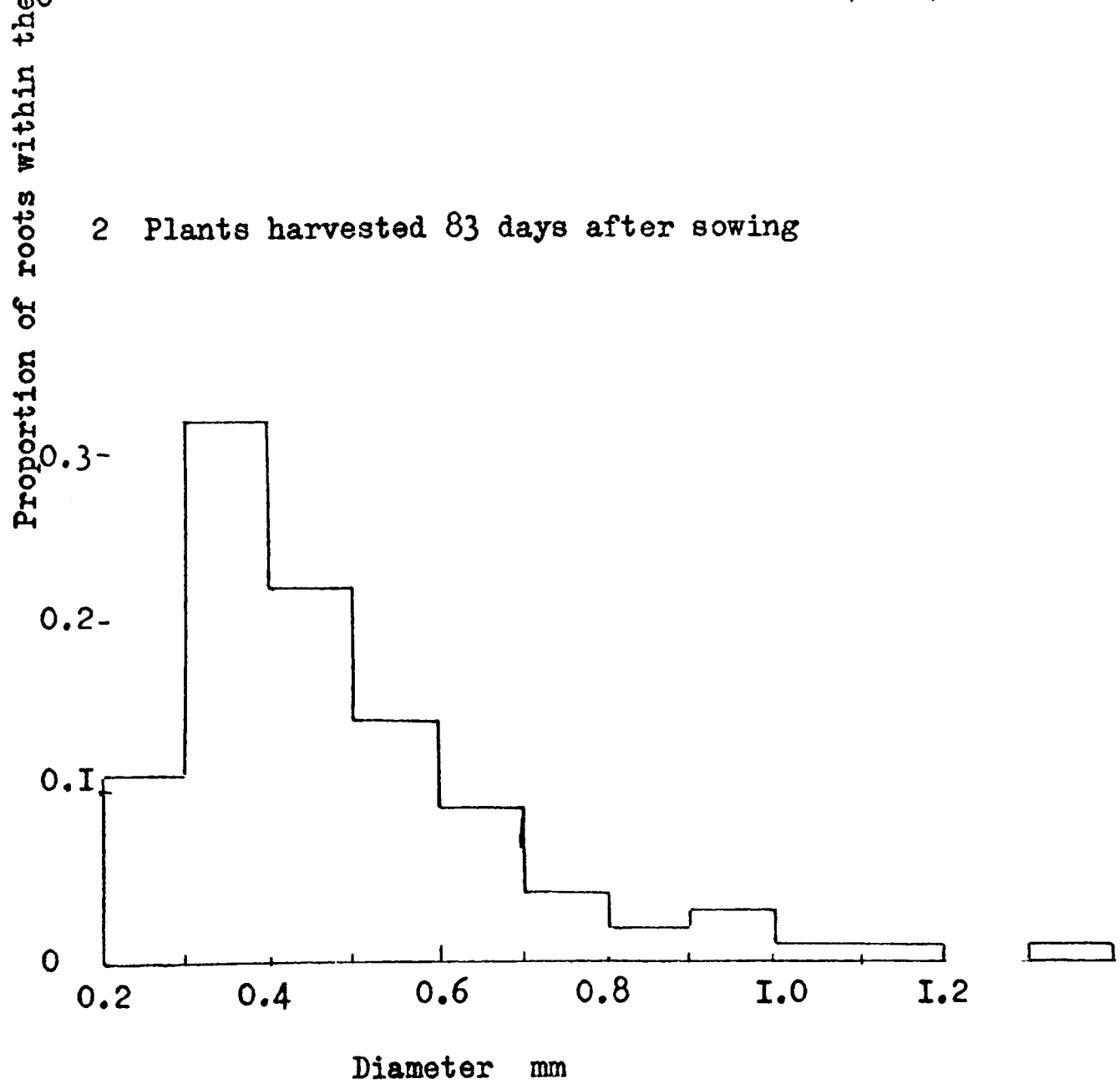
Fig.4.8.

HISTOGRAMS SHOWING THE DISTRIBUTION OF ROOT DIAMETER OF THE SOIL GROWN LEEKS

I Mean of plants harvested on day 49, 62 and 70 after sowing



2 Plants harvested 83 days after sowing



CATION UPTAKE BY LEEKS FROM JOE SOIL

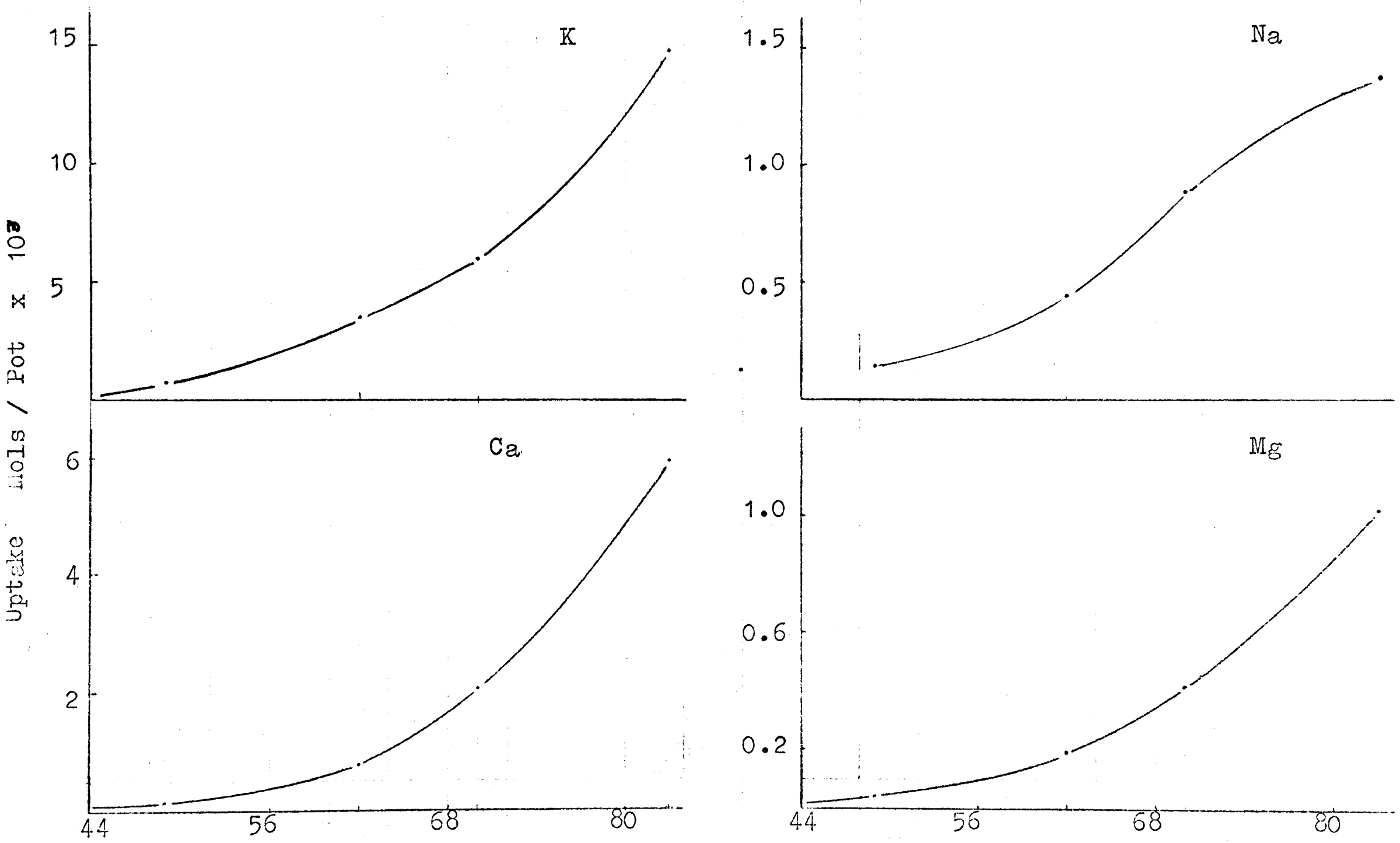


Fig.4.9.

ANION UPTAKE BY LEEKS FROM POT SOIL

Fig.4.10

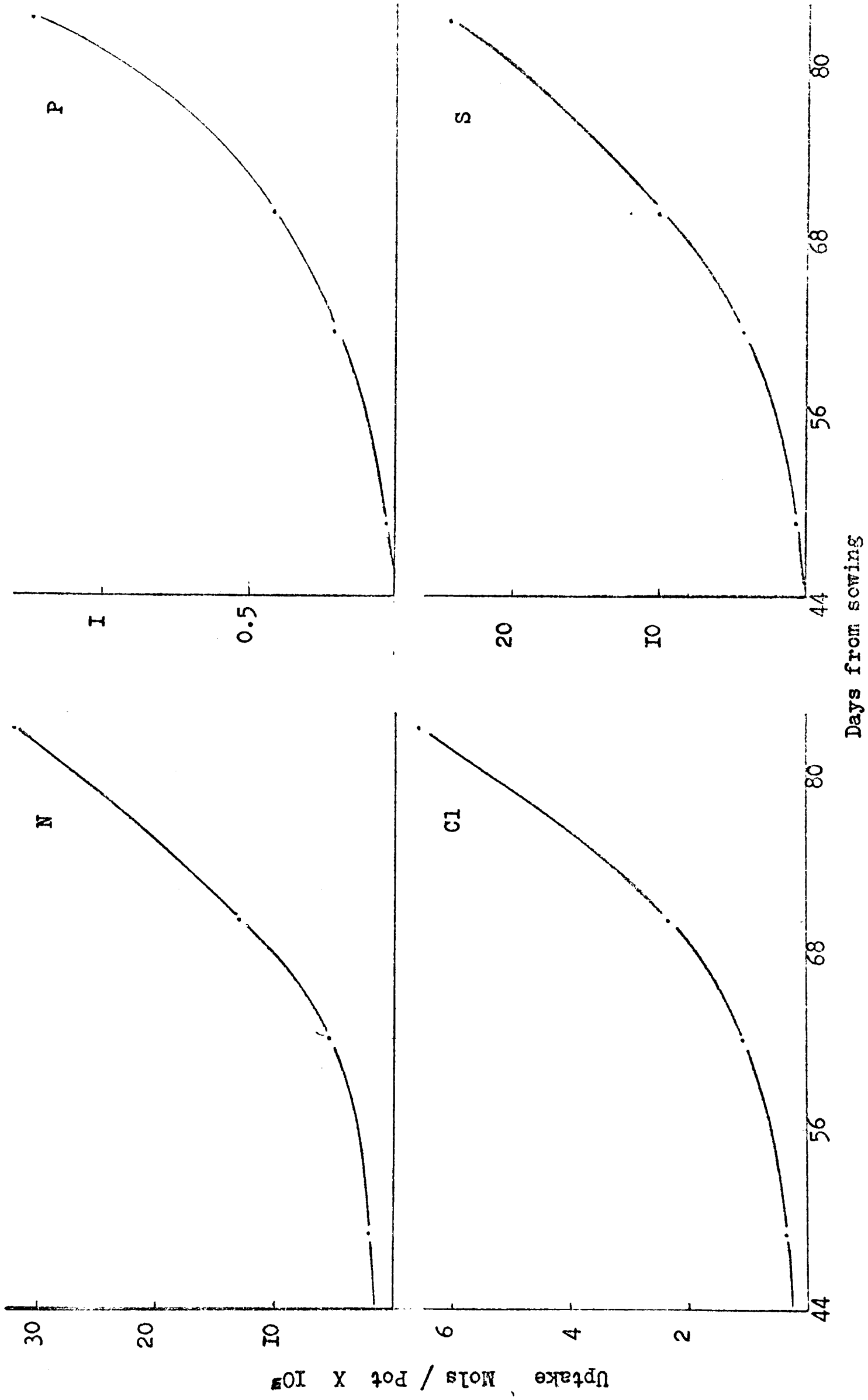


Figure I5

DATA ON LEEK PLANTS FROM POTS

FRESH AND DRY WEIGHTS (grams)

(coefficients of variation in brackets below)

Date	Days after sowing	Harvest	Shoot		Root		Total	
			FW	DW	FW	DW	FW	DW
16.6.	49	1	3.83 (16)	0.32 (15)	2.02 (18)	0.087 (21)	5.85 (15)	0.41 (21)
29.6	62	2	20.8 (18)	2.02 (17)	9.15 (16)	0.34 (24)	30.0 (17)	2.36 (17)
7.7.	70	3	44.0 (12)	4.48 (12)	23.7 (26)	0.90 (28)	67.7 (16)	5.38 (14)
18.7.	83	4	124.1 (22)	11.3 (24)	43.2 (30)	1.63 (35)	167.3 (22)	12.9 (24)

Table 4.3 a

Harvest	Root % of Total DW	Root Length cm	cm of root / mg total DW	Interharvest period	Relative Growth Rate
1	21	627 (22)	1.5		
				1	1.3
2	15	2372 (30)	1		
				2	1.0
3	17	5340 (26)	1		
				3	0.7
4	13	11739 (39)	0.9		
Mean	16		1.1		

Table 4.3 b

SHOOT % OF ELEMENTS IN DRY WEIGHT

Harvest	K	Na	Mg	Ca	N	P	Cl	S
1	5.98 (11)	0.17 (49)	0.17 (9)	1.34 (8)	4.26 (21)	0.32 (10)	2.97 (5)	0.57
2	4.81 (6)	0.13 (40)	0.14 (13)	1.30 (17)	3.35 (12)	0.27 (7.3)	1.65 (15)	0.53
3	4.23 (8)	0.14 (29)	0.14 (12)	1.43 (15)	3.5 (9)	0.24 (12)	1.53 (15)	0.59
4	4.85 (10)	0.16 (32)	0.17 (11)	1.77 (22)	3.8 (9)	0.31 (7)	1.96 (20)	0.45
Mean								

Table 4.3 c

ROOT % OF ELEMENTS IN DRY MATTER

Harvest	K	Na	Mg	Ca	N	P	Cl	S
1	4.40 (11)	3.02 (19)	0.51 (11)	1.75 (23)	3.37	0.24 (15)	1.48	1.42
2	2.32 (21)	2.26 (31)	0.49 (10)	1.66 (15)	3.07	0.30 (11)	0.96	0.88
3	4.0 (23)	1.54 (17)	0.42 (17)	2.11 (21)	2.95 (15)	0.25 (7)	1.33 (13)	0.67
4	2.70 (10)	0.78 (28)	0.36 (17)	1.72 (22)	2.33 (18)	0.24 (27)	0.84 (27)	0.72

Table 4.3 d

SHOOT AND ROOT % OF ELEMENTS IN DRY MATTER

Harvest	K	Na	Mg	Ca	N	P	Cl	S
1	5.57	0.78	0.24	1.43	4.07	0.30	2.66	0.75
2	4.45	0.45	0.19	1.35	3.31	0.27	1.49	0.58
3	4.19	0.37	0.19	1.54	3.41	0.25	1.50	0.60
4	4.58	0.24	0.19	1.76	3.61	0.30	1.82	0.48
Mean	4.70	0.46	0.20	1.52	3.60	0.28	1.87	0.60

Table 4.3 e

in Table 4.4 Even a non adsorbed anion like nitrate was not seriously depleted on average.

Table 4.5 shows the mean nutrient inflows for each ion over the three inter-harvest periods. Most of these fell with time, sodium quite drastically, in line with its diminishing percentage in the shoot. Calcium inflows remained nearly constant and older plants contained a greater fraction of their cations as calcium than the younger plants. If we assume that all the N was absorbed as NO_3, the sum total mean anion inflow exceeded the total mean cation inflow in each period. Therefore on averagethe roots must have either excreted HCO_3^- or OH^- ions or absorbed H^+ ions in order to maintain electroneutrality. Values of mean HCO_3^- or OH^- outflow are given in Table 4.8.a (Anions-Cations). These were calculated by difference, and are unlikely to be very accurate as they embody all the errors in the values for all the other ions.

The transpiration rate increased steadily from June 10 as did plant weight Only one decrease in transpiration rate occurred, and this was during a period of dull wet weather between June 17 and June 19. The mean transpiration ratios for harvests one to four respectively were 280, 240, 230 and 230 g. water transpired /g. plant dry matter produced. Plants in pots of different sizes had similar transpiration rates over the same period. Fig.4.11 shows tha graph of $\log_{10}$ of the mean total water transpired, T (grams), plotted against time, t (seconds). The formula of the resulting straight line was,

$$\log_{10} T = 1.415 + 0.46.\ t.\ 10^{-6}.$$

By differentiating this expression an equation for transpiration rate was derived. Thus, $dT/dt = (1.06.e^{(3.26+1.06\ t/10^6)}) / 10^{-6}$

Mean water inflow rates were determined by dividing values of dT/dt by root length, L. Successive values of water inflow midway between the four harvests were 0.24, 0.23 and 0.24 g./cm/sec x 10^{-6} .Expressed as water fluxes, V, these values were 1.28, 1.22 amd 1.57 cm/sec x 10^{-6}.

4.9.b. Soil Solution Concentrations

A table of the mean soil solution concentrations from different pot sizes

Fig.4.11

Log of Water Transpired per Pot Against Time

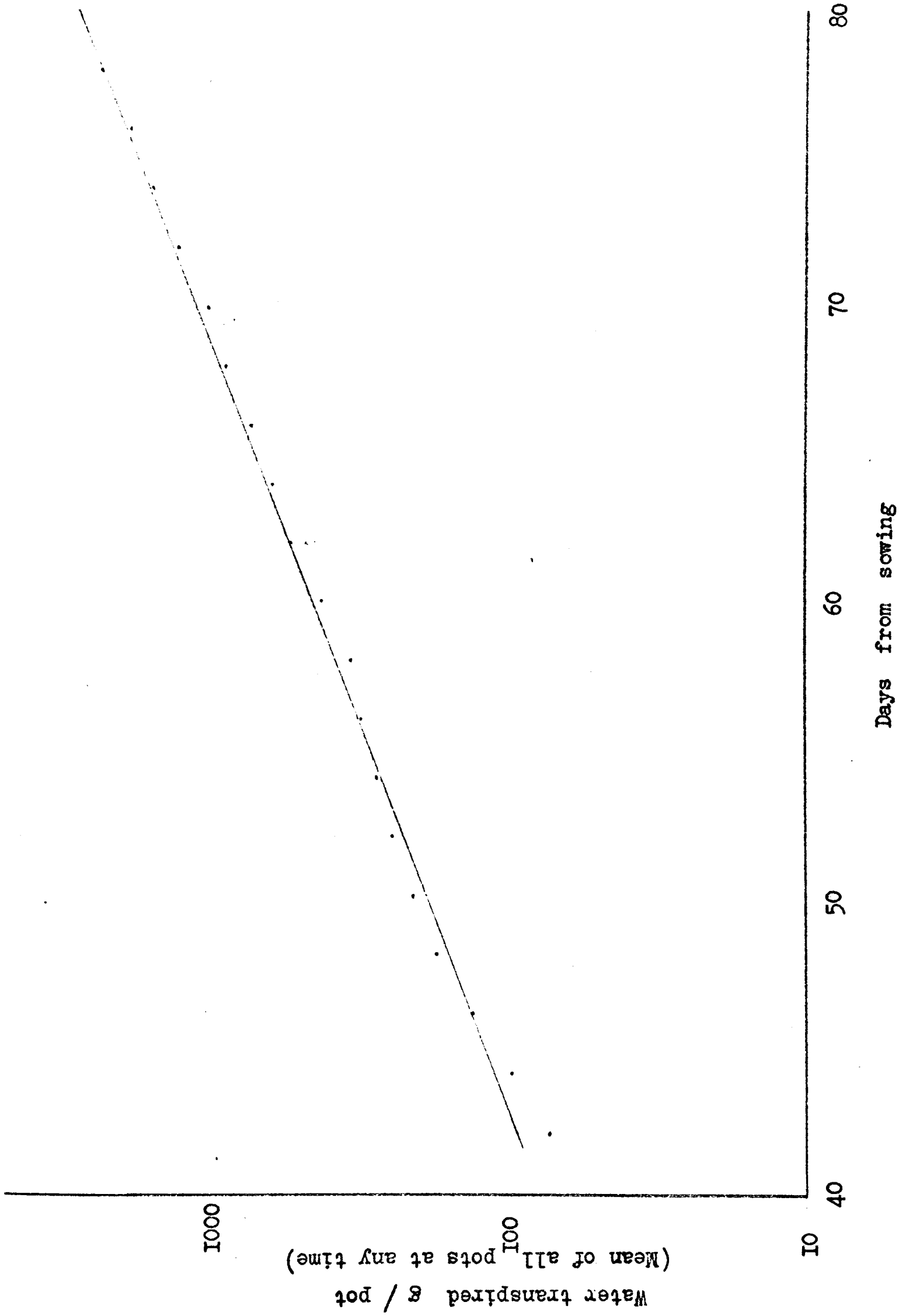


Table 4.4

THE TOTAL DEPLETION OF EXCHANGEABLE NUTRIENTS FROM POT SOIL

Harvest		1	2	3	4
Pot Volume (cc soil)		2900	7350	13400	33300
% of the available nutrients (exchangeables) initially present removed at harvest time.	Element				
	K	2.0	4.2	4.8	5.0
	Na	2.1	3.5	4.1	2.5
	Mg	0.23	0.52	0.63	0.60
	Ca	0.04	0.09	0.13	0.16
	N	9	11	14	14
	P	0.09	0.28	0.30	0.36
	Cl	3.7	5.4	6.4	7.5
	S				

MEAN INFLOWS INTO LEEK ROOTS IN POT EXPERIMENT

Standard deviations of mean inflows in brackets below (9 degrees of freedom)

Day	Inter-harvest period	Water $cm^3/cm/s$	K	Na	Mg	Ca	N	P	Cl	S
			Mols / cm / s x 10^{-13}							
49										
	1	0.24	14.8	2.15	1.01	4.4	23	1.2	5.1	2.3
62			(2.4)	(0.26)	(0.18)	(0.70)	(0.17)	(0.17)	(0.76)	
	2	0.23	11.8	1.64	0.85	4.8	30	0.82	4.7	,,
70			(2.4)	(0.12)	(0.15)	(0.58)		(0.19)	(1.3)	
	3	0.24	10	0.48	0.68	4.4	21	0.94	4.7	,,
83			(3.1)	(0.27)	(0.22)	(1.4)		(0.29)	(1.6)	
	Mean	0.24	12	1.4	0.85	4.5	25	1.0	4.8	,,

Table 4.5

and at different sampling dates is given in Table 4.6. Fig.4.12 compares the concentration of calcium with that of potassium, showing that the monovalent ion varies less drastically as is predicted by the Ratio Law, and that the concentration ratio $K/\sqrt{Ca}$ was almost constant. On the whole, the concentrations were surprisingly similar, and further calculations were based on the overall mean soil solution concentrations.

In such a soil as this, soil solution concentrations are largely controlled by the level of the non-adsorbed anions nitrate and chloride. If we assume there was no nitrification or denitrification in the course of the experiment, then two factors must have determined the way in which these ions changed in concentration with time: the extraction of soil water by plants would have tended to increase their concentration, and ion uptake would have tended to diminish it. For chloride, concentration by plant water absorption exceeded dilution by ion uptake, and the concentration was calculated to increase from its measured/mean level of 0.8 x 10^{-3} Eq/L to 0.97 x 10^{-3} Eq/L. In fact, the final initial measured concentrations were 1.1 x 10^{-3} Eq/L in good agreement with expectations. For nitrate, despite the greater proportion of uptake (assuming that all N was absorbed as NO_3) the concentrations should also have risen slightly. In fact, the final samples showed a slight decrease in concentration, perhaps indicating that some denitrification or microbial uptake was occurring. In all soil solution samples the sum of the cations approximately equalled the sum of the anions, the overall mean values differing from each other by only about 4%. This is not a significant difference since the sums are based on eight separate analyses.

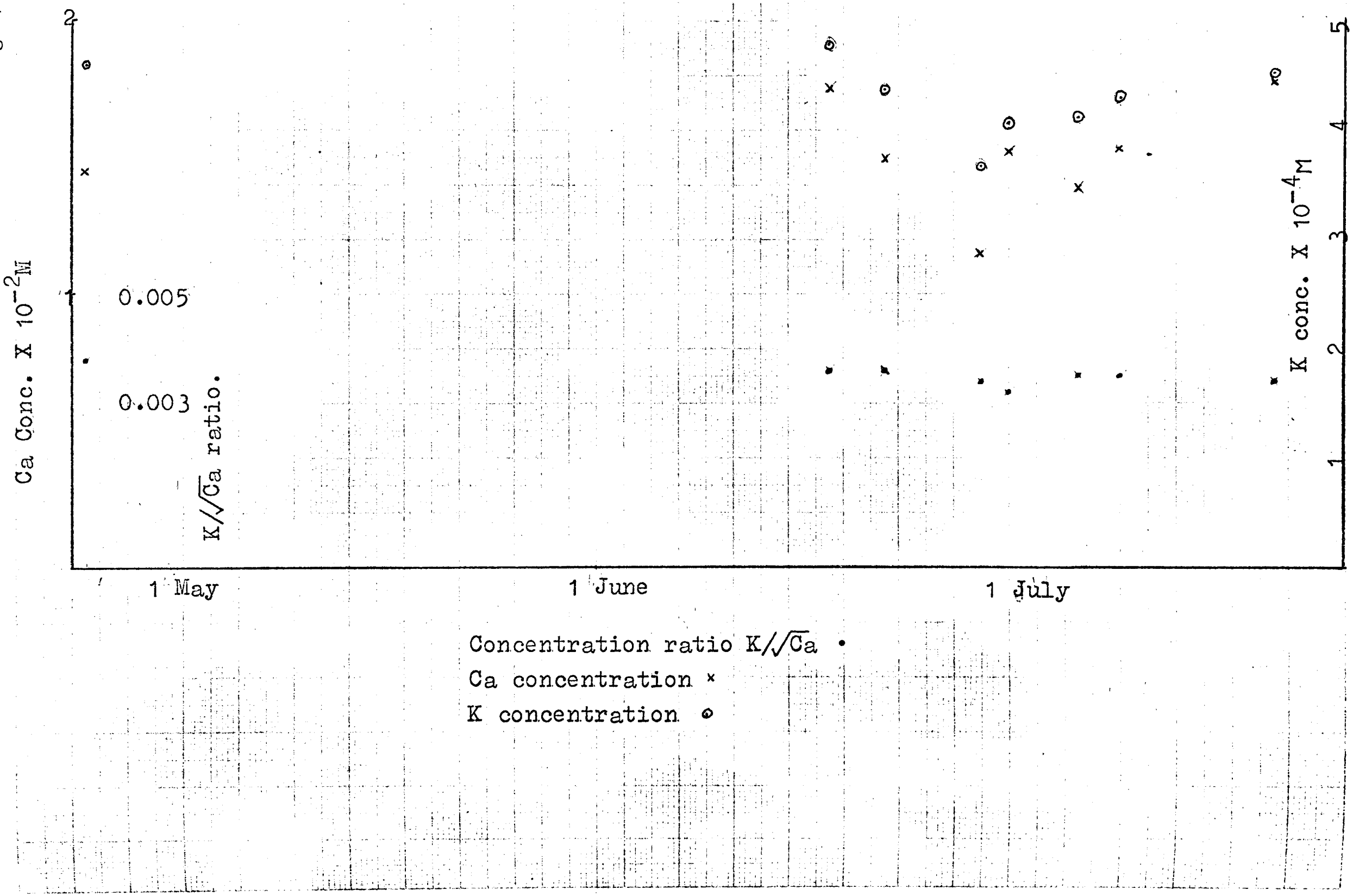
4.9.c. Factors Contributing to the Calculated Diffusion Coefficients

The soil bulk density was the same in all pots at a value of 1.165 . oven dry soil per c.c. Soil volumes were measured at planting and at harvest time to check for any shrinkage, and this did not occur.

From the data on soil volume and water content, V_L was calculated for the different pots at sowing and harvest time. The plan was to harvest all pots

Fig. 4.12

MEAN K AND Ca CONCENTRATIONS AND THE CONCENTRATION RATIO $K/\sqrt{Ca}$ IN SOIL SOLUTION SAMPLES TAKEN ON DIFFERENT DATES.



SOIL SOLUTION CONCENTRATIONS

Table 4.6

Mols/Litre X 10^{-3} Coefficients of variation of the 12 individual analyses in brackets below results.(as %)

Pot vol. ml.	Ion / Sampling date	K	Na	Mg	Ca	NO_3	Cl	P
2900	25.4	0.45	1.74	0.69	14.8	25.0	8.5	0.018
	16.6	0.48 (5)	1.94 (10)	0.69 (3)	17.6 (3.3)	25.0 (3.8)	-	0.017 (23)
6300	25.4	0.46	1.77	0.72	16.4	22.0	8.2	0.023
	20.6	0.44 (6)	1.59 (9)	0.60 (10)	15.0 (11)	22.7 (6)	8.9 (3)	0.024 (13)
	29.6	0.40 (8)	1.61 (8)	0.64 (10)	15.2 (11)	19.7 (7)	9.8 (5)	0.023 (13)
11500	25.4	0.49	1.86	0.65	13.5	20.0	8.1	0.023
	27.6	0.37 (14)	1.33 (20)	0.51 (14)	11.6 (16)	20.6 (9)	9.1 (5)	0.020 (18)
	7.7	0.43 (7)	1.69 (13)	0.64 (13)	15.3 (14)	20.1 (7)	10.7 (5)	0.018 (20)
28500	25.4	0.44	1.76	0.55	13.8	21.0	7.8	0.010
	4.7	0.41 (9)	1.59 (13)	0.57 (17)	13.9 (15)	20.6 (5)	8.6 (3.5)	0.021 (18)
	18.7	0.45 (9)	1.67 (17)	0.70 (14)	17.8 (9)	18.7 (10)	10.0 (6)	0.021 (26)
Mean of all analyses		0.43 (11)	1.65 (17)	0.62 (15)	15.1 (16)	20.6 (12)	9.1 (10.5)	0.021 (24)

Mean SO_4 conc. 2.5

Mean ΣCations- ΣAnions = 33.4-34.7 = -1.3 me/L.

The mean values were used in all subsequent calculations.

when they had lost about 20% of their initial water content. Initially, V_L was 0.39 cc of water/cc soil, and at harvest, it ranged from 0.288 to 0.315 with a mean of 0.297. For the purposes of calculation final V_L was taken as 0.30 cc water/cc soil.

The mean value of f_L at a V_L of 0.39 was calculated as 0.307 with a coefficient of variation of 16%. from the results from three replicate measurements. A value of 0.30 was used in subsequent calculations. Rowell, Martin and Nye (1967) showed that in the range of V_L from 0.15 to 0.4, f_L varied linearly with V_L, and their graph was used here, to estimate an f_L of 0.2 at the final V_L of 0.30. Hence, the initial value of $V_L f_L$ was approximately equal to 0.12, and the final value of $V_L f_L$ was estimated as 0.06 .

In subsequent calculations the mean value for $V_L f_L$, $\overline{V_L f_L}$, of 0.09 was used.

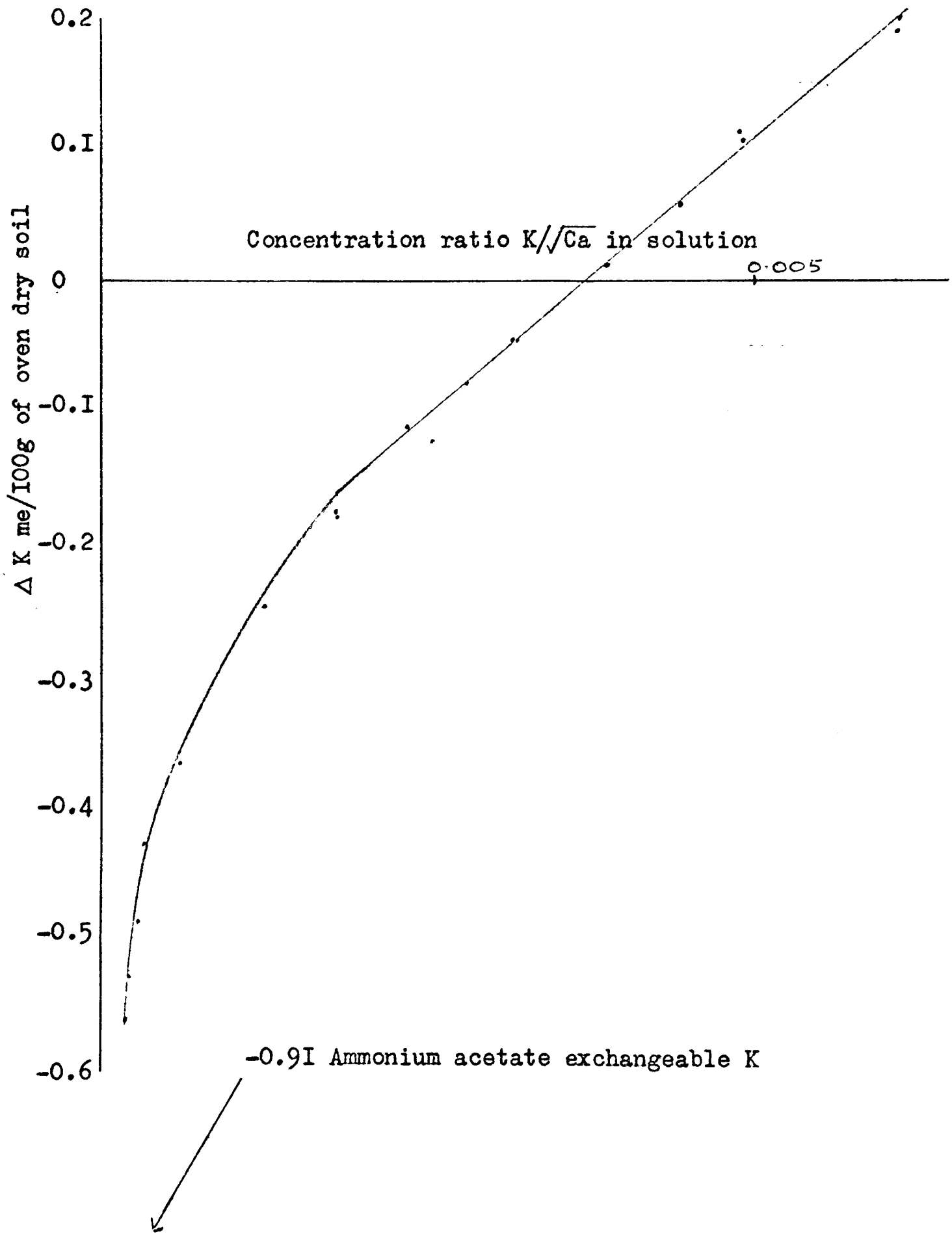
The Q/I plots for K, Na and Mg are shown in Figs. 4.13, 4.14 and 4.15. Fig.4.16 shows these curves converted to the exchange isotherms reigning at the bulk density and soil solution concentration of the soil. From the slopes of the curves in Fig.4.16., the buffer capacities at any concentration can be determined. The isotherms are linear over the major portion of the range from the initial equilibrium level downwards, and hence, $\frac{dC_L}{dC}$ and therefore, D is constant over this range. The null point activity ratios should be equal to the activity ratios for ions in the soil solution (Moss,1963). This was shown to be the case for potassium and, after allowing for soluble salts, for sodium, but the null point for magnesium was about 20% lower than was expected from the mean $\frac{Mg}{Ca}$ concentration ratio in the soil solution.

Figure 4.17 shows the phosphate desorption isotherm in 3.30×10^{-2}N.$CaCl_2$ solution at pH 7 and 25°C. This isotherm has been taken as appropriate to the conditions around roots in the plant experiment. The isotherm is curved, hence the value of $\frac{dC_L}{dC}$ varies with C_L and for this reason the value of D is concentration dependent.

The isotherm at pH 8 (see Fig. 4.18) gave more erratic points but there was no indication of greater solution phase concentrations than at pH 7; if

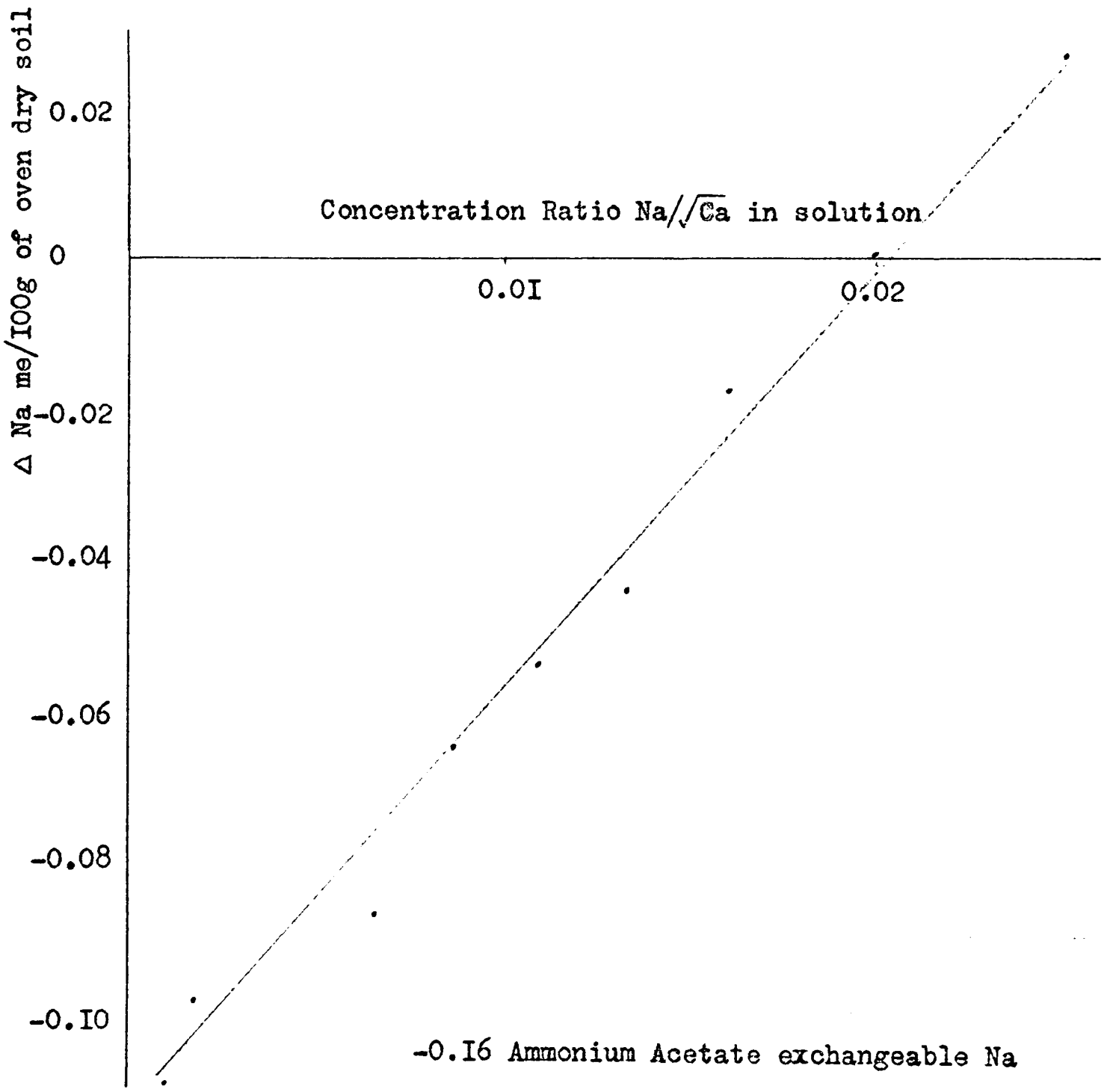
K Q/I FOR WYTHAM SILT LOAM

Fig.4.13



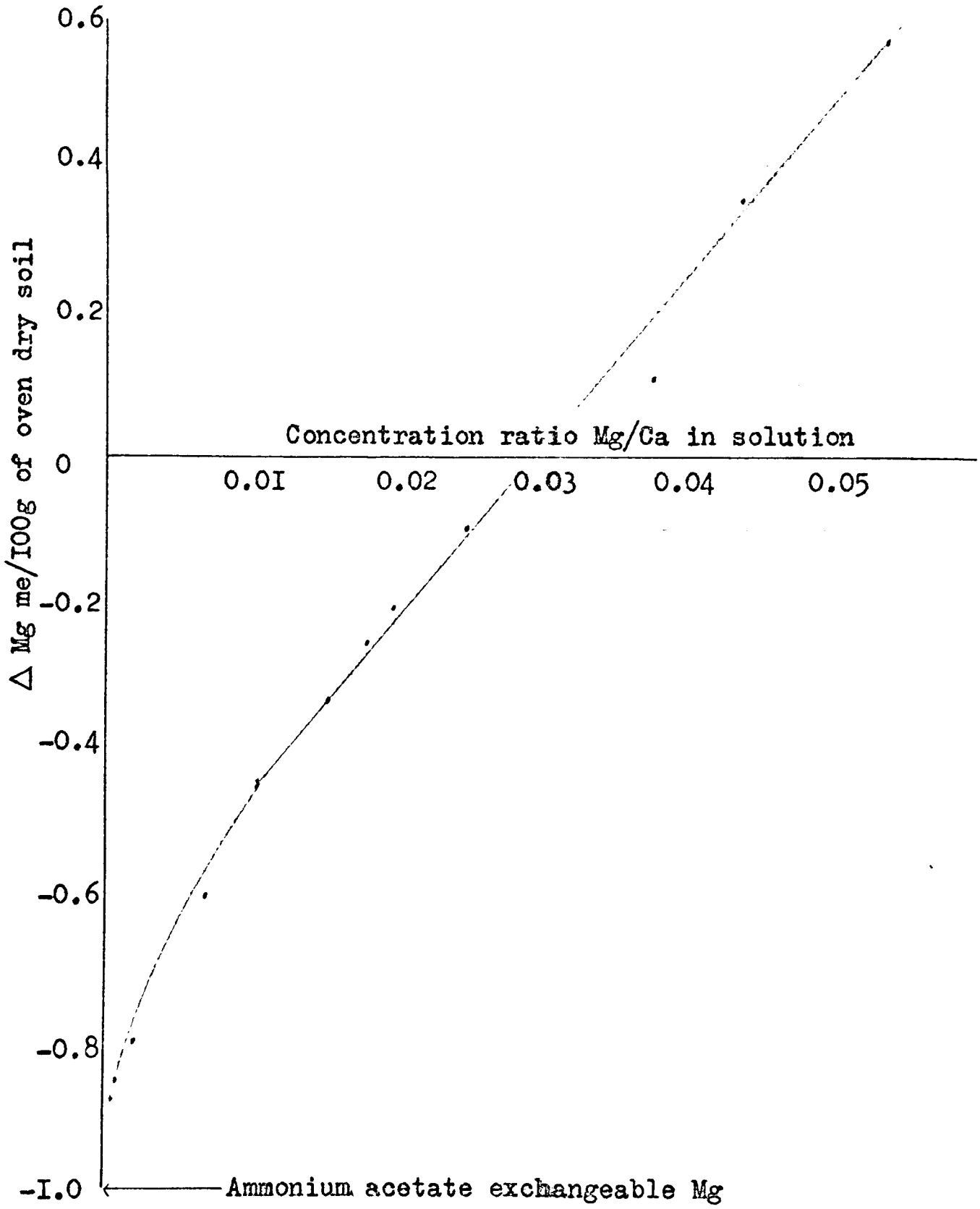
Na Q/I FOR WYTHAM SILT LOAM

Fig.4.14



Mg Q/I WYTHAM SILT LOAM

Fig.4.15



CATION EXCHANGE ISOTHERMS AT MEAN BULK DENSITY AND ANION CONCENTRATION OF POT SOIL

Fig.4.16

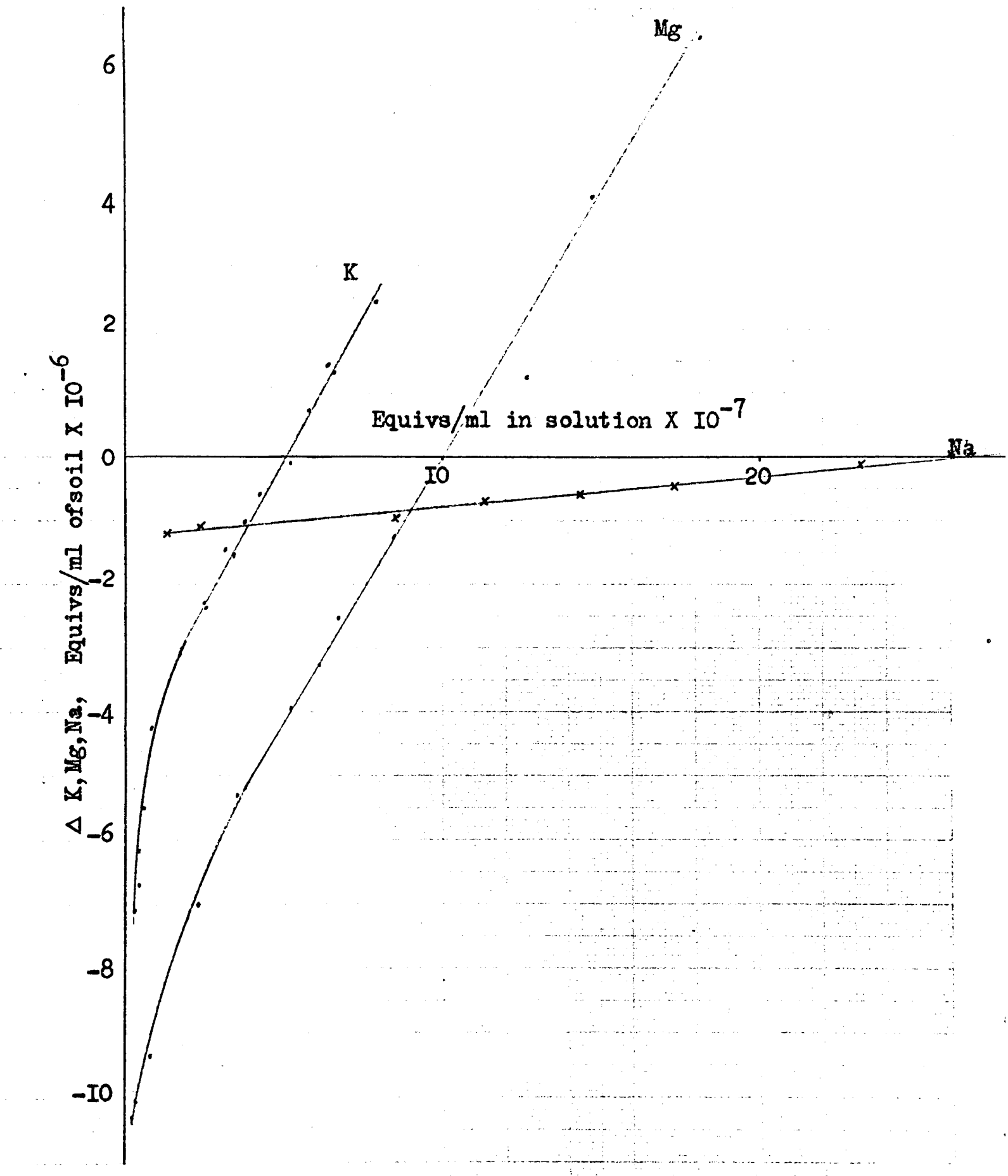


Fig.4.17

P DESORPTION ISOTHERM OF WYTHAM SILT LOAM IN I.65M $CaCl_2$ AT pH 7

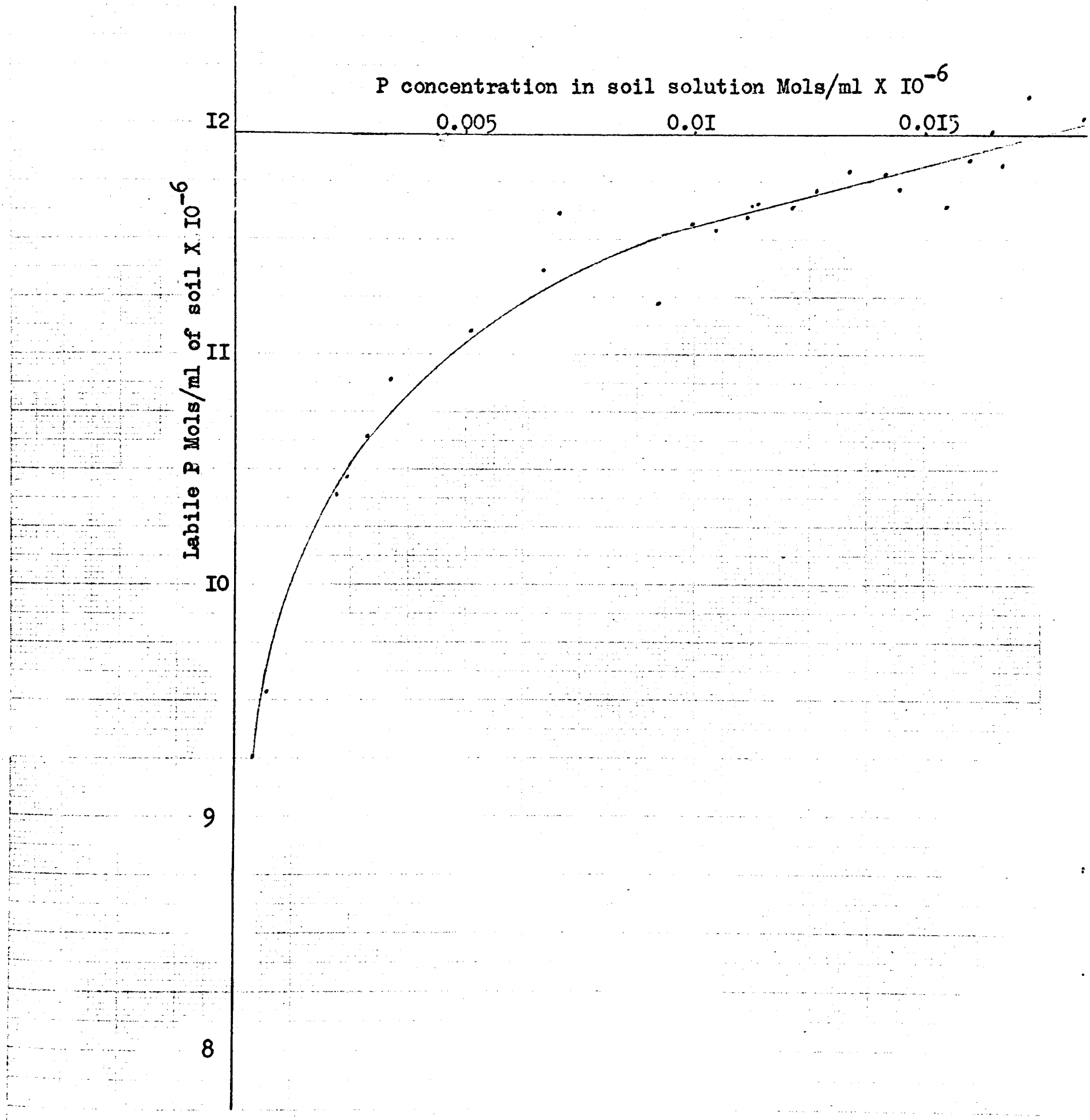
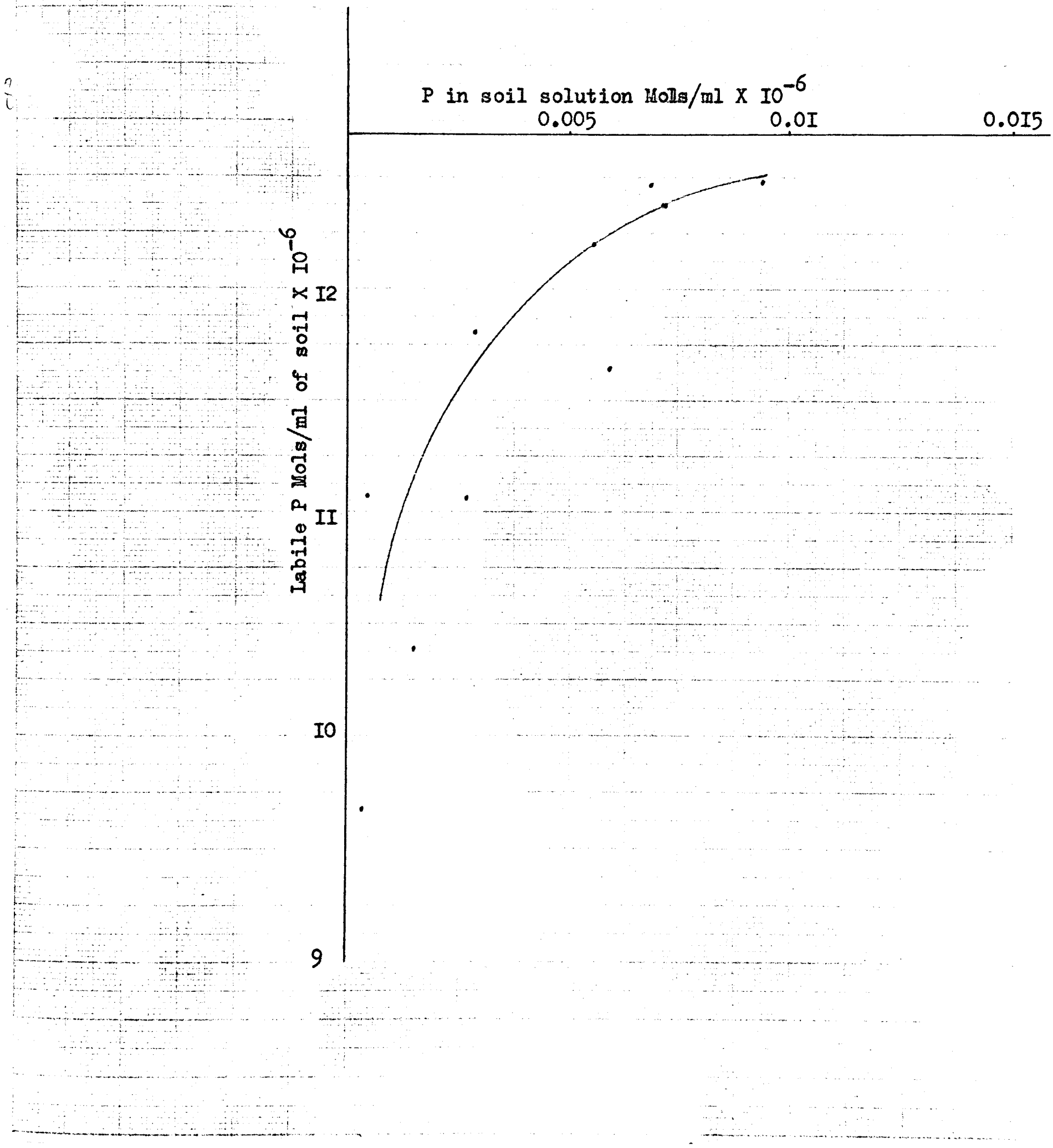


Fig.4.18

P DESORPTION ISOTHERM OF WYTHAM SILT LOAM IN I.65M $CaCl_2$ WITH THE pH RAISED TO 8



anything solubility appeared slightly diminished. A systematic investigation into the effects of a decreased pH was not undertaken, but in the first attempts to obtain a high soil solution to soil ratio (1g of soil to 5000 and to 2000 cc of solution) the pH decreased to 6.3. Presumably there was insufficient soil to buffer the system against the pH of the pure $CaCl_2$ solution, which was about 5.7. These two desorptions showed considerably more P in solution than similar volumes maintained at pH7 by addition of $Ca(OH)_2$ solution. Thus, in contrast to the Greensand soil of Bagshaw and Nye (pers. comm.) there is no indication of greater solubility with an increase in pH, but some indication of its increase with a decrease in pH. Perhaps this is to be expected in a soil containing free calcium carbonate, where the dominant phosphate solids are probably forms of calcium phosphate, the solubility of which diminishes with increasing pH (Larsen, 1967).

The isotopically exchangeable phosphate in the soil, P_E, was 1.1 m equivs per 100 g of dry soil for the first isother,. The specific activities determined for the isotherm at pH 8 indicated that the labile fraction adsorbed on the solid was slightly greater; 12.7×10^{-6} as opposed to 12×10^{-6} Moles of P per ml. of moist soil. This suggests that very slow adsorption from the solution was still proceeding after the initial six weeks of equilibrium, since the pH 8 isotherm was determined on the same soil after about a further three weeks of moist aerated storage.

The buffer capacity of NO_3 and Cl was $1/V_L$, since these ions are not adsorbed, hence D simply equals $D_L f_L$. Although evidence of slight sulphate adsorption was found, the time needed for a complete desorption isotherm could not be spared, and it too was treated as a non-adsorbed ion like Cl and NO_3. As will be apparent from the calculations for Mg and Na in 4.9.d. below, the root surface concentration of a slightly buffered ion, which tends to accumulate at the root surface, is only slightly affected by the exact value of D and hence by the value of the buffer capacity used to calculate D. Thus the error involved in ignoring the slight adsorption of labile sul-

phate was small.

Values of D_L were derived from Parsons (1959) and multiplied by $\overline{V_L f_L}$ and $\frac{dC_L}{dC}$ to calculate D values. The values are given in table 4.7.a. along with a summary of the rest of the soil data (tables 4.7.a. and b.) Diffusion coefficients for calcium were calculated assuming it to be an unbuffered ion like NO_3 and Cl. Since the exchange complex was largely saturated with Ca ions, and since increases rather than depletions of Ca occurred at the root surface, then little net adsorption of Ca could have occurred in the rhizosphere, and bulk diffusion must have occurred as though the ion was unbuffered. A similar deduction was made by Passioura and Frere (1967). If the concentration of Ca and Mg increased by an equal proportion at the root surface, then the same argument should apply to Mg, and it too should diffuse as though it were unbuffered. With Na, the Ratio Law predicts that an increase in Ca, Mg and Na in solution at the root surface would lead to an increase in the proportion of Na adsorbed relative to Ca and Mg. But the adsorption of Na in Wytham Silt Loam was so weak that this effect would not be important for small increases in solution concentration. In fact calculations (see 4.9.d. below) indicated that the percentage increase in Ca at the root surface was greater than that of Mg and Na. Hence, there was a rather complex situation concerning Mg and Na diffusion away from the roots. Diffusion coefficients were calculated considering Mg and Na as both buffered and unbuffered ions, which should represent the extremes for possible values of D in the rhizosphere.

4.9.d. Results found by applying Equation 3.X

The data given in sections 4.9.a, b and c were used to calculate values of M, the apparent mass flow contribution to inflow. Equation 3.X was applied to the data for each nutrient for all three interharvest periods and values of $C - \overline{C_{LR}}$ and $\bar{\alpha}$ were calculated. Values of M and $\overline{C_{LR}}$ are given in table 4.8 and $\overline{\alpha}$ in 4.9.

Apparent mass flow supplied an excess of all ions except K and P. The

SUMMARISED SOIL DATA

Nutrient	K	Na	Mg	Ca	NO_3	Cl	P	SO_4
Mean soil sol'n conc. Eq/L X 10^{-3}	0.43	1.65	1.24	30.2	20.6	9.1	0.021	5.0
Exchangeable ions me/100g oven dry soil	0.91	0.16	1.0	23.3	-	-	1.1	-
Buffer capacities Eq/ml dry soil / Eq/ml solution	9.2	0.53	8.2	-	-	-	40 b is variable this is minimum value	-
dC_L/dC in pOt Eq/ml solution / Eq/ml soil	0.105	1.15	0.12	$1/V_L$	$1/V_L$	$1/V_L$	0.019	$1/V_L$
D_L Self diffusion coef. in dilute sol'n cm^2/sec X 10^{-5}	1.98	1.35	0.70	0.78	1.92	2.03	0.90	1.08
$D' = D_L V_L f_L$ cm^2/sec X 10^{-6}	1.78	1.22	0.63	0.70	1.72	1.82	0.81	0.97
D Diffusion coef. in soil cm^2/sec X 10^{-7}	1.87	14	0.76	19.5	48	51	0.20	27

Table 4.7 a

SUMMARISED SOIL DATA

Bulk density g oven dry soil/cc	V_L	Water Potential bars	f_L	$V_L f_L$	$\overline{V_L f_L}$
1.165	0.39	-0.04	0.3	0.12	
					0.09
1.165	0.30	-0.28	0.2	0.06	

The upper row of values refersto conditions at planting out time, the lower ones are mean harvest time values.

Table 4.7 b

RESULTS DERIVED FROM THE MEAN INFLOWS INTO LEEK ROOTS USING THE MODIFIED PASSIOURA EQUATION (EQUATION 3.X)

Harvest	Date	Days after sowing	Interharvest period	Root radius $\bar{r}$ cm	Water Inflow $cm^3/cm/s$ $x10^{-6}$	$\sum^{A}$ Anion inflows Eq/cm/s $x10^{-13}$	$\sum^{C}$ Cation inflows Eq/cm/s $x10^{-13}$	A- C Eq/cm/s $x10^{-13}$
1	16.6	49		0.028				
			1	0.03	0.24	33.9	27.8	6.1
2	29.6	62		0.032				
			2	0.03	0.23	40.1	24.7	16.0
3	7.7	70		0.026				
			3	0.026	0.24	31.2	20.6	10.6
4	18.7	83		0.022				

Table 4.8.a.

See continuation sheet 4.8.b. →

Interharvest period	K Inflow $\overline{I}$ Mols/cm/s x10^{-13}	App.mass flow M Mols/cm/s x10^{-13}	$\overline{C}_{Lr}$ Mols/cm^3 x10^{-7}	$\overline{C}_{Lr}$ / C_{Li}	M / $\overline{I}$	Na Inflow $\overline{I}$ Mols/cm/s x10^{-13}	App.mass flow M Mols/cm/s x10^{-13}	$\overline{C}_{Lr}$ Mols/cm^3 x10^{-7}	$\overline{C}_{Lr}$ / C_{Li}	M / $\overline{I}$
1	14.8	1.04	1.10	0.26	0.07	2.15	3.96	17.30	1.05	1.84
2	11.8	0.99	1.80	0.42	0.084	1.64	3.80	17.50	1.06	2.3
3	10	1.04	2.00	0.46	0.104	0.48	3.96	18.20	1.11	8.3

See continuation sheet 4.8.c. →

Interharvest period	Na unbuffered					Mg				
	Inflow $\bar{I}$ Mols/cm/s $\times 10^{-13}$	App.mass flow M Mols/cm/s $\times 10^{-13}$	$\bar{C}_{Lr}$ Mols/cm^3 $\times 10^{-7}$	$\bar{C}_{Lr}/C_{Li}$	$M/\bar{I}$	Inflow $\bar{I}$ Mols/cm/s $\times 10^{-13}$	App.mass flow M Mols/cm/s $\times 10^{-13}$	$\bar{C}_{Lr}$ Mols/cm^3 $\times 10^{-7}$	$\bar{C}_{Lr}/C_{Li}$	$M/\bar{I}$
1	2.15	3.96	17.50	1.06	1.84	1.01	1.49	6.46	1.04	1.47
2	1.64	3.80	17.70	1.07	2.3	0.85	1.42	6.51	1.05	1.67
3	0.48	3.96	18.60	1.12	8.3	0.68	1.49	6.70	1.08	2.2

Table 4.8.c.

See continuation sheet 4.8.d. →

	Mg unbuffered					Ca				
Interharvest period	Inflow $\bar{I}$ Mols/cm/s $\times 10^{-13}$	App.mass flow M Mols/cm/s $\times 10^{-13}$	$\bar{C}_{Lr}$ Mols/cm^3 $\times 10^{-7}$	$\bar{C}_{Lr}/C_{Li}$	$M/\bar{I}$	Inflow $\bar{I}$ Mols/cm/s $\times 10^{-13}$	App.mass flow M Mols/cm/s $\times 10^{-13}$	$\bar{C}_{Lr}$ Mols/cm^3 $\times 10^{-7}$	$\bar{C}_{Lr}/C_{Li}$	$M/\bar{I}$
1	1.01	1.49	6.67	1.08	1.47	4.4	36	177.5	1.18	8.2
2	0.85	1.42	6.75	1.09	1.67	4.8	35	176.4	1.17	7.4
3	0.68	1.49	7.05	1.14	2.2	4.4	36	179.7	1.19	8.2

Table 4.8.d.

See continuation sheet 4.8.e. →

Interharvest period	SO_4 Inflow $\bar{I}$ Mols/cm/s $\times 10^{-13}$	App.mass flow M Mols/cm/s $\times 10^{-13}$	$\bar{C}_{Lr}$ Mols/cm^3 $\times 10^{-7}$	$\bar{C}_{Lr}/C_{Li}$	$M/\bar{I}$	PO_4 Inflow $\bar{I}$ Mols/cm/s $\times 10^{-13}$	App.mass flow M Mols/cm/s $\times 10^{-13}$	$\bar{C}_{Lr}$ Mols/cm^3 $\times 10^{-7}$	$C_{Lr}/\bar{C}_{Li}$	$M/\bar{I}$
1	2.3	6	27	1.09	2.6	1.2	0.050	-	-	0.04
2	,,	,,	,,	,,	,,	0.82	0.048	-	-	0.06
3	,,	,,	,,	,,	,,	0.94	0.050	-	-	0.05

These are mean figures for all harvests

Table 4.8.e.

		NO_3				Cl		
Inflow I Mols/cm/s $x10^{-13}$	App.mass flow M Mols/cm/s $x10^{-13}$	C_{Lr} Mols/cm^3 $x10^{-7}$	C_{Lr}/C_{Li}	M/I	Inflow I Mols/cm/s $x10^{-13}$	App.mass flow M Mols/cm/s $x10^{-13}$	C_{Lr} Mols/cm^3 $x10^{-7}$	C_{Lr}/C_{Li}	M/I
23	49.5	216.2	1.05	2.15	5.1	22	97.2	1.07	4.3
30	47.5	212.6	1.03	1.66	4.7	21	96.8	1.06	4.45
21	49.5	217.4	1.06	2.36	4.7	22	97.7	1.07	4.65

VALUES OF THE MEAN ROOT ABSORBING POWER $\bar{\alpha}$

Interharvest period	K	Na	Na unbuf.	Mg	Mg unbuf.	Ca	NO_3	Cl	SO_4	PO_4
					$\bar{\alpha} \times 10^{-6}$ cm/s					
1	71	0.66	0.65	0.84	0.81	0.13	0.56	0.28	0.45	
2	35	0.50	0.49	0.69	0.67	0.14	0.75	0.26	0.45	
3	30	0.16	0.16	0.62	0.59	0.15	0.59	0.29	0.52	

Table 4.9

order of increasing oversupply was Mg, NO_3, SO_4, Na, Cl and Ca by factors of about 2,2,3,4,4 and 8 respectively. A greater proportion of the fluxes was supplied by mass flow in the last interharvest period, when water uptake rate was continuing to rise steeply, but ion uptake rate was decreasing slightly. Despite the large oversupply by mass flow, the calculated root surface concentrations did not rise greatly above the average solution concentration. For calcium, which was supplied in greatest excess by mass flow, a 15% mean increase in C_{LR} was calculated. This conclusion was reinforced by comparison of these results with one of the numerical solutions of Passioura and Frere (1967) with very similar conditions.

Conditions	$\bar{r}$ cm	$\bar{v}$ cm/sec	D_L cm/sec	$\frac{C_{LR}}{C_{Li}}$	t days
Passiours and Frere	0.02	2×10^{-6}	10^{-6}	1.12	7
Present (approximately)	0.03	1.3×10^{-6}	10^{-6}	1.15	7

Their computed C_{LR}/C_{Li} increased to 1.12 in less than an hour and then increased very slowly. The differences in parameters between the two cases should oppose themselves, since the lower $\bar{v}$ in our experiment should lead to lower values of C_{LR}/C_{Li} but the larger $\bar{r}$ should have the converse effect. Root absorption of calcium was only 1/8 of the apparent mass flow supply in the experiment and this condition should be very similar to the no absorption boundary situation of Passioura and Frere. The calculated values of $\overline{C_{LR}}$ are discussed in Chapter 6 in the light of the assumptions listed in Chapter 3.5.

Chapter Five

THE PHOSPHATE FLOW TO LEEK ROOTS IN SOIL

5.1 Computation of the Theoretical Phosphate Supply to Roots

5.1.a. Introductory Discussion

As has been mentioned already, the desorption isotherm for P in the soil was markedly curved (see Fig.4.17). This meant that the diffusion coefficient was concentration dependent. Equation 3.IV describes the inflow into a cylindrical sink with a constant surface concentration absorbing nutrients from a medium in which the nutrients have a constant diffusion coefficient. Thus, two approximations are implied in applying this equation to the diffusion of phosphate to roots. The first, that the boundary concentration is constant, is not serious, and, as for other ions, results from this equation are very similar to those using $F = \alpha C_L$ as the boundary condition (see 3.3 above). However, the smaller the value of D the more rapidly g, the instantaneous flux parameter, changes with time and the bigger the discrepancy between the two boundary conditions will be (Drew 1966, p.157). Thus, this approximation becomes less satisfactory the smaller D becomes and we can expect less reliable results for P than say K. However, later evidence (5.2 below) will show that even for P this is not a serious difficulty. The second important condition or approximation involved in equation 3.IV is that of a constant D, and this has been less thoroughly considered before. Equation 3.IV is derived from that of Jaeger and Clark (1942) describing the heat flow to a cylinder from an infinite medium with a constant thermal conductivity. However, Crank and Henry (1949) have shown that in many cases of concentration dependent diffusion to a planar sink, the values of the mean diffusion coefficient, $\bar{D}$, that can be calculated from total uptakes, using the formula which relates the total uptake by the sink to time, approximate closely to the values of the integral diffusion coefficient (D) over the concentration range considered. The formula

they used to calculate $\bar{D}$ is strictly applicable only to diffusion in a medium where D is constant, but $\bar{D}$ was within 20% of (D) for a number of functions relating D and C. Therefore, it is reasonable to assume that the converse procedure will also give approximately correct results and that, given a value of (D), one could substitute in equations that strictly apply only to diffusion in a medium with a constant D and obtain reasonable values for the total uptake and hence the mean flow to the sink.

The integral diffusion coefficient (D) is easily calculated given the desorption isotherm since,

$$(D) = \frac{1}{C_2 - C_1} \int_{C_1}^{C_2} D\,dC = \frac{D_L v_L f_L}{C_2 - C_1} \int_{C_1}^{C_2} \frac{dC_L}{dC}\,dC$$

$$= D' \quad \frac{C_{L2} - C_{L1}}{C_2 - C_1} = D' \quad \frac{\Delta C_L}{\Delta C} \quad . \quad \text{(equation 2.II).}$$

where, $D' = D_L v_L f_L$

$\frac{\Delta C_L}{\Delta C}$ is the mean slope of the desopption isotherm between the limits of C_L considered (see Chapter 2 for a further discussion of (D).)

In order to calculate the phosphate flow to roots using this approach, different values of $\frac{\Delta C_L}{\Delta C}$ were used to calculate different values of (D). From this a mean flux parameter $\bar{g}$, describing flux to the surfaces of the leek root system, could be calculated in the way described in 3.3 above. Using values of (D) it was possible to use equation 3.X to predict the flows to root surfaces with different values of C_{LR}. But diffusion to roots is a case of cylindrical diffusion and the conclusions of Crank and Henry (1949) referred to above justifying the approach, concerned diffusion to a plane surface. Consequently there remained some uncertainty in adopting this approach to determine the theoretical inflow.

In order to provide a fully satisfactory theoretical prediction of inflow which could be confidently compared both with measured values and approximately calculated predictions, the appropriate data were entered into a computer programme which generated numerical solutions to the problem. The programme was written in Fortran by Mr.P.H.Nye.

5.1.b. Details of the Computer Programme

The programme was able to calculate the inflow, total uptake and concentration gradients round a root at any time given the values of C_{Li}, $D_L v_L f_L$ (or D'), $\bar{r}$, α, v the water inflow into the root and the buffer power b or, where b is variable, a function relating b to C_L.

The programme used the Crank-Nicholson finite difference method (Crank 1956) to provide solutions to the differential equation describing simultaneous diffusion and mass flow to a cylinder (equation 3.I).

The boundary conditions were:

$$t = 0 \qquad a \geq r \qquad C_L = C_{Li}$$

$$t > 0 \qquad a = r \qquad F = \alpha C_{LR}$$

$$t > \theta \qquad a \to \infty \qquad C_L \to C_{Li}$$

If there is considerable depletion at the surface of a cylindrical diffusion sink of small radius, the concentration gradients near to the surface of the sink are very steep. If, as here, diffusion coefficients are concentration dependent, then near the root surface the value of D will change drastically with distance. Thus, in order to use a finite difference method satisfactorily in regions where C and hence D are changing markedly, the calculation must be based on small steps of space and time. The programme had variable time steps, so that the finite difference computations could be performed over much shorter times early as opposed to later in the diffusion period. Thus, calculating accuracy was concentrated where it was most needed. It had

previously proved impossible to obtain solutions without using excessive computer time running a similar programme without the variable time step facility.

Space steps were 0.005 cm and the initial time step was 21.625 seconds. There was 1 space step inside the root and 145 space steps outside the root stretching to 0.7 cm from the root axis. The pg programme was run for 100 time steps equivalent to 0. to 21 days real time. The early time steps increased by a factor of 2 for each of the first ten steps and thereafter the time step was held constant at one hundred times the initial time step.

As mentioned above, the programme needed an input of the relation between C_L and b. The shape of the phosphate desorption isotherm (Fig.4.17) approximates to an inverse exponential curve of the form given by:

$$C_L = a\, e^{-k\Delta P}$$

where ΔP = the amount of exchangeable P removed from the soil in moles/cc and a and k are constants.

thence, $\log_e C_L = \log_e a - k\Delta P$

Here ΔP was plotted against $\log_e C_L$ and an almost perfect straight line was obtained. The slope of the line was -k and the intercept with the ΔP axis was $\log_e a$. The resulting equation was:

$$C_L = 0.177 \times 10^{-7}\ e^{-1.4 \times 10^{6}\ \Delta P}.$$

By differentiating this equation it can be shown that

$$b = \frac{dC}{dC_L} = \frac{1}{kC_L} = \frac{7.08}{10^{7} C_L}$$

This relation between b and C_L was entered into the computer programme.

5.1.c. The Computer Input Data

The programme was run with several different conditions thereby testing the effect on P inflow of changes in the different input parameters. The effects were examined of 1, different values of root absorbing power a, 2,

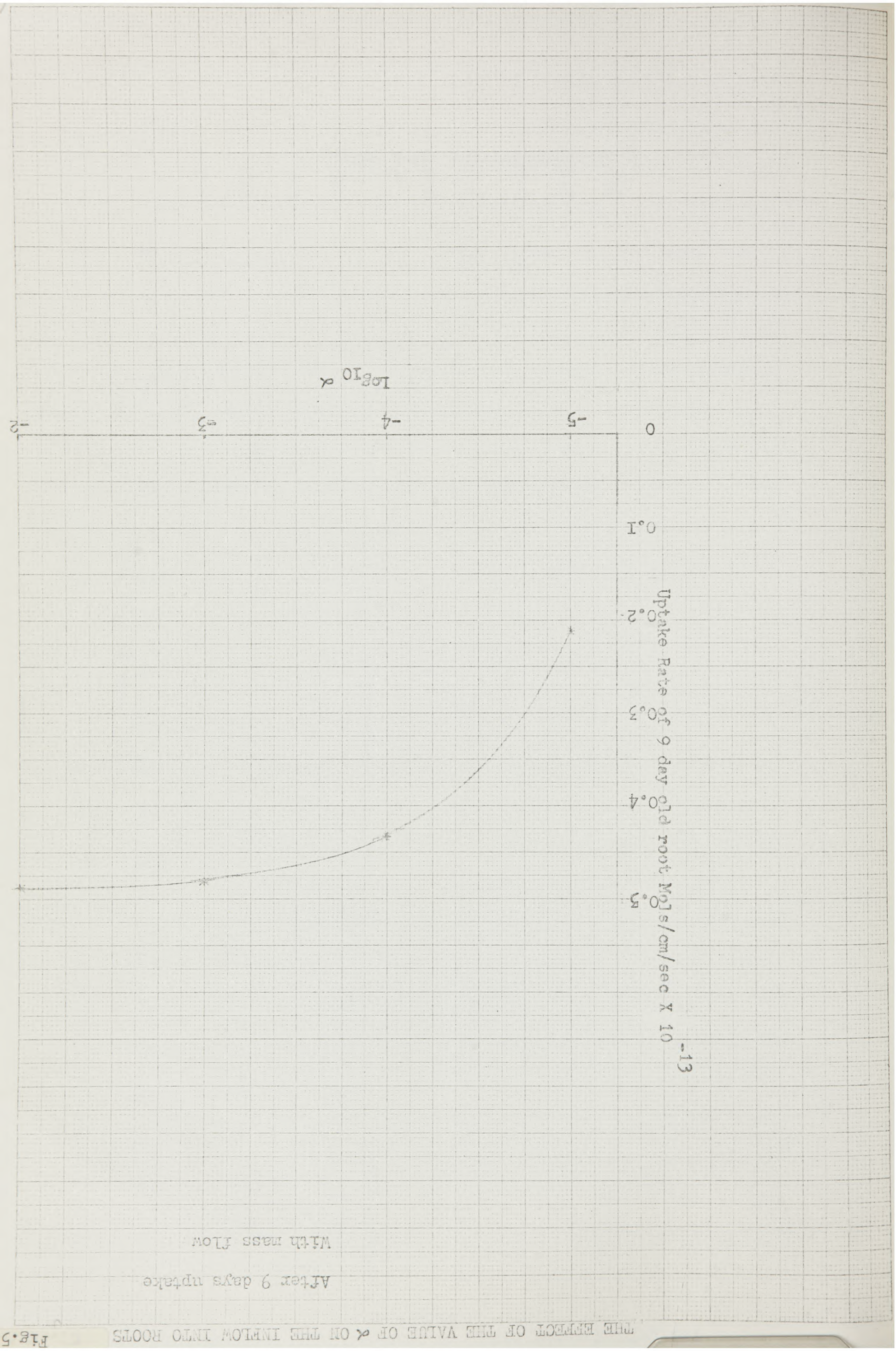
the presence or absence of mass flow and 3, the presence of a variable as opposed to a constant D. The runs are tabulated below along with details of the important input parameters.

Run	Initial Soil Solution concentration C_{Li} Mols/cm^3	$D_L v_L f_L$ cm^2/sec	Root Radius r.cm	Water Flux at the Root Surface V cm/sec	Buffer Power b	Root Absorbing Power cm^2/sec
1	1.77×10^{-8}	0.81×10^{-6}	0.03	1.3×10^{-6}	Variable with b = $\frac{7.08}{10^7 C_L}$	10^{-2}
2	"	"	"	"	"	10^{-3}
3	"	"	"	"	"	10^{-4}
4	"	"	"	"	"	10^{-5}
5	"	"	"	0	"	10^{-3}
6	"	"	"	0	Constant with b=40	10^{-3}
7	"	"	"	0	Variable	10^{-3}

Run 7 had the space and time steps halved and gave results almost identical with 5 showing that the choice of space and time steps in runs 1 to 6 was sufficiently small for accurate results.

5.1.d. Computer Output Data

Fig.5.1. illustrates the effects of the value of α on the inflow rate at a given time. Above a certain value of α the root is effectively a zero sink and inflow is controlled totally by diffusion (Nye 1966a) In the case of P diffusion considered here, it is clear that an α of 10^{-3} cm/sec is virtually as effective as an α of 10^{-2}. Even an increase of an α from 10^{-5} to 10^{-4} only doubles the inflow, showing diffusion in soil to be partially limiting the inflow in this range of α. In Fig.5.2. the inflows can be seen to decrease with time. The inflow into ten day old roots is only 55% that into one day old roots when $\alpha = 10^{-2}$. This illustrates the



THE EFFECT OF THE VALUE OF α ON THE INFLOW INTO ROOTS

Fig.5.1

THE INSTANTANEOUS INFLOW OF PHOSPHATE INTO ROOTS WITH DIFFERENT VALUES OF α .

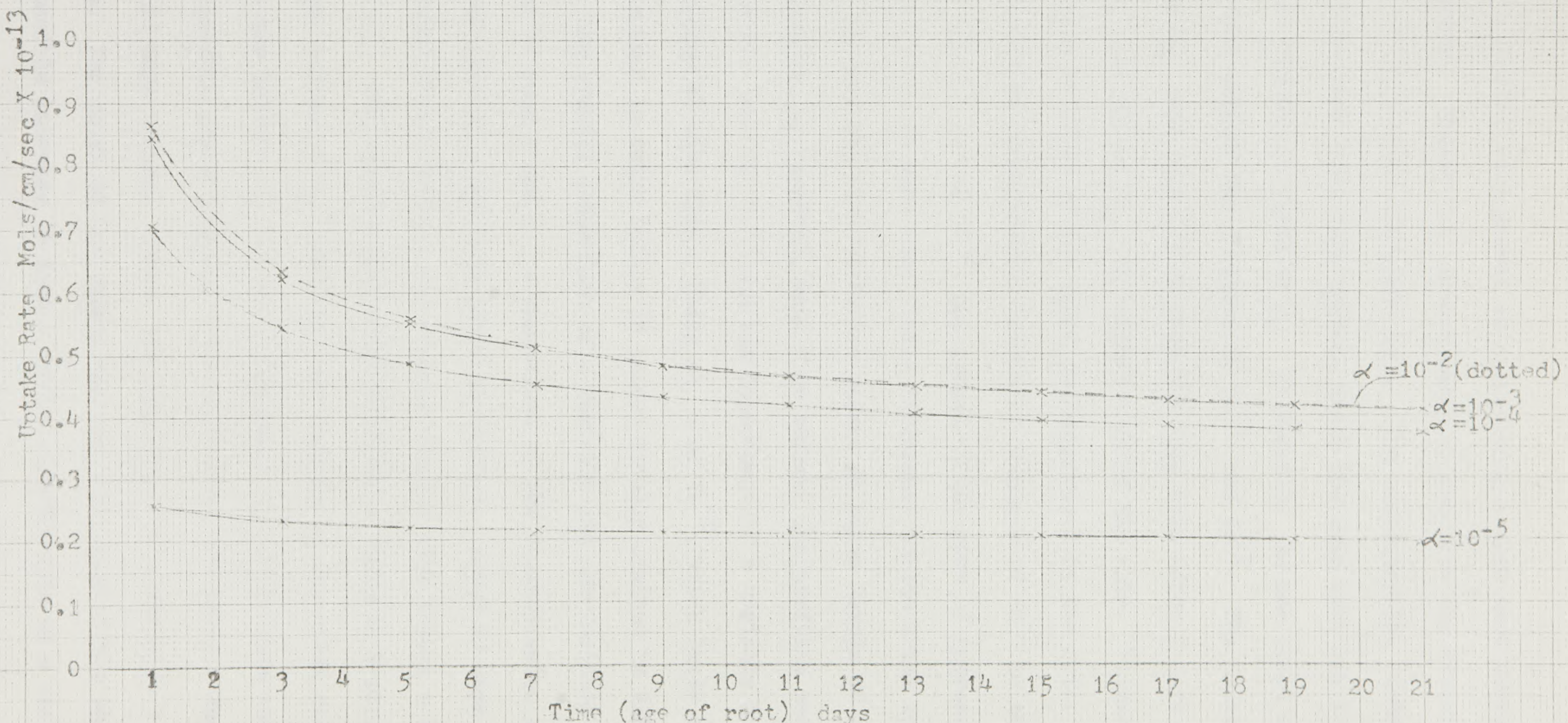


Fig.5.2

importance of continued root growth in maintaining a high mean phosphate flow into a root system. Figure 5.2. also clearly illustrates the diminishing effectiveness of successive increases in α. The concentration distance profiles round roots after nine days uptake, about the mean root age in the pot experiment, are plotted in terms of C_L in Fig.5.3. As one would expect the profiles are very similar for α values of 10^{-3} and 10^{-2}. The point where C_L was 90% of C_{Li} was only 2.5 mm from the root axis after 9 days and the point where C_L was 50% of C_{Li} lay within 1 mm of the axis. Figure 5.4 shows the same profiles in terms of the total exchangeable P in the soil. Although root surface solution concentration decreased with an α of 10^{-2} to about one tenth of that with an α of 10^{-3}, the spread of the zone of increased depletion was so narrow as to make very little difference to the total uptake in the two cases despite the high buffering powers at these levels of depletion.

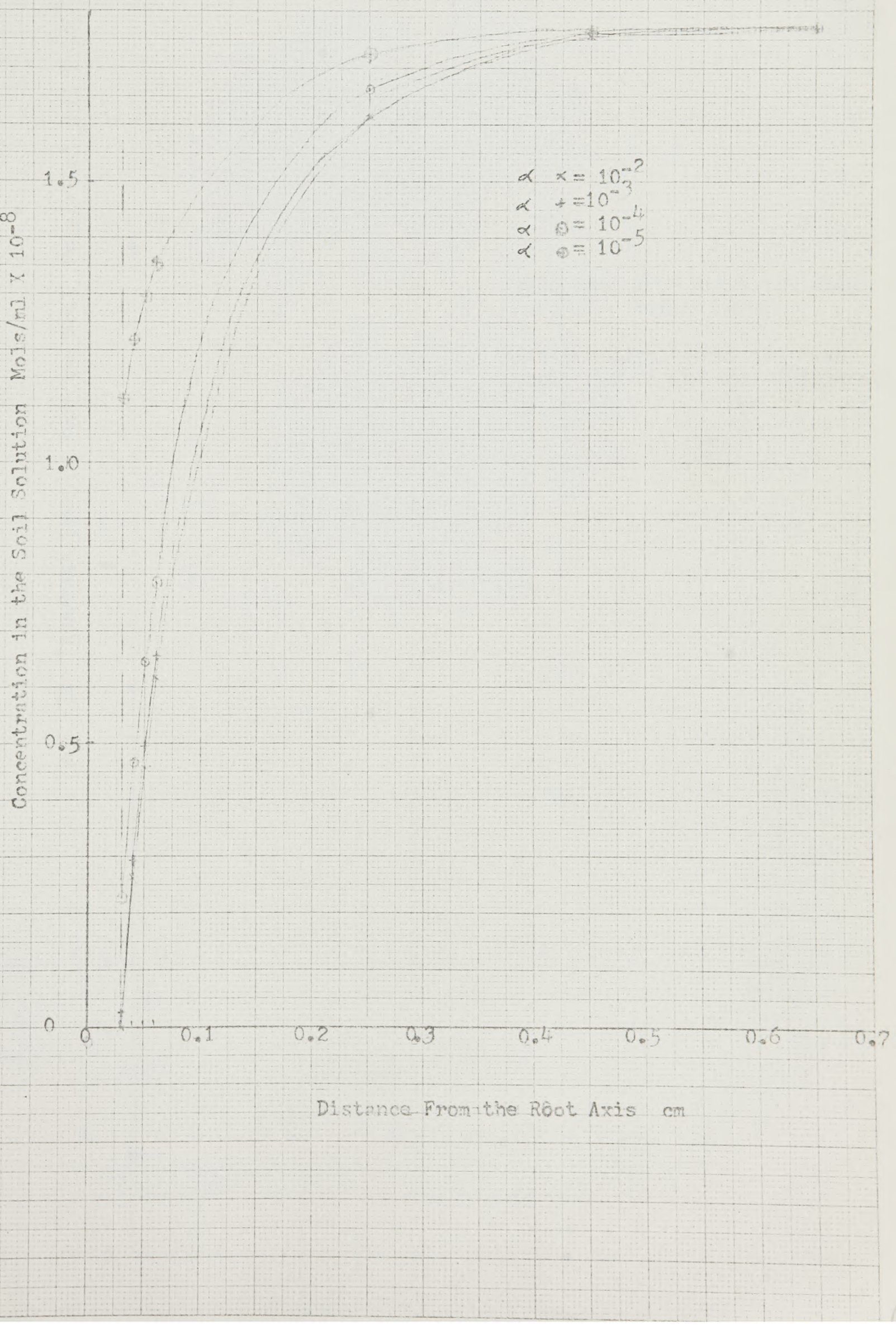
For phosphate, as expected, mass flow affects the profiles and inflows only very slightly (see Fig 5.5) and the importance of a variable b was assessed in the absence of mass flow. Using an α of 10^{-3}, which leads as we have seen to a situation in which inflow is almost totally limited by diffusion to the root surface, the crucial comparison of a variable and non-variable buffer power was made in runs 5 and 6. A comparison of the concentration profiles at 21 days from runs 5, 6 and 2 is given in Fig.5.5. After 21 days, the soil solution concentration profiles were closely similar with either a constant or a variable b. The computations which included a variable b predicted only slightly larger values of C_L near the root surface at any given time. Fig. 5.6. compares the inflows in the two situations. The difference between inflow with a variable and a constant b was only about 15% after 1 day's uptake and 8% after 21 days uptake. Hence, the importance of a variable b diminishes with root age. For roots of the dimensions and life span of the experimental leeks, the possible increase in mean P inflow attributable to a variable b was of small importance, but the possible increase in inflow would be greater for shorter lived roots or roots with root hairs.

Fig.5.3

THE EFFECT OF THE VALUE OF α ON THE SPREAD OF DEPLETIONS IN PHOSPHATE CONCENTRATION ROUND ROOTS

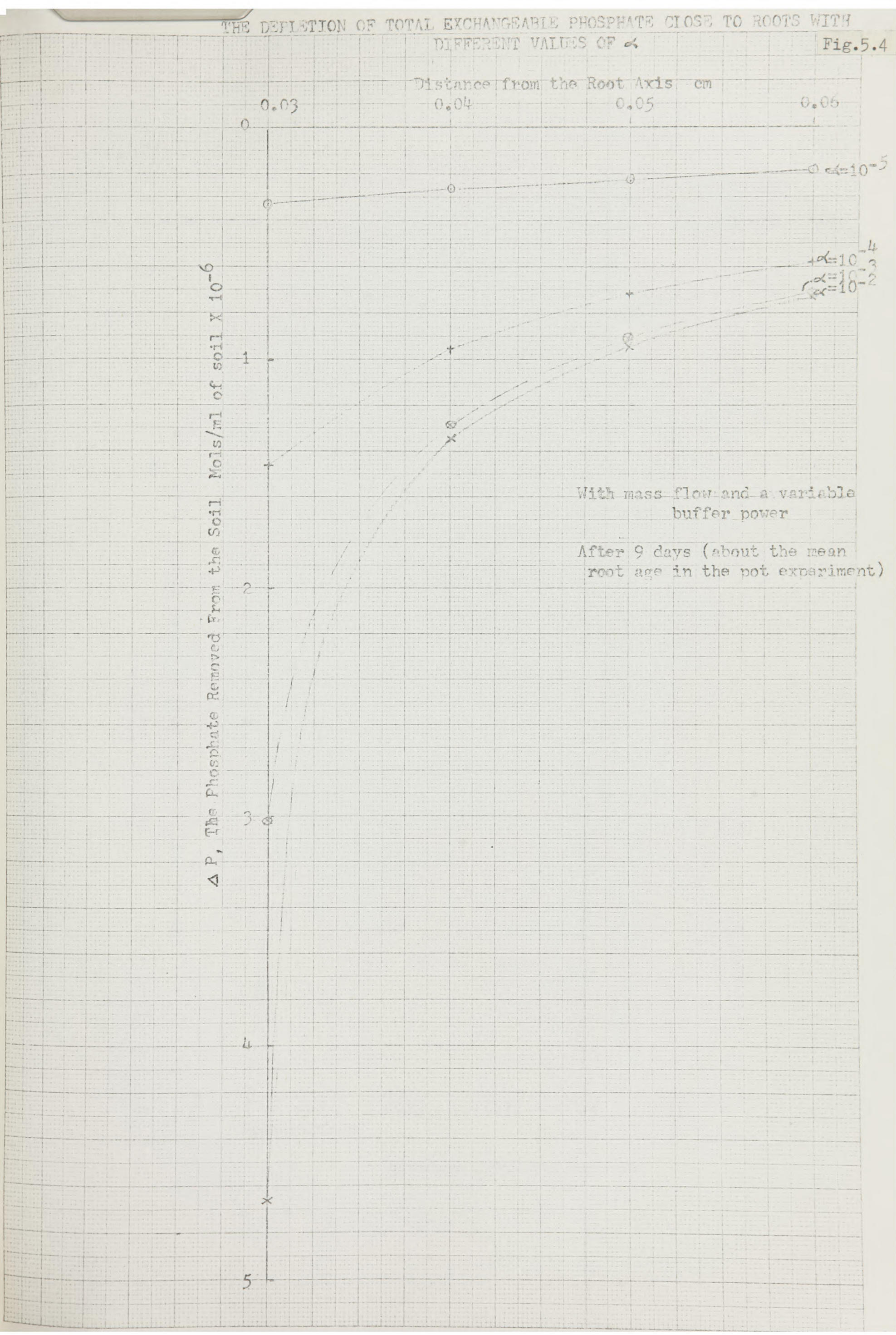
With mass flow and a variable buffer power.

After 9 days (about the mean root age in the pot experiment)



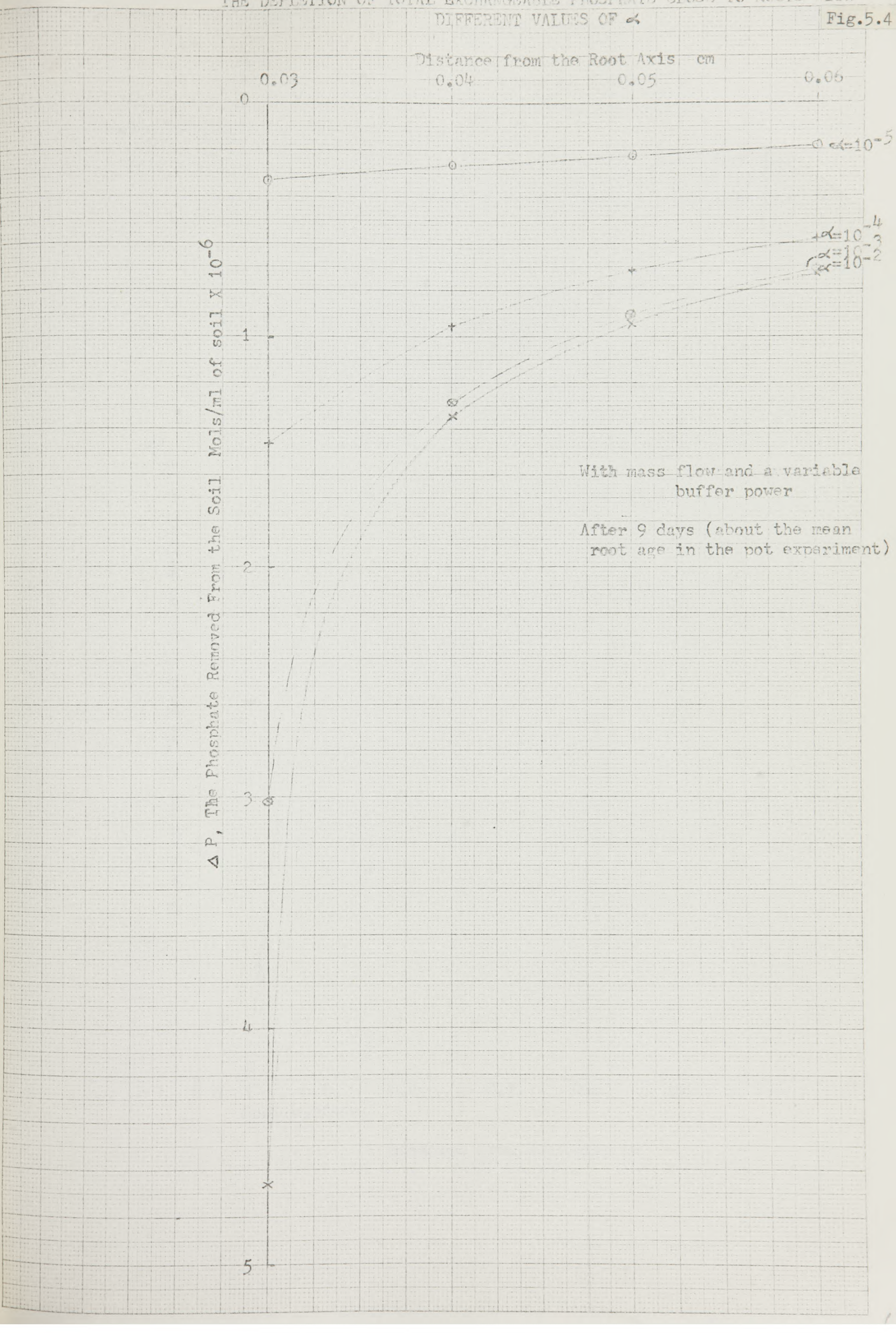
THE DEPLETION OF TOTAL EXCHANGEABLE PHOSPHATE CLOSE TO ROOTS WITH DIFFERENT VALUES OF α

Fig.5.4



THE DEPLETION OF TOTAL EXCHANGEABLE PHOSPHATE CLOSE TO ROOTS WITH DIFFERENT VALUES OF α

Fig.5.4



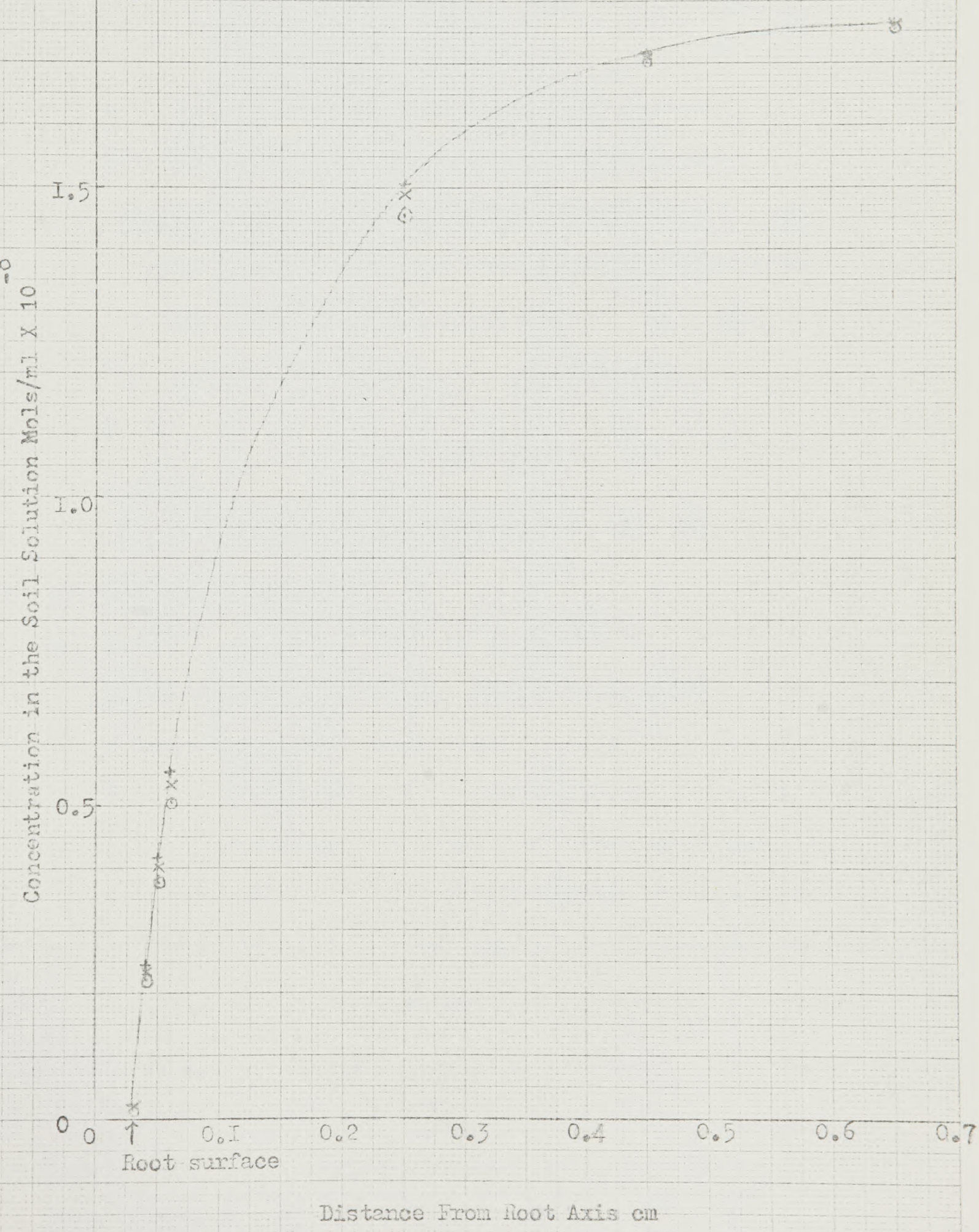
THE EFFECTS OF MASS FLOW AND A VARIABLE BUFFER POWER ON PHOSPHATE CONCENTRATION PROFILES ROUND ROOTS

Fig.5.5

After 21 days uptake

$\alpha = 10^{-3}$ in all cases

\+ Variable b and mass flow
× Variable b no mass flow
⊙ Constant b and mass flow



Nye (pers.comm.) has pointed out that where roots with high α's are closely spaced and liable to compete, the presence of a variable b is likely to be of more significance than was the case above. Root competition diminishes the inflow of nutrients into roots of high absorbing power (i.e. high α) when the depletion zones of adjacent roots overlap (Baldwin and Tinker, 1971 in press). The results above indicate that, given two adjacent roots with a high α for P, then when b is variable as opposed to constant, depletion zones will spread out slightly less rapidly and will take slightly longer to overlap. Further, concentrations in solution will decrease more slowly when overlap does occur, if b increases as C_L diminishes. Hence, the reduction in mean inflow due to root competition will be less important where b is variable, and the mean inflow with a concentration dependent D will differ by an increasing fraction from that with a constant D as depletion zones overlap more and more.

5.1.e. The Calculation of the Theoretical Inflow into the Leek Root System from the Computer Output Data.

The computer print out gave values of the inflow and total uptake at two day intervals from 1 to 21 days. From the root growth curve the proportion of the total root length in successive two day long age classes was calculated. Thus the proportion of the root system aged between 0 and 2, 2 and 4 and so on to 20 and 22 days was calculated. For interharvest periods 1 and 2 the straight line plot of log root length against time was used in this calculation (see Table 4.3.b. for raw data). For interharvest period 3, the length of root in each age class was estimated from Fig.4.7. The mean flow into the root system was calculated by multiplying the proportion of roots in each age class by the inflow, given by the print out, into the roots of the mid age of the class and summing these products. For the roots from 0 to 2days old where the computed inflow was decreasing comparatively rapidly with time, the contribution to the mean inflow was calculated by multiplying the proportion of roots by the average flow into roots from 0 to 2 day old.

This calculation of the mean inflow was very similar in principle to that for calculating $\bar{g}$ described in detail in page 4.6.c.

The values of the mean flow into the root system for the different runs are tabulated below:

Run	α	Points to Note	Mean Inflow Interharvest Periods 1 & 2	Mols/cm/sec x 10^{-13} Interharvest Period 3
1	$\alpha = 10^{-2}$	Variable b Mass Flow	0.67	0.62
2	$\alpha = 10^{-3}$	" "	0.66	0.61
3	$\alpha = 10^{-4}$	" "	0.54	0.51
4	$\alpha = 10^{-5}$	" "	0.22	0.22
5	$\alpha = 10^{-3}$	" No Mass Flow	0.64	0.59
6	$\alpha = 10^{-3}$	Constant b No Mass Flow	0.55	0.52

Thus it seems that the presence of a variable b could account for, at most, about a 15% increase in mean P inflow over the case where b remained constant.

5.2. RThe vCalculation of the Theoretical Inflow Using the Integral diffusion Coefficient and the Analytical Equation (Equation 3.X)

The integral diffusion coefficient, for diffusion to the roots,

$$(D) = D' \frac{C_{Li} - C_{LR}}{C_i - C_R} \quad \text{(See Equation 2.II)}$$

was calculated for a number of values of root surface P concentration C_R. In each case except (1) below $C_i - C_R$ was calculated from the equation,

$$C_L = 0.177 \times 10^{-7} \, e^{-1.4 \times 10^{6} \Delta P}$$

by substituting the required C_{LR} for C_L and hance obtaining the value of ΔP which equals $C_i - C_R$. The five calculations presented are:

1) The buffer power constant at 40 with $C_{LR} = 0$.

2) Depletion at the root surface down to the end of the measured isotherm where ΔP was 2.8×10^{-6} mols/cc, C_{LR} was 0.36×10^{-9} mols/cc and (D) was 5×10^{-9} cm^2/sec.

3) C_{LR} was 10^{-10} mols/cc giving a ΔP of 3.75×10^{-6} mols/cc and (D) of 2.66×10^{-9} cm^2/sec.

4) C_{LR} was 10^{-11} mols/cc giving a ΔP of 5.4×10^{-6} mols/cc and (D) of 1.85×10^{-9} cm^2/sec.

5) It was assumed that all the exchangeable P was removed at the root surface hence ΔP was 12×10^{-6} mols/cc and (D) was 1.2×10^{-9} cm^2/sec.

The minimal concentration of phosphate in solution needed to support plant growth and uptake varies with species. (see Asher and Loneragan 1967b). Olsen (1950) found such a minimal concentration at 10^{-10} mols/cc whereas Barley (1970) quotes 10^{-11} mols/cc, hence both cases 3 and 4 above were chosen. Case 5 above is in fact extremely unlikely to apply since plants have been shown to be unable to remove all the exchangeable phosphate from soil even in conditions of exhaustive cropping (Mattingley and Talibudeen 1961). It should be noted that in calculations 3, 4 and 5 it was assumed that the isotherm follows the exponential equation beyond the measured points.

Case	Predicted Mean Inflow Mols/cm/sec x 10^{-13}	
	Interharvest Periods 1 and 2	Interharvest Period 3
1	0.57	0.50
2	0.77	0.65
3	0.87	0.73
4	0.98	0.83
5	1.32	1.08

A comparison of these inflows with the computer predictions in 5.1.e. shows a hearteningly close agreement between case 1/here and computer solution 6. Thus where the diffusion coefficient was constant the predicted mean inflow to the root system was almost the same from both methods of calculation, despite the known approximations in calculating $\bar{g}$. This result imparts further confidence in the modified Passioura equation (equation 3.X) as a sufficiently accurate tool for the calculation of the possible inflows to roots when the value of α is large, given that D is constant or almost so.

When (D) is highly concentration dependent, this equation predicts inflows which are considerably greater than the numerical solution indicates are possible. Thus, the equation 3.X is satisfactory where b is constant, but where b increases with decreasing concentrations it predicts inflows that are too high. As mentioned above equation 3.X derives from a heat inflow equation which assumes a constant diffusivity so it is not surprising that it yields erroneous results when D becomes very variable.

5.3. The Comparison of Theoretical with Measured Phosphate Inflows.

If the maximum inflows predicted by the numerical solution are compared with the measured inflows, we find that the measured values are higher than the predicted values

	Mean Inflow into Leek Roots Computer Predicted	Mols/cm/sec x 10^{-13} Measured
Interharvest Period 1	0.67	1.2
Interharvest Period 2	0.67	0.82
Interharvest Period 3	0.62	0.94

The standard deviation of the measured values was about ± 0.2, hence we can say that measured fluxes were about 1 x 10^{-13} mols/cm/sec.

Taken overall the measured mean inflows showed reasonably close agreement with the theoretical maximum supply rate from the soil. The agreement is such

that the most likely hypothesis to explain the observed mean inflows is that the root system had a uniformly high α for phosphate and was virtually a zero sink for phosphate throughout its length. Experimental errors and the minor effects overlooked by the assumptions upon which the theoretical analysis is based are probably sufficient to explain the discrepancy between the observed and the theoretical results. However, large effects due to factors that were not accounted for cannot be entirely ruled out.

Of the assumptions in 3.5., those that require particular discussion for phosphate are;

2) The root is a simple sink for water and nutrient ions.

A number of the organic anions that roots can exude (Rovira 1969) could in some circumstances displace adsorbed phosphate from soil solids (Hingston, Atkinson, Posner and Quirk,1968).

The results from the P desorption isotherms (see 4.9.c.) indicated that an increase in pH in the rhizosphere was unlikely to have altered the rate of P supply by diffusion in this soil.

3) The soil is initially homogeneous.

Even sieved soil can hardly be regarded as homogeneous over the short distances through which P diffuses. However, although points along the root may be supplied by microvolumes of soil containing different P concentrations and having different P diffusion coefficients, these properties should average out along the root to give the mean P concentration and mean P diffusion coefficient of the soil. Therefore, theoretical calculations of inflow based on the mean P concentration and diffusion coefficient should not be misleading for this reason.

The possible effect of mycorrhizal fungi on phosphate supply to roots should not be overlooked.

As with most crops the roots of leeks can be colonised by fungi of the genus Endogone that form endotropic mycorrhiza. Mosse (pers.comm,) found evidence of hyphae in the cortex of dried root material from the pot experiment

that were probably Endogone sp. In a phosphate deficient soil infection of onions with Endogone has been shown to increase P inflow into roots by a factor of about four in comparison with that into the roots of non-infected plants in the same soil. (Sanders and Tinker in press).

The fungi can probably increase the P inflow into roots by increasing the absorbing surface area and extending it into undepleted zones well away from the root surface. (Sanders and Tinker, 1971 in press.) They thus change the geometry of the absorbing system. The hyphae of Endogone in grasses have been reported as 20 to 27 μ in diameter giving rise to branches 7.5 to 10μ in diameter. These permanent hyphae have been seen to give rise to ephmeral laterals 3 to 5 μ in diameter (Nicholson, 1959 and 1960). The mycelium extends to a distance of 1 cm. or more into the soil from the root in the active vegetative condition in several species and the hyphae have been shown t to penentrate roots with a frequency varying from 2.6 to 21 junctions per millimetre of root, The density of hyphal penetration increases with decrease in soil nutrient status and it increases with time during the growing season. This question of mycorrhiza casts some uncertainty over out conclusions about phosphate supply in the experiment. (Nicholson 1959 and 1960). However, in soils of high P status such as fertilised Wytham silty loam, the presence of mycorrhiza has been observed to increase total P uptake only occasionally (Daft and Nicholson 1966, Holevas, 1966, Peuss 1958). In assessing the importance of myccorhiza as opposed to their mere presente, measurements of P inflows into infected and non-infected root systems are critical.

Chapter Six

A DISCUSSION OF THE RESULTS AND THE CONCLUSIONS FROM THE POT EXPERIMENT

The mean ion flows around the roots are summarised diagramatically in fig.6.1. The diagram is based on the mean of the inflow values for all the three interharvest periods. The mean ionic concentrations at the root surface as calculated by equation 3.X. are summarised diagramatically in fig.6.2. Again, this is based on the mean of values for all three interharvest periods. As well as the concentrations at the root surface, it was possible to estimate the concentration profiles around roots for K and P. Profiles of P were presented and discussed in Chapter 5, figs. 5.3, 5.4, and 5.5. Fig. 6.3 shows the expected K concentration profile around the roots after five and a half and after sixteen days. This is based on the curves of Olsen and Kemper (1968 p.100). This profile ignores the effect of mass flow but fig. 5.5. gives us reason to believe that mass flow would compress the profile only slightly.

As pointed out in Chapter 3.5., estimates based on equation 3.X involve a range of assumptions. The importance of the assumptions in this experiment is now considered in the order listed there.

1) The flow of nutrients can be described by an appropriate form of the diffusion equation with suitable boundary conditions.

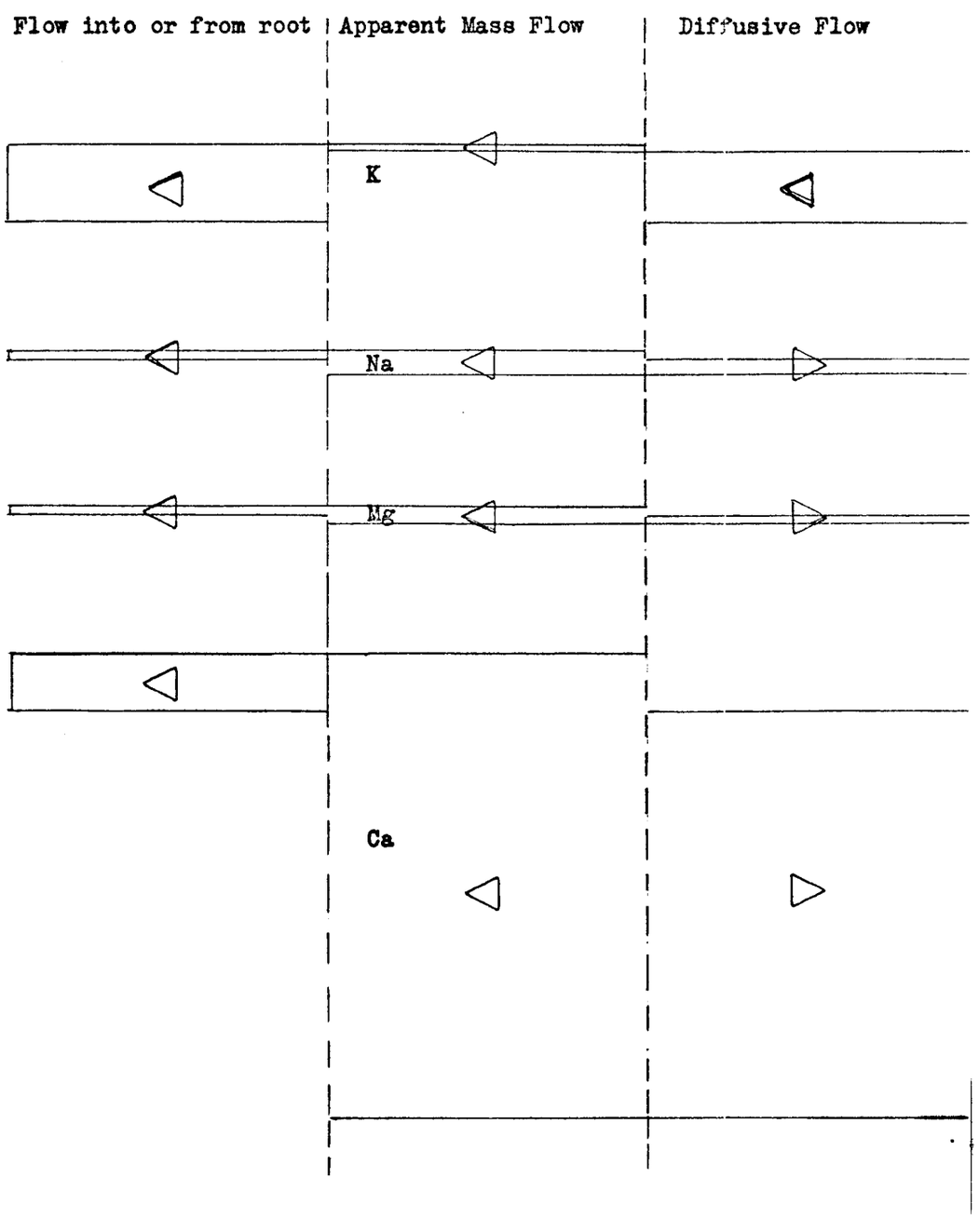
This assumption seems reasonable for all ions except bicarbonate. HCO_3 ions will react with H+ and be neutralised to CO_2 and H_2O as they diffuse away from roots, so that we are dealing with a diffusion plus reaction system and a more complicated mathematical treatment taking into account the rates of both processes is really required. HCO_3 diffusion in soil has been investigated in this laboratory (Ramzan 1970). Fig.6.4. shows the major proton-donating reactions that occur in soil. The HCO_3 concentration at any point in the rhizosphere depends on the HCO_3 outflow from the root, the diffusion coefficient of HCO_3 in the soil, the rate at which HCO_3 reacts to form CO_2 and water and the time for which the root

Fig.6.1

THE MEAN INFLOWS INTO OR OUT OF ROOTS IN THE POT EXPERIMENT AND THE RHIZOSPHERE AS INDICATED BY THE PASSIOURA EQUATION(EQUATION 3.X)

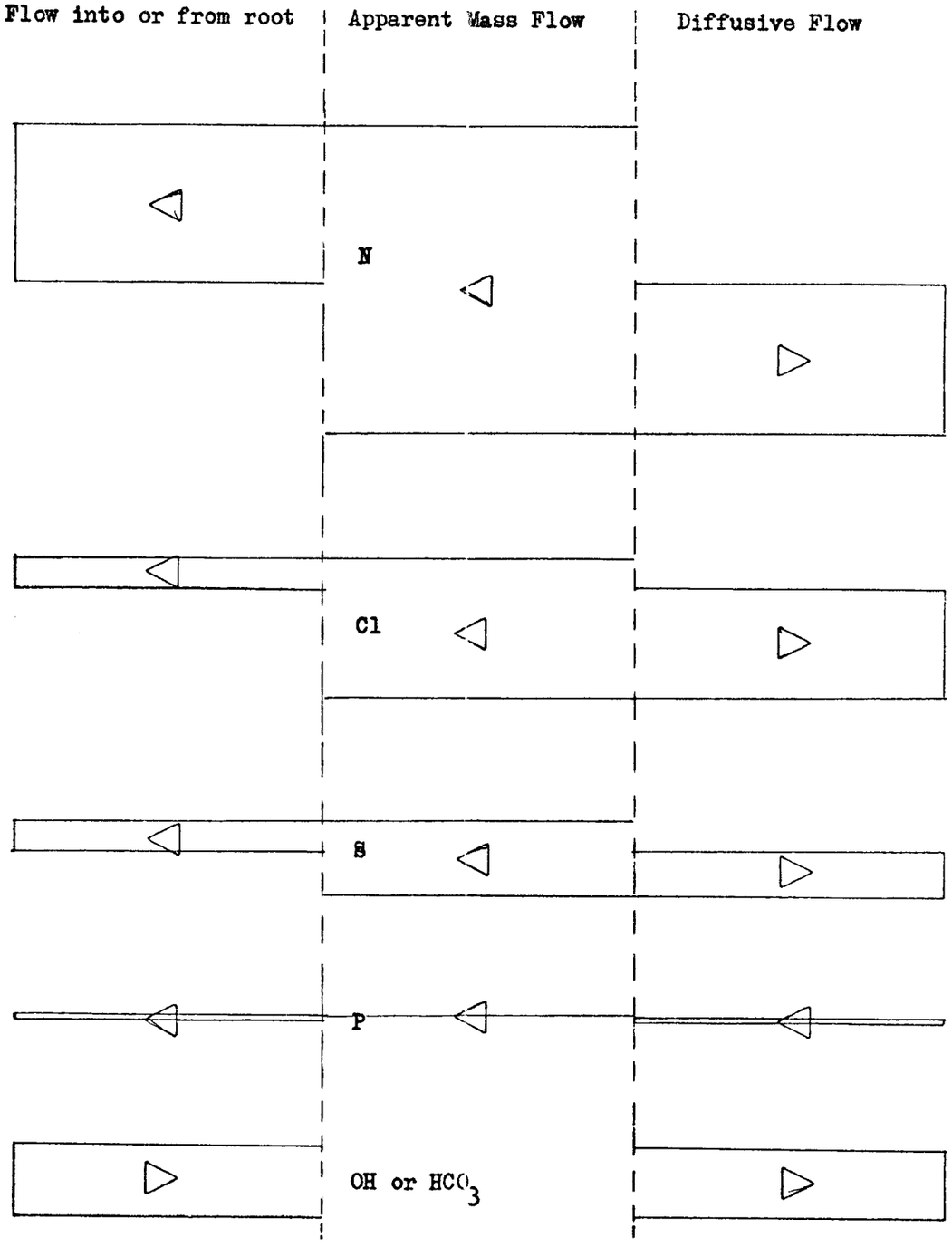
CATIONS

Scale: I mm = I X 10^{-13} Mols / cm of root / sec



MAGNITUDE AND DIRECTION OF THE DIFFUSIVE AND APPARENT MASS FLOW COMPONENTS OF INFLOW IN THE

ANIONS



THE MEAN SOIL SOLUTION NUTRIENT CONCENTRATIONS AT THE ROOT SURFACE OF THE POT LEEK PLANTS COMPARED WITH THAT IN THE BULK OF THE SOIL AS PREDICTED BY THE PASSIOURA EQUATION (EQUATION 3.X)

(Average of the three interharvest periods shown in the table)

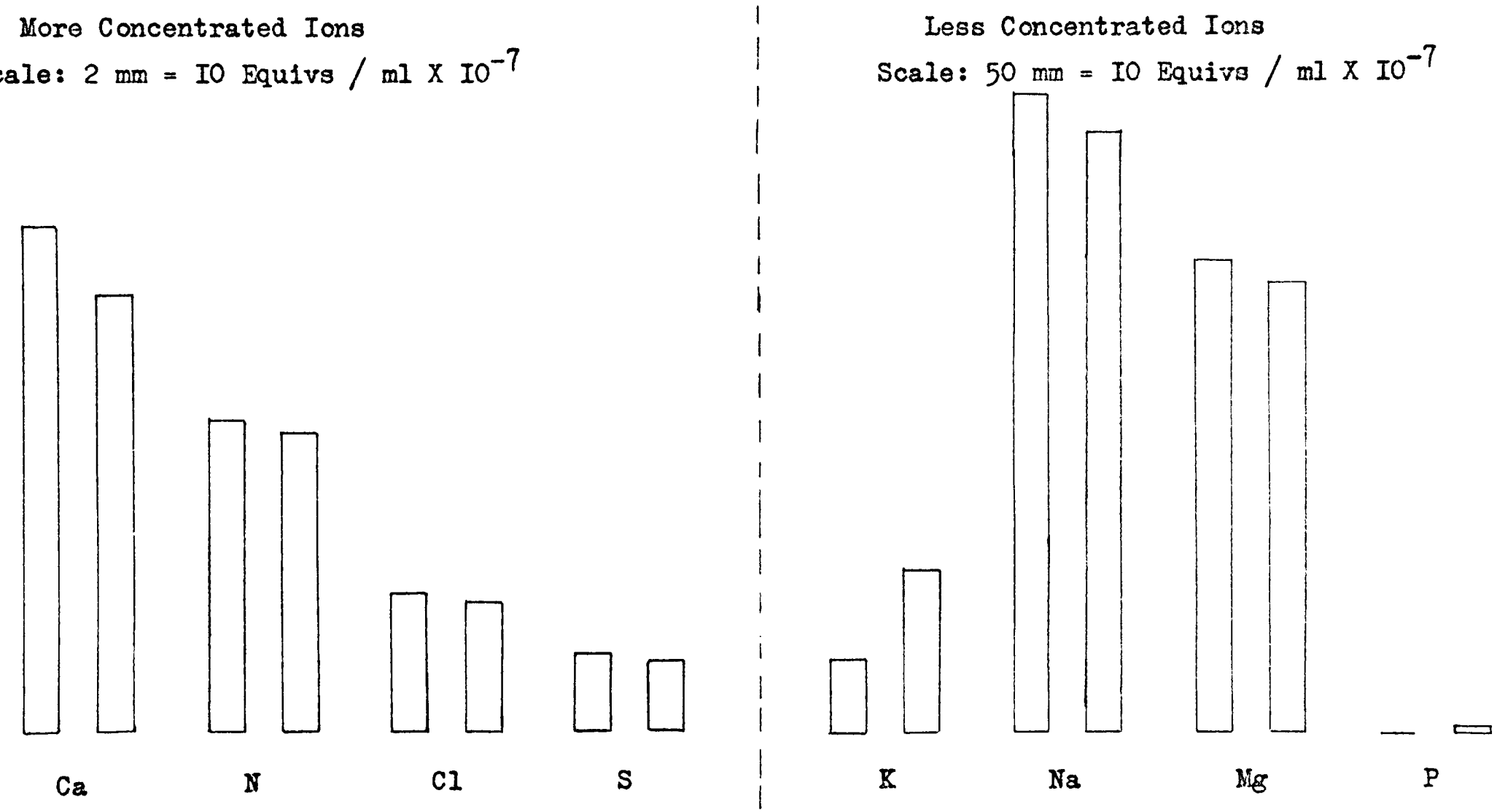


Fig.6.2

Root Surface Concentration C_{LR} to Left , Bulk Soil Concentration C_{LI} to Right .

Fig.6.3

K CONCENTRATION DISTANCE PROFILES ROUND LEEK ROOTS IN POT EXPERIMENT

(Based on Olsen and Kemper I968 p I00 profiles describing diffusion to a cylindrical sink. Mass flow should slightly compress the profiles)

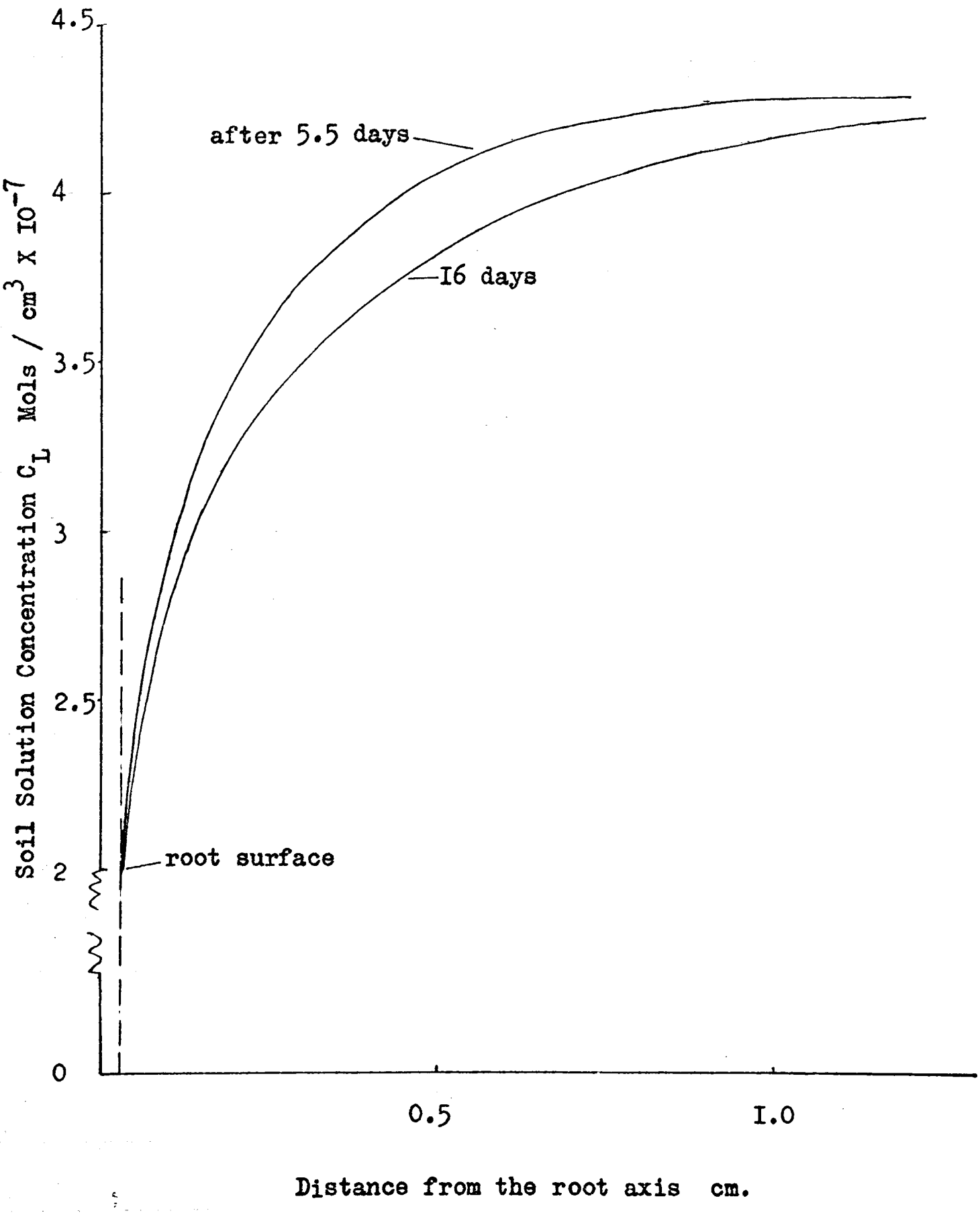
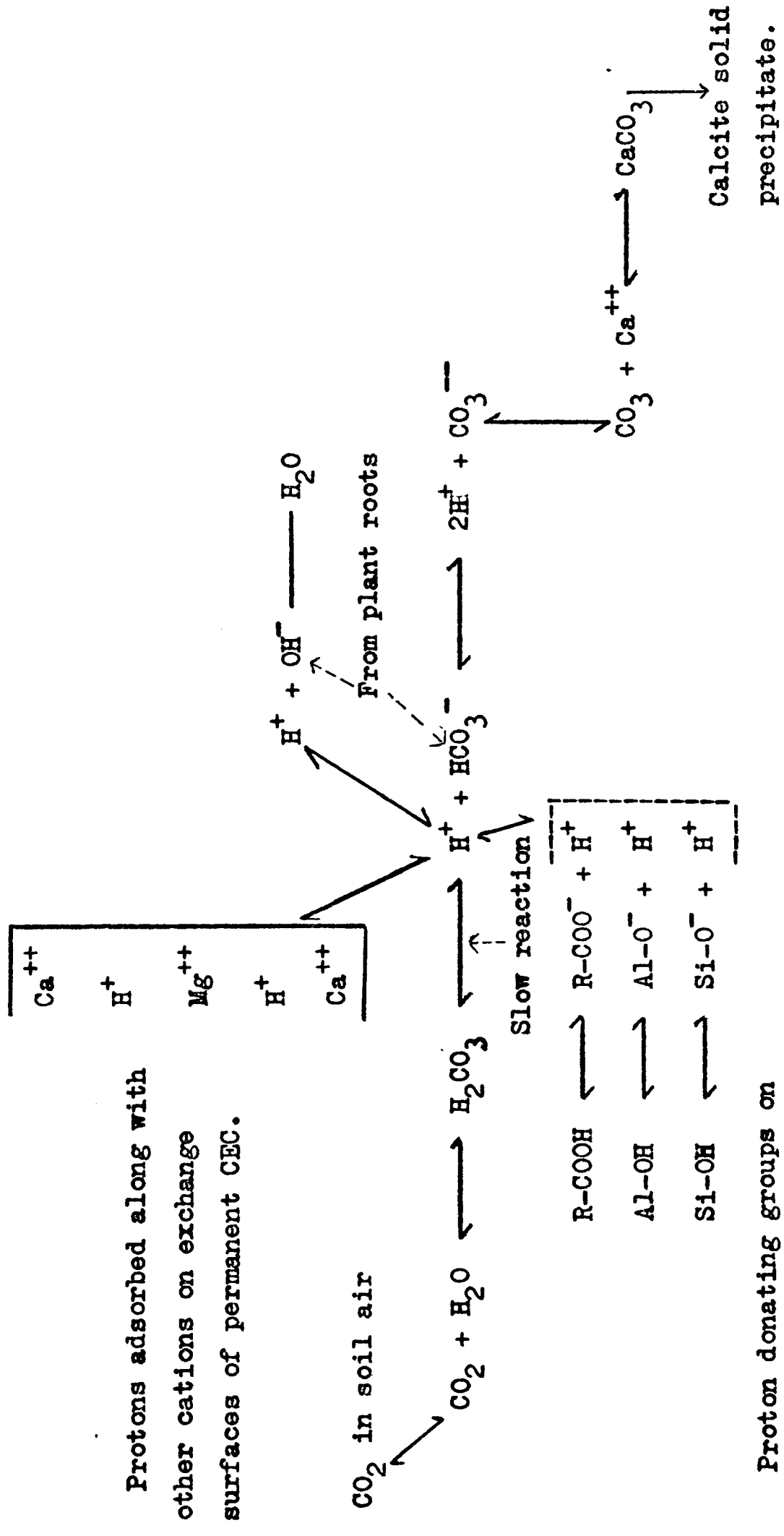


Fig.6.4

THE MAIN REACTIONS DONATING PROTONS TO THE SOIL SOLUTION AND NEUTRALISING HCO_3^- OR OH^- PRODUCED BY PLANT ROOTS



has been excreting HCO_3. The reaction rate is a function of the rate constants and the proton activity or pH in the solution. This pH at any time is determined by the initial pH in solution and the ability of the soil to buffer pH changes in the solution around roots. This in turn depends on the rate at which protons can be donated to the rhizosphere by diffusion from a distance and by proton donating reactions. Ramzan (1970) has found that it takes one to two days for added bicarbonate to come to equilibrium with aerated soil suspensions. This must mean that much HCO_3 remains as this ionic species for a considerable time after excretion from roots and it may diffuse far from the root before neutralisation.

Consideration of the situation round the experimental leek roots suggests that the neutralisation reaction may well have been slow because the proton concentration in the rhizosphere was low. This follows from the relatively high pH of 7 of the bulk soil solution and the calcareous nature of the soil which would bufferthe solution against any decrease in pH. The soil was also moist with a high diffusion coefficient for ions in solution. Remembering also, Ramzan's (1970) finding that the equilibrium of HCO_3 is an intrinsically slow series of reactions in soil, it seems likely that in the pot experiment diffusion away from the root would have dissipated the HCO_3, outflows with little neutralisation in the rhizosphere. HCO_3 probably behaved very similarly to those nutrient ions oversupplied by mass flow, in which case, the root surface concentrations of HCO_3 predicted by equation 3.X are probably a reasonable mean of what were in reality somewhat higher daytime and lower night time concentrations.

3) The soil is initially homogeneous.

The initial homogeneity of the soil was ensured by a thorough mixing and equilibrium prior to the experiment.

4) Roots are cylindrical with constant dimensions.

Leek roots appear almost perfectly cylindrical and the thickness of any one root is almost uniform except at the very tip. Different roots did differ in diameter; the younger primary adventitious roots tended to be thicker than

the older ones, and secondary roots were also thinner than the primaries from which they branched. In the calculations, a mean value of radius $\bar{r}$ was used. The different components of equation 3.X are not simple functions of $\bar{r}$ and this approximation probably leads to some slight error.

5) All flow to roots is radial.

The leek roots were sparsely branched and did not produce root hairs hence the number of tips and junctions where flow was not radial were few.

6) Diffusion coefficients remain constant in the soil round roots.

Diffusion potentials may have been created by the back diffusion of those ions that were accumulated at the root surface. The ions involved were mainly Ca, NO_3, Cl, and HCO_3. These have D_L values of 0.78, 1.92, 2.03 and 1.2 x 10^{-5} cm^2/sec respectively. In solution, the co-diffusion of Ca and these anions would give rise to a diffusion potential accelerating Ca and retarding the anions. Such an effect may have increased the anion accumulations and decreased the cation accumulations with respect to those given in fig.6.2 and Table 4.8.

Turning to $V_L f_L$, therewas no indication of soil compaction due to root growth; the bulk density of the soil was the same at the beginning as at the end of the experiment. The roots emerged from the soil dry and shiny and there was no mucigel apparent. Using the equation of Gardner (1960), and his values of water diffusivity and capillary conductivity for a sandy soil, a maximal estimate was made of the decrease in matric suction at the root surface. This was 0.005 bars, corresponding to a negligible decrease in V_L. This suction gradient could have occurred if the water uptake rate were four times the measured mean rate and if V_L in the body of the soil were 0.3. Such conditions may have occurred during a period of maximal transpiration with the soil in its driest condition just prior to a harvest. Using Gardner's (1960) values of diffusivity and capillary conductivity for a loam soil, a suction drop of only 0.0015 bars was calculated. This evidence indicates that $V_L f_L$ did not vary with distance from the root surface. However,

Whisler, Klute and Millington (1970) present theoretical evidence that even in moist soils the water flow into roots attains a limiting value which is of the order of the mean water flows that have been observed. Where the water inflow is thus limited, they predict a sharp decrease in soil moisture content near the root. If this were the case, $V_L f_L$ would be markedly decreased near the root surface leading to significant accumulations of ions at the root surface. In an autoradiographic experiment using anions growing in Upper Greensand soil labelled with $S^{35}O_4$ and in conditions of high transpiration, I was unable to detect any root surface accumulation until the soil was dry overall (See Chapter 7). This suggests that in practice $V_L f_L$ does not diminish sharply near roots in moist soil and that the accumulations predicted by 3.X are not likely to be misleading for this reason.

7) The soil around roots is infinite in extent.

As shown in table 4.4 the overall depletion of the soil was not great, even for the non adsorbed anions. Since 42% of the roots were in the top quarter of soil volume, if 42% of nutrients absorbed by the plants had been removed from this volume at harvest the corresponding depletions of the initially present/exchangeable nutrients would have been K 8%, Na 6.5%. Mg 1%, Ca 0.26%. NO_3 22%, Cl 12%. Hence, even if depletion had been localised in this way, the average depletion in the top quarter of the pot would not have been very great. If all the roots had been equally spaced throughout the soil volume the mean distance between them would have been 1.8 cm. In fact, the mean distance between roots in successive depth layers was 1.3, 1.6, 2.6 and 2.9 cm. With the diffusion coefficients given in Table 4.7.a. the spread of depletion zones would have been about 0.4 cm for K, and 0.12 cm for P in 7 days, which was approximately the mean root age. Mass flow should compact these depletion zones (Nye and Marriott (1969)). Even so the K depletion zones of adjacent roots probably overlapped to some extent in the top quarter of the pots resulting in slightly greater root surface depletions than were calculated. It is unlikely that the P depletion zones of adjacent roots overlapped to a significant extent. Thus

it seems probable that the effects of inter-root competion on $\overline{C_{LR}}$ were small in this experiment.

8) No nutrient supply from alternative sources.

The results reported on 4.7.d. and Fig.5.6 showed that K fixation, rather than slow release, occurred in the experimental soil until the activity ratio $K/\sqrt{Ca}$ in solution was reduced to about 40% of its initial level. From the experimental results a mean value of $\overline{C_{LR}}$ of about 0.4 C_{Li} was predicted (Table 4.8.). The slow release of K could not therefore, have prevented such decreases in C_{LR} from occurring. A similar conclusion can be drawn for P, where, as described in 4.7.e., there was no evidence of the slow release of P into solutions as low as 0.02 C_{Li}

Turning to the possibility of mineralisation, the constancy of N concentrations in the soil solution on different dates (see Tabel 4.6.), showed that there was no important net mineralisation of this element during the growing period. The slight tendency of N concentration to decrease suggests rather that microbial nitrate fixation or denitrification was occurring. (See also 4.9.b.). The local mineralisation of N, or other nutrients in the rhizosphere remains an uninvestigated possibility.

9) Water Inflow (uptake rate/cm of root) is constant.

Passioura and Frere (1967) present a solution to the situation where water inflow into a root in soil varies according to a cosine curve for 12 hours, with a midday peak, and then ceases for 12 hours. Their mean water inflow over 24 hours was 1×10^{-6} $cm^3/cm^2/sec$, and the values of their other parameters were $r = 0.02$ cm, $D = 10^{-6}$ cm^2/sec and $\alpha = 0$. On the first day, C_{LR}/C_{Li} rose to 1.21 just after midday and fell almost in parallel with transpiration until evening, then fell very slowly through the night until it was about 1.02 after 24 hours. A similar pattern occurred succeeding days but C_{LR}/C_{Li} at the end of night increased slightly after each day. After 8 days, C_{LR}/C_{Li} was 1.15 at the end of the night period. Clr/Cli rose to 1.4 just after midday on day 9. For comparison, the mean root age in our experiment was 8 days. Passioura and Frere's values of the parameters

involved were very similar to the Ca data from our pot experiment. Transpiration rates in our experiment were not measured over days or fractions of a day, but the day lengths were longer than 12 hours and trans piration rates probably did not vary so drastically over any particular 24 hours. The roots were slightly thicker and some calcium uptake was occurring. All these factors would tend to diminish the increase in C_{LR} compared with Passioura and Frere's case. It seems reasonable to regard the values of C_{LR} in table 4.8. for those ions that accumulated at the root surface, as means of what were, in reality, higher daytime and lower night time values. Extreme values of C_{LR}/C_{Li} for Ca, the most heavily accumulated ion, were probable somewhat less than the extremes given above from Passioura and Frere's work.

Turning now to the effect of root age on water permeability, Rosene (1937) found that in onion roots which are very similar to leek roots, all regions between the root cap and the base could absorb water. Measurements were made on roots up to twenty two cm long. An average of ten roots showed a mean water uptake rate changing less than 20% along the first 7 cm from the tip. Thus, this evidence suggests that most of the roots of a young leek plant will be similar to one another in their permeability to water.

In considering the water flow into all roots as equal, we also ignore the possible effect of root position in the pot. The driving force for water flow towards roots is the difference between the matric suction at the root surface and that in the surrounding bulk soil. Although the calculation above showed that a maximal gradient of -0.005 bars in matric suction was sufficient to drive the measured water flows in the driest mean state of the soil, the differences in water potential between soil in the densely rooted upper regions of the pot and the lower regions may have been much greater. At harvest, soil near the bottom of the pots appeared and felt moister. It is quite likely that water inflow per centimetre of root was somewhat greater in the moister lower regions in the later stages of uptake just before harvest. If differences in root density had led to differences in soil water content between different

parts of the pot there might have been a certain amount of non-radial water flow upwards in the pots. This could also have led to differences in ionic diffusion coefficients in different regions of the soil. No data were collected on differences in water content at different levels; such detail was not reached in this experiment. Current work in the laboratory is investigating the effects on nutrient and water uptake of root density at different depths in pots. (Baldwin and Tinker pers.comm.).

10) α constant along all roots.

The experiments described in Section 3 showed that leek roots up to fifty days old were capable of absorbing P and Ca. As regards K, the oldest roots only, which were about fifty days old, showed a consistent inability to absorb K. In the pot experiment described in Chapter 4, the mean root age was about seven days, and only a small fraction of the roots was more than twenty days old. Hence, there was some experimental justification for the assumption of a constant α, On the other hand, there was also evidence, from the experiments in Section 3, of wide differences in the uptake ability of similar roots, even of those of the same age. Such differences however, revealed no pattern which could be incorporated in an analysis based on equation 3.X. The implications of this are discussed in Chapter 11.

* * * * * *

In conclusion, if we return to the questions posed at the beginning of Chapter 4 (4.1.); we have been able to account for the experimentally observed uptake in terms of the model for root behaviour which is described in Chapter 3. On the basis of this model, it appears that all roots acted as almost zero sinks for phosphate. There was at least a 60% depletion in K at the root surface, and if any roots were not absorbing K, then K depletions around the active roots would have been even greater. As discussed in this chapter, water inflow rate probably varied with time of day, however, as Fig.5.5 illustrates, and as the results of Nye and Marriott 1969, indicate, the presence of

absence of mass flow would not have altered the depletion profiles of K or P by very much. Hence, for P amd K, we can be fairly certain as to the validity of the values of $\overline{C_{LR}}$ in Table 4.8., and as to the reality of the depletion profiles in Figs. 5.5 and 6.3. For those ions where $\overline{C_{LR}} / C_{Li} > 1$, values of $\overline{C_{LR}}$ are uncertain in the light of a number of the above assumptions, and their values of $\overline{C_{LR}} / C_{Li}$ in Table 8.should be taken as only approximate mean values that are subject to certain assumptions. However, it seems probable that increases in solution concentration at the root surface were not very large, at most up to 1.4 C_{Li}. Such root increases were unlikely to have had a very significant effect either on root physiology or on nutrient availability. Of course, the evidence of this experiment alone confirms only the feasibility of the model for root behaviour described in Chapter 3. This model certainly provides the simplest possible explanation of the results, but we cannot dismiss on this evidence, the possibility that some other factors were important, for example nutrient solubilisation by organic root exudates. The data from the experiment are interesting and useful in that they provide real values for a number of parameters that can be related to the several theoretical treatments of nutrient flow to roots that exist in the literature (see Chapter 3.1). This type of experiment should also be a generally useful approach to the study of nutrient uptake from different soils and by different plant species, and the results of such experiments should become more illuminating as more results are collected and compared.

Chapter Seven

AN EXPERIMENTAL INVESTIGATION OF ACCUMULATIONS OF SULPHATE IN THE RHIZOSPHERE CAUSED BY MASS FLOW

7.1 INTRODUCTION

For those ions that were oversupplied to roots by mass flow in the pot experiment above, the calculated values of C_{LR}/C_{Li} were less than 1.2. The numerical solutions to equation 3.I of Passioura and Frere (1967), Marriott and Nye (1968) and Nye and Marriott (1969) all indicated that, in moist soils, values of $\overline{C_{LR}}/C_{Li}$ were unlikely to increase greatly until many days had elapsed. However, the theoretical analysis of water flow to roots made by Whistler, Klute and Millington (1970) indicated that in conditions of high transpiration even in a fairly moist soil V_L may diminish markedly near the root surface. If this were the case, f_L would also be low near the root, and the consequent low values of D would favour the accumulation of ions at the root surface. Wray (1970) measured mass flow accumulations round roots in soil but his system consisted of a root in a thin layer of soil and water flow and diffusion were constrained to a planar geometry. Where a root is surrounded by soil on all sides, accumulations are not so likely to occur as in Wray's planar geometry. Barber, Walker and Vasey (1963) presented an autoradiograph of an accumulation of S^{35} around a maize root, which they believed was caused by oversupply by mass flow, but they gave no experimental details. Barber and Ozanne (1970) grew four species of plants in Ca^{45} labelled soil; they obtained autoradiographs showing faint accumulations near the roots of three species and slight depletions round those of the remaining species. Those species that showed an accumulation had absorbed less Ca than was supplied by apparent mass flow, whereas the other (lupin) had absorbed more Ca than was supplied by apparent mass flow. Barber and Ozanne therefore attributed the accumulations to oversupply by mass flow. In contrast, Wilkinson, Lonergan and

Quirk (1968) produced autoradiographs showing depletions of Ca^{45} around wheat roots, although calculations showed that apparent mass flow should have supplied ten times more calcium to the root than the plant had absorbed. Thus, the direct experimental evidence for mass flow accumulations in the rhizosphere is rather meagre and conflicting. It seems likely that on theoretical grounds however that mass flow accumulations are not very significant except in conditions of high transpiration from a rather dry soil. To test this an experiment was designed to observe the accumulation of ions in the rhizosphere of a plant that was transpiring and progressively drying the soil. The plant root was grown against a window in a block of soil one centimetre deep, hence the geometry of diffusion and water flow was hemicylindrical.

Ions accumulate at the root surface if $V/_{\alpha} > 1$ (Nye and Spiers 1964, Nye and Marriott 1969). The value of C_{LR}/C_{Li} at the root surface after an infinite time with constant values of V and D is $V/_{\alpha}$. The rate at which C_{LR}/C_{Li} approaches this limiting value depends on the value of rv/Db (Nye and Marriott 1969). Only when rv/Db is greater than 1 does C_{LR}/C_{Li} rise very rapidly. When rv/bD is 1 and v/α is large, C_{LR}/C_{Li} increases to about 1.5 after twenty four hours and about 2 after 10 days. Mean values of v of about 5×10^{-6} cm/sec have been measured (Ogata, Richards and Gardner, 1960); if we take r as 0.03 cm then this yields a value for rv of 0.15×10^{-6} cm^2/sec. If we take D_L as 10^{-5} cm^2/sec, rv/Db will become greater than 1 only when $V_L f_L$ is less than 0.015. Rowell et al. (1967) found that $V_L f_L$ was 0.015 when V_L was about 0.18. Porter et al.(1960) showed that the value of soil matric suction, τ, at which $V_L f_L$ was as low as 0.015 depended on the soil texture. In many clay soils, V_L does not decrease to 0.18 until the matric suction is less than - 15 bars. This is in the range of suction where wilting drastically slows transpiration rates (Slatyer,1967 p.77). A decrease in transpiration rate must diminish values of v, and it is unlikely that values of rv/Db greater than 1.0 will occur in clay soils; consequently mass flow accumulations are probably only small in heavy soils. In sandy soil on the

other hand V_L may diminish to values less than 0.18 at matric suction around -1 bar. It seems likely therefore that fairly large accumulations occur in light soils when the soil is moderately dry.

7.2. Experimental Methods

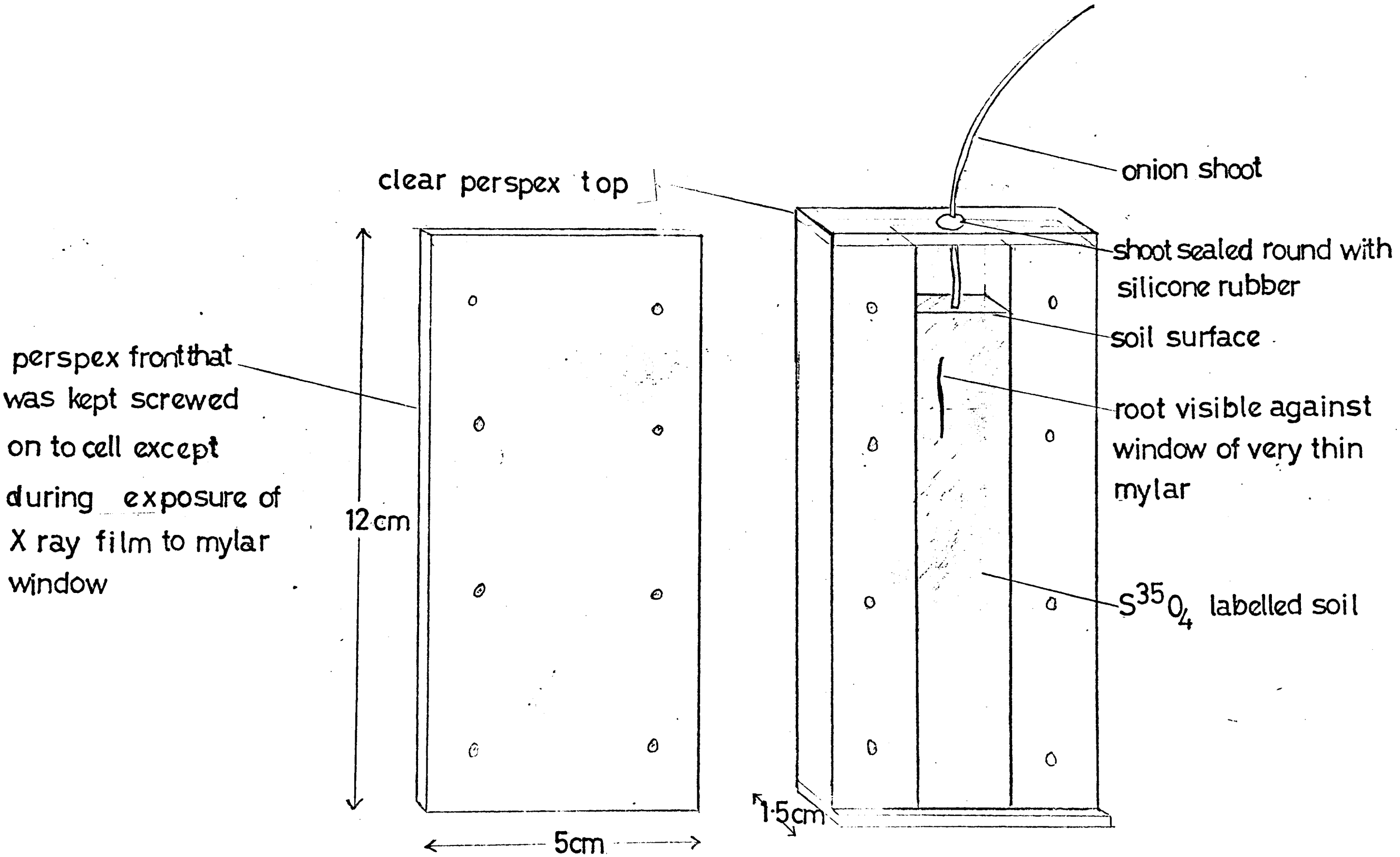
The parameters that should be measured for a fully satisfactory analysis of mass flow accumulations are v, C_{LR}/C_{Li}, the relations between α and C_{LR} and the relation between V_L and f_L. From these data, values of rv/Db and V/α can be calculated and used to calculate values of C_{LR}/C_{Li}, which can be compared with the measured values. It was decided to measure accumulations of SO_4 around onion roots using S^{35} autoradiography. The soil chosen was a mixture of 50% byweight air-dry Upper Greensand Sandy Loam (U.G.S.) sieved to pass a 0.295 mm sieve and 50% acid washed fine sand (BDH Ltd) UGS soil was chosen because it does not adsorb SO_4, and there also exist a number of measurements of the relation between f_L and V_L for the soil (Rowell et al.1967, Dunham, unpublished information). S^{35} was chosen because it has a soft β^- emission suitable for high resolution autoradiography (Rogers,1969). The F.1 hybrid onion variety "Mustang" was chosen as the experimental plant.

The soil and sand were mixed air dry and then evenly packed into perspex cells 2 cm wide by 1 cm deep. A 10 cm long column was packed in this way (See Fig.7.1.) One side of the cell was removable, and between the removable side and the soil was placed a sheet of extremely thin (3.5 μ thick) Mylar film. (made by Dupont Ltd). This served to protect the X ray film from the soil during exposure of the autoradiographs. The Mylar film was sufficiently thin to retain a very short film-soil distance, and hence to obtain high resolution exposures. The packed and assembled cell was placed on a small tension table, and and wetted from below, using a solution containing the following;

$CaSO_4$	0.4×10^{-3} Mols/L
$Mg(NO_3)_2$	0.25×10^{-3} Mols/L
$K H_2 PO_4$	0.20×10^{-3} Mols/L

24 μCi/ml. $S^{35}O_4$.

DIAGRAM OF THE CELL USED TO STUDY S^{35} ACCUMULATION AROUND AN ONION ROOT



the cell was made of perspex

FIG 7.1.

The soil was saturated with this solution, then excess solution was removed by applying a suction of -28 cm of solution to the soil column and leaving the column overnight to equilibrate. The cell was then removed from the tension table, and the base was sealed with perspex and tape. A single onion seed was placed on top of the soil next to the Mylar 'window' and a clear perspex top was screwed on to the cell. The assembled cell was surrounded by a black polythene envelope that excluded light from all but the top of the soil where the seed was. The complete assembly was placed in a growth cabinet set as follows; 25°C, 3000 foot-candles light intensity at leaf level, continuous light and minimum humidity. It was hoped that these conditions would lead to high transpiration rates and large values of V, and avoid the complication of diurnal variations in V brought about by the cessation of transpiration during night periods. The cell was inclined at an angle of 30° to the vertical with the Mylar window facing downwards, to encourage roots to grow along the window.

The onion germinated in one day and the primary root was visible two days after sowing, down to 2 cm below the soil surface. At this time, the first autoradiographs were made. The cell was removed from the growth cabinet, its front was removed and in the dark room the cell was laid with the Mylar window downwards on a sheet of Kodirex X ray film. The film was exposed for one hour, after which time the cell was reassembled and returned to the growth cabinet. The developed autoradiograph clearly showed the initial uniformity of labelling in the soil. (Fig.7.2.). The picture was rather faint, and subsequently a longer exposure time was used.

A small hole was then made in the top of the cell and the cotyledon was allowed to emerge. Subsequently, the cell was weighed daily to follow the water loss. An identical cell without a plant was kept in the same conditions and weighed along with the planted cell. The amount of water transpired was calculated as the difference in water lost between the planted cell and the plantless control. Root growth against the window was observed and measured every, day as was shoot growth. Three days after sowing the primary root had achieved

its maximum length of 2.9 cm. The root had a uniform diameter of 0.6 mm. The seedling leaf continued to lengthen until six days after sowing, when its length was 6.5 cm. Subsequently, no lateral roots, secondary shoots or adventitious roots appeared. Under the microscope, the tip of the root appeared slightly swollen and club shaped. New growth was clearly inhibited and it seems likely that the level of S^{35} was sufficient to suppress cell division. Despite the cessation of growth, the root and shoot appeared healthy, and remained turgid until twenty two days after sowing, by which time the shoot was wilting because the soil had dried to the permanent wilting level.

A second autoradiograph was made seven days after sowing. The film was applied to the 'Mylar' window in the dark room. The cell was then returned to the growth cabinet to expose the film "in situ" and to avoid the possibility of any accumulation zone that existed being dissipated by back diffusion during a long exposure in the dark. This time the film was exposed for three hours. Unfortunately, a certain amount of light leaked into the black polythene envelope which surrounded the cell and darkened the edge of the film somewhat. However, the region showing the central part of the soil column and the root was not affected in this way (see Fig.7.2.) Further autoradiographs were exposed thirteen, sixteen and twenty two days after sowing using an exposure time of two hours.

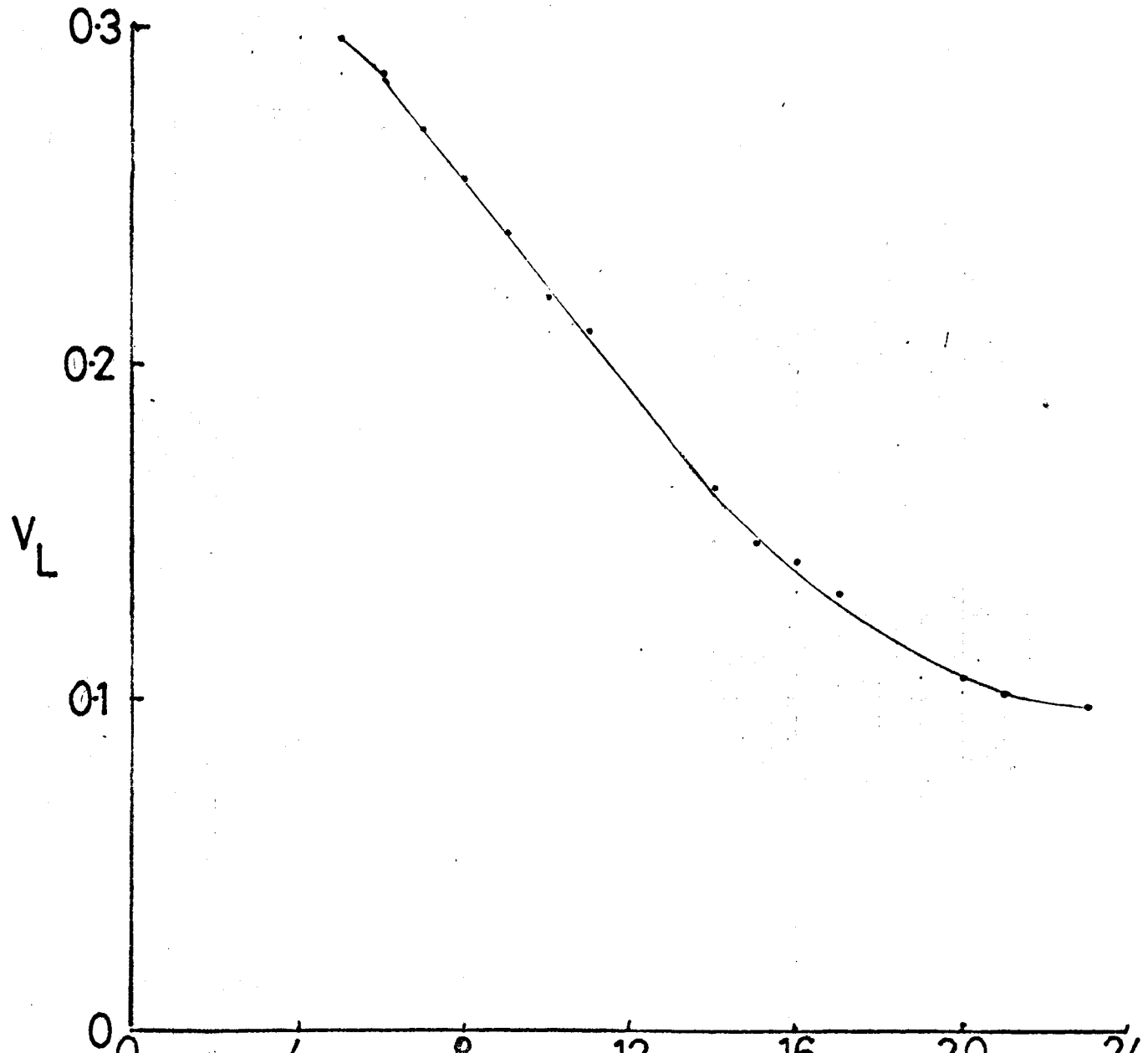
The density and shape of the darkened S^{35} accumulation zones on the autoradiographs were measured using a microdensitometer which scanned across the root zone with a 0.5 mm diameter beam of light. Scans were made across the root zone of all the autoradiographs at successive 4 mm steps from the surface of the soil. In this way the progressive accumulation of S^{35} at the same point on the root was recorded. In a separate experiment, a water characteristic of the soil was determined, using a pressure membrane apparatus.

7.3. Results and Discussion

Fig.7.2. shows a photograph of the autoradiographs from five successive dates. Fig.7.3. shows the relationship between transpiration and time, and

FIG 7.2.

THE WATER TRANSPIRED AND THE CHANGE IN V_L WITH TIME IN THE CELLS FOR AUTORADIOGRAPHY



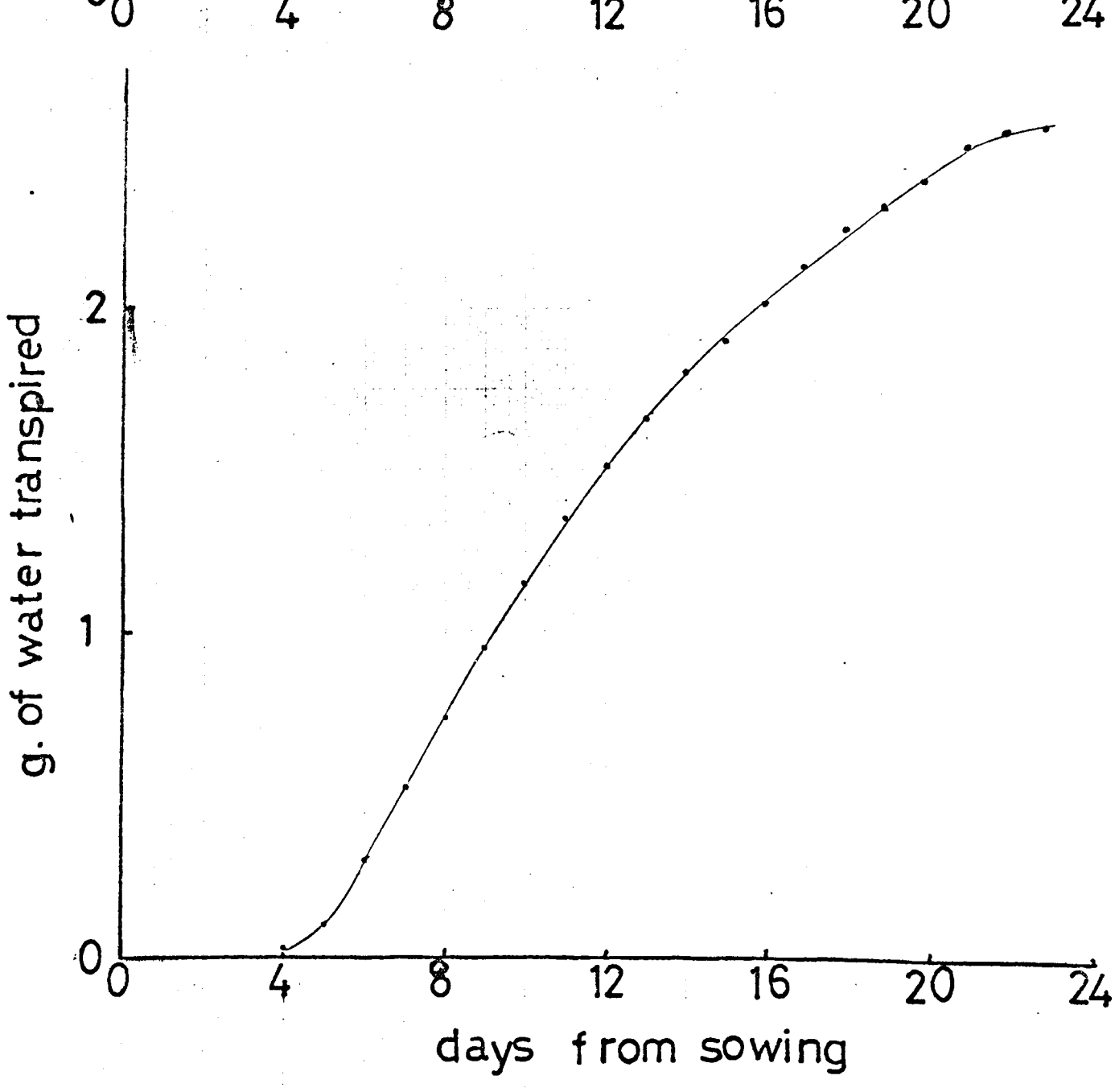
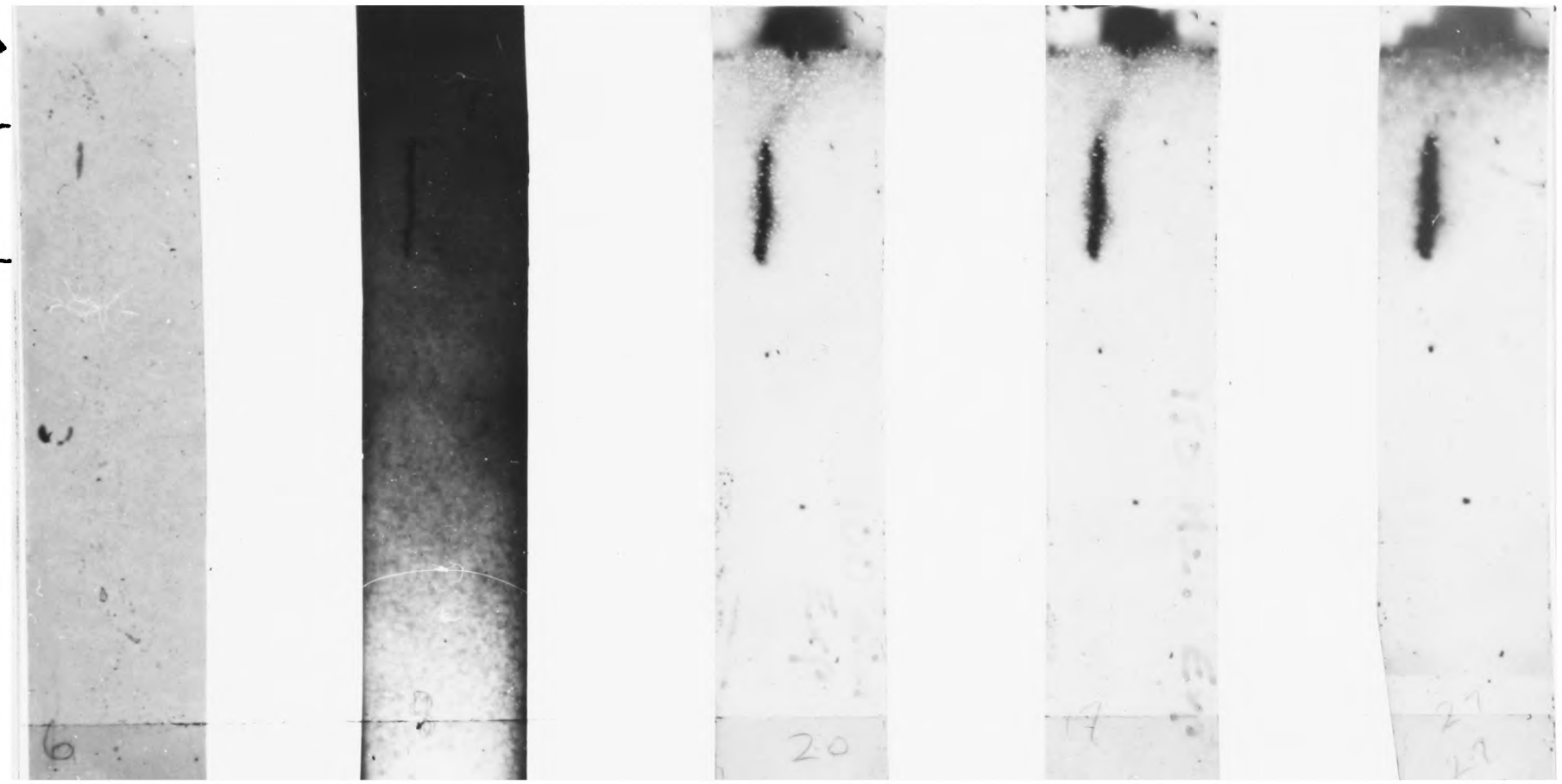


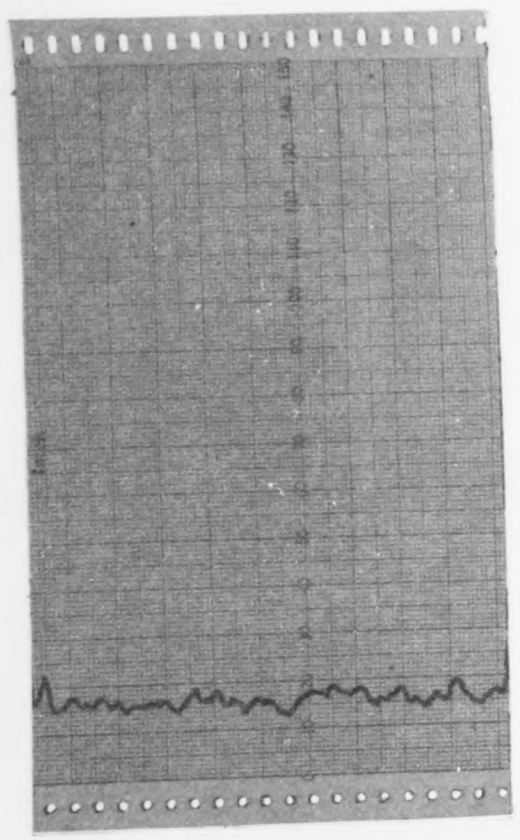
FIG 7.3. A SEQUENCE OF AUTORADIOGRAPHS SHOWING THE BUILD UP OF MASS FLOW ACCUMULATIONS OF $S^{35}O_4$ NEAR AN ONION ROOT IN SOIL



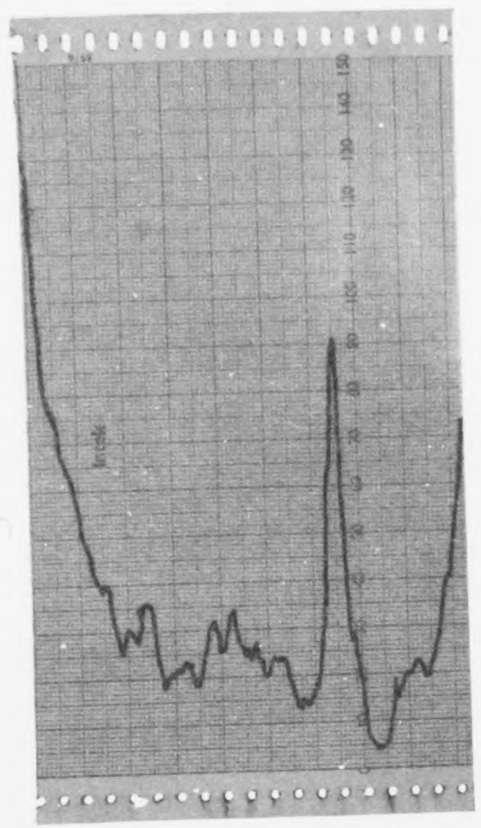
days from sowing → 2 7 13 16 22

DENSITOMETER SCANS ACROSS AUTORADIOGRAPHS OF S^{35} ACCUMULATION NEAR AN ONION ROOT

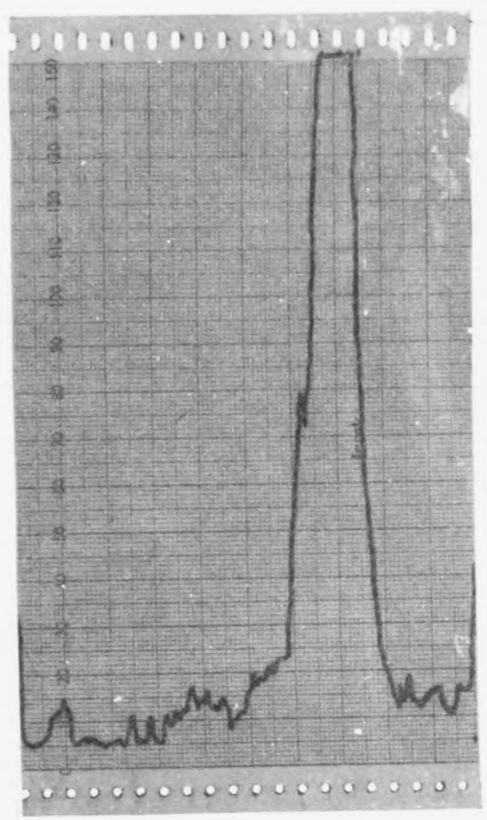
SCANS TRAVERSING THE ROOT ZONE 20 mm BELOW THE SOIL SURFACE ARE SHOWN, FROM THE AUTORADIOGRAPHS TAKEN 2, 7, 13, AND 22 DAYS AFTER SOWING.



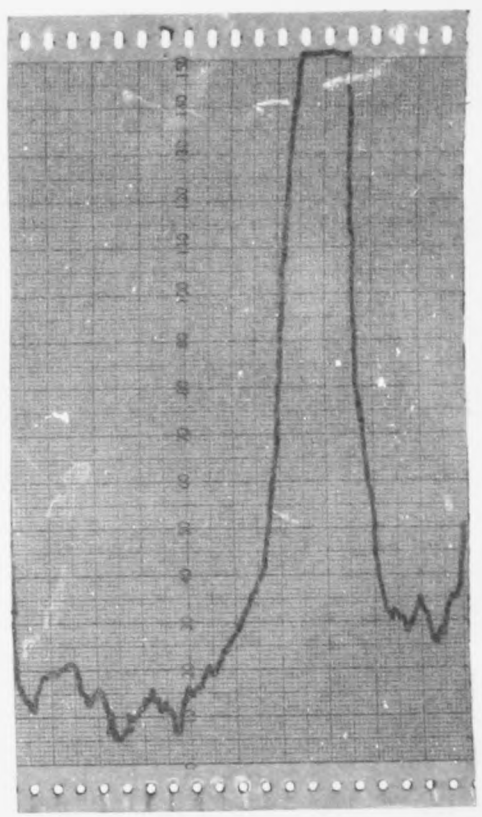
DAY 2



DAY 7



DAY 13



DAY 22

SCALE: 2·3 cm OF SCAN EQUALS 1 cm ORIGINAL

FIG. 7.4.

Fig.7.4

TABLE 7.1.

DATA DETERMINING THE VALUES OF rv/bD AT THE TIMES WHEN THE AUTORADIOGRAPHS WERE MADE

DAYS FROM SOWING	MEAN v_L	$\bar{F}$ (mean matric suction in soil, bars)	v cm/sec x 10^{-6}	f_L (from Rowell et al 1967)	$D_L v_L f_L$ x 10^{-6}	rv/bD
2	0.295	0.028	0	0.270	0.86	0
7	0.255	–	4.7	0.205	0.56	0.25
13	0.163	0.60	3.0	0.065	0.11	0.79
16	0.132	1.5	2.7	0.035	0.050	1.62
22	0.100	6.7	0.80	0.020	0.022	1.11

$D_L v_L f_L = bD$

soil water content, V_L, and time. Table 7.1. lists the values of mean V, mean V_L and mean soil matric suction, τ, at the times when the autoradiographs were made. The data of Rowell et al (1967) were used to estimate f_L at each date, and values of rv/Db were calculated. Fig.7.4. shows densitometer scans across the autoradiograph of root zone at two locations on three successive dates. The values of V_L and τ are means for the whole cell; V_L must have been somewhat lower, and τ somewhat larger in the root zone. The values of V approach those found by Ogata et al (1960) as a mean for alfalfa plants in a moist sandy loam. The higher values of V are similar to the largest values measured by Wray (1970) for onion seedlings under conditions of high transpiration. α was not measured in a separate experiment, but since growth ceased after six days, it seems probable that α was rather low thereafter.

The first two autoradiographs show peaks of S^{35} activity in the same position as the root. The width of the zone (less than 1 mm) in both of these is similar to the diameter of the root (0.6 mm) and probably represents S^{35} accumulation within the root itself. In the third and subsequent autoradiographs, the zone of S^{35} accumulation is clearly wider than the root, and the scans (Fig.7.4.) show that the zone had increased to a width of about 3 mm by 22 days after sowing. V_L had fallen to 0.163 by day thirteen, when the third autoradiograph was taken. The estimate of rv/Db showed it to be 0.079. at this time (see Table 7.1.). Thus the accumulation became apparent only when V_L fell to this low level as was expected from the theoretical predictions of Nye and Marriott (1969). Also in accord with theory, the accumulation zone appears as a narrow zone of greatly increased concentration. The major difficulty with the experiment was in distinguishing between a true accumulation and plant uptake. Ideally such experiments require a suitably labelled compound in the soil colution that is very little absorbed by the cells of the plant root. Only by using such a substance would it be possible unequivocally to distinguish extremely local accumulations from root absorption. However, the resolution of the present autoradiographs is sufficiently good to show that 7 days after

sowing, when values of V were at their highest and when V_L was 0.255, there was no zone of accumulation spreading into the soil particles of the rhizosphere. Thus, at a V_L which is lower than the lowest that occurred in the pot experiment of Chapter 4, and with values of V which are greater than those recorded in the pot experiment (see 4.9.a.) , we see no evidence of large mass flow accumulations in the rhizosphere. This adds weight to the conclusion that mass flow accumulations were not very great in the pot experiment (see Chapter 6). In drier soils however large accumulations clearly can occur. If V_L decreases below about 0.2 and V remains high, then salt concentrations in the rhizosphere may increase to levels that retard plant growth (Slatyer 1967). In the conditions of this experiment, Ca SO_4 concentration in the rhizosphere probably rose to a level sufficient to precipitate gypsum in the rhizosphere. The maximum solution concentration of Ca SO_4 that can exist in soil solution is about 1.4 x 10^{-2}.M. The SO_4 concentration initially present in the soil was 0.4 x 10^{-3} M. Overall drying of the soil must have increased the average SO_4 concentration to 0.12 x 10^{-2} M. If Ca concentration was about the same and if C_{LR}/C_{Li} reached a value of ten or above, precipitation was likely. The average matric suction in the soil was -0.6 bars when the accumulations became apparent. Such a suction is adequate for plant growth and transpiration and must commonly occur under field conditions, so that in very sandy soils it is reasonable to expect mass flow accumulations in the rhizosphere to be of some agricultural significance.

The only other well-documented autoradiograph that we traced, of accumulation zones in the rhizosphere are those of Ozanne and Barber (1970) using Ca^{45}, but their evidence is contradicted by that of Wilkinson, Loneragan and Quirk (1968). In both these experiments the plants were watered daily and we can therefore assume that the soil was not in the dry state that the theory of Nye and Marriott (1969) predicts as necessary for large mass flow accumulations to occur. The explanation for the conflicting results of different workers using Ca^{45} may lie in the work of Ramzan (1970), who showed that, when bicarbonate loaded resin papers were placed in blocks of some soils, calcium accumulated

in the soil adjacent to the resin paper. The explanation lay in the local increase in pH caused by the entry of bicarbonate into the soil. This has caused a local increase in pH dependent cation exchange capacity upon which Ca was adsorbed and this had increased the total concentration of Ca in the soil near the resin paper. The same effect could occur around roots and cause an accumulation of Ca in the rhizosphere not attributable to mass flow. In conditions where cation uptake exceeds anion uptake, roots may exude H^+ ions; the latter could displace Ca from exchange sides in the rhizosphere, thereby diminishing the overall Ca concentration there. Thus, pH changes brought about by root activity can change cation concentrations in the rhizosphere. Using a non adsorbed anion such as sulphate in the above experiment, there should be no possibility of confusion between accumulations due to pH changes in the rhizosphere, and those due solely to excess supply by mass flow.

SECTION III

INVESTIGATIONS INTO THE FRACTION OF ROOT SYSTEMS ACTIVE IN NUTRIENT UPTAKE.

Introduction

The model used to analyse the transport of ions and water to roots in embodied in Equation 3.X. assumed the equal activity of all roots. Experiments to investigate the validity of this assumption were performed using methods developed by Russell and Sanderson (1967), at the A.R.C. Letcombe Laboratory. They have developed a technique for measuring the uptake of ions by short sections of the roots of whole plants growing in solution culture. It was decided to investigate the uptake rate of different regions of leek roots using the same technique and facilities were kindly provided for this work to be performed at Letcombe.

The experimental work falls into three parts described in Chapters 9, 10 and 11 respectively. Chapter 9 describes a long term experiment in which the growth rate and the mean nutrient inflows in the nutrient culture conditions were established. Chapter 10 describes experiments to determine what fraction of a radioactivity labelled nutrient absorbed in 24 hours was exchangeable at the end of the 24 hours and not indicative of a net plant uptake. Chapter 11 describes experiments in which the uptake of radioactivity labelled nutrient ions by short sections of roots of different ages was measured. The nutrients investigated in the latter experiments were P, K and Ca. These were chosen because P and K were both found to be seriously depleted at the root surface in the experiment described in Section 2 whereas Ca, in contrast, was found to be accumulated at the root surface to a greater extent than any other nutrient. The isotopes used were P^{32}, K^{42} amd Sr^{85}. Sr^{85} was taken as equivalent to Ca as regards its rate of absorption from solution by roots over twenty four hours (Russell and Squire 1958).

The account of experimental work is prefaced by Chapter 8, a short dis-

cussion on the physiology of nutrient uptake from which it should become clear why information on exchangeable nutrients and the longer term uptakerate was necessary in order to interpret measured uptakes by roots of different ages and in order to relate this work to the previous experiment on nutrient uptake in soil.

In Chapter 11 the results of other workers on the uptake rate of roots of different ages are discussed. Chapter 11 concludes with a discussion of the experimental findings in relation to the soil's ability to supply nutrients to roots. From this some conclusions are drawn as to the relevance of such results in understanding root behaviour in natural soil conditions.

Chapter Eight

A SURVEY OF THE PHYSIOLOGY OF PLANT NUTRIENT UPTAKE

8.1. A General Review

As in the soil, solute will move within plants by diffusion down any gradients of electrochemical potential that occur and also by mass flow as, for example, in the transpiration stream. In addition, ions may be transported across membranes against an electrochemical potential gradient by transport mechanisms coupled to metabolic processes which provide the energy needed; this is termed active transport. (Briggs, Hope and Robertson 1961, Sutcliffe 1962, Jennings, 1963).

Plant tissues including those of the root, contain a complex pattern of cells and membranes of different permeability to solutes and with differing capabilities for active uptake. Cellulose cell walls are freely permeable to water and to solutes of molecular weight less than about 5000. Cytoplasmic membranes are permeable to water molecules but show varying permeability to solutes. Non polar solutes can diffuse readily into cytoplasm but strongly ionised solutes cannot, and their uptake by cytoplasm seems to be largely due to active transport (Collander 1959). Cell walls that are impregnated with hydrophobic substances like wax, suberin and lignin are not permeable to water or to ionised solutes (Collander, 1959).

Plant tissues also vary in the resistance they offer to the mass flow of water and in their rate of solute uptake. For example, when roots are subjected to osmotic stress their resistance to inflowing water can decrease within minutes and their ion uptake rate rapidly increases (Brouwer, 1954 b). These changes seem to involve two independent cytoplasmically controlled processes.

Prolonged changes in conditions can lead to anatomical changes that affect the resistance to water inflow and probably the solute uptake ability of roots. For example, roots in dry soil generally have suberin extending down the epidermal layers to much nearer the tip than those in moist soil and such roots

present a greater resistance to water inflow (Kramer,1969, Slatyer,1967). The indications are that both the ion uptake rate of roots, and the resistance they present to water inflow, show adaptive changes both in the long and short term and thus that they will vary with conditions of growth.

About 10% of the volume of young roots that have been centrifuged to remove surface water film, is in equilibrium with the external solution. There are no barriers to solute diffusion between this volume, which has been termed the water free space, W.F.S., and the external medium (Briggs et al.1961) A further fraction, of about 10%, of the root volume contains fixed negative charges which hold exchangeable cations. This is known as the Donnan Free Space D.F.S. The charge derives from dissociated carboxylic acid groups which are probably located mainly in the pectic substances of cell walls. (Briggs et al.1961). The remaining region of the tissue has been termed the osmotic volume, O.V., and consists of the cytoplasmic regions and vacuoles that lie enclosed by differentially permeable membrances and that can behave like osmometers. The O.V. is not homogeneous and doubtless finer compartmentation exists within it (Briggs et al. 1961).

Nearly all living plant tissue contains W.F.S., and D.F.S. and O.V. but the free space of intact roots does not extend into the stele since ions are retained in high concentrations there when the roots are immersed in distilled water (Arisz, Helder and van Nie,1951). There is thus a strong barrier to free diffusion between the stele and the cortex, probably in the cytoplasm of the endodermis (Weatherly,1968).

The net influx of an ion into the vacuoles and cytoplasms of the osmotic volume, involving active transport, is the difference between an influx and efflux of the ions (Jennings,1963). Thus, ions within the O.V. may interchange with similar ions outside. This is quite different from the simple physical exchange of ions in the free space; ions from within the "metabolic pool" of cells must interchange across the cytoplasmic membrances. The efflux does not seem to be simply associated with permanently leaky membranes since both influx

and efflux can be inhibited by poisons and low temperature indicating physiological control of both (Jennings,1963). Phosphate is most frequently discussed in this connection. Reports conflict on the degree of P interchange in and out of the O.V. of roots, but a rapid turnover of P between wheat (Hevesy,1946) and barley (Russell and Martin,1953) roots and the medium has been reported.

The pathway of ion absorption into intact plants is still uncertain: Hoagland (1948 p.89) showed that the entry of radioactivity labelled ions into whole plants did not progress as a uniform wave across the root cortex, into the stele and then to the shoot but that the labelled ions appeared in the shoot before the root tissue was saturated with activity. The pathway to the stele has been envisaged as a series/parallel network of regions of varying conductivity to ions. The cytoplasm and the cell wall free space are probably the routes for transport across the cortex (Laties,1969). Root cell vacuoles seem to act more as competing sinks than as part of the pathway for transport to the shoot. There is strong evidence for a "valve" at the endodermis forcing ions en route into the stele to pass through cytoplasm (Weatherley ,1968).

To summarise then, many processes are involved in ion uptake by plants. The magnitude of effluxes, influxes, fluxes due to the different transport mechanisms, permeability barriers and free space will vary with tissue anatomy and physiology and with the condition of the whole plant, for example, its salt status. The balance of these processes may change within minutes of a change in external conditions but they must be adjusted as the plant grows in order to adapt it to a changing environment. We can picture the plant as a variable "leaky bag" of solution with a regular transpirational influx of water which, when growing, is also a net sink for those solutes that are incorporated in new tissue.

8.2. Implications for the measurement of Net Flows into Roots

For an understanding of the ion flows towards roots in the soil, we can ignore most of the intraplant complexity. What we require is a knowledge of the

net uptake rate of water and ions by roots and how this varies with position along the root and also with time at any one position along the root. The mean net inflow into a root system will be related to the plant growth rate, the ion concentration in the new tissue and the length of root. (Nye and Tinker, 1969). However, the above discussion of physiology indicates two particular precautions necessary for experimenters hoping to measure inflows into plant roots and to extrapolate their measurements from one situation to another.

The first is the variability of the uptake processes and their sensitivity to changing environmental conditions. Only for roots grown in similar conditions can we expect inflow rates to be similar. The second, more specific point, concerns the use of the short term inflow of radioactive isotopes to measure net inflows. Firstly, a considerable fraction of the radioactivity absorbed by a root placed in a labelled solution will simply represent isotopic exchange between the free space of the root and the medium. Secondly, if the net influx into the plant osmotic volume is the resultant of an influx and an efflux of the same ion species, then, upon introduction of the label to the medium, the specific activity of the inflowing ions can be expected to be greater than that of the outflowing ions. Hence, the initial uptake of label by the osmotic volume will overestimate the net influx.

Hence, both influx and efflux from the osmotic volume and ion exchange with the free space will tend to cause an overestimate of net inflows when the short term uptake of isotopically labelled nutrients is used to estimate the net inflows.

Chapter Nine

THE MEASUREMENT OF MEAN NUTRIENT INFLOWS INTO LEEK ROOTS IN SOLUTION CULTURE

This Chapter describes an experiment to measure mean nutrient inflows into the roots of leeks in solution culture. From the results it was possible to ascertain the degree of similarity in mean nutrient inflow between the plants grown in solution culture and those grown in soil (see Chapter 4). It was also possible to see if the values of mean inflow were the same as the averages of the measured short term flows into small segments of the roots (Chapter 11).

The environment of the solution grown plants was made as closely similar as possible to that of the soil grown plants by making the nutrient solution similar to the mean soil solution. Nevertheless, the experiment had to be performed in the greenhouse in winter, and despite supplementary lighting, the light intensity was certainly lower than that in the soil experiment.

9.1. Experimental Procedure

9.1.a. Growing the plants.

The procedures followed and the root and shoot environment at each stage of growth are outlined below.

I) Germination - from 0 to 7 days.

Seeds of Leek, Carter's selected variety Musselburgh, were germinated on filter papers moistened with deionised water at a constant temperature of 20°C in a Saxcil growth cabinet.

2) Seedling Stage - from 7 to 20 days.

Seeds from which the radicle was just emerging were transferred to the surface of moistened coarse sand in 4" plastic pots. These were watered from below using the prepared nutrient solution described below.

The seedlings were grown with a 16 hour day and a 1700 to 2000 foot candle light intensity from Phillips Colour Match fluorescent tubes. The temperature was 20°C and the relative humidity was 60 to 70%.

3) Greenhouse Growth - from 20 days until harvest.

Batches of twenty six plants were washed out of the sand and placed in black polythene containers which held 26 Litres of nutrient solution. The plants were supported in circular holes above the solution with a cushion of foam polyethylene around the leaf bases. The solution was aerated and mixed by a stream of filtered compressed air which emerged from a fine bubbler. The concentrations of the major nutrients in solution were the same as the average in the pot soil solution, except for phosphorus, which was decreased to half its bulk soil solution concentration to make some allowance for the depletion in concentration to be expected at the root surface in soil. The concentrations in moles/L. x 10^{-3} were:- Ca 15, Mg 0.6, K 0.42, Na 1.6, NO_3 22, H_2PO_4 0.01, Cl 8, SO_4 1.6. The solutions were prepared from laboratory grade $CaNO_3$, $MgCl_2$, K_2SO_4, Na_2SO_4, $CaCl_2$ and KH_2PO_4. In addition a standard minor nutrient mixture was added to give concentrations in μ moles/litre of 9.22 Fe EDTA, 9.22 H_3BO_3, 0.16 $Cu\,SO_4\,5H_2O$, 3.6. $MnSO_4.4H_2O$, 0.016 $(NH_4)_6\,Mo_7O_{24}\,4H_2O$ and 0.77 $ZnSO_4.7H_2O$. The pH was adjusted to 6.5 with NaOH. The greatest change in pH was a decrease to 5.5 during 5 days uptake by 35 day old plants. With P concentration as low as this in solution, nearly 40% of the P in the container immediately after a solution change could have been absorbed in 4 days by 25 fifty day old plants withdrawing P at the mean rate. Thus, when the plants had become large, the P concentration in solution could have fallen to about 60% of the original value. Similar plants, used for single segment experiments (see Chapter 11) were taken only 2 days after a solution change. Uptake could not have significantly diminished the concentration of any of the other ions in the solution. No precipitation of salts was observed during the experiment.

The plants were grown in a greenhouse with a constant air temperature of 20°C. The winter daylight was supplemented by Phillips HLRG 400 Watt lamps suspended three feet above the plants. During darkness these gave a light intensity of 1300 foot candles at leaf level. Light intensity was not allowed to fall below this during the sixteen hours of daily illumination. This regime

gave about 40 Cals/cm^2/day of incident light energy, which is about 25% of the daily income of incident light energy in June in Britain, so the light energy incident on the plants was well below that in the soil experiment.

9.1.b. Harvesting and Analysis of the Plants

Statistically, the most efficient sampling procedure for following plant growth and nutrient uptake is to sample a few plants frequently rather than a larger number less frequently (Radford 1967). For this reason small regular samples were taken. Particular interest centred around mean inflow rates into the roots of plants of the same age as those used in the short segment uptake experiment described in Chapter 11. The latter plants were 49 days old, so samples were taken rather more frequently around 49 days, i.e. on days 20, 27, 34,39,43,49 and 53 from sowing. All plants were assigned a number and samples for any harvest were selected using random number tables. At each harvest nine plants were taken. Three were used for N analysis, three for the analysis of other ions and three for root length measurement. Upon transfer to the 26 Litre containers, 36 seedlings were sampled, quantities of 12 being used for N analysis, other ions and root length measurement respectively. At harvesting plants were removed from the nutrient solution and their roots were washed by two ten second rinses in deionised water. The roots were cut from the shoots and both roots and shoots of those to be chemically analysed were left to air dry overnight in small beakers. They were then dried in the oven at 70°C and stored in a dessicator until weighing, after which they were transferred to 50 ml acid washed conical flasks ready for digestion and analysis.

Plants were analysed separately except for the seedlings which were grouped in fours to give sufficient material for one analysis. Roots and shoots were analysed separately. One group of each sample was analysed for N using a microkjeldahl technique. On others Ca, K, Mg and Na were determined by flame photometry and P by colorimetry using the method of Truog and Meyer. The prepared samples were analysed by staff of the Letcombe Laboratory under the supervision of Mr.K.Gunn.

The roots of the plants harvested on days 20 and 27 were photographed and a print of known scale was produced. The root length was determined from the print with a map measuring wheel. This proved to be a rapid and simple method of measuring these roots because they were much straighter than those grown in soil. At later harvests root lengths were measured with a ruler.

9.2. Experimental Results

The weight, root length and nutrient content of the plants increased over the period from day 20 to day 53 after sowing. Graphs of the log of dry weight, root length and nutrient content are shown in Figs.9.1.a. and 9.1.b. From the lines fitted to the uptake data, equations of the form $\bar{U} = C.e^{kt}$ were written for all nutrients where,

$\bar{U}$ = the total nutrient content of plants at time t (Moles)

t = the time in seconds from germination (germination was taken as 7 days after sowing)

C and k are constants derived from the graph lines.

The equations obtained from Figs.9.1.a. and b were:

For K $\bar{U} = 2.7.e^{0.079t}$

Na $\bar{U} = 0.70.e^{0.055t}$

Mg $\bar{U} = 0.34.e^{0.044t}$

Ca $\bar{U} = 1.06.e^{0.072t}$

N $\bar{U} = 4.80.e^{0.072t}$

P $\bar{U} = 0.45.e^{0.070t}$

It is evident from the values of k that the relative rates of uptake of the different nutrients were similar apart from Mg and Na, both of which were diminishing in tissue concentration relative to the other nutrients, as time passed.

By differentiating these equations expressions for the mean nutrient uptake rates were obtained. From these and the root length data the mean inflows on day 43 after germination were calculated. The values are listed in Table 9.2.

Fig.9.1 a

GROWTH AND NUTRIENT UPTAKE OF LEEKS IN WATER CULTURE

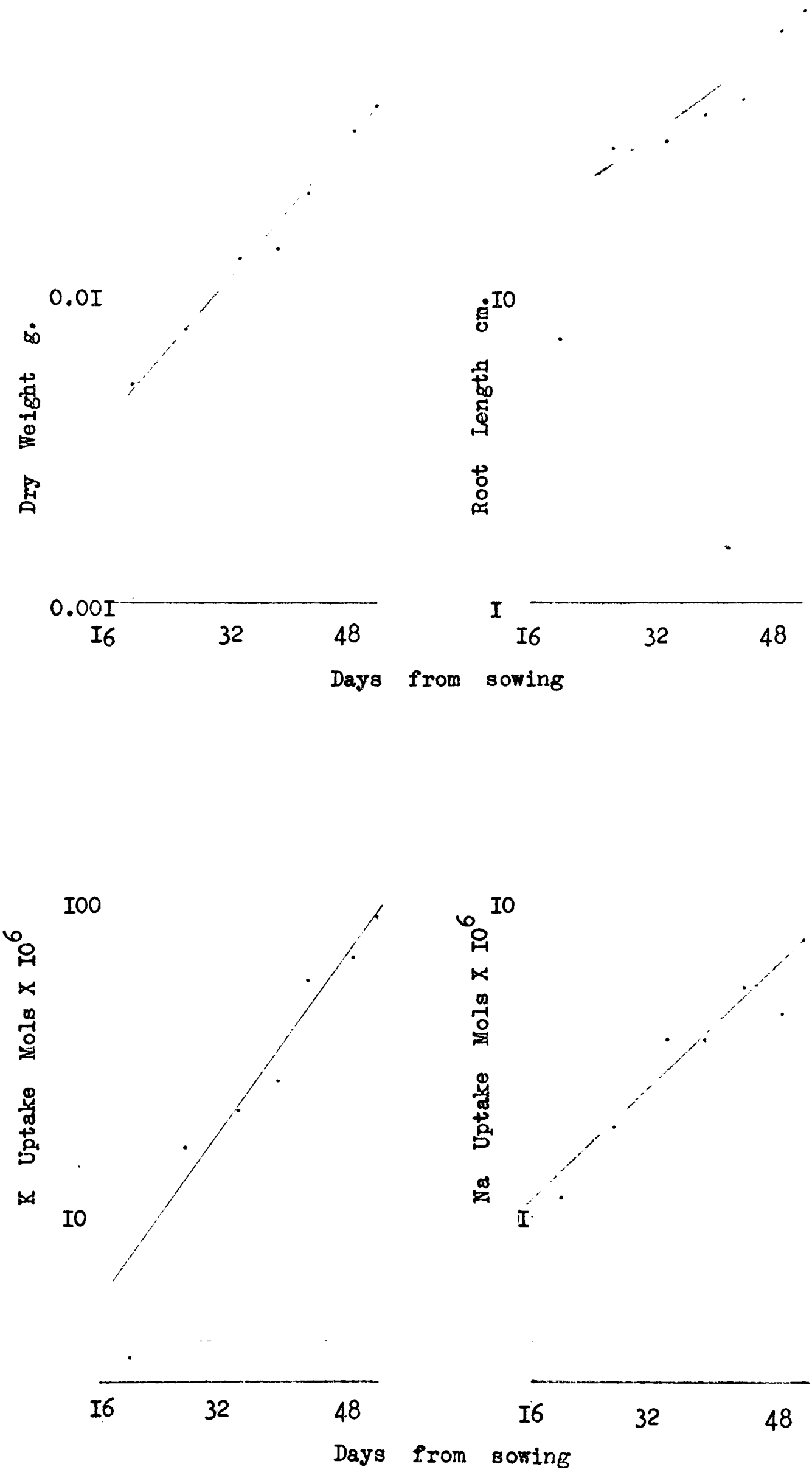
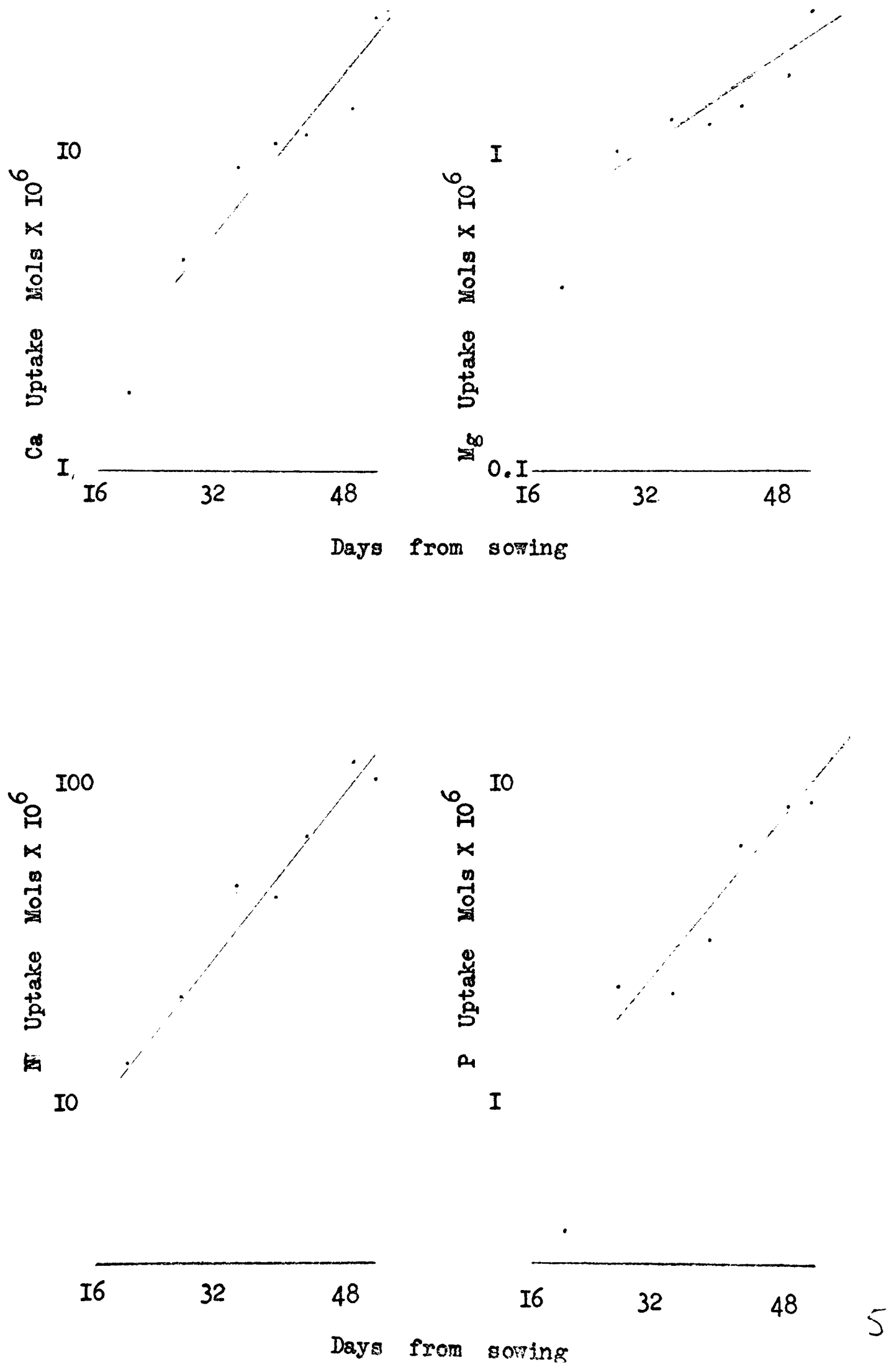


Fig.9.1. b

GROWTH AND NUTRIENT UPTAKE OF LEEKS IN WATER CULTURE



5

Table 9.1

GROWTH DATA FOR LEEKS IN WATER CULTURE

(% coefficient of variation in brackets below)

Days after sowing	Total dry weight(DW)g	Root DW / Shoot DW	Root length cm per plant
21	0.0053 (43)	0.32 (30)	7.25 (52)
28	0.0088 (29)	0.32 (16)	30 (19)
35	0.0132 (37)	0.21 (24)	32 (6)
40	0.0141 (24)	0.22 (15)	39 (21)
44	0.0217 (34)	0.18 (15)	44 (20)
50	0.0341 (30)	0.18 (24)	74 (33)
53	0.0414 (32)	0.17 (20)	85 (23)

Mean Relative Growth Rate (days 28 to 53)
= 0.063 g/g/day.

Mean of 2.32 cm of root/mg of plant dry weight.

NUTRIENT CONTENT AND INFLOW DATA FOR LEEKS IN WATER CULTURE

Element	K	Na	Mg	Ca	N	P
Mean % of dry matter						
Shoots	7.3	0.32	0.18	2.6	4.7	0.63
Roots	6.0	1.1	0.25	1.7	4.6	0.61
Total	7.0	0.49	0.19	2.3	4.7	0.62
(soil pots)	(4.7)	(0.46)	(0.20)	(1.52)	(3.6)	(0.28)
Mean nutrient Inflow	9.0	0.53	0.40	2.5	8.9	0.79
(in soil pots)	(12.2)	(1.42)	(0.85)	(4.5)	(25)	(1.0)

Mols/cm/s x 10^{-13}

Table 9.2

Here, then, Inflows were calculated in a different way from that described in 4.6.b. The present procedure is preferable if an equation describing the time course of uptake can be determined since data from all harvest dates, not just two, go into the calculation of the uptake rate at any time. Here curve fitting by eye was considered accurate enough, but given the form of the equation, for example exponential or polynomial, it is possible to find the line of maximum likelihood for the data using the least mean square deviation criterion familiar in fitting regression lines (Loneragan unpublished information). Computer programmes for fitting exponential equations to growth data have been written (Radford,1967).

The weight, nutrient content and nutrient inflow data for these plants are summarised in Tables 9.1. and 9.2. Mean inflow values from the soil experiment are included in Table 9.2. for comparisons.

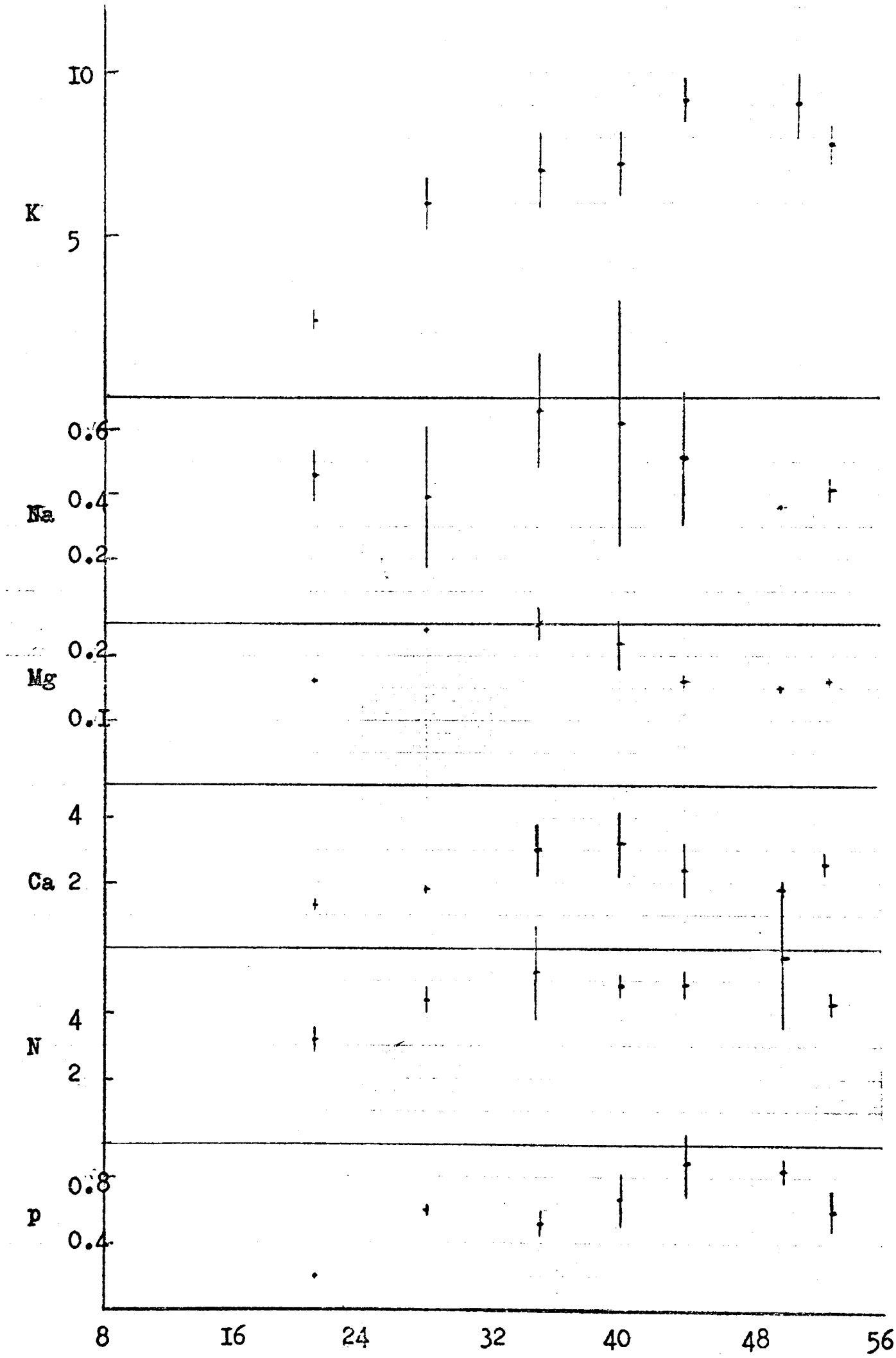
The mean nutrient content of the samples from each date are shown in Fig. 9.2. The standard errors show the variability that existed. For a sample of only 3 plants, the value of the statistical parameter t at the 5% level of probability is about 4, so that there are no significant differences in nutrient content between successive harvest except between days 21 and 28, that is, between the seedlings at transplanting to solution culture and after one week's growth in solution culture. Here there is an indication of a generally low nutrient content in the seedlings which is particularly marked for K and P. In drawing the lines in Fig.9.1. (a and b) uptakes at day 20 were ignored, since they clearly did not always fall on the same line as later points, and the inflow rate around 50 days was of particular interest. Thus there must have been a higher mean inflow rate into the seedlings between days 21 and 28 than would be derived using the exponential equations above.

A useful figure for estimating the mean inflow into roots from dry weight and nutrient content data alone is the root length per unit of total plant dry weight. This figure was calculated here to see how it varied between individual plants. In fact about a two-fold range was found at any one date,

% NUTRIENT CONTENT OF LEEKS GROWN IN WATER CULTURE

Fig.9.2

Means for each harvest and standard errors based on the analysis of three plants each.



different plants varying from about 1.5 to 3 cm of root per milligram of total dry weight. The mean was 2.2 cm of root per mg. of plant dry weight.

The water culture plants afforded an excellent opportunity to measure root diameters which are needed to convert uptake rates in terms of root length into those in terms of root surface area or volume. Diameters were measured on plants 53 days from sowing (about the age of plants in single segment experiments). Diameter was measured systematically every centimetre along the roots. The histogram in Fig.9.3 shows the results obtained from five plants with a mean root length of 68 cm each.

9.3. The Comparison between Soil Grown and Solution Culture Grown Plants

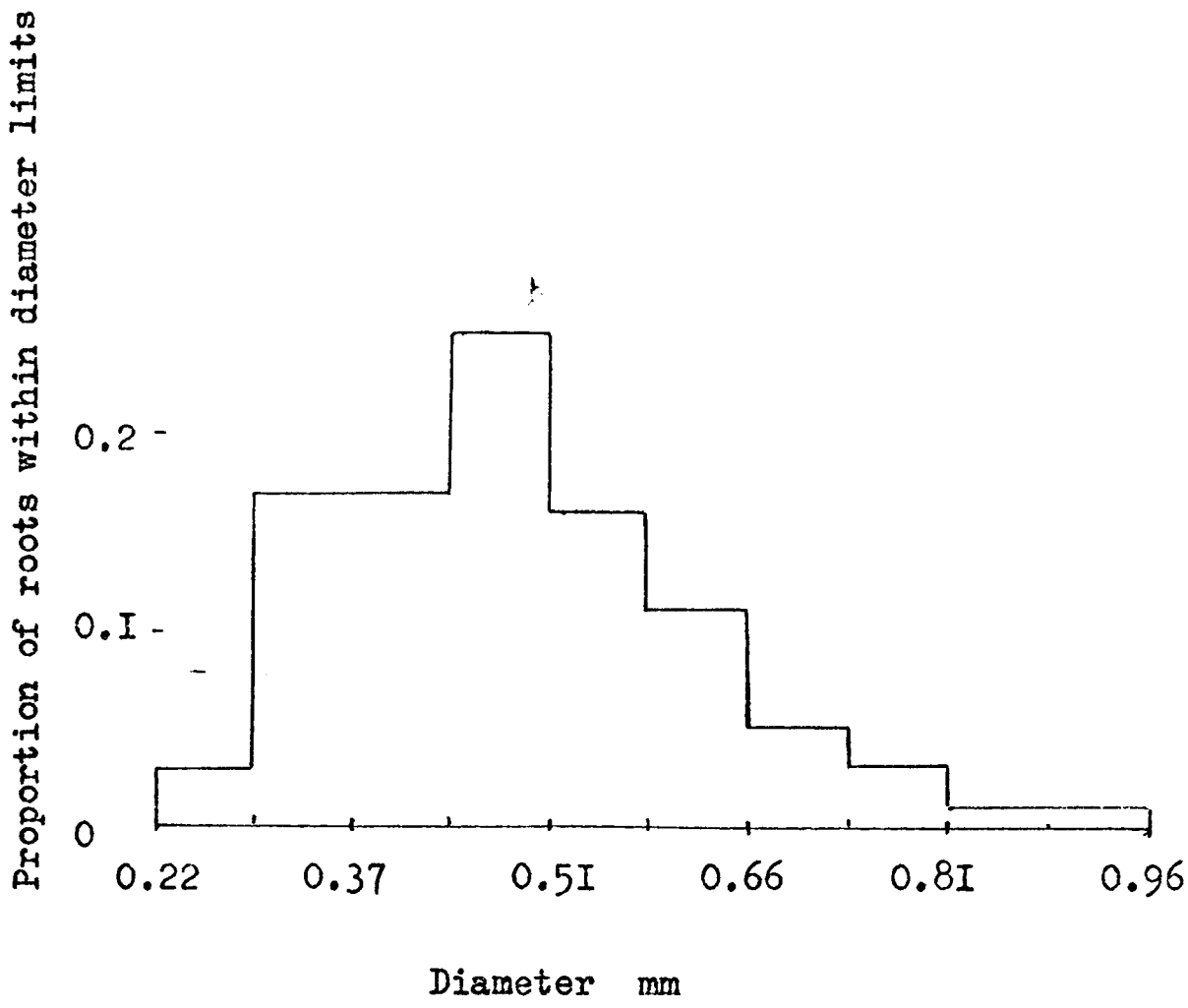
The plants in the water culture grew only about half as quickly as those in the soil experiment, probably because of the lower light intensity in the water culture experiment. The respective growth rates were 0.063 and 0.133 g/ g/ day. The percentage nutrient content of the tissues was higher in the water culture plants than the soil plants for all elements except Na and Mg. Despite their lower growth rate the water culture plants had a greater length of root per mg of dry matter than those in the soil; the mean value were 2.2 and 1.1 cm/mg respectively. This is rather surprising since one would expect a low light intensity and a plentiful supply of water and nutrients to increase shoot/root ratio. (Brouwer,1962).

The values of mean nutrient inflow were generally higher in the soil experiment (see Table 9.2.). However, the mean inflows of K, P and Ca found in solution culture were at least 60% of those into the soil grown roots. If we consider the mean inflows to be an indicator of root system nutrient demand, then the nutrient demand of both the soil and solution grown root systems were similar for K, P and Ca and it seemed reasonable to suppose that measurements of the inflow of these nutrients into short segments of the solution grown roots would be relevant to the soil experiment.

Fig.9.3

HISTOGRAM SHOWING THE DISTRIBUTION OF ROOT DIAMETER IN WATER CULTURE LEEKS

Plant age 53 days from sowing



Chapter Ten

ISOTOPIC EXCHANGE EXPERIMENTS WITH WHOLE PLANTS

In the root segment experiments to be described in Chapter 11, the uptake over twenty four hours of a radioactively labelled ion was to be used to estimate the net uptake rate of roots of different ages. It was therefore essential to know what fraction of the isotope intake was due to the exchange of labelled for unlabelled ions in the roots, and not indicative of the net nutrient uptake rate, (see Chapter 8). Hence, the purely exchangeable fraction of the Sr^{85} absorbed by whole leek plants in 24 hours was determined as described below.

10.1. Experimental Procedure.

Three sixty five day old leek plants (65 days from sowing) which had been grown in the greenhouse conditions described in 9.1.a. were placed in a 2 L. jar of the nutrient solution described in 9.1.a. containing about 0.04μCi of Sr^{85} per cc. This was about 1% of the activity used in the circulating solution in the segment experiments. (See Chapter 11.1). The plants were grown for 24 hours in growth cabinets with a 2000 foot candle leaf level illumination, a 16 hour day, a 20°C air temperature, and a 70% relative humidity.

After 24 hours, the plants were removed from the labelled solution, the roots were drained of excess solution and lightly blotted with tissue in a manner identical to that followed when the segment experiments were harvested (see 11.1.a.). Then they were immersed in a series of solutions in the following sequence:

Solution - 200 mls of:-	Distilled Water			Initially Unlabelled Nutrient Solution								
Time in minutes after the start of the immersions that the roots were removed from the solution.	2	10	20	21	22	25	30	40	60	120	360	1440

At each change the roots were drained and shaken free of excess solution.

After removal of the plants, 5 ml of 10% HNO_3 was added to each solution

and it was evaporated to about 5 ml. on a hot plate. Solutions then transferred to polystyrene vials and made up to 10 ml. and the γ emission was assayed on a scintillation counter. Samples of the original labelled nutrient solution were also counted. Nitric acid digests of the plant roots and shoots were counted to determine the activity remaining in the plants after removal from the last solution.

10.2. Results and Discussion

Fig.10.1. shows the graph, obtained when counts remaining in the plant were plotted against time. In Fig.10.1 counts have been converted to terms of calcium uptake on the assumption that Ca and Sr are identical as far as plant absorption is concerned. (See Russell and Squire, 1958).

The curve shows a very rapid initial rate of loss of exchangeable Sr gradually declining to a low leakage rate. It shows a sharp break at 20 minutes corresponding to the time at which roots were immersed in nutrient solution as opposed to distilled water, thereby releasing exchangeable Sr^{85} from the D.F.S.

When the roots were immersed in the exchange solutions a number of simultaneous processes would have been occurring, namely:-

1) Ion exchange of labelled Sr^{85} for unlabelled cations in the D.F.S., primarily Ca.

2) Diffusion of labelled ions out of the root and of unlabelled ions in.

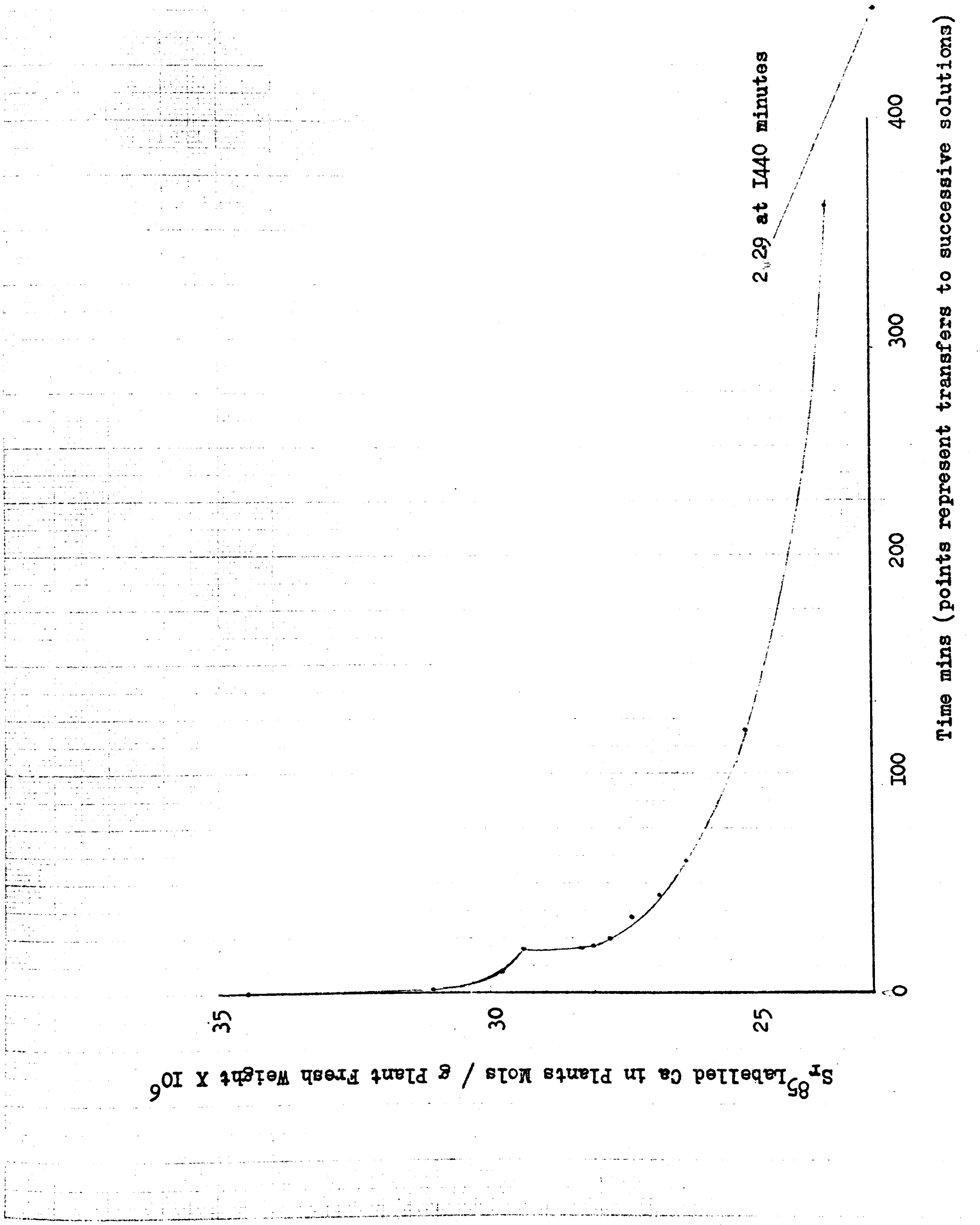
3) Uptake of ions into the root O.V.

4) Efflux of ions from the O.V.

The very slight loss of activity between four and twenty four hours was probably due to 4 indicating the slowness of this process. Similarly, 3 was probably slow in comparison with 1 and 2. Thus we have a situation where processes 1 and 2 rapidly tend to establish equilibrium between the free space and the external solution but where 3 and 4 are superimposed and give rise to a continuing slight efflux. By extrapolating the final part of the curve to time zero the effect of 4 can be roughly eliminated and the intercept with the time axis gives an estimate of Sr^{85} in the root free space and in the water film

THE LOSS OF LABELLED CALCIUM ABSORBED IN THE PREVIOUS TWENTY FOUR HOURS FROM LEEK PLANTS IN WATER CULTURE

Fig.10.1



that adhered to the roots.

Fig.10.1. shows that about 30% of the initial total plant Sr^{85} uptake was exchanged after twenty four hours. This was equivalent to about 60% of the initial root content of Sr^{85}. From Fig.10.1. it was also estimated that Sr^{85} equivalent to about 4.5×10^{-6} Moles of Ca per g. of fresh root was rapidly lost to distilled water and was hence in the W.F.S. The Ca concentration in the nutrient solution was about 15×10^{-6} Moles/g. Hence 1 g of root appeared to hold the equivalent of 0.3 g. of nutrient solution in a freely diffusible form, in other words, 30% of the root weight appeared to consist of W.F.S. and external water films.

10.3. The Possible Efflux of Nutrients from the Root Osmotic Volume.

Although the above experiment gives us a good estimate of the exchangeable ions in the D.F.S., W.F.S., and water films adhering to the roots, there still remains the possibility that net uptake rates could be overestimated since cell uptake is usually the resultant and of an influx and an efflux from the osmotic volume (see 8.2.). Upon immersion of unlabelled roots in labelled solution inluxing ions are liable to contain a greater proportion of isotopes than ions of the same species effluxing from the initially unlabelled osmotic volume of the roots. However, it seems likely that the measured uptake of non rapidly exchangeable ions was a good measure of the net uptake (influx minus efflux) into the root osmotic volume for two reasons. First, in the above experiment the rate of loss of Sr^{85} decreased to an extremely low level between 4 and 24 hours and this probably represented slow leakage from the osmotic volume. Secondly, the overall calcium uptake rate in the 24 hour period was estimated from Sr^{85} uptake as 2.7×10^{-13} mols/cm of root/sec. If we deduct 30% as rapidly exchangeable Ca, we get a mean inflow of about 2×10^{-13} Mols/cm of root/sec. This was very similar to the mean Ca inflow of 2.5×10^{-13} Mols/cm/sec into the roots of 50 day old plants given in Table 9.2. Thus there is no suggestion that the inflow rate, of Sr^{85} labelled Ca was greater than the expected mean net Ca inflow, indicating that any overestimate of net inflow,

due to a possible underestimating of the true efflux from the osmotic volume, was small.

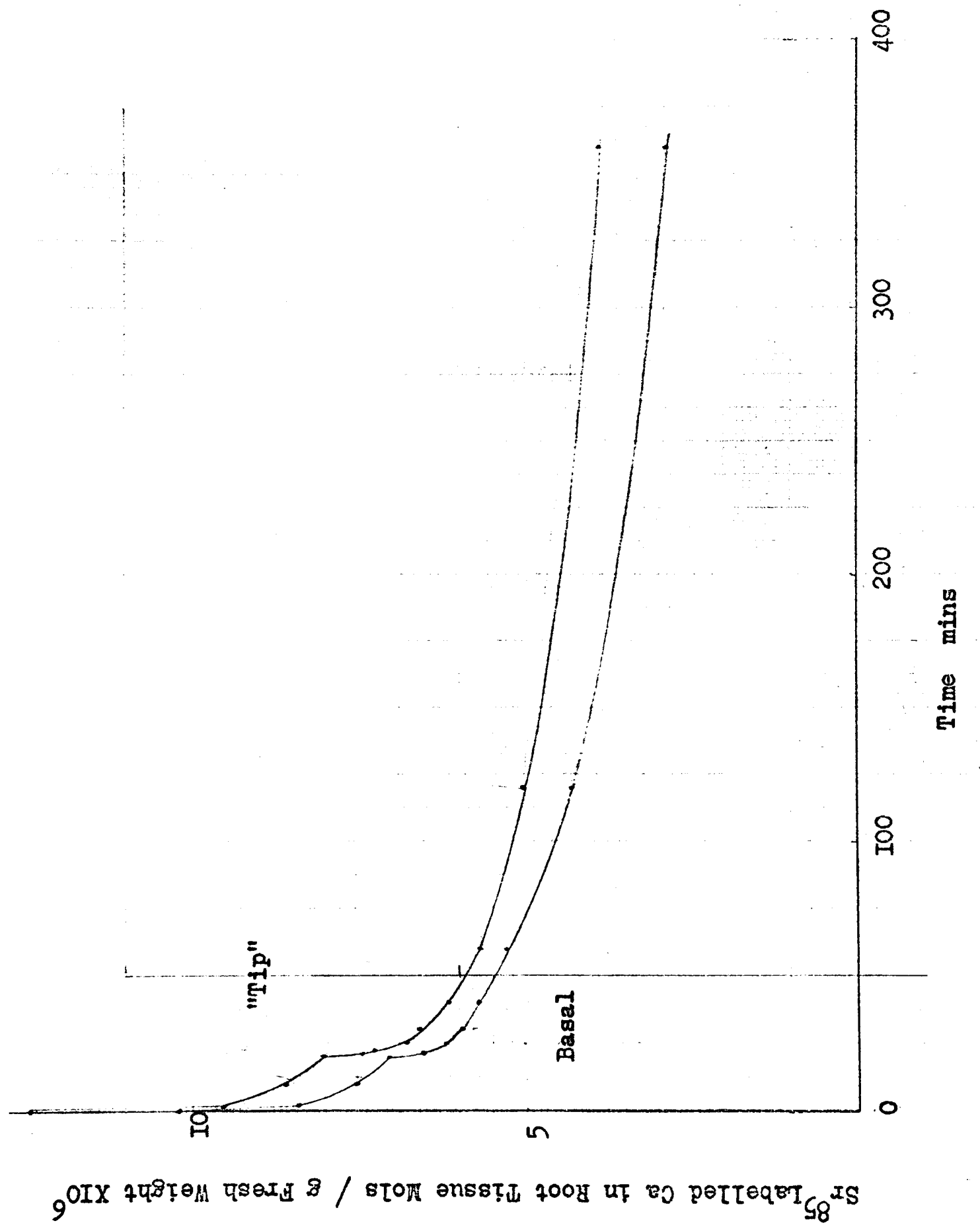
10.4. The Exchangeable Sr^{85} in Roots of Different Ages

In the segment experiments the intention was to compare uptakes of young and old root sections. The data in the above isotopic exchange experiment allows us to deduct the mean contribution of free space ions from the apparent uptake, but there still remains the possibility that the W.F.S. and D.F.S. of roots of different ages are very different, which could lead to big apparent differences in the uptake rate between young and old roots. Therefore, the exchange properties of sections of basal and apical roots of 70 day old leeks were compared. The plants were labelled by growing for 19 hours in nutrient solution containing 2μ Ci/ml Sr^{85}. 3 cm sections were cut from basal parts of the roots and from apical regions, excluding the apical 0.5 cm itself. Cut sections from each region were batched separately, wrapped in nylon gauze and passed through the series of immersiona described in 10.1. above. The results are shown graphically in Fig.10.2.

The younger roots appear to hold slightly more exchangeable ions per gram but both sets are very similar and no serious misconceptions about their relative uptakes rates could stem from a difference in exchange capacity.

Fig.10.2

THE LOSS OF LABELLED CALCIUM ABSORBED IN THE PREVIOUS TWENTY FOUR HOURS FROM EXCISED BASAL AND TIP SEGMENTS OF LEEK ROOTS



Chapter Eleven

THE MEASUREMENT OF NUTRIENT UPTAKE BY DIFFERENT AGED SEGMENTS OF THE ROOTS OF INTACT PLANTS

11.1. Experimental Prodedure

The method used was that of Russell and Sanderson (1967), which in outline involved growing plants for 24 hours in nutrient solution with a single short segment of the root of each plant sealed into an inner tube of the same solution containing two radioactively labelled nutrients. After 24 hours, the plants were harvested and their radioactivity assayed, from which the uptake of labelled nutrients by the enclosed segment was determined.

Root segments from three different regions of the roots were used, basal, middle region about 10 cm from the root tip and tip region about 1 cm behind the root tip. These are referred to as Basal, Mid and Tip segments respectively, and their respective ages were approximately 27, 10 and 1 days. The age of the Basal segments was known since during growth, seedlings had been transferred from sand to solution 29 days before the experiment, in three experiments and 58 days before the experiment in one experiment and the roots formed in sand were crinkled, unlike those formed in water culture, which were smooth. As basal segments were chosen immediately below the crinkles, this fixed their age at about 27 days or 56 days in the one case. Mid and Tip segments were chosen from those actively growing adventitious roots which were outmost in their attachment to the shoot, and the ages of the segments were known approximately since these roots increased in length by about 1 cm per day.

As mentioned above four separate experiments were performed; the first three on plants 49 days from sowing and the last on 78 day old plants. In the first two experiments P^{32} and Sr^{85} were used and in the last two P^{32} and K^{42}. In each of the four experiments there were four tanks containing eight plants of which two were control plants and two each of the remaining six were allocated to the Basal, Mid and Tip treatments.

The control plants had no root in the inner tube. Their purpose was to

assess the uptake of the labelled ions that had leaked out of the inner tube either via the experimental plant or the seal.

Leek plants grown in the greenhouse conditions described previously (9.1.a. above) were used. The plants were taken from the greenhouse and mounted in the tanks shown diagramatically in Fig.11.1. The plants were held in the perspex frame by polythene tape, then the roots were teased apart and the chosen root segment was mounted in the inner tube. The roots were kept immersed in solution during all these manipulations.

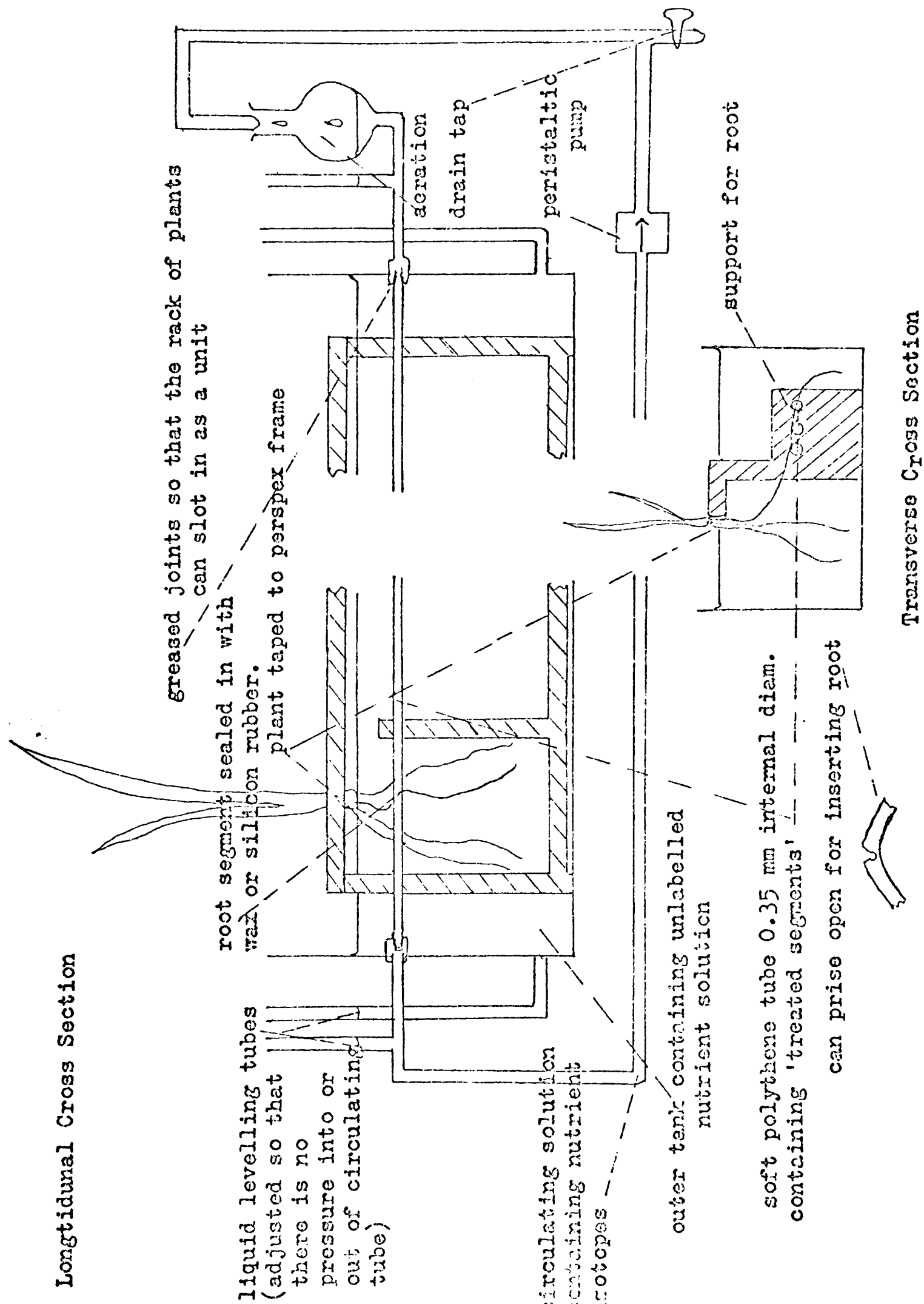
In experiment 1, roots were sealed in the tube with anhydrous lanolin warmed to 45°C followed by a mixture of 50% colophony resin and 50% paraffin wax. In experiments 2, 3 and 4, the roots were sealed in with Silastomer 9159 Cold Cure Rubber made by Midland Silicones Ltd. This made a much shorter seal. All seals were tested for leaks by introducing a 0.005% solution of the fluorescent green dye uranyl into the tube and looking for leakage. Sanderson (personal comm.) has shown that neither uranyl nor silicone rubber in nutrient solutions affects the strontium or phosphorus uptake rate of the whole root system of barley plants.

After the sealing, the mounted plants were transferred to nutrient solution in the 6 L. tanks in growth cabinets and left undisturbed for two hours. The growth cabinet settings for the experiment were 2000 foot candles at leaf level, a 16 hour day, 20°C air temperature and 60 to 70% relative humidity. Next the inner tube was connected to the pump (see Fig.11.1), drained and filled with radioactive nutrient solution. The time was noted and the pump was switched on to start circulating the labelled solution.

24 hours after adding the active solution, the inner tubes were drained and the plants racks were disconnected and removed. The plants were removed from the rack, and the roots and shoots of each plant were placed into a previously weighed flask after a quick blotting on absorbent tissue. The treated segments were removed separately and placed on a slide and their mean diamter measured using a microscope with a scale in the eyepiece. A note was made of

APPARATUS FOR STUDYING THE UPTAKE OF IONS BY REGIONS OF INTACT ROOT SYSTEMS

Fig. 11.1



any unusual visible features of the segments. Plant material was digested in about 7 ml of hot concentrated nitric acid, after which the digests were evaporated down to about 1 ml and transferred to polystryene vials and made up to 10 ml with water for counting.

The roots, shoots and segments of each plant and a sample of the original [illegible] inner tube solution were counted. The isotopes, their relevant properties and the counting methods are tabulated below.

Isotope	Half-life	Emission	Counting method
P^{32}	14.3 days	β^-	Liquid counting using a G.M.tube β^- detector.
K^{42}	12.5 hours	β^- and γ	
Sr^{85}	64 days	γ	γ scintillation counting

The specific activity of the circulating solutions was about 4 µCi/ml for Sr^{85}, 0.2 µCi / ml for P^{32} and 0.5 µCi/ml for K^{42} at counting time, which was about forty eight hours after the introduction of the active solution to the plants.

The major features of all four experiments are tabulated in Table 11.1.

Where the double label of K^{42} and P^{32} was used, β^- counts were determined in the samples straight after digestion. Then they were left for a week, after which time, the K^{42} had virtually all decayed. They were then recounted. The remaining counts could all be attributed to the P^{32} present and by correcting for P^{32} decay to the time of the first count, the P^{32} contribution to the first count could be calculated by difference. Least significant difference values at the 0.05 level of probability (L.S.D. 0.05) for the difference, Total counts minus P^{32} counts, were calculated. Any differences less than L.S.D. 0.05 were dismissed as non-significant and as showing no indication of a K uptake. Such non-significant differences were few in experiment 4 and in most cases differ-

SUMMARY OF SEGMENT UPTAKE EXPERIMENTS

All had 4 tanks x 4treatments (3 root regions + controls) x 2 replicates = 32 plants.

Experiment	Plant age days	Isotopes applied	Method of sealing roots	Comments
1	49	$P^{32}$and Sr^{85}	Lanolin+wax	Leakage of Sr
2	49	,,	Silicon rubber	Large P leakage some of Sr
3	49	$P^{32}$and K^{42}	,,	Large P leakage
4	78	,,	,, a deliberately long seal.	Little leakage of P or K.

Table 11.1

ences were about seven times L.S.D.$^{0.05}$, except in the case of the control plants, none of which had significant K uptake.

Uptakes of Ca, P and K were calculated in terms of Moles by converting from the counting data. Samples of the labelled nutrient solution initially added to the inner tube were counted in parallel with the plant digests. The ionic concentrations in this solution were known, hence the counts per Mole could be determined for each labelled nutrient. Knowing this, and assuming that the specific activity of the solution remained constant over the 24 hour uptake period, the Moles of each element absorbed from the circulating solution could be calculated from the number of counts found in the plant digests. It has been assumed here that P^{32} and K^{42} behaved identically to P^{31} and K^{39} and that Sr^{85} was identical to Ca with regard to its rate of absorption over 24 hours. (Russell and Squire,1958).

Any radioactivity in the plants measured external to the treated segments had been termed "translocated uptake" although only if there was no leakage from the inner tube and hence no uptake of radioactive ions by the roots other than the enclosed segment was it all truly translocated.

11.2 Leakage from the Treated Segments

One of the difficulties of the experiments was the large leakage of isotopes from the inner tubes to the outer tank solution by a pathway impermeable to the uranyl dye. P leakage in experiments 2 and 3 was so large as to make the control plant uptake almost as great as the amount found external to the enclosed segment in the treated plants. The same was to some extent true of Sr uptake in experiments 1 and 2. Sr uptake by the control plants was considerable in experiment 1 where P leakage was small, so that some difference in the mechanism of leakage of the two elements is apparent. K leakage was small in both experiments 3 and 4. Thus K and P also seem to differ in their mode of leakage. Similar leakage was reported in barley roots by Russell and Sanderson (1967). Their experiments indicated that it was affected by root metabolism; P leakage being reduced by the metabolic inhibitor dinitrophenol (DNP) and Sr leakage being enhanced, again indicating a difference in the methanisms involved. The root cor-

tex was suggested as the probable pathway of longitudinal transport leading to leakage (Russell and Sanderson, 1967). Brouwer (1954 b) found movement of P^{32} away from similar treated segments of broad bean roots. Most of such P^{32} was within 3 mm of the segment boundary after 24 hours uptake and, in contrast to this work and that of Russell and Sanderson (1967), he observed no leakage into the outer tank solution. The greater P leakage in experiments 2 and 3 than in 1 was puzzling. The only difference between these experiments lay in the sealing of the segments into the inner tube, the more easily handled silicon rubber being used in 2 and 3 and the wax mixture in 1. The wax tended to cover a longer section of root around the seal, and this suggested that the difference might lie in the greater length of seal in experiment 1. In experiment 4 therefore the region of root around the seal was deliberately coated with rubber for a distance of 3 to 4 mm on either side of the seal. The outer tank solution was also changed after 18 hours in this experiment to minimise uptake of any isotopes that had leaked. As the results indicate (Fig.11.2 a and b), these measures drastically reduced the uptake of leaked P by control plants.

These observations on leakage may be understandable in terms of diffusion through the cortical free space. Clearly there must have been a gradient of isotope concentration between the cortical free space of the treated segments and that of the adjacent roots. The leaked isotopes may have diffused longitudinally through the cortical free space out of the treated segments and thence escaped into the outer tank solution. The fact that a long seal in experiment 1 appeared to prevent P leakage but not Sr leakage suggests that the mobility of Sr was greater than that of P in the cortex. Such differences in mobility may be explicable in terms of diffusion coefficients in the cortical free space. It may be possible to apply the same theory to diffusion of ions in the free space of plant tissues as has been applied to ionic diffusion in soil, since in both media, we have to consider the diffusion of ions through tortuous water films which surround surfaces with a predominantly negative fixed charge. If so, the extended form of equation 2.I should be applicable,

$$D = D_L v_L f_L \frac{dC_L}{dC} + D_S$$

where D_s is the diffusion coefficient for the "solid associated" diffusion of ions along charged surfaces and within the electrical double layers (see Nye,1966 a). The relative importance of the liquid and solid associated pathways depends on the proportion of the diffusion path that is occupied by double layers.In moist soil, as discussed in Chapter 2, D_s is negligible. However, it may be, that, within the cortical free space of roots, the electrical double layers occupy a much greater proportion of the diffusion pathway than in moist soil. If this is true, then negative adsorption may exclude anions like phosphate from much of the diffusion pathway (Olsen and Kemper,1968), whereas cations like Sr would be able to diffuse through the electrical double layers.

11.3 Results and Discussion

11.3.a. Summarised Results.

The individual uptakes for each plant are presented in Figs.11.2.a, 11.2.b, 11.3 and 11.4. The graphs all follow the same sequence, so that the uptake of both of the labelled elements absorbed by a particular root segment can be compared.

Root segments of all three age groups appear capable of the uptake and translocation of Ca, and K and P, but the variation between different segments is very striking. A transformation of the data to log (x + 1), where x is the raw value was necessary in order to make the variance of control plant uptakes and treated plant uptakes similar. Using the transformation an analysis of variance of the results was possible. This showed that the P content external to the segments in experiments 2 and 3 was not significantly different from the control plant content. Leakage into the outer tank solution must have caused the large control uptake and these experiments were not used in arriving at conclusions regarding P uptake.

Mean values of total uptake and translocated uptake for each ion were cal-

ROOT SEGMENT UPTAKE EXPERIMENTS

The uptake of radioactive nutrients through the segments by each plant is shown in the following four graphs in histogram form. The eight replicates from each root region in each experiment are grouped together and follow the sequence of pairs of replicates from tanks I,2,3 and4 respectively. The same sequence is followed in all graphs so that the uptake of different nutrients by the same plant can be compared. Any spaces in the sequence are simply missing values.

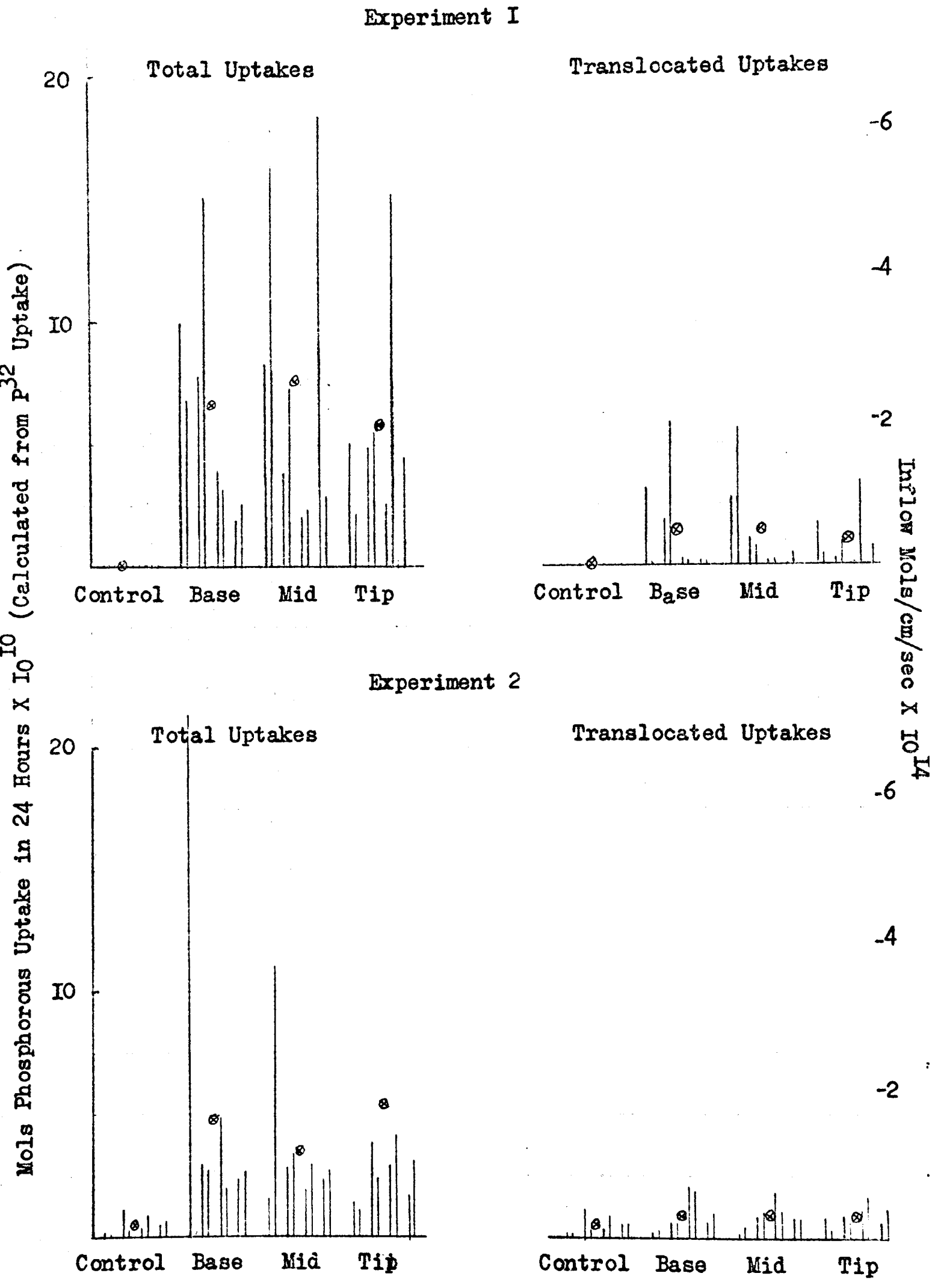
The symbol ⊗ indicates the mean uptake from each root region in each experiment.

Scales in terms of total uptake in Mols/24 hours and converted to Inflow Mols/cm of root/sec are represented.(the segments were 0.35 cm long)

All radioactivity found external to the treated segments is termed 'Translocated Uptake' although this is only truly translocated from the segment if leakage and hence control uptake is small.

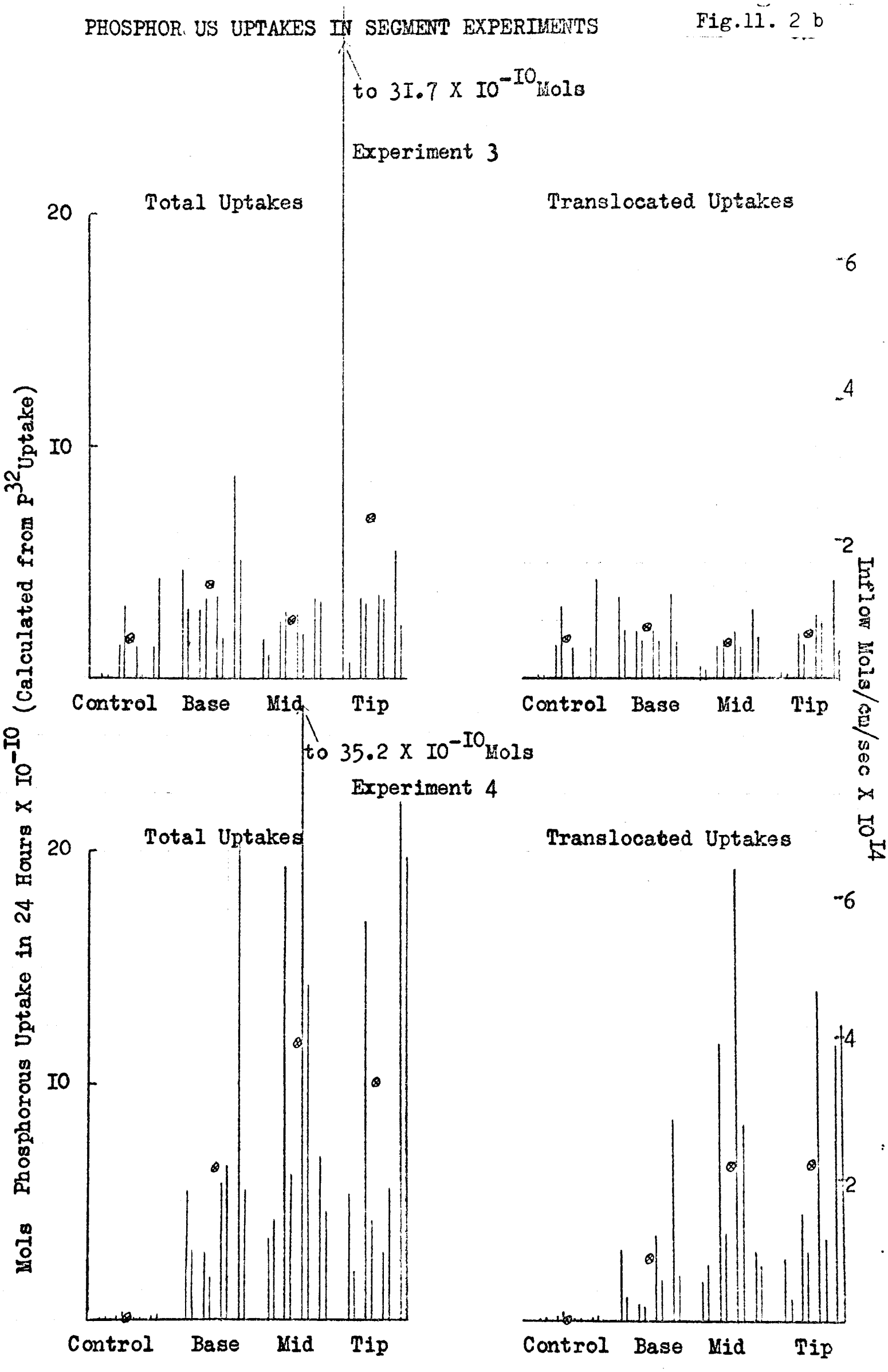
PHOSPHORUS UPTAKES IN SEGMENT EXPERIMENTS

Fig.11.2 a



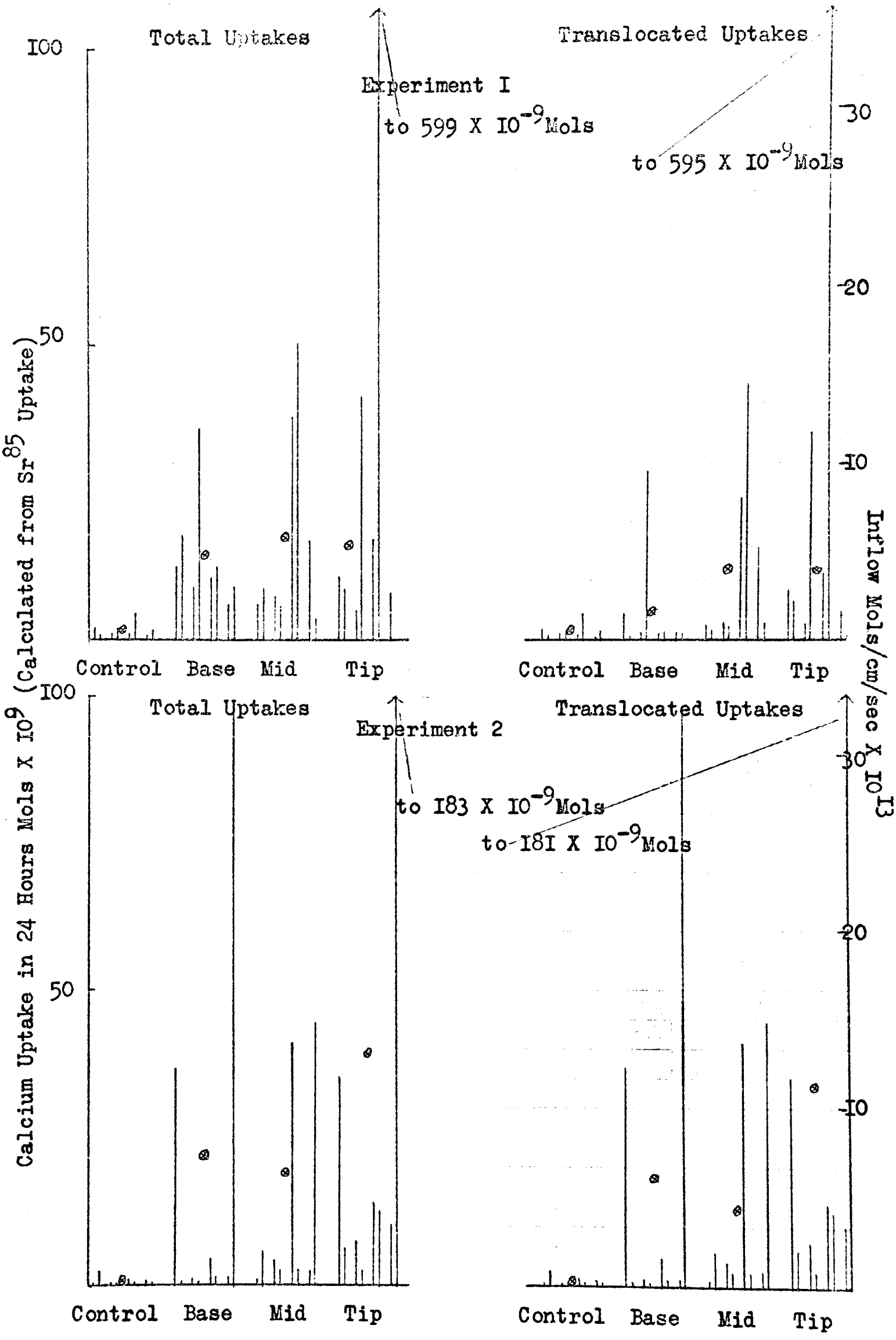
PHOSPHORUS UPTAKES IN SEGMENT EXPERIMENTS

Fig.11. 2 b



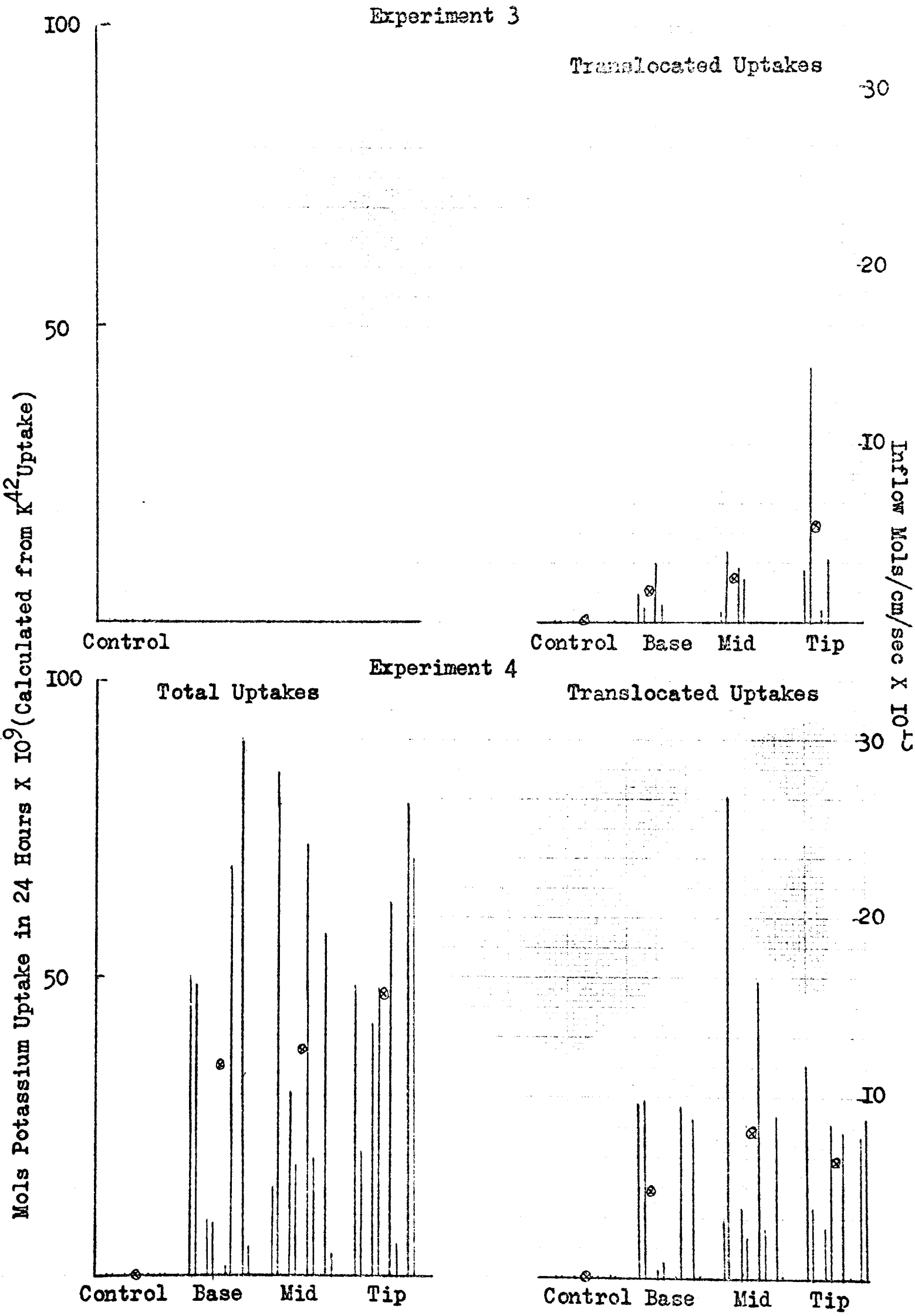
CALCIUM UPTAKES IN SEGMENT EXPERIMENTS

Fig.11.3



POTASSIUM UPTAKES IN SEGMENT EXPERIMENTS

Fig.11.4



culated by combining all values from experiments 1 and 2 for Sr, 1 and 4 for P, and 4 and 3 for K. The standard errors of the mean uptake values and the mean of all values transformed to log (x + 1) were determined, and differences between the mean uptakes of the three root regions were tested for significance. No significant differences (at the 0.05 probability level) were found between the mean total uptakes or mean translocated uptakes of different root regions using either the raw or the transformed data.

The mean inflow rates into these segments of root are summarised in Table 11.2

In summary, significant differences in the uptake of different root regions were not apparent, and roots of all ages upto 27 days old appeared able to absorb and translocate phosphorus, potassium and strontium (i.e. calcium). The uptake rate was highly variable between visually similar root segments in different plants.

11.3.b. Exchangeable Ions in the Treated Segments.

The freely exchangeable Sr^{85} in the roots was a highly significant fraction, as pointed out in 10.2 above, and consideration has been given to this factor in the detailed discussion of calcium uptake results below. From the Sr^{85} exchange experiment we can make an estimate of how much P and K occurred as freely diffusible ions in the roots, $H_2PO_4^-$ being an anionm would not be adsorbed by the cation exchange sites in the roots and would not appear in the D.F.S. The fraction of K adsorbed by cation exchange would be small in roots immersed in this nutrient solution, since it contained only 0.42 me/L K as against 30 me/L Ca, and since Donnan Systems are highly selective in adsorbing bivalent ions in competition with monovalent ions(Briggs et al,1961,p.28). Thus, freely exchangeable ^{32}P and ^{42}K would be primarily in the root W.F.S. and in the water films adhering to the roots. This was estimated to be roughly 30% of the root volume (see 10.2). Hence, if we assume equilibrium between the external solution and the solution in the W.F.S., the exchangeable ^{32}P and ^{42}K uptake can be estimated as 0.3 x the root volume x the concentration of ^{32}P and ^{42}K in the ex-

MEAN INFLOW RATES INTO 0.35cm SEGMENTS OF LEEK ROOTS (averages from all four experiments)

Element	Total Inflow				Translocated Inflow			
	Base	Mid	Tip	Mean	Base	Mid	Tip	Mean
	Mols / cm / s x 10^{-13}							
Ca	6.8	5.9	9.6	7.4	5.3	5.3	4.6	5.1
K	11.6	12.7	15.6	13.3	3.8	6.1	6.0	5.3
P	0.21	0.32	0.26	0.26	0.07	0.13	0.13	0.11

Table 11.2

ternal solution. Hence, allowance for exchangeable P and K in the roots could be made in the segment experiments since the volumes of the root segments were measured and the specific activity of the nutrient solution that surrounded them was known. In all four experiments less than 1% of the mean P^{32} content of the treated segments could be attributed to free space P^{32}. The same was true of the K^{42} in experiment 4. Thus we can safely ignore the contribution of freely diffusible P^{32} and K^{42} to the apparent uptake of the treated segments .

11.3.c. Calcium (Strontium) Uptake.

Although the differences between the control plant content and the treated plant translocated Sr were not great for many of the treated plants, some had a vastly greater Sr uptake than the controls. These plants clearly translocated large amounts of Sr from the treated segments. At first it was thought that such plants had damaged segments allowing a direct mass flow of labelled ions into the stele and up the xylem, but microscopic examination showed visible damage in only one case. Similar results have been obtained with segments of barley roots where it has also been shown that high uptakes cannot be induced by deliberately damaging segments with a needle (Clarkson, pers.comm.). There was no apparent correlation between a high Sr uptake and translocation and a high P uptake and translocation except in the case of the one visibly damaged segment.

The mean Sr (Ca) inflow of 7.4×10^{-13} mols/cm/sec or 6.0×10^{-13} after deducting the free space Sr in the segments (see 10.2), was greater than the expected mean uptake rate of 2.5×10^{-13} as found for Ca in the long term experiment (see Table 9.2). Examination of Fig.11.3 shows that translocation from a few segments with exceptionally high Sr uptake accounts for most of the observed mean uptake.

11.3.d. Potassium Uptake.

The mean inflow of potassium, 13.3×10^{-13} mols/cm/sec, was close to the expected mean inflow of 10.8×10^{-13} mols/cm/sec from longer term experiments. Once again, variation between segments was obvious and similar roots had total uptakes ranging from almost zero to just over twice the mean. As stated in

11.1 above, Experiment 4 was conducted with 78 day old plants, upon which it was possible to select 57 day old basal segments. These were located on the first formed primary root which was short in comparison with the later formed roots and it had clearly ceased to grow. Unfortunately of the eight plants designated for the "Basal" treatment, only four still had this root in a healthy state. In the remaining four plants this root was showing signs of decay. Hence, the basal segments of the latter four plants had to be chosen from adventitious roots and their age was not certain. However, the four 57 day old basal segments translocated very little K, whereas the other basal segments translocated a similar quantity of K to the Mid and Tip segments of younger roots (see Fig.11.4). It was also striking that these 57 day old basal segments did translocate P at a rate similar to that of much younger roots (see Fig.11.2). There was no correlation between the K and P uptake of any root segments. An interesting observation was the very high uptake and fraction translocated by one mid segment that was subsequently seen to be giving rise to a lateral, suggesting high K uptakes occur where lateral roots permeate the stele and endodermis. P uptake by this segment was not exceptional. Thus there were several indications that the mechanisms of K and P uptake in the roots were fundamentally different.

11.3.e. Phosphorus Uptake.

The mean P inflow into the enclosed segments was 0.26×10^{-13} mols/cm/sec. This was considerably lower than the long term mean inflow of 1.04×10^{-13} mols/cm/sec. A few of the high individual uptakes approached 1×10^{-13} mols/cm/sec but only one exceeded it. The reasons for the low mean inflows are not apparent. We cannot attribute it to an overall depletion of P in the nutrient solution, since the P^{32} activity of the circulating solution at the end of the 24 hour uptake period was 95% of its initial level. A second guess might be that leakage from the segment reduced apparent uptake, but this does not stand careful consideration. Algebraically one can show that with these relative lengths of roots in the inner and outer solutions and these relative volumes of the inner and outer solution, any leakage would lead to a slightly increased up-

take of labelled P. Thus if we designate by the following symbols,

U = uptake rate of P^{32}

L = root length

α = root absorbing power for P

C_L = concentration of P^{32} in solution

C_{LS} = initial P^{32} concentration in the inner tube solution

x = P^{32} leaked from the inner tube to the outer solution

$Suffix_i$ e.g. U_i, C_{Li}, L_i = within the inner tube

$Suffix_o$ e.g. U_o, C_{Lo}, L_o = within the outer solution

Now, α should on average be the same for roots in the inner and outer solutions. There were 40 cc. of solution in the inner tube and 6000 cc. in the outer tank. There was also 0.35 cm. of root per plant in inner tube and 49 day old plants had on average about 70 cm. of root, so that 70 cm. of roots can be taken as in the outer tank.

Hence, L_o = 70cm. and L_i = 0.35 cm.

If x moles of P^{32} had leaked from the inner to the outer solution

$$C_{Li} = (C_{Ls} - x/40) \text{ and } C_{Lo} = x/6000.$$

If there was no P^{32} leakage $U_{no\ leak} = \alpha.C_{Ls}.L_i$

If there was leakage, $U = \alpha.(C_{Ls} - x/40).L_i + \alpha.C_{Ls}.L_o$

$$U = \alpha.C_{Ls}.L_i + \alpha.x/6000.L_o - \alpha.x/40.L_i$$

$$U = U_{no\ leak} + \alpha.x.(L_o/6000 - L_i/40)$$

$$U = U_{no\ leak} + \alpha.x.(70/6000 - 0.35/40)$$

$$U = U_{no\ leak} + 0.0004.\alpha.x.$$

Thus, if leakage occurred, we would expect a slightly greater mean uptake of P^{32} per plant than in its absence. Hence, it seems that P inflows were genuinely low; possibly the transfer and handling had affected the uptake ability of the plants.

With the caution that the mean P uptake rate was only about a quarter that expected. it does appear that P uptake, like Ca and K, fluctuates as much as

twenty fold between apparently similar segments of root. Experiment 4 showed quite clearly the ability of roots as old as 56 days to absorb and translocate P at rates similar to those of young roots.

11.4 The Sporadic Nature of Nutrient Uptake

The experiments suggest that Ca, K and P inflow into leek roots may be very sporadic. The overall mean inflow could be due mainly to high inflow into a small proportion of the total root length or into the whole root system for only a small proportion of the time to some combination of the two. We can speculate about distribution of high inflow both in space, i.e. along the root system and in time. One could envisage individual roots having "spots" along their length where high uptake rates are maintained over a long period. Alternatively, one whole root from base to tip along with its branches may have a much greater uptake than the rest of the root system for a limited period. If roots on leeks connect to and supply particular leaves, then one might expect the period of leaf expansion to coincide with an exceptionally high inflow into the corresponding root. Evidence for such connections is lacking, and vascular bundles into different leaves and roots normally anastomose along their length in higher plants (Esau, 1953). Further, Baldwin (pers.comm.) has shown that injection of a single leaf of the related onion plant with P^{32} will label all roots, suggesting no strict one leaf/one root connection in plants of the genus Allium. Another possible explanation for the observed variation of inflow into different root segments is that whole plants go through cycles of low and high nutrient uptake rate and inflow.

11.5 A Review of Published Work on the Relation between Nutrient Uptake and Root Age

Nutrient uptake by different root regions has been studied in several ways including;

I. The attachment of sealed micropotometers to different regions of the root and subsequently,

a) Measuring the rate of concentration decrease in the solution

surrounding defined root regions. (Gregory and Woodford, 1939; Brouwer, 1954 b.)

b) Measuring the rate of uptake and translocation of a nutrient ion isotope by a defined root region (Russell and Sanderson, 1967; Wiebe and Kramer, 1954; Grasmanis and Barley, 1969).

2. The placing of the roots into solutions containing nutrient ion isotopes for periods sufficient to allow uptake but very little translocation, followed by the washing out of the isotopes in the root free space and the determination of the quantity of isotopes in root regions of different ages. (Rovira and Bowen, 1966; Bowen, 1969).

3. The growing of roots through discs of soil containing a nutrient ion isotope and following nutrient uptake by successive harvests of replicate plants. In this way, changes in the nutrient uptake rate can be measured as the roots in the soil disc become older. (Drew, 1966; Drew, Nye and Vaidyanathan, 1969; Drew and Nye, 1970).

All of the above except the work of Russell and Sanderson, of Brouwer and that reported in 11.1 to 11.4 above have been done using seedlings. Further, only a limited range of ions and a few plants species have been investigated so far.

Of the solution culture methods, I.a) is probably the best since the net uptake rate is measured and uncertainties about the extent of exchange do not confuse the situation. Fuller details about the plants, their pretreatment and the uptake period are listed in Table 12.1. (See Chapter 12). Brouwer, Gregory and Woodford, and Grasmanis and Barley found NO_3 uptake all along the apical 15 cm of broad bean and pea roots. Uptake rates were maximal in the apical 2 cm and diminished to about 40% of the maximum 10 to 15cm from the tip. Brouwer observed a similar pattern for Cl in his beans. For P he found uptake throughout 15 cm of root with a maximum in the apical 3 cm and indications of another peak around 15 cm where lateral root apices were emerging. Rovira and Bowen found a similar pattern of P uptake in wheat and in pine seedling roots using method 2. They showed uptake throughout a 12 cm root with peaks 0.5 cm from the

apex and in the region of lateral emergence. Brouwer's and Wiebe and Kramer's work indicated that the greatest fraction of the uptake was translocated from the region 3 to 4 cm from the apex. In summary, uptake can occur throughout the apical 10 or 15 cm of solution grown roots, but there seems to be a region of greatest potential uptake 0.5 to 2 cm from the tip and a possible second peak of uptake ability in the region of lateral root emergence.

In soil, Drew (1966) found no indication of any decrease in the P uptake rate of onion roots over 16 days after entering a labelled soildisc. P uptake rate continued at a constant mean rate over successive 3 day periods. The rate was the same whether the rest of the root was in similar unlabelled soil or in nutrient free sand. It is likely in this case that diffusion to the root surface was limiting the uptake rate and hence any decrease in α as the roots aged had no effect on uptake rate (see Chapter 3.4.). In estimating the uptake rate of different aged roots in soil it is important to bear in mind the ability of soil to supply nutrients as well as the inherent uptake ability of roots. For K also, Drew found a similar constant inflow over 16 days. Interestingly, the K uptake uptake rate was about twice as great when the rest of the root was in nutrient free sand rather than soil, indicating differences in root demand (α) depending on the K status of the whole plant which in this case was determined by the K supply to the rest of the root. The later points on Drew's graph for the soil/soil system indicate a slowly diminishing uptake rate unlike the graph for the soil/sand system, suggesting that, where K is plentifully available to the root systems as a whole, there is a tendency for α to diminish with root age. There are indications in Drew's work that the root demand coefficient (α) of any short section of root, may depend on the nutrient status or requirements of the whole plant. Perhaps the root demand coefficient of different age fractions of roots will prove to be an adaptive variable, in which case it is unlikely that any rigidly defined correspondence between root uptake ability (α) and root age will be found.

A careful note was made of the variability in the published uptake rates

in view of our finding of great differences between apparently similar roots. Many published results are the mean values from several plants bulked together for chemical analysis so that individual plants variation is not known. Rovira and Bowen (1966) report a coefficient of variation of about ± 40% for the total uptake of P^{32} by sterile wheat roots, and they remark on differences in the uptake pattern along visually similar roots. Bowen (1969) comments on the even greater variability in his experiments of non-sterile roots. Wiebe and Kramer (1954) also remark on the irregularities in P^{32} uptake found in their initial (unpublished) work. They found that the growth of seedlings in flowing culture prior to experiments diminished the variability. Possibly, microbes are less able to accumulate in flowing cultures.

It is reasonable to expect the microbial infection of roots to be rather sporadic and to attribute some variability in short term uptake to differences in the amounts absorbed by microorganisms at different spots along the root. Microorganisms can have a great affinity for nutrients and a rapid rate of nutrient uptake and turnover (Barber, 1968). Over the long term, however, it is difficult to envisage the occurrence of a constantly expanding microbial biomass at the surface of each bit of root/as a permanent sink for nutrients. It seems likely that short term uptake experiments using isotopes in solution culture magnify the importance of microorganisms on the uptake rate of roots and they will probably appear less important in longer term experiments.

Variation in microbial infection is one possible explanation for the great variability in uptake found along roots in the leek experiments. However, similar variations were found in the amounts translocated and these were not correlated with the amount of nutrient remaining in the absorbing segment. It is difficult to see how micro organisms could cause such variation in non local accumulation of nutrients.

Another reason for the variation in uptake rate may have been the greater age of our leek plants as compared with the seedlings used in most of the published work mentioned. As plants become older it is possible that the physio-

logy and anatomy of small regions of roots will show a greater degree of variation in properties; an older root system has undergone a greater degree of random fluctuation in environment than a young one and has had a greater scope for variation in internal development. Seedlings, on the other hand, may be lass variable; their roots all emerge from similar seeds, and short sections are more likely to have experienced a constant internal and external environment during their formation than are small regions of the root of an older plant.

Despite the qualifications in the latter paragraphs, it does seem from the experimental results discussed in 11.3., and from those comments on variability in the literature, that the great differences in the short term uptake rates of similar roots on different plants present a problem to physiologists and soil scientists alike. The problem seems to warrant further investigation which could throw light on the underlying physiology of nutrient uptake in whole root systems. In section 11.6 below, the implications of such behaviour for studies of the nutrient flow to roots in soil are considered.

11.6 The Uptake Rate of Different Fractions of the Root System in Soil

The experiments described in 11.1 to 11.3 gave no indication of any differences in the average uptake rate of P or Ca by roots of different ages in solution culture. Only for K was there evidence that the inflow into very old roots was negligible. However, roots of this age constituted only a very small fraction of the total root length at the time of the experiment. The results of other workers discussed in the last chapter indicate that NO_3, Cl and P are absorbed along at least the apical 10 or 15 cm of solution grown roots. Their evidence indicates that on average the uptake rate of these ions is about twice as large in the apical region as compared to several centimetres behind the tip. Thus there is some evidence that the absorbing power of younger roots is greater than that of older roots.

What has not been explicitly reported or fully discussed before is the finding of immense differences in the uptake rate of visually similar segments of root from all parts of the root system of different plants in solution cul-

ture. The possible patterns of uptake that could explain these observations have been discussed in 11.4. The question of whether roots in soil could behave like this is now considered. We must question whether the mean inflow into a root system can normally be the result of high inflows into a fraction of the roots and low inflows into the rest. For the purpose of this discussion it matters little whether inflows are consistently higher into younger roots, as the results of some workers suggest, or whether, as here, the inflow is high into a fraction of the roots that cannot be identified as of a particularage group.

The degree to which root uptake can be non-uniform in soil depends on the degree to which the rate of nutrient supply to the root surface limits the inflow. This depends on the magnitude of the required mean inflow and on nutrient mobility in the soil, which is of course, different for different nutrients. Here we consider whether the mean inflows into leek roots found in the pot experiment (see Chapter 4) could have been due to absorption by a fraction of the total root length (see Chapter 3.4 for a fuller discussion of the theory).

If we consider calcium first, it was shown that a large excess was supplied to the roots by mass flow (see 4.9.d.). It seems entirely possible that the observed mean inflow could have resulted from localised inflows many times the mean or from occasional periods of very high inflow. A variation in α along the root would affect the value of C_{LR} at different points along the root. Accumulations occur at the root surface if v/α is greater than one. If, at certain points, along the root, v/α for calcium was less than one, then depletions would have occurred there. If this had been the case, then v/α in remaining roots would have been greater than $\overline{v/\alpha}$. However, as pointed out in 4.9.d. it made little difference to the value of C_{LR} whether v/α was ∞, as in Passioura and Frere's (1967) numerical solution, or 8 as v/α proved to be for Ca in the pot experiment. Hence, even if the mean inflow of Ca in the soil was due to a few roots with a very high α, the values of $\overline{C_{LR}}$ in Table 4.8. can still be taken as approximately correct for all but the inevitably small proportion of roots with values of v/α close to or lower than one.

Nitrate and chloride could similarly have been absorbed by a fraction of the roots and so too could Na, S and Mg. In fact, all the ions that were over-supplied by mass flow could have entered the roots in a non uniform way. The abundance and mobility of these ions is such that non-uniform uptake is a possibility in most agricultural conditions. Only when soils are dry, or for the cations, when the anion, usually nitrate, concentration in solution is low, will the nutrient mobility be reduced to such an extent that the soil will not be able to supply inflows of the magnitude of those into leek roots. Only in these circumstances can we expect a uniform distribtuion of absorbing power along the root to be particularly advantageous.

Turning to phosphate, the P inflows of individual root segments in solution differed by as much as twenty fold and presumably the root absorbing power was similarly variable. However, it was shown in 5.3. that the observed mean phosphate inflow in soil could barely be accounted for if all the roots were a zero sink. Consequently a sporadic P uptake would be even less able to account for the observed mean inflows. Moreoever, the results reported in 5.1.d. and Fig.5.1. showed clearly that large differences in α for P had little effect on inflow in soil and that above an α of 10^{-3} cm/sec the root was virtually a zero sink for P. Thus our knowledge of P diffusion in soils makes it seem unlikely fo that P inflow was localised or sporadic in the soil and it does reinforce the view that P is adsorbed by old as well as young roots.

Much the same can be said about K inflow. Here soil supply was partially rate limiting, but the root was not a zero sink and inflows about double those observed were possible. This being the case, it is again clear that a twenty fold variation in the uptake rate between different sections of the root length in the soil was an impossibility. We have to admit, though, that the mean K inflow may have been the result of double the mean inflow into half the roots and that a cessation of K absorption by old roots was possible in the soil.

These conclusions about P and K inflows in soil emphasize the importance

of considering the transport of nutrients in soil when thinking about the significance of quite striking experimental observations on nutrient uptake rate from solution. Without the coherent overall model of soil supply and plant demand we might have concluded from the experiments described in 11.1 that the P and K uptake of typical roots is highly sporadic or localised along their length.

SECTION FOUR

CONCLUDING CHAPTERS

Chapter Twelve

MEAN NUTRIENT FLOW RATES INTO PLANT ROOT SYSTEMS

In this Chapter the literature on the mean flow rate of nutrients into plant roots is reviewed and discussed. The factors intrinsic to plants that determine mean nutrient inflow are outlined and the potential usefulness of nutrient flow analysis is discussed.

12.1 A Review of Published Work

Table 12.1 summarises the mean uptake rates of N, P, K and Ca reported from a wide variety of experiments. The rates are given in terms of mean inflow and mean specific absorption rate (S.A.R.), which is defined as the uptake rate per gram of fresh root per second. Such uptake rates are of interest (1) for comparing a crops requirement for nutrients with the ability of a soil to supply nutrients (See Chapter 3.4.) and (2) as a comparative measure of the efficiency in nutrient absorption of a given quantity of roots on different crops or in different soil conditions (see Williams 1948).

The usefulness of inflow or specific absorption rate as a measure of nutrient flow really depends on the purpose of the investigation. Uptake per unit weight is clearly important to those interested in root efficiency and there is some evidence that in solution culture the uptake rate per unit of root weight has a more constant value than uptake per unit length (Russell and Sanderson,1967).(Clarkson and Sanderson,1970). This may also be true for mobile nutrients such as nitrate in soil, but for the immobile nutrients such as K and P, it is clear that diffusion to root surfaces is frequently the rate determining step in the overall flow. For plants in soil uptake rates in terms of inflow are essential to a proper understanding of the uptake process (Brewster and Tinker,1971).

Although there is an abundance of literature on the uptake of field crops through the season there is a dearth of information on root length in the field. No reports of simultaneous root growth and uptake analysis by field crops were found apart from Welbank's unpublished data. Hence, as indicated in the table, several

A Literature Survey of the Nutrient Inflow and Specific Uptake Rate of Roots

Table 12.1

Author	Species	Age at start of experiment Days after germination	Period over which uptake measured	Experimental Conditions †	Uptake Region	Root radius cm	Mean Inflows. Mols/cm/s x 10^{-13} and Mean Specific Absorption Rates Mols/g of root fresh wt/s x 10^{-10}				Notes
							N	P	K	Ca	
Bowen (1969)	Pinus radiata	21	20 mins	Growth cab./soln./ full nutrients	Apical 12 cm of primary root	0.045		0.7 0.11			Sterile conditions. Uptake greater by non-sterile roots. 5×10^{-6} M.P.
Bowen & Rovira (1966)	Wheat	4	15 mins	"	Apical 8 cm of primary root	0.02**		3 2.38			Sterile conditions 5×10^{-6} M.P.
Brewster (1971)	Leek	49	24 hours	"	0.4 cm sections in all root regions	0.03		0.26 0.09	16 5.5	9.6 3.4	10^{-5} M.P.; 4×10^{-4} M.K.; 15×10^{-3} M.Ca
Brouwer (1954)	Broad bean	42	8-24 hours	Growth cab./soln.	Apical 12 cm of secondary root	0.05	21 2.65	7 0.88			No nutrients before experiment. 10^{-3} M.NO_3; 3×10^{-3} M.P.
Grasmanis & Barley (1969)	Pea	8	30 mins	"	Apical 13.5 cm of primary root	0.03	5.5 2.0				Value is for NO_3; larger for NH_4. No N before experiment. 1.5×10^{-6} M.NO_3.
Gregory and Woodford (1939)	Broad bean	seedlings	23 hours	"	Apical 5 cm of primary root	0.15	390 5.5				Single preliminary experiment. No nutrients before experiment. 8×10^{-3} M.NO_3.
Russell & Sanderson (1967)	Barley	21	24 hours	Growth cab./soln./ full nutrients	3.5 mm of seminal root 1 cm from apex	0.02		0.15 0.12			3×10^{-6} M.P.
					lateral root	0.01		0.05 0.4			
					nodal root	0.03		0.15 0.05			
Asher & Ozanne (1967)	Vetch	10	31 days	Greenhouse/soln./ full nutrients	Whole root system	0.02*			3.1 2.5		Calculated from RGR, K percentage and root/shoot ratio. Various concs. tested. Values for vetch 2.5×10^{-5} M.K.; Capeweed 9.5×10^{-5} M.K.
	Capeweed	10	31 days	"	"				13 10		
Bange (1959)	Maize	20	1 hour	"	"	0.02*			13 10		Various concs. tested. Value is for 2×10^{-4} M.K.
Brewster (1971)	Leek	14	53 days	"	"	0.03	13 4.5	1.0 0.37	11 3.8	2.5 0.88	22×10^{-3} M.NO_3; 10^{-5} M.P.; 4×10^{-4} M.K.; 15×10^{-3} M.Ca.
Hackett (1969)	Barley	7	7 days	"	"	0.025	12 6.1	1.7 0.86	11 5.6		21×10^{-4} M.NO_3; 10^{-4} M.P.; 4×10^{-4} M.K.
			14 days	"	"	0.015		0.80 1.1	1.5 2.1		
Lastuvka & Minar (1970)	Pea	0	42 days	"	"	0.02*	8.7 6.9	0.93 0.74	4.3 3.4		Various concs. tested; the inflows did not vary with age Values for 3.3×10^{-4} M.NO_3; 8×10^{-5} M.P.; 3×10^{-4} M.K.
Asher and Loneragan (1967)	Mean of 8 pasture sp.	10	18 days	"	"	0.02*		1.4 1.1			Various concs. tested. Values for 5×10^{-6} M.P.

	11 grasses & cereals			"	"	0.013*				0.28 0.4	Various concn. tested. Values for 10^{-4} M.Ca.
Minar & Lastuvka	Maize	0	32 days	"	"	0.02*	31 25	4.2 3.5	11 9		3.3×10^{-3} M.N ; 0.8×10^{-3} M.P; 3×10^{-3} M.K.
Bagshaw, Vaidyanathan & Nye (1969)	Onion	7	10 days	Growth cab./soil discs	1 cm of primary root	0.03**			4-55 1-20		Inflows measured in 44 soils of different K status.
Drew & Nye (1969)	Perennial rye grass	7	4 days	"	"	0.02**			10 8		Wide range of values found for soil/sand systems with different fertilizer levels.
Drew, Vaidyanathan & Nye (1969)	Onion	7	10 days	"	"	0.03**			21 7.5		
Drew & Nye (1970)	Onion	7	10 days	"	"	0.028		1.0 0.4			Values are for Upper Greensand soil.
	Rye grass	7	5 days	"	"	0.015		1.6 2.2			A wider range of values found in a fertilised clay soil.
Brewster (1971)	Leek	30	42 days	Outside/pot soil/ fertilised	Whole root system	0.03	25 8.8	1 0.35	12 4.2	4.5 1.6	
Keay, Biddiscombe & Ozanne (1970)	Mean of 8 pastures	0	29 days	Greenhouse/pot soil/fertilised	"	0.02*		2.5 2			Assumed that roots are 6% dry matter.

Lewis & Quirk (1967)	Wheat	35	14 days	Growth cab./pot soil fertilised	"	0.02		0.14 0.11 0.30 0.24 0.65 0.51			Increasing P additions with max. growth at highest values.
Newman (1971)	Wheat	35	14 days	Greenhouse/pot soil/no fertiliser	"	0.015**	0.5 0.7	0.08 0.11			
Sanders & Tinker (1971)	Onion	0	31 days	Growth cab./pot soil/fertilised Mycorrhizal plants Non-mycorrhizal plants	" "	0.036 0.03		1·7 0·4 0·37 0·13			
Welbank (1962)	Impatiens parviflora	28	14 days	Outdoors/pot soil/fertilised	"	0.02*	11 8.5				Root assumed to be 6% dry matter.
Welbank (1970)	Wheat	28	28 days	Outdoors/field soil/fertilised	"	0.013	7 13.2	0.5 0.95	2 3.8		
		56	28 days			0.013	1 1.9	0.1 0.19	0.5 0.95		
Williams (1948)	Oats	9	10 days	Greenhouse/sand culture/full nutrients	"	0.015*	5 7	0.6 0.8			Results decreased greatly with time, max. values given here.

† Unless otherwise stated, plants were grown in the same conditions prior to the experiment.

(1) Some authors gave uptake rates per unit root length and we had to assume a root radius to calculate specific absorption rates. In other cases the reverse was true and a radius had to be assumed to calculate inflows. In all such conversions fresh roots were taken to have a density of 1 g/cc.

* Root fresh weight given - radius assumed
** Root length given - radius assumed

(2) In all cases the rates have been averaged over the period of time and length of root given in the table.

(3) Where rates have been measured in a range of solution concentrations, the uptake rates quoted are those for the minimum concentration that gave near maximum plant growth rates, unless it is stated otherwise in the table.

(4) For uptake periods of the order of days, where uptake rates were not given by the original authors they have been calculated by the formulae of Brewster and Tinker (1970) and Williams (1946).

of the values make assumptions about either nutrient content or root length.

The values in Table 12.1 come from a wide variety of experiments ranging from a few minutes uptake from solution to several weeks uptake by a field crop. It is interesting that the inflow of NO_3 into soil grown leek plants approaches values observed in short term experiments in solution using peas and broad beans. The nitrate inflows into the older cereal plants seem considerably lower, suggesting that leeks have a comparatively high mean inflow. The short term uptake rates of P into defined root regions are similar to the mean inflows in many longer term experiments, which suggests that most of the roots were active in phosphorus uptake in these longer term experiments. The similarity of nutrient inflows in many different experiments is interesting. It suggests that inflow or specific absorption rate of the roots of plants well supplied with nutrients and in a phase of rapid growth may be approximately constant. However, certain results in the table do illustrate that nutrient inflows can differ considerably and it is worth considering the factors we might expect to affect the mean inflow into roots.

12.2. Factors Affecting the Mean Nutrient Absorbing Power, α, of Root Systems

Plant factors that affect root nutrient uptake rate have been discussed by Williams (1948), Loneragan (1968) and Nye and Tinker (1969). The following equation, embodying some terms well known in plant growth analysis can be written.

$$12.1 \quad \bar{I} = \frac{dU}{dt} \Big/ L = \frac{W}{L} \cdot X \cdot \left[\frac{1}{W} \frac{dW}{dt} + \frac{1}{X} \cdot \frac{dX}{dt} \right] = 2\pi\bar{a}\bar{r}\,\overline{C_{LR}}$$

where, $\bar{I}$ = Mean inflow

U = Nutrient content of plant

W = Dry weight of plant

L = Root Length of plant

X = Proportion by weight of nutrient in the plant dry matter.

t = time

The general effects of age and of different environmental changes on the terms in equation 12.1 are already known. We now consider each term.

1. $\frac{W}{L}$. The reciprocal of the Specific Root Length. This is a major adaptive variable in plants. Work on Shoot-Root fresh weight ratios, which pro-

bably reflect W/L satisfactorily, indicates that W/L decreases in conditions of nutrient and water scarcity, tending to maintain overall plant uptake rates despite diminishing inflows. W/L also decreases in conditions of high light intensity, tending to counteract increases in inflow due to the high Relative Growth Rates that occur in such conditions (Brouwer,1962). Temperatures vary in their effect, and many plants have a maximum shoot root ratio around one temperature (usually in the range 20°-30°C) (Brouwer,1962, Nielson and Humphries,1968). A large root length to shoot ratio may explain the low mean inflows found by Newman (1970) (See Table 12.1) for wheat growing in an unfertilised sand-soil mixture. Brouwer (1962) states that the shoot-root fresh weight ratio tends to be constant in any particular set of conditions for a plant species in each phase of its growth. After an initial rise to the ratio from the seedling stage, the ratio remains constant unless conditions are changed. The switch from vegetative growth to flowering in annual plants is often accompanied by an increase in the shoot root ratio.

2.X. Nutrient concentration in plant dry matter. X is rather variable, partly because plants will absorb nutrients in excess of their requirements for maximum growth if the nutrients are freely available, (Asher and Loneragan,1967 a and b). X tends to be very high in seedlings and to diminish as plants age, hence $\frac{dX}{dt}$ is usually negative. Sharp decreases in X when annuals flower are well known and these correlate with the increase in shoot-root ratio mentioned above. In conditions of nutrient deficiency, where plant growth rate is slowed, the tissue concentration of the non deficient nutrients can increase as Hackett (1969) reported in barley plants.

3. Relative Growth Rate. Plant growth creates the ultimate sink for nutrients and its rate varies with species, with light intensity up to a maximum, with temperatures around an optimum which depends on species, and with nutrient supply at levels well above those at which deficiency symptoms are visible (Asher and Loneragan,1967a,Asher and Ozanne,1967, Loneragan and Snowball,1969a,Lastuvka and Minar,1970). Growth rates usually decrease with age in seeded crops and this is probably the reason for diminishing inflows into older plants,(see for example, the data of Biddiscombe, Keay and Ozanne,1969).

The way in which these different factors combine and result in an actual mean inflow or specific uptake rate differs with species and depends on its growth pattern, age and on the way in which the different components of equation 12.2 are affected by a particular environment. A few examples illustrate the point. Inflows into leek roots (see Table 4.5.) and the barley roots of Hackett (1969) diminished with time. In both cases R.G.R. and X decreased and overcompensated for an increase in W/L. In contrast, Lasturka and Minar (1970) found undiminished inflow rates into the roots of peas up to 7 weeks old and even a slight increase around podding time, since here a decrease in W/L overcompansated for decreases in R.G.R., and X did not change greatly. In another experiment, Hackett (1969) grew barley in solutions deficient in either K or P. The deficiencies slowed growth, including root growth, but the tissue concentration of whichever of K or P was non deficient was doubled in comparison with that of plants grown with no nutrient deficiency and the mean inflow of whichever of K or P was non deficient was increased by about 50% in comparison with that into normal plants.

12.3. The Efficiency of a Typical Root System

The quantity of carbohydrate expended in root growth and maintenance per mole of nutrient absorbed by the roots may be a useful criterion of root system efficiency. Such a concept could link studies of nutrient flow into roots with those of crop growth analysis. From Table 12.1 typical values of S.A.R. in Mols/g. root fresh weight/sec. x 10^{-10} appear to be about 10 for N, 1 for P, 5 for K and 1.5 for Ca. These values were derived from experiments in young plants with relative growth rates of about 0.15 g./g./day and about 6% dry matter in the fresh root tissue. (See Table 5.3.b. and Asher and Loneragan 1967 for example.).

In such a plant, we can make a rough estimate that there will be;

1) used in synthesising new root tissue,

5.8×10^{-10} Moles of carbohydrate/g.root fresh weight/sec.

2) used in root respiration,

6.8×10^{-10} Moles of carbohydrate/g.root fresh weight/sec.

3) hence, used in root growth and maintenance,

12.6×10^{-10} Moles of carbohydrate /g. root fresh weight/sec.

The values for root respiration are based on the data of Huck, Hageman and Hansen (1962), who found that whole maize plants in solution culture had a root respiration rate equivalent to about 55 μL.O_2 /Hr/g. fresh root. For the above mean S.A.R. values, the Moles of carbohydrate expended in root growth and maintenance per Mole of nutrient absorbed are 1.26 for N, 12.6 for P, 2.52 for K and 8.4 for Ca.

12.4. Agriculturally Significant points arising from present knowledge of Nutrient Flows to Roots.

Table 12.1 suggests that nutrient inflows into Leeks and Onions are maintained at a high level over a longer period than is true of cereals. This agrees with the fact that these two vegetables are known to require a very fertile soil for good growth. With regard to the inflows required by plants at different stages of growth, the data of Hackett(1969) on barley, suggests that the nutrient inflow into seedlings is particularly high. Although the specific root length is usually large in seedlings, nutrient concentrations and growth rates are also high. Thus the seedling stage may be a critical time for nutrient supply roots because high inflows are required. In addition the leaf area of seedlings is small relative to their size and in early spring, when most seedlings emerge under temperate region farming, the potential evapotranspiration is low, hence water inflows and the resultant mass flow contribution to nutrient supply will often be small at the seedling stage. These points may partly explain the need for fertile seedbeds and the susceptibility of seedlings to suppression by nutrient competion (Rhodes,1970).

Another critical period for nutrient supply to roots may occur at flowering time in some crops. The work with peas of Lasturka and Minar (1970) showed that nutrient uptake continued at an undiminished rate as flowers formed. Salter and Drew (1965) showed that root growth ceases at flowering time in peas and it is known that pea yield is very sensitive to the soil moisture level at flowering time (Salter and Goode,1967). It seems likely that the oneed for a moist soil may well be to facilitate nutrient mobility and to maintain the supply of nu-

trients as well as water to pea roots at flowering time.

12.5 Future Possibilities for Nutrient Flow Analysis

Nutrient flow analysis promises to be an increasingly useful experimental approach along the lines established here. Comparisons of nutrient flow to roots in different soils should be a useful test for our theories of nutrient flow to roots in soil. The correlation of such soil studies with an extended form of plant growth analysis, in which root lengths and weights are measured, should enable us to relate the efficiency of roots in supplying nutrients to shoots to the soil's ability to supply nutrients. If information on the diameter of roots, the length and number of root hairs, the root growth rate and the root distribution within the soil were recorded in nutrient flow experiments it may prove possible to explain differences in the responses of different species to a given level of soil fertility by differences in their root morphology. The results of such studies should enable us to understand better why we sometimes get a "growth response to nutrients."

A good example of how flow analysis can be used to investigate differences in nutrient supply under different soil conditions has recently been reported by Sanders and Tinker (1971). They showed that the inflow into mycorrhizal union roots growing in a P deficient soil was about four times greater than that into non mycorrhizal roots in the same soil. Further it was theoretically impossible for diffusion to the root surface alone to have maintained the inflow into the mycorrhizal roots.

The practical utility of a more detailed knowledge of the nutrient flows into different crops could be considerable. If the nutrient inflow required by different crops for maximum growth were known and also if any differences in the required inflow of crops at different stages in their growth were known, it should indicate how soil fertilify should be modified to best suit the growth of different crops. Such knowledge would be a useful addition to field trials for discovering more precise and efficient fertiliser practices. With a fuller knowledge of the different ways that plants adapt to differences in soil fertility the more exciting possibility arises of 'designing' and breeding plants and root systems to exploit different soils in the most productive fashion.

This is discussed further in Chapter 13.

Chapter Thirteen

CONCLUDING DISCUSSION

13.1 The Established Picture of Nutrient Movement Round Roots

It was concluded in Chapter 6 that equation 3.X provides a possible explanation for the uptake of an experimental crop. There is now considerable experimental evidence in support of the model of nutrient flow to roots described in Chapter 3. A similar mathematical approach has been applied to the inflow into single 1 cm. sections of root. Using onion seedlings, Drew, Nye and Vaidyanathan (1969) and ryegrass seedlings Drew and Nye (1969), were able to explain differences on observed K inflows in different soils in terms of differences in the potential supply by diffusion; Drew and Nye (1970) did the same for phosphate. Farr, Vaidyanathan and Nye (1968) described a method for directly measuring ion concentration gradients near roots which they illustrated with K and Ca depletions and H accumulations. Using the latter method, concentration gradients adjacent to roots of Cl and P, that are in reasonable agreement with the theory of mass flow and diffusion in soil (see Chapter 3) have been measured (Dunham, unpublished information). In situations where supply by mass flow greatly exceeded uptake, Wray (1970) measured the accumulation of sulphate ions round roots in soil and showed that they too were in accord with theoretical expectations.

An understanding of the theory of nutrient movement in soil gives us considerable insight into some of the processes of plant nutrition. As a basis for discussion, we can consider the supply of nutrients to a "typical" plant. From Table 12.1 it appears that mean inflows of 10^{-12}, 10^{-13} and 10^{-12} Mols/cm/sec of N, P and K respectively are typical of young, rapidly growing plants. Thus, if we take a 20 day old plant with 20 g. of root per 100 g. of total dry matter, 6% dry matter in the fresh root tissue, a root radius of 0.025 cm, and a transpiration ratio of 300 g. of water transpired per g. of dry matter produced, it follows that the plant will have a root length of 1680 cm/g. of dry matter and a

mean water inflow of 3.1×10^{-7} g/cm/sec. To supply the above mean inflows of N, P and K by mass flow alone would require soil solution concentrations of $3.2\ 10^{-3}$ M. for NO_3, 3.2×10^{-4} M. for P and 3.2×10^{-3} M. for K. Such a value is quite possible for N in agricultural soils, and mass flow will often be important, but such concentrations of P and K are well above those in a normal soil and we make little error if we assume that these elements are supplied by the diffusion process alone (See also Chapter 6.)

Water and nitrogen may not be absorbed by the same portion of the root system (Black,1968), in which case, nitrate also will be supplied primarily by diffusion (Barley,1970). If we take it that our "typical" plant has a relative growth rate of 0.15 g/g/day and a constant ratio of root length to plant weight, it follows that the mean root age is 4.5 days. If we take a root radius of 0.025 cm and a root hair length of 0.05 cm, and consider uptake from a soil with buffer powers of 50 and 10 for P and K respectively, we can calculate (using equation 3.X.) the average depletion at the root surface ($\overline{C_{LR}}$) needed to supply, by diffusion, mean inflows of 10^{-12}, 10^{-13} and 10^{-12} Moles/cm/sec of N, P and K respectively. Here we assume that root hairs cause the rapid and uniform depletion of the cylinder of soil around the root occupied by the hairs and that material arriving at the edge of this cylinder is transported rapidly into the plant (Nye,1966, Drew and Nye,1969). The average depletions in soil solution concentration $\overline{\Delta C_L}$ required in both a moist and a dry soil are tabulated in table 13.1 along with the "average" spread of the depletion zones and the percentage of the uptake coming from within the hair zone. The moist soil is taken as having a value of $V_L f_L$ of0.09 and the dry soil a $V_L f_L$ of 0.01.

(see Rowell, Martin and Nye (1967) and Porter, Kemper, Jackson and Stewart (1960)).

The results in Table 13.1 illustrate the importance of the different variables involved in equation 3.X. We now consider them separately.

C_{Li} Obviously C_{Li} the initial soil solution concentration, represents the upper limit of C_L, hence C_{Li} sets an upper limit to the possible mean inflow into a given root system. However, Table 13.1 shows that this maximum inflow depends on soil moisture content and on the effective radius of roots. The greater value of C_L necessary to supply a given inflow in a dry soil is one reason

Table 13.1

DEPLETIONS, DEPLETION ZONE SPREADS AND ILLUSTRATIONS

OF THE EFFECTS OF ROOT HAIRS FOR N, P AND K

		Moist Soil $v_L = 0.3, f_L = 0.3$		Dry Soil $v_L = 0.1, f_L = 0.1$	
		No Root Hairs	With Root Hairs	No Root Hairs	With Root Hairs
Values of C_L required to supply mean inflow Moles/L	N	0.4×10^{-3}	0.26×10^{-3}	3.3×10^{-3}	2.45×10^{-3}
	P	4.0×10^{-5}	1.07×10^{-5}	19.0×10^{-5}	2.63×10^{-5}
	K	2.6×10^{-4}	1.2×10^{-4}	16.4×10^{-4}	4.8×10^{-4}
% of nutrients coming from within root hair cylinder	N		0.2		1.3
	P		14.5		36.0
	K		3.0		013.0
$\sqrt{Dt}$ cm (an approximate measure of the spread of the depletion zone)	N		1.50		0.86
	P		0.08		0.026
	K		0.26		0.09

why nutrient uptake rates may decrease in dry soils.

$\bar{r}$. Root hairs can be thought of as increasing the "effective root radius" (Drew and Nye,1969). The values of ΔC_L in Table 13.1. clearly show the potential importance of effective root radius for immobile nutrients like P and K for which the soil has a high buffering capacity and its small importance for a mobile unbuffered nutrient like NO_3.

$D_L V_L f_L$ (or D') Values of C_L were greater, and values of $\sqrt{Dt}$ were smaller, in the dry soil where D' was diminished. Hence, given the same inflow in a moist and in a dry soil, inthe dry soil depletion will be greater at the root surface but narrower in its spread away from the root.

b. Although buffer capacity does not appear in equation 3.X. directly, its effect is felt through the value of $\bar{g}$ (see Chapter 3). A comparison of the calculations for the three different nutrients, show that an increase in b somewhat diminishes the ΔC_L required to supply a given inflow, but that it causes a proportionately greater reduction in $\sqrt{Dt}$. A nutrient with a high value of b, e,g, P, will have a narrow steep depletion profile around the root, whereas a nutrient with a low value of b, e.g. NO_3 will have shallow depletions that spread far from the root surface. Thus b as well as D' affects the shape of the depletion profile around roots.

t. The value of t, the time for which a root has been absorbing nutrients, does not appear directly in Equation 3.X. but again it determines the values of $\bar{g}$. In terms of Equation 3.X. t is a measure of the growth rate of a root system; the lower t the higher the root growth rate. Fig.4.2. shows that the rate of change of $\bar{g}$ decreases as $Dt/\bar{r}^2$ increases, hence the effect of t on the value of ΔC_L required to supply a certain mean inflow is most significant for those nutrients which have low values of D.e.g.P and will also be mere significant in a dry soil, where D is reduced than in a moist soil. It should be emphasized that the results of calculations like those in Table 13.1. and consequent conclusions about the effects of r, b, C_{Li} andD', depend on t, i.e. on the mean age of the roots that are being considered.

Clearly we can understand many effects on crop uptake of variations in soil and plant properties in terms of the theory discussed in Chapter 3. However,

the model of nutrient uptake discussed in Chapter 3 applies to uniform soil conditions. Soils in the field show heterogeneities in physical and chemical properties which are frequently accentuated by localised applications of fertiliser. The irregular nature of rainfall is yet another complexity. An understanding of the nu-trient uptake of a crop in such a situation requires a quantitative knowledge of 1) the movement of nutrients through soil, 2) the movement of water through soil, 3) the demand of roots for nutrients (i.e. $\overline{\alpha}\,\overline{r}$, see Chapter 3.4) and water, 4) the growth of roots including the distribution of root growth in relation to heterogeneities of nutrient concentration and water potential in the soil. There is extensive knowledge of (1) and (2) (See Slatyer 1967, Childs,1969). As regards (3), values for the mean nutrient demand $(\overline{\alpha r})$ of many species can be derived from the extensive literature on the relation between concentration in solution and uptake rate (Asher and Loneragan,1967, Longragan and Snowball 1969, Carroll and Loneragan,1969, see Table 12.1 for others). The discussion in Chapter 11.6 showed, however, that there is uncertainty about the local values of αr at different points on the root system. There is considerable knowledge of root growth and its adaptation to heterogeneities in nutrient concentration in the soil (e.g. Duncan and Ohlrogge 1958, Whittington,1968) but there does not yet seem to be a generally applicable quantitative model of root growth and growth pattern that could be combined with a knowledge of factors (1), (2) and (3) to provide a theory to account for nutrient uptake in field situations.

3.2 Inter Root Competition for Nutrients

One of the assumptions in applying equation 3.X to plant uptake was that of no inter-root competition for nutrients (see Chapter 3.5 and Chapter 6). It was concluded in Chapter 6 that this was an acceptable approximation in the pot experiment described in Chapter 4, but the exploitation of the soil is commonly more intense than was the case in the experiment, and root densities are frequently sufficient for the depletions of adjacent roots to overlap. In such conditions, values of $\overline{C_{LR}}$ will diminish more rapidly than would be the case if depletions did not overlap. If α remains constant, there will be a consequent reduction of mean inflow into the roots. With the help of an electrical analogue of the

root-soil system (Sanders, Tinker and Nye,1971), a mathematical analysis of nutrient diffusion to, and nutrient uptake by, competing roots has become possible (Baldwin, Tinker and Nye in press), The calculations tabulated in 13.1 illustrated the general nature of depletions of NO_3, K and P which form a useful spectrum of ions of contrasting mobility in soil.

For NO_3 it is generally true that,

b is small, α is low and depletion zones shallow and widely spread. For P, b is large, α is large and depletion zones are narrow and deep. For K, b is fairly large, α is also fairly large and depletion zones are deep but fairly wide.

(see Baldwin, Tinker and Nye in press, Barley 1970).

Given a fairly dense root system the wide and shallow depletions of NO_3 around adjacent roots will soon overlap and a general decrease in the NO_3 concentration in the soil solution will occur, the rate of which will depend on the root density (cm of root per cm^3 of soil). If α remains constant the mean inflow into the roots will diminish as C_L diminishes.

For K, depletion zones may overlap with the root densities typically found in soil (see Newman 1969). Furthermore the depletions of K are sufficiently local for the pattern of roots in relation to each other to be of some potential significance. Given the same average root density, $\overline{C_{LR}}$, and hence the mean inflow of K, will diminish less rapidly where roots are regularly spaced as opposed to where they are clumped.

For P, depletion zones are so localised that only at unusually high root densities could mean inflows be reduced by competition.

In general, the nutrient uptake rate of a root system depends on the values of α, $\bar{r}$, b, D^1, t (root age, a function of root growth rate) and root density. Reductions in C_{LR} due to root competition may lead to diminishing mean inflows. This will affect the different nutrients to different extents again depending on the values of α, r, b, D^1, t, root density and for K, the local distribution of roots. The situation can now be analysed with the aid of an electrical analogue (Baldwin, Tinker and Nye in press) and it should be possible

to find approximate "correction factors" which could be used to modify equations like 3.X to make allowance for the effects of root competition. Hence, the extension of nutrient flow analysis to situations of greater root density than those reported here is possible and such experiments are already in progress (Baldwin pers.comm.).

13.3. The Consequences of the Dynamic View of Plant Nutrition for Concepts of Nutrient Availability and Soil Fertility.

It will be clear from the above that measurements of the intensity or quantity of available nutrients in soil alone cannot predict the uptake of a crop. The dimensions, growth rate, nutrient demand, density and distribution of roots also affect the flow of nutrients from soil to plants. Nye (1963) stressed how difficult it was to extrapolate the results of field trials and correlated soil tests from one situation to another, and some of the reasons for this can now be understood.

A practicable approach to soil fertility would be to ask, "Can this soil supply the nutrient inflows required for the maximal growth of the crop we wish to grow?". Mean inflows into actively growing crops were listed in Table 12.1 and most were fairly similar. Much information exists about the root dimensions of different crops (Kutschera 1960, Weaver 1926, Weaver and Bruner,1927). Such data should enable crude estimates to be made of the value of $\overline{\Delta C_L}$ and hence of C_{Li} required to supply typical mean inflows to different species, assuming that they have a high α. For example the figures in Table 13.1 indicate that, in moist soil conditions, to supply a mean P inflow of 10^{-13} Moles/cm/sec into a leek or onion root system with its absence of root hairs would require an initial soil solution concentration of about 4×10^{-5} Moles/L P. By comparison a spring rape plant with its dense root hairs, might well be able to derive the same mean P inflow from a soil with concentration of only about 1×10^{-5} Moles/L.P in the soil solution.

13.4 The Breeding of Efficient Root Systems

An efficient crop is considered, for the purposes of this discussion, to be one which produces the maximum possible harvestable dry matter as shoot or stor-

age tissue. In this light, the energy devoted to root respiration, the growth of unharvestable feeding roots and the absorption of nutrients not required to maintain growth rates, is regarded as a loss and an efficient crop will keep it to a minimum. There is a certain mean tissue concentration of nutrients, X_{MIN}, which is sufficient just to maintain maximum relative growth rates in a given crop. If the tissue concentration falls below X_{MIN} then plant growth rate is diminished (see for example Asher and Loneragan 1967 a and b). An efficient root system can be regarded as one which maintains X_{MIN} in the plant tissues but which does not devote energy to the "luxury consumption" of nutrients.

The ability of a plant to maintain X_{MIN} depends on the nutrient uptake rate of its root system keeping pace with the plant growth rate. The maximum possible mean inflow of a nutrient into a root system, $\overline{I}_{MAX}$, occurs when the root surface acts as a zero sink for the nutrient. In such a situation nutrient uptake rate is totally determined by diffusion to the root surface. It was shown in Chapter 3.4. that the extent to which diffusion limits uptake depends on the value of $\overline{\alpha r}$. Amongst the macronutrients, the value of $\overline{\alpha r}$ is most frequently largest for P. Hence, provided micronutrients are not limiting, the minimum size of root system to maintain a given crop growing at its maximum rate may frequently be specified as the minimum root length needed to maintain X_{MIN} for P in the tissues when the root surface acts as a zero sink for P. In this sense, the ultimate limit to root efficiency may be said to be set by P, the most immobile major nutrient in soil. As a generalisation, we can say, that the limit to the efficiency of a given root system in a given soil is set by $\overline{I}_{MAX}$ for the nutrient with the largest value of $\overline{\alpha r}$.

Corresponding to $\overline{I}_{MAX}$ it follows from equation 12.I that there is a certain $\overline{SAR}_{MAX}$ for the root system. i.e.

$$\overline{SAR}_{MAX} = \frac{\overline{I}_{MAX}}{\pi \overline{r}^2} = \frac{2\alpha}{\overline{r}^2}$$

It was argued in 12.3 that the efficiency in nutrient uptake of a root system can be measured in terms of the quantity of carbohydrate devoted by the plant to

root growth and respiration per mole of nutrient absorbed. This is related to $\overline{SAR}$ and has a minimum value in a given soil determined by $\overline{SAR}_{MAX}$. Gardner (1965,Equation 54) presents an alternative equation to 3X for describing the diffusive flow to a young root that is a zero sink for nutrients, i.e. I_{MAX} for a young root. The equation reads,

$$I_{MAX} = 2\pi D' C_{Li} \left[1 \Big/ \sqrt{\frac{\pi D' t}{(b+1) r^2}} + \frac{1}{4} \right]$$

For a highly buffered nutrient like phosphate, $b + 1 \approx b$. Hence,

$$I_{MAX} = 2 D' C_{Li} \left[1 \Big/ \left(\frac{1}{r} \sqrt{\frac{\pi D' t}{b}} \right) + \frac{1}{4} \right]$$

$$I_{MAX} = 2\pi D' C_{Li} \left[r \Big/ \sqrt{\frac{\pi D' t}{b}} + \frac{1}{4} \right]$$

Therefore at a given root age, t,

$$I_{MAX} = p\, r + q \text{ where p and q are constants.}$$

As an approximation it follows that $\overline{I}_{MAX} = \overline{p}\,\overline{r} + \overline{q}$. From this it is clear that an increase in $\overline{r}$ leads to higher $\overline{I}_{MAX}$ for a young root system, The increase in $\overline{I}_{MAX}$ brought about by an increase in r is less marked for an older root system (see Gardner 1965 equation 55). Now as pointed above, $\overline{SAR}_{MAX} = \frac{\overline{I}_{MAX}}{2\overline{r}^2}$ hence it follows that $\overline{SAR}_{MAX} = \frac{\overline{p}\,\overline{r} + \overline{q}}{\overline{r}^2} = \frac{\overline{p}}{\overline{r}} + \frac{\overline{q}}{\overline{r}^2}$.

Thus $\overline{SAR}_{MAX}$ can increase more than inversely proportionally to $\overline{r}$ as $\overline{r}$ decreases. This has the interesting consequence that a certain rate of nutrient absorption can be sustained by a lesser weight of thin roots than thick roots when both are acting as zero sinks for nutrient diffusion. If we reach a stage where $\overline{SAR}_{MAX}$ is just sufficient to maintain X_{MIN} for a certain crop it may be possible to breed varieties of the crop with finer roots and thereby increase $\overline{SAR}_{MAX}$, producing a variety that can maintain X_{MIN} with less energy devoted to root growth and maintenance. The most efficient root form on the basis of this analysis would be a very thin root with a high value of α. The value of α may be related to root volume in which case it may not prove possible to breed very fine roots with values of α sufficiently high to cause the root to act as a zero sink;in other words,there is probably some physiological limit to the ab-

sorbing power of very fine roots. Within limits however, particularly with crops like the onion and leek which have rather fat roots, it may prove possible to breed improved plants by selecting for finer roots. Such varieties should be capable of maintaining inflows adequate for good growth on soils of lower nutrient concentration than the present varieties can.

In fact, the root densities of many crops in the field seem so large as to make it seem unlikely that their roots behave as zero sinks even for P (see Newman 1969). Also, roots proliferate in regions of high nitrate concentration in soil (Duncan and Ohlrogge 1958) which seems wasteful from the point of view of plant efficiency since the mobility of nitrate is such that a single root can withdraw the N from a large volume of soil, given time. Thus it would seem that plants frequently devote more energy to root growth and maintenance than is necessary to provide themselves with nutrients. However, Tinker (pers.comm.) and Newman (1970) have both speculated that, since many root systems have evolved in competitive situations, the important characteristic for species survival is not the root system efficiency as considered above but the ability of a root system to absorb nutrients, particularly nitrate, rapidly before competitors can remove it from the soil. Hence, there may have been evolutionary selection pressure in favour of dense root systems. If this is the case, it seems possible that more efficient crop varieties might be bred by recognising and reversing the selection for dense root systems, provided that competition from weeds is controlled.

Dense root systems may be competitively advantageous, but when it comes to cultivation in a controlled monoculture, they may well be inefficient. The situation is analogous to that of shoot competition for light. Here, it became clear that the selection for breeding of the strongest plants from a crop field selects the most competitive plants, which tend to be the tallest and the best competitors for light. As a result many crops are unnecessarily tall and their shoot form, far from being the most efficient for the interception of light includes much bulky and unneeded stem. The idea of designing crops from physiological and ecological principles and of synthesizing the design

from individuals with certain desirable attributes, not simply breeding from strong individuals in a competitive stand, is transforming plant breeding. It has already contributed greatly to crop productivity, notably the International Rice Research Institute tropical "wonder" rice varieties. It is reasonable to assume that a similar situation exists for root systems with selection favouring competitive rather than necessarily desirable root forms. Similar increases in crop efficiency may therefore be attainable by recognising and reversing this trend.

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Redacted article "Nutrient Cation Flows in Soil Around Plant Roots" can be found at

https://www.soils.org/publications/sssaj/abstracts/34/3/SS0340030421