THE GROWTH AND ACTIVITY OF WHEAT ROOT SYSTEMS

by

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ABBREVIATIONS

C = concentration of diffusible ions in the whole soil (moles / cm^3).

C_l = concentration of ions in the soil solution (moles / cm^3).

C_i = initial concentration in the soil.

C_r = concentration of ions at the root surface (moles / cm^3).

D = diffusion coefficient of ion in soil (cm^2 / sec).

D_l = diffusion coefficient of the ion in free liquid (cm^2 / sec).

D_w = water diffusivity.

F = flux of ions (uptake in moles /cm^2 of root surface / sec).

F_w = water flux.

I = inflow of ions (uptake in moles / cm of root length / sec).

I_w = inflow of water.

K_w = hydraulic conductivity.

L = root length (cm).

L_v = root length per unit volume of soil (cm / cm^3).

U = content of nutrient (µg or moles / plant).

f_l = geometric tortuosity of the liquid pathway.

r = root radius.

t = time.

v_l = fraction of the soil volume occupied by liquid.

x = distance.

α = root uptake coefficient (cm / sec).

αr = root demand coefficient (cm^2 / sec).

θ = volumetric water content of soil.

ψ = water potential.

ψ_r = water potential at the root surface.

ψ_s = water potential in bulk soil.

γ = complex functions of Dt / r^2.

ABSTRACT

A knowledge of root growth and the activity of separate members of the root system is necessary before a comprehensive understanding of plant water and nutrient uptake is possible.

The literature describing the developmental characteristics of wheat root systems is first reviewed. Methods of examining root systems in the field are compared, and studies of the contribution of seminal and nodal roots, and the effects of soil environment are discussed. Finally, nutrient and water uptake are considered mainly from the literature concerned with soil processes supplying nutrients to the root surface. The literature survey highlights the scarcity of field studies of water and nutrient uptake compared to laboratory studies and the poor understanding of the ways in which soil water status affects root growth and activity.

An experiment in which spring wheat was grown in soil columns in a controlled environment is reported. Water was withheld during growth and the consequences for root growth and nutrient and water uptake followed. Nodal root growth was also restricted but this treatment was largely inconclusive because of the limited time during which conditions comparable to those in the field could be maintained.

It was decided from these experiments to work with a field crop; a major study of the micro-climate and growth of winter wheat was in progress, so it was appropriate to examine in detail the growth and functioning of the crop's root system. A number of experiments were set up but this thesis mainly describes the root growth, and associated nutrient and water uptake of the normal field-grown crop. Measurements of root dry weight and length, plant nutrient content and water use are reported in early sections, with subsequent calculations of nutrient and water

inflow; the possible contribution of mass-flow to plant nutrient is considered.

A pattern of nutrient inflow not previously reported was found and possible explanations are discussed. The influence of soil properties, root distribution and atmospheric conditions on water inflow are also examined.

The work shows the importance of field studies in understanding root growth and activity, and puts forward a number of suggestions for future progress.

1. INTRODUCTION

"Resistance to nutrient transfer cannot be inferred from knowledge of soil properties alone; nor is it sufficient to know in addition how well the roots can absorb".

"The resistance offered by the soil to the transfer of nutrients to the roots depends upon the size and shape of the paths along which nutrients must travel".

Barley (1970).

Our knowledge of how roots develop and grow in soil has lagged behind our understanding of the interactions between the shoot and its environment. This has arisen largely because of the inaccessibility of roots and also because to study them in situ often leads to the destruction of the very environment that it is desired to measure. Recent advances in the methods available for studying root systems have allowed progress to be made in a relatively short time.

In comparison, theoretical knowledge of the soil processes involved in supplying the plants' requirement of water and nutrients is well advanced; the problem lies mainly in measuring those factors indicated as important in the theoretical analyses. Work in solution culture and with simple root systems growing in soil has increased the understanding of the absorption characteristics of roots and of the soil processes supplying nutrients to the roots. Despite all this, the relative importance of the various processes to field-grown crops throughout the growing season is not clear. Neither is it known to what extent yield differences on different soils, with similar climates and optimum fertiliser applications, arises from differences in root physiology or from differences in root morphology.

This thesis describes work undertaken in an attempt to measure the growth of the wheat root system under typical conditions and to determine how growth may be changed by soil conditions (particularly soil water status). In addition, uptake rates of water and nutrients were investigated and attempts made to distinguish the relative importance of the soil processes contributing to crop nutrition.

2. LITERATURE REVIEW

2.1. Production and growth of wheat roots

While many environmental factors may influence the size of a root system (Burström, 1963), it is possible to describe in general terms, the growth of the system. Monocotyledons differ from dicotyledons in that the primary root (and subsequent laterals) originating in the embryo does not constitute the entire root system.

When a wheat grain is planted, the root sheath (coleorhiza) breaks through the pericarp and shortly after the primary root appears through the end of the root sheath. A pair of roots above the primary root break through the root sheath followed shortly by a second pair above the first. This gives the commonly observed pattern of five seminal roots (Percival, 1921; Troughton, 1962; Peterson, 1965). After these five roots have attained a considerable length, a sixth root may appear, but this is not common. These roots are all attached below the insertion of the coleoptile and appear to be genetically determined.

In addition to these six seminal roots a pair of roots may develop immediately above the divergence of the coleoptile and coleorhiza. The production of these coleoptile (Percival, 1921), coleoptile-node (Troughton, 1962) roots is, in the opinion of Taylor and McCall (1936) related to food reserves in the grain.

Compared to the seminal root system, the development of nodal roots (adventitious roots) from the nodes is affected markedly by environmental conditions. Few observations have been made on the rate of differentiation of nodal roots or on the number produced

(Milthorpe and Moorby, 1974). However, it is generally thought that each node of the main shoot produces a pair of roots with higher nodes, slightly below or above ground level, producing four to six. In contrast, each tiller develops a single nodal root from its basal node but higher nodes may produce larger numbers of roots (Peterson, 1965).

The production of nodal roots has been shown by a number of workers (Simmonds and Sallans, 1933; Manner, 1957; Pinthus, 1969) to be related to the production of tillers. A difference of opinion seems to exist as to when the roots are produced; that is whether they precede (Manner, 1957) or succeed (Pinthus, 1969) the appearance of tillers. Since a tiller may well have been differentiated without necessarily being visible to the naked eye, the appearance of the root relative to the shoot is likely to be an environmental function.

As growth of the root axis proceeds, new primordia are differentiated in the pericycle and give rise to primary lateral roots. The location of these laterals is related to the vascular pattern of the parent root and this generally results in linear arrays of laterals along the length of the root (Mc Cully, 1975).

Root hairs arise from the elongation of epidermal cells toward the proximal end of the zone of elongation on each axis and lateral but these are frequently lost after a few weeks as the epidermis is sloughed off and the root suberises or ages.

Barley (1970) presents a summary of the most pertinent geometrical data for cereal roots growing in topsoil and this is reproduced in table 2.1.

The drawings of Francis Bauer reproduced in an article by Carruthers (1892) outlining the life of the wheat plant from seed to seed provide an excellent pictorial record of the production of wheat roots.

Table 2.1 Geometrical data for cereal roots growing in topsoil

	Order of Root				
	Main	Primary lateral	Secondary lateral	Tertiary lateral	Root hair
Diameter (cm)	5×10^{-2}	2×10^{-2}	1×10^{-2}	5×10^{-3}	1×10^{-3}
Number of roots per cm of root of next higher order	-	2	1	5×10^{-1}	1×10^{3}
Length (cm) per cm^3 of soil	1	5	2	5×10^{-1}	1×10^{3}

From Barley (1970)

To avoid confusion in the text that follows, the terminology used at the A.R.C. Letcombe Laboratory has been adopted unless otherwise stated. This was defined by Hackett (1968) and is summarised below:

Axis - each cylinder of root tissue developed from the seed or stem.

Primary laterals - branches borne on the axis.

Secondary laterals - branches borne on the primary laterals.

Tertiary laterals - branches borne on the secondary laterals. Each axis plus laterals is a root and each root a member of the root system.

Seminal axes - derived from initials present in the embryo.

Nodal axes - developed from the growing shoot.

2.2. Depth of rooting

The depth of rooting is of great agricultural importance especially if water or nutrients may be in short supply (Pearson,1974). It has long been realised that the wheat root system is not restricted to the plough layer. In one of the earliest studies, Weaver (1926) found that the roots of winter wheat had grown to a depth of 2 metres and many laterals were present down to 1.4 metres. He pointed out, however, that depth of rooting will be affected markedly by soil type and the presence of compact layers. Despite the early realisation of these modifying agents on root growth, Pearson (1974) is still able to state that we are unable to define the optimum root system for a given crop, soil and climatic condition.

In addition to studying the total depth which a root system may attain, it is also important to know the rate at which it becomes established and thereby secures an uninterrupted supply of water and

nutrients. For example, if the topsoil is prone to rapid drying, a variety may be at an advantage if it quickly establishes a deep root system. Russell (1971) discusses these "critical periods" of root growth but, at present, there are few quantitative results available for assessing their occurrence. In general, the main axes of wheat elongate at rates from 0.5 to 3 cm per day (Barley 1970) and an average value of approximately 1 cm per day is typical in field experiments (Weaver, 1926; Welbank, Gibb, Taylor and Williams, 1974).

2.3. The relative importance of seminal and nodal roots

Nodal roots differ from seminal roots not only in the site of production but also morphologically and anatomically. Nodal axes are thicker than seminal axes and possess a larger number of xylem vessels (12-16) compared with the 6-8 vessels of the seminal axis (Jackson, 1922).

A difference of opinion exists about the relative importance of the two root systems. Nelson (1946) states that the functioning of the seminal root system is temporary and supplies only the seedling stage of the plant; the permanent root system arises adventitiously and during the changeover period from seminal to nodal root system there may be a period of weakness in the plant. An earlier writer (Hector 1936) reports, however, that . . experiments lead to the conclusion that the seminal roots of wheat are functional throughout the life of the plant.

There has also been some disagreement whether or not the two root systems have distinct and specific functions (Williams, 1962). The reasons for this apparent controversy probably lie in the limited techniques available to the experimenter prior to the introduction of

radioisotopes in addition to some poor experimentation.

One of the better, earlier experiments was conducted by Krassovsky (1926) using a split root technique. The major conclusions he reached are as follows:

a) The seminal roots were active in supplying water and nutrients to the plant until harvest.

b) The seminal roots appear to supply principally the main stem; the nodal roots, the tillers.

c) The removal of the nodal roots stimulates the growth and activity of the seminal roots.

d) The seminal roots absorb almost double the amount of water per unit of dry weight in comparison to the nodal roots.

Other observations tending to confirm the first conclusion are the reports by Locke and Allen (1924) of the possibility of field grown wheat plants reaching maturity supported only by the seminal roots when soil physical conditions (drying and crusting of the soil caused by a combination of weather conditions) did not allow the development of the nodal root system.

Further evidence is supplied by the experiments of Sallans (1942) who concluded that the contribution of nodal roots to total plant growth was about 60% of total yield. Taken individually, however, the nodal roots contributed less than the individual seminal roots.

Despite these experiments, the question of relative physiological activity of both systems is still open to debate. Williams (1962) working with perennial ryegrass was unable to ascertain whether the seminal roots are inherently capable of absorbing much greater amounts of nutrients in relation to their size than nodal

roots, but on the evidence available the possibility could not be ruled out. In contrast Boatwright and Ferguson (1967) conclude that the nodal roots of wheat are physiologically more active than the seminal roots although no root length or weight data are presented to support such a statement.

2.4. Methods available for studying root systems

Until recently methods available for studying root systems were very limited in number and this in turn has meant that our knowledge of the size and shape of the underground part of the plant has not progressed as far as our understanding of the above ground part of the plant.

Much of the early work was of a descriptive nature (Weaver, 1926) involving careful excavation of the soil around the roots and subsequent drawing. A certain degree of artistic licence is probably essential in this type of approach but the technique did allow the assessment of spatial relationships and the contribution of each root member to the whole system. This approach is the basis for the "pin-board" technique of Schuurman and Goedewaagen (1965) and the modification using a wire cage and nylon thread (Gooderham, 1969; Bloomberg,1974). While these techniques allow the three - dimensional distribution of roots to be ascertained, they are very time consuming, and in the majority of studies, there is little need for this type of information. Most recent methods have, therefore, concentrated on either the extraction of roots or *in situ* measurements aimed at quantifying particular characteristics such as depth of rooting, quantity of roots in a given horizon or the relative distribution of roots within the profile.

a) Depth of rooting

Extraction of a soil core using an auger and subsequent washing out of the roots using fine jets of water is the method commonly applied in studies of this type. The problems inherent in this approach are discussed by Welbank et al (1974) but the roots separated may also be kept for dry weight or length measurements.

An alternative approach requires the use of a radioisotope. The method involves labelling a volume of soil at a particular depth with an active isotope (Hall et al, 1953: Bassett, Stockton and Dickins, 1970) and after a suitable period of time the plant tops are monitored for activity. The presence of radioisotope in the tops implies the presence of roots at that depth whereas the absence of isotope does not necessarily mean there were no roots at that depth, but that no roots were present in the small volume of soil labelled.

A simpler technique is described by McGowan (1973) and utilises the drying profiles under crops as measured by neutron probe and tensiometer studies. A good relationship is observed between the measured rooting depth by excavation and the estimated rooting depth from neutron probe data. The method will obviously not work if no appreciable drying occurs.

b) Length or dry weight of roots

Excavation of the roots using an auger (Welbank et al, 1974) or a pin-board (Schuurman and Goedewaagen, 1965) and subsequent washing with water leaves the roots and organic matter accessible. The problem then arises of separating the live roots from dead roots and other organic matter. No easy way of doing this exists for routine determinations and picking out impurities with forceps is the method most frequently employed. Dry weight

is determined by drying the roots in an oven at 75°C for 24-48 hours.

The measurement of root length was until recently a very difficult operation involving the separation of the individual roots and then measurement with either a ruler or map measuring wheel (opsiometer). Neither of these techniques is particularly accurate since the separation of very fine, short roots is extremely tedious and almost impossible to achieve. Newman (1966) devised a technique based on the chance of a randomly orientated root spread over a given area intersecting a series of straight lines. The equation giving the length of root (L) is

$$L = \frac{\pi N A}{2H}$$

where A = area over which roots are spread (cm^2).

H = total length of straight lines (cm).

N = number of root intersections with the straight lines.

In an article comparing the methods available for measuring root length, Reicosky, Millington and Peters (1970) conclude that while no significant improvement in precision was obtained using Newman's method over the ruler or opsiometer, the time involved in making a measurement was considerably reduced. The time element was the incentive to Rouse and Phillips (1974) to develop a machine for measuring root length. Using a photo-electric cell, the instrument counts intersections of roots with a series of parallel straight lines. The principle is identical to Newman's method but by making the straight lines parallel and the distance between them $2/\pi$

L is equal to N independent of A.

Melhuish and Lang (1968) propose a method for determining length based on counting the number of roots observed at a given plane in a resin-impregnated block. The method is very time consuming and depends upon a random distribution of roots within the soil. Using a similar approach, Baldwin, Tinker and Marriott (1971) injected plants with radioactive phosphorus and drove a photographic plate supported by a metal frame into the soil. A spot was produced on the film where live roots had been cut, and from the number of spots it was possible to calculate the root density. This method is restricted in practice to shallow rooted crops and sandy soils. A further development by Baldwin and Tinker (1972) allows the estimation of lengths of two interpenetrating root systems using radioistopes of different energies.

All of these techniques involve destructive sampling but the use of a rhizotron (Taylor, Huck, Klepper and Lund, 1970) has the advantage that continuous observations can be made on the same root system. Against this, however, are the possible problems raised by introducing a planar glass surface into the soil, which may cause root accumulation at the glass / soil interface.

c) Distribution of roots within a soil profile

Length and dry weight data if collected in discrete layers down the profile, may obviously be used to describe the distribution of roots within the profile.

Because of the limitations involved in separating roots from soil, a number of indirect methods have been evolved to overcome this problem. Rubidium-86 has been shown to distribute itself almost uniformly throughout the root system of the plant (Russell and Ellis, 1908) and by injecting the isotope into plants Ellis and Barnes (1973)

have been able to estimate the relative distribution of living roots under field conditions. The isotope emits energetic gamma radiation and samples of root within the soil can be counted accurately.

The methods all involve destructive sampling but a development using Potassium-42 and a counter mounted beneath the soil in an aluminium access tube may overcome this problem. (Mercer, Lay, Harris and Belford, 1975).

2.5. Root and shoot growth

It is a truism that the root and shoot are dependent one upon the other and neither is fully functional for long if the other is removed. The root receives carbohydrates and other substances from the shoot but in return provides essential nutrients, water and hormones. Underground and aerial parts of the plant should not, therefore, be studied in isolation because factors influencing one part of the system will directly or indirectly affect the other.

Precise relationships between root and shoot are extremely difficult to define but it is generally assumed that within limits a balance must exist between the activities of the two systems. Changes in plant growth resulting from changes in the environment have caused a number of workers to postulate the existence of an equilibrium under all conditions.

In an attempt to describe quantitatively the relationship between the size and activity of root and shoot systems, a model has been constructed (Thornley, 1972) based upon the semi-empirical relationsnip deduced by Davidson (1969):

Root mass x specific absorption rate $\propto$ shoot mass x specific photosynthetic rate.

The model is based on vegetative growth of a two component system (root and shoot), one supplying nitrogen, the other carbon. The conclusion reached is that plants possessing a number of chemical activities, each essential for growth, will, when undergoing steady state growth in a constant environment, adjust their growth so that the total activities bear a constant ratio to each other independent of environment. This "precise balance" or "functional equilibrium" hypothesis (Brouwer, 1963b) has recently come under attack as being inadequate to describe the observed responses (Troughton, 1974). For example, changes in the growth of the root relative to the shoot do not necessarily reflect changes in the rates of activities of the two systems, and sink size and demand have effects on the rates of water and nutrient absorption.

The non-steady state is, perhaps, the main feature of growing plants and when all the factors influencing root and shoot growth are taken into account, the complexity of interactions seems unlikely to produce an equilibrium. An approach based on kinetics might lead to greater understanding.

Burström's statement (1963) that the partnership between root and shoot is not voluntary "but a case of hard competition for the necessary compounds" is perhaps a better hypothesis from which to start than an idea of an ill-defined equilibrium.

2.6. Influence of the soil environment on root growth

As has been shown, any adverse effect of the environment on the root will also affect shoot growth. Leaving aside consideration of the balance of these effects, a number of soil conditions are known

to affect root growth. A precise evaluation of the importance of every factor is impossible because each interacts with the other.

a) Soil mechanical properties.

The pressures required to reduce root elongation have been studied for many years; work of Pffefer summarised by Gill and Bolt (1955) showed that the maximum longitudinal pressure exerted by a root is approximately 10 bar and the maximum radial pressure, 5 bar. Soil strengths of this order have been reported as reducing the elongation rate of pea and cotton roots (Gerard, Mehta and Hinojosa, 1972). Experiments at the Letcombe Laboratory (Goss and Ward,1975) have shown however, that very small external pressures, as low as 0.2 bar will halve the elongation rate of barley seminal axes, but within 30 minutes of removal the rate is as rapid as its pre-contact level. This transient effect has been shown over a wide range of pore diameters provided they are smaller than the root and suggest that the pressures reducing root extension are only a small fraction of those which living roots have been found to exert when rigidly confined. This difference in values may arise because pressure applied to a soil body does not represent the pressure immediately surrounding an expanding root.

Difference of opinion exists as to whether mechanical impedance influences the developmental pattern of the root system. Schuurman (1971) growing oats found that in general variation of soil density did not materially change the fundamental development but did alter the rate and hence quantity of roots produced. Goss (1974) has found that mechanical impedance causes more laterals to be formed per unit length of root and they arise only on the side of the root where the force has been applied. The larger number of laterals under impeded conditions might, in part, be due to incomplete expansion of cells;

lateral number per cell remaining constant.

In addition to bulk density, the number of pores larger than the roots is important since roots will tend to follow the line of least resistance. This is in contrast to the rigid probe of a penetrometer and it is not surprising that penetrometer techniques have not proved widely applicable for assessing resistance to root penetration except under extreme conditions.

b) Soil water.

Soil water matric potential interacts with soil bulk density and for any level of mechanical resistance, elongation of roots is restricted as potential decreases. Matric potential will affect plant turgor which in turn affects the ability of a root to overcome resistance (Mirreh and Ketcheson, 1973).

The literature on soil water / root relationships is very difficult to interpret and apparent water affects may depend more upon oxygen, mineral - nutrient supply or soil strength. Interpretation is further complicated because water is rarely uniformly distributed throughout the soil.

An early experiment (Hendrickson and Veihmeyer, 1931) showed that roots will not grow into soil containing less water than the permanent wilting percentage. More recently, experiments (Portas and Taylor, 1976) with corn and tomato roots showed that soil water potentials below -50 to -100 bars were required before root growth into those "dry" areas ceased and if the soil was wetted rapid elongation ensued. However, if the soil dries around a root, root elongation is favoured but branching reduced so that the root rapidly extends over a large distance (Stålfelt, 1960 as quoted by Burström, 1963).

c) Aeration.

Because of the inter-relationship between aeration, water supply and structure, the results of physiological investigations into the subject are frequently contradictory (Brouwer, 1963a). Plant roots require oxygen for aerobic respiration but the percentage of oxygen required to maintain full growth varies between species (Stolzy, 1974); 5% seems an average value. Most crop plants prefer well-aerated soils but many are able to grow in oxygen-deficient soils because of modifications to the root cortex enabling diffusion of air within large air cavities. Root growth is normally depressed more than shoot growth and growth reduction in non-aerated plants is commonly accompanied by water stress.

The effects of lack of oxygen under anaerobic or partially anaerobic conditions are also confounded by the possible presence of ethylene. Root and shoot weights are reduced under these circumstances, root extension is inhibited while lateral root growth in barley is stimulated (Crossett and Campbell, 1975).

d) Temperature.

Temperature will affect all processes occurring within the plant and for this reason much attention has been paid to the subject. A common criticism of the experiments performed is that root and shoot temperatures are rarely varied independently, For this reason, it is often difficult to reach definite conclusions about the optimum temperatures for a particular species.

Brouwer (1962) working with a wide range of crop plants showed that a broad optimum temperature range of about 10°C exists and the main difference between crops appear in the region of transition to the minima and maxima. A root temperature of 25°C gave optimal growth for all crops under consideration and temperatures

of 5°C and 40°C greatly inhibited growth. When root temperature is reduced, leaf growth reacts rapidly and at 5°C growth terminates completely after two days (Brouwer 1963a). This immediate reaction is brought about by changes in the water balance of the plant, the low root temperature causing a reduction in water conductivity in the root thereby inhibiting water uptake.

Reviews by Nielsen and Humphries (1966) and Nielsen (1974) show that literature expounding the effect of root temperature on morphological development is sparse in comparison with that dealing with dry-matter changes. Low temperatures generally cause roots to become thicker and less branched and elongation of the individual cells is also reduced. Initiation of nodal roots by corn is affected by temperature (Allmaras and Nelson, 1973) and as Lal (1974) has shown, modification of soil temperature by mulching may have important consequences for yield.

The interaction of temperature with other environmental conditions especially water supply and available nutrients means, however, that while root temperature effects are being observed other soil conditions must be well defined (Nielsen, 1974).

e) Nutrients.

Increasing the quantity of available nutrients in the soil will result in increased root and shoot growth until an unfavourable osmotic potential is reached.

The light and nitrogen supply of the plant are generally recognised as the factors regulating the balance between carbohydrate and protein production in the plant (Burström, 1963). A higher concentration of nitrogen in the rooting zone results in larger plants but the root:shoot ratio decreases (Welbank et al, 1974). The reasons for this relative decline in the size of the root system

are not clear but it may arise because of the comparatively smaller amounts of carbohydrate available in the roots or an improved transport of mineral nutrients from the root to the shoot, or, more likely, a combination of both. Combined with the relatively reduced root system is a higher transpirational area and this may lead to problems of obtaining adequate water supplies to maintain the greater growth of the shoot.

Under most conditions, however, nutrients are not supplied uniformly to the soil and it has been observed that roots proliferate preferentially in those regions where high concentrations abound (Miller, 1938; Weaver and Clements, 1938; Passioura and Wetselaar, 1972). The work of Passioura and Wetselaar (1972) describing the growth of wheat roots with banded ammonium sulphate and urea shows both toxicity and stimulation effects depending upon the time of observation after the initial application.

These varied responses have been the subject of a number of laboratory experiments to determine the morphological response to millimolar concentrations of nitrate supplied to localised regions of the root axis (Hackett, 1972; Drew, Saker and Ashley, 1973; Drew and Saker, 1975). Lateral root initiation and extension is locally stimulated but extension of the axes is little affected. This result was also produced by ammonium and phosphate application (Drew,1975) but potassium promoted lateral growth throughout the entire root system. The reasons for this apparent contrast remain unexplained but the possibility of a threshold concentration above which initiation of laterals is not limited might explain the result.

Since these latter experiments have been performed in conditions where water is readily available, the extrapolation of the results to the field must be treated with caution.

2.7. Nutrient uptake by plant roots

a) Soil and plant processes.

The processes involved in moving a nutrient from a point in the soil into the plant shoot can be divided into three stages (Barber, 1962) -

a) movement of the nutrient from the soil to the root surface.

b) movement of the nutrient from the root surface into the interior.

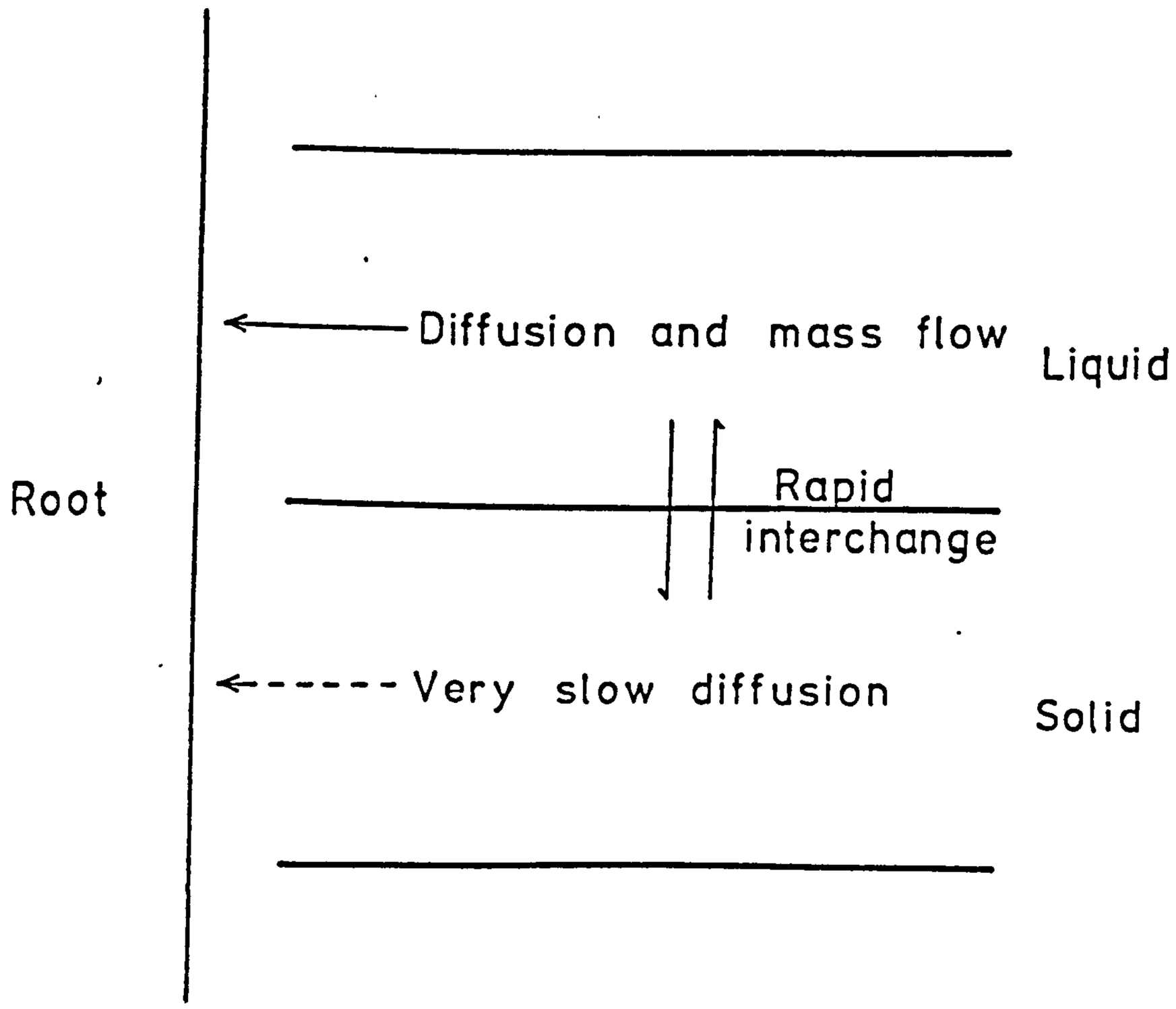
c) translocation of the nutrient from the root to the shoct.

Until comparatively recently, process a) had received far less attention than the other two processes largely because the nutrition of plants was considered to be characterised by the total quantity of available nutrient in the soil. Schofield (1955) stressed that "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 pool"; he thereby introduced the concept of intensity of supply. Under most circumstances, however, it is not the thermodynamics of equilibrium which control nutrient supply to the roots but the kinetics of movement.

The present approach to plant nutrition is to consider nutrient availability, over short time periods at least, in relation to mobility and proximity to absorbing surfaces (Bray, 1954; Barber, 1962). Movement to the root surface is illustrated by Nye (1968a) and occurs either by convection (mass-flow) or diffusion within the soil solution or by very slow diffusion from the soil solids (fig 2.1.)

The contribution of mass flow to the uptake of nutrients has been assessed by Barber, Walker and Vasey (1963) for a corn plant. Using an estimated value for the quantity of water transpired in the accumulation of one gram dry weight and knowing the concentration

Fig.2.1. Movement of nutrients to the root surface (after Nye,1968a)



of ions in the soil solution, they showed that the whole of the plants Ca and Mg, but only part of its K and P, could be swept in by the transpiration stream. As Nye(1968a) points out, these conclusions are based on averages over the whole season and the initial early growth often occurs when temperatures and transpiration are low. There are also problems in defining the concentration of ions in the soil solution; most workers base their calculations on the initial concentration rather than the concentration at the root surface.

Calcium and magnesium concentrations within the plant are frequently lower than those which might be provided by a simple mass-flow mechanism indicating some form of selection at the root surface. Increased concentration of some ions at the surface with high transpirational rates has been shown using autoradiography by Barber (1962) and Wray and Tinker (1969) for strontium and sulphate ions respectively.

Evidence that diffusion may play a critical role in the supply of nutrients to plants, particularly potassium and phosphorus, is provided not only by the figures of Barber et al (1963) but also by autoradiography showing depletion of these ions around roots (Walker and Barber, 1961; Lewis and Quirk, 1967). The application of diffusion theory to plant nutrient supply is now well established and has been reviewed by Nye(1968b) and Olsen and Kemper (1968). The amount diffusing across a unit area in unit time under a concentration gradient dc/dx is given by Fick's 1st Law of Diffusion;

$$F = -D \frac{dc}{dx} \qquad (1)$$

where F = ionic flux along the X axis.

D = diffusion coefficient.

The diffusion coefficient (D) in soil will be less than the diffusion

coefficient of the ion in free solution and can be obtained from the approximate expression (Nye, 1966a).

$$D \simeq D_l \, v_l \, f_l \, \frac{dC_l}{dC} \qquad (2)$$

These equations show that the quantity of ions supplied by diffusion depends upon the concentration of ions in the soil and their intensity. and that diffusion will be lowered as the soil dries out through the effects of volumetric water content on the diffusion coefficient.

Diffusion to the root will occur when the concentration at the root surface is lowered relative to the ambient solution and a concentration gradient is set up. The concentration at the root surface will be determined by the balance between the plant demand (root absorbing power) and the soil's ability to supply. Boundary conditions at the root surface must be stated and the most commonly applied expression to describe the uptake of ions (Passioura, 1963; Nye, 1966b) is of the form :

$$F = \alpha C_{lr} \qquad (3)$$

$$\text{or} \quad I = 2\pi\alpha r C_{lr} \qquad (4)$$

The latter expression is used most because root length is easier to measure than root surface area but both show the importance of α

(root absorbing power) or αr (root demand coefficient) (Nye and Tinker, 1969). Values of αr are still largely unknown for a number of plants and knowledge of its variation with size of root, age of root or demand of the plant shoot is scanty although theoretical models exist (Nye, 1973).

Where mass flow and diffusion occur simultaneously the situation is more complex and the precise equation is stated by Nye and Spiers (1964). For practical purposes, however, this equation differs little from the much simpler Passioura (1963) equation except where large accumulations of salts occur around the roots (Marriott and Nye, 1968).

$$I = 2\pi(C_i - C_r) D\gamma + I_w C_{li} \qquad (5)$$

or by combining with equation 2

$$I = 2\pi D_l v_l f_l (\Delta C_l / \Delta C)(C_i - C_r) D\gamma + I_w C_{li}$$

$$\therefore \quad I = 2\pi D_l v_l f_l (C_{li} - C_{lr}) D\gamma + I_w C_{li} \qquad (6)$$

These equations regard diffusion and mass flow as separate and additive whereas they interact and for this reason $I_w C_{li}$ is referred to as the "apparent mass flow" (Brewster and Tinker, 1970). Equation 6 differs from 3 because it uses different boundary conditions (fixed concentration; variable concentration respectively) but a fixed concentration is reasonably correct.

Inflow (I) can be readily calculated to give a mean value between harvests using growth analysis formulae (Williams, 1948).

$$I = \frac{U_2 - U_1}{t_2 - t_1} \times \frac{\ln(L_2 / L_1)}{L_2 - L_1} \qquad (7)$$

This approach makes two assumptions which may be invalid. Firstly it assumes that root growth proceeds according to an exponential growth curve and secondly that the rate of uptake per unit length is constant. Khasawmeh (1975) has developed equations for mean uptake rates allowing for either linear or exponential growth curves, while the use of "dynamic" methods of growth analysis (Hunt, 1973) allows calculation of instantaneous inflow values.

It is also important to remember that not all parts of the root system may be absorbing equally. This is the reason for the factor γ in equation 6 which attempts to make allowances for the time for which the sink has been operating (Passioura, 1963). Clarkson and Sanderson (1971) have shown, however, that this factor may not be as important as previously thought for some ions.

At present, measurements of mean inflow seem to offer the best possibility for dealing with complete plants. Average inflow values for the major nutrients are given in a comprehensive review by Brewster and Tinker (1972);

N	10×10^{-13}
P	1×10^{-13} g atoms / cm root / sec
K	10×10^{-13}

Inflow values for field grown crops are sparse and changes throughout the growing season have rarely been studied. Brewster and Tinker (1970) working with young leek plants found inflows to decrease throughout the growing period for sodium, potassium and magnesium, while those for calcium remained constant. Field grown corn plants (Mengel and Barber 1974a and b) had similar mean inflows for two consecutive years despite large grain yield differences and inflows for all ions studied generally decreased throughout the growing season.

b) Influence of root hairs on nutrient uptake.

Because root hairs may substantially increase the surface area of the root system (Dittmer, 1937) it has been assumed that they are important in the uptake of nutrients from soil; the greater surface area should mean that uptake of those nutrients supplied predominantly by diffusion should be enhanced. In cereals in particular, the root hairs persist for many weeks and thin-walled hairs are found on nearly all parts of the root system (Barley, 1970). The evidence that they increase nutrient uptake is, however, inconclusive largely because of the difficulties in obtaining a suitable control.

The theoretical advantage of roots possessing root hairs has been assessed using diffusion equations (Lewis and Quirk, 1967b; Drew and Nye, 1970) but these suffer from uncertain boundary conditions. Autoradiographs have shown intense depletion of phosphorus in the zone of root hair proliferation using rape (Bhat and Nye, 1974a) and wheat (Lewis and Quirk, 1967a). Changes in sorption characteristics could account for depletions, however, through changes in root exudates or rhizosphere micro-organisms.

Barley and Rovira (1970) showed that uptake of phosphate by wheat and barley from stirred solutions was not affected by root hairs but uptake was appreciably increased by root hairs on pea roots in a clay soil. To prevent root hair development they compacted the clay and compared this with phosphate uptake in less dense material where root hairs had developed normally. Other effects of the compaction treatment (on the impedance to diffusion, for example) were ignored. In contrast, Bole (1973) concluded that root hair development of wheat did not regulate the phosphorus uptake.

Comparison of the depletion zones around onion roots (without root hairs) and rape roots (with root hairs) showed narrower depletion

zones around onion roots (Bhat and Nye 1974b). Coupled with this, a lower uptake rate and a closer relationship between observed and predicted uptake for onions suggested the importance of root hairs in increasing phosphorus supply. The effect of root hairs is not simply to increase surface area but root induced changes in buffer power and phosphorus concentration in solution in the rhizosphere, through changes in rhizosphere pH, may make a quantitative analysis of their affect on diffusion very difficult (Bhat and Nye, 1973).

In addition to these uncertainties, the major importance of root hairs may be in their maintainance of liquid continuity between cell and soil water in unsaturated soils (Barley, 1970). Their role in these circumstances still needs investigation.

c) Influence of mycorrhizal associations on nutrient uptake.

Recent work (Sanders and Tinker, 1971; Ross and Gilliam,1973; Khan, 1975) has shown the beneficial effects of endotrophic mycorrhizal associations on plant uptake of phosphate in moderately phosphorus deficient soils. A review by Sanders and Tinker (1973) concludes that this increased inflow is probably due to the formation of a more dispersed root system by the external fungal mycelium. Additions of phosphate fertiliser to the soil decreases the extent of mycorrhizal infection (Sanders and Tinker, 1973; Khan 1975) and on typical agricultural soils in this country their contribution is unknown.

2.8. Water uptake by plant roots

The problems concerning the quantitative description of water uptake by plants are similar to those of nutrient uptake and an understanding of plant water uptake is required for the mass-flow component of nutrient uptake from the soil. Theoretical developments

have followed the same course with initial concern for quantities of water, then availability of water and more recently with the rate at which water is supplied to the root surface.

Water movement in soils is based on two equations which for movement in one direction may be written ;

Steady Flow - Darcy's Law

$$F_w = -K_w \frac{d\psi}{dx} = -D_w \frac{d\theta}{dx}$$

Unsteady Flow

$$\left(\frac{d\theta}{dt}\right)_x = \frac{d}{dx}\left[K_w \frac{d\psi}{dx}\right] = \frac{d}{dx}\left[D_w \frac{d\theta}{dt}\right]$$

The mechanism of water flow is convective (mass flow) and, therefore, dependent on pore radius. Changes in soil water content will affect K_w and D_w and the relationship between K_w and D_w with θ is dependent on whether the soil is wetting or drying.

Uptake of water by roots is mathematically described by Gardner (1960) and Cowan (1965) assuming the root to be a line sink of uniform radius and uniform absorbing properties within an infinite soil volume.

The unsaturated flow to the surface of cylindrical systems is given by

$$\frac{\partial\theta}{\partial t} = \frac{1}{r}\frac{\partial}{\partial r}\left[r D_w \frac{\partial\theta}{\partial r}\right]$$

and when the above assumptions are made

$$\psi_s - \psi_r = \frac{I_w}{4\pi K} \left[\ln \frac{4D_w t}{r^2} - 0.577 \right]$$

Equations of this form show the water uptake rate from a soil layer is proportional to the water potential difference between the bulk soil and root surface and that the pattern of water use depends upon the root distribution, root permeability and soil water content and conductivity properties (Gardner, 1960). The assumptions involved in the derivation of these equations have been discussed by Tinker, (1976) and the principal point of disagreement has been the magnitude of the difference $\psi_s - \psi_r$. Newman (1969a) states that the values used by Gardner and by Cowan for I_w are overestimates and concludes that drying out of the soil around roots (i.e. an appreciable rhizosphere resistance) is unlikely - given typical field values for evaporation - until the soil is near or beyond the permanent wilting point (Newman, 1969b).

Few experiments have been conducted to test the validity of these theoretical equations because of the difficulties in measuring small changes in water content or potential close to the root surface. However, Dunham and Nye (1973) using onion roots showed that potential gradient near the root was steeper in drier soil as predicted by the theory; this despite a substantial decrease in transpiration in the drier soil. Water potential gradients in moist soil were very small. Taylor and Klepper (1975) using more complex cotton root systems showed that the water uptake was proportional to rooting density but that a large resistance was present in the pathway from root epidermis to root xylem causing water uptake to be proportional to the water potential difference between root xylem and bulk soil (rather than

between root surface and bulk soil) and to the hydraulic conductivity of the soil-root pathway.

Further evidence in support of the single root model is provided by Allmaras, Nelson and Voorhees (1975) who also found that water inflow increased as soil hydraulic conductivity increased.

Typical values for I_W are summarised in table 2.2. and compared with values used in theoretical models. The comparison shows the high values of I_W used in the early models and explains the initial concern with soil resistance as a limit to uptake. The values ignore the non- linear demand for water throughout the day but this is perhaps a factor of 2 or 3 and not an order of magnitude.

Mean values also hide the non-uniform velocity of water entry over the root surface. Although unsuberised roots are more permeable than suberised roots, they constitute a relatively small part of the total. The effects of suberisation on water inflow are shown by Graham, Clarkson and Sanderson (1974) who found a 7-fold decrease in barley and marrow water uptake rate over a 90 hour period with contemporancous suberin deposition in the endodermis. Suberin was present at distances greater than 8 cm from the root tip in seminal axes of barley and in those circumstances suberised areas contribute approximately half of the water taken up by the main axes.

Despite the possible variations in uptake with time and physiological state of the root, the information so far available suggests that the rhizosphere resistance to flow is unlikely to be an important restriction to uptake in most circumstances and that water uptake is proportional to rooting density (for a profile at a uniform water potential) independent of their depth (Taylor and Klepper 1971 and 1975). Definite conclusions are not possible until

Table 2.2 Typical values for water inflow found experimentally compared with values used in models

Author	Crop	Average inflow ml/cm root/day	Range
Taylor & Klepper (1971)	Cotton		early season 0.1 → 3.1; late season 0.03 → 0.86
Lawlor (1972)	Ryegrass	7×10^{-4}	
Dunham & Nye (1973)	Onion	0.022	
Allmaras et al (1975)	Soybean	0.03	5×10^{-6} → 0.5
Gardner (1960)		0.1	
Cowan (1965)		0.16	

quantitative description of root configuration and properties are available (Gardner and Ehlig, 1962; Tinker, 1976) - an echo of Barley's thoughts on nutrient uptake.

2.9. Summary of literature and introduction to experimental work

It is evident from the literature that although a generalised outline of wheat root growth exists, the environmental effects on growth (particularly with-holding water) are not understood. Neither is it clear what the relative importance of the seminal and nodal root systems is nor how changes in soil water status and root growth are reflected in nutrient uptake.

Work reviewed about diffusion and mass flow of nutrients has largely been concerned with single-root studies and only in a few cases have attempts been made to work with the more complex problems associated with multiple root systems. Brewster and Tinker (1970) have analysed cation flows to leek plants grown in pots in the field and Mengel and Barber (1974b) have measured the nutrient inflow for field grown corn plants. Apart from these, there is no information on the size of nutrient fluxes for field grown plants or its variation throughout the growing season. If such information were available it might be possible to calculate the levels of available soil nutrients required to maintain growth or, alternatively, the extent of the root system necessary to supply required nutrients (Mengel and Barber,1974b)

Three inter-related problems present themselves:

1) The influence of soil water status on plant growth and nutrient uptake.
2) The relative importance of seminal and nodal roots.
3) The contribution of mass flow and diffusion to total nutrient uptake.

The first part of the experimental work combines a study of the effects of with-holding water from spring wheat plants in the early stages of growth with an assessment of the possible role of nodal roots. This work was conducted in a controlled environment cabinet with plants grown in columns but because root growth was restricted by the size of the columns, the work was transferred to the field. Root growth, nutrient uptake and water use of field grown winter wheat plants was measured and, in addition, calculations were made of the relative importance of mass flow and diffusion in supplying plant nutrients throughout the growing season.

3. EXPERIMENTS IN CONTROLLED ENVIRONMENT LABORATORIES

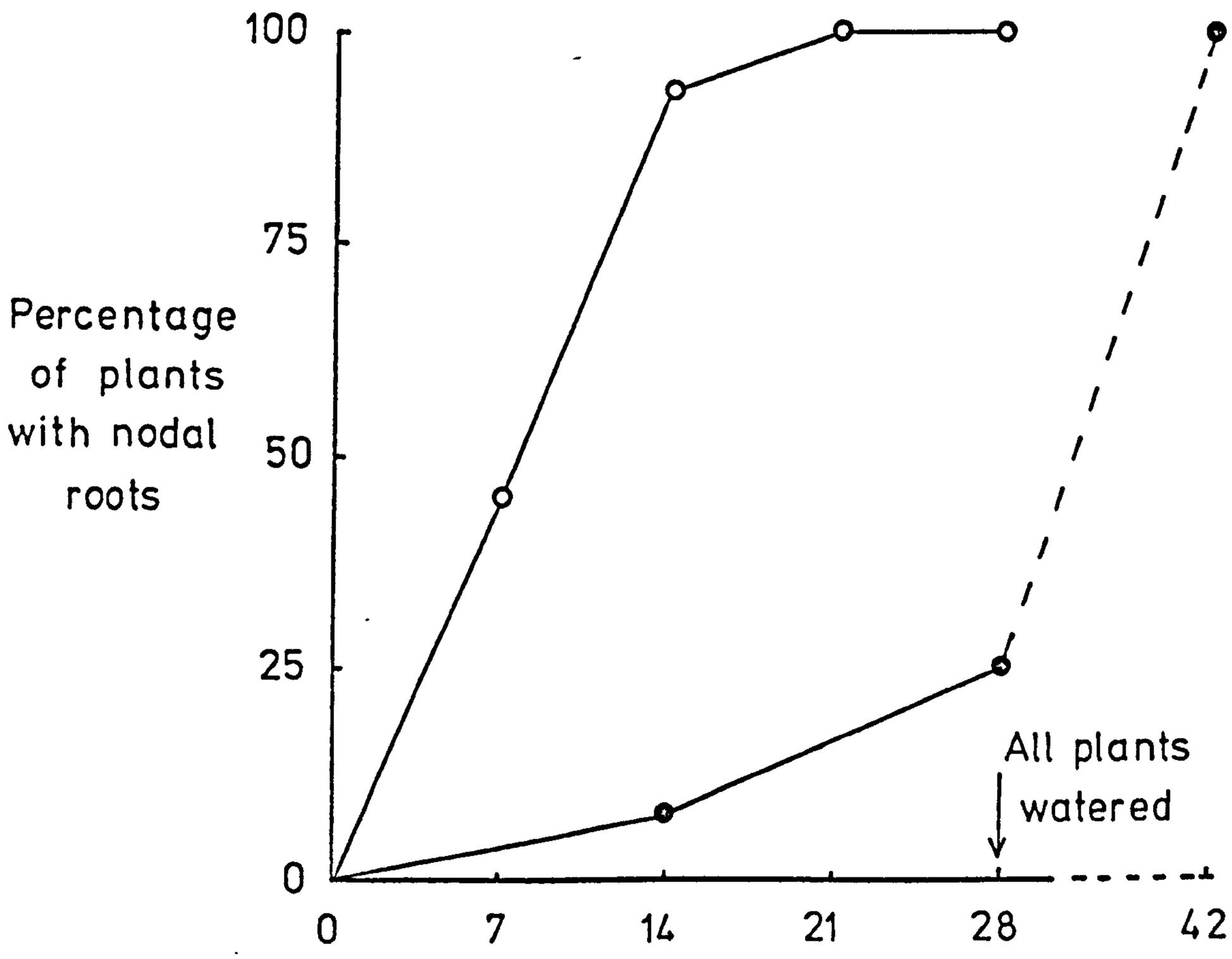
3.1. Introduction

The purpose of the experiments was to determine the effect of soil moisture conditions and the importance of nodal roots during the early growth of spring wheat. An early experiment with spring wheat and ryegrass showed that if the soil was allowed to dry out, both root and shoot growth decreased. Figure 3.1 shows the results for an experiment with ryegrass grown in pots containing a sandy loam topsoil. When the topsoil was maintained in a moist condition, nodal root production was rapid and within 21 days all the plants possessed nodal roots; where the topsoil was allowed to dry out, however, only 25% of the plants possessed nodal roots. On subsequent watering the roots grew and within 14 days nodal roots were present on all plants.

These initial results suggested that topsoil moisture status could have an important influence on the growth of the root system and provided a method to regulate root growth. However, the dry topsoil treatment not only reduces nodal root development but also reduces water and nutrient conductivity to the roots and may also affect seminal root growth. For these reasons, an assessment of the nodal root contribution to the plant cannot be made by simply comparing plants grown in wet and dry soil.

Several possible methods for controlling nodal root growth were examined including cutting off the roots or attempting to bind around the site of production with elastic tape. These studies showed that the most suitable method was to place the seedling in a small plastic pot and thread the roots through a hole in the bottom; any nodal roots produced are restricted to the small pot and unable to

Figure 3.1. The production of nodal roots by ryegrass



explore the surrounding soil (fig. 3.2.).

As a result of these preliminary experiments, three treatments were examined:

1) Soil moisture content maintained nearly constant and all roots allowed to develop.
2) Soil moisture content maintained nearly constant and only five seminal roots allowed to develop.
3) Soil allowed to dry out and all roots allowed to develop.

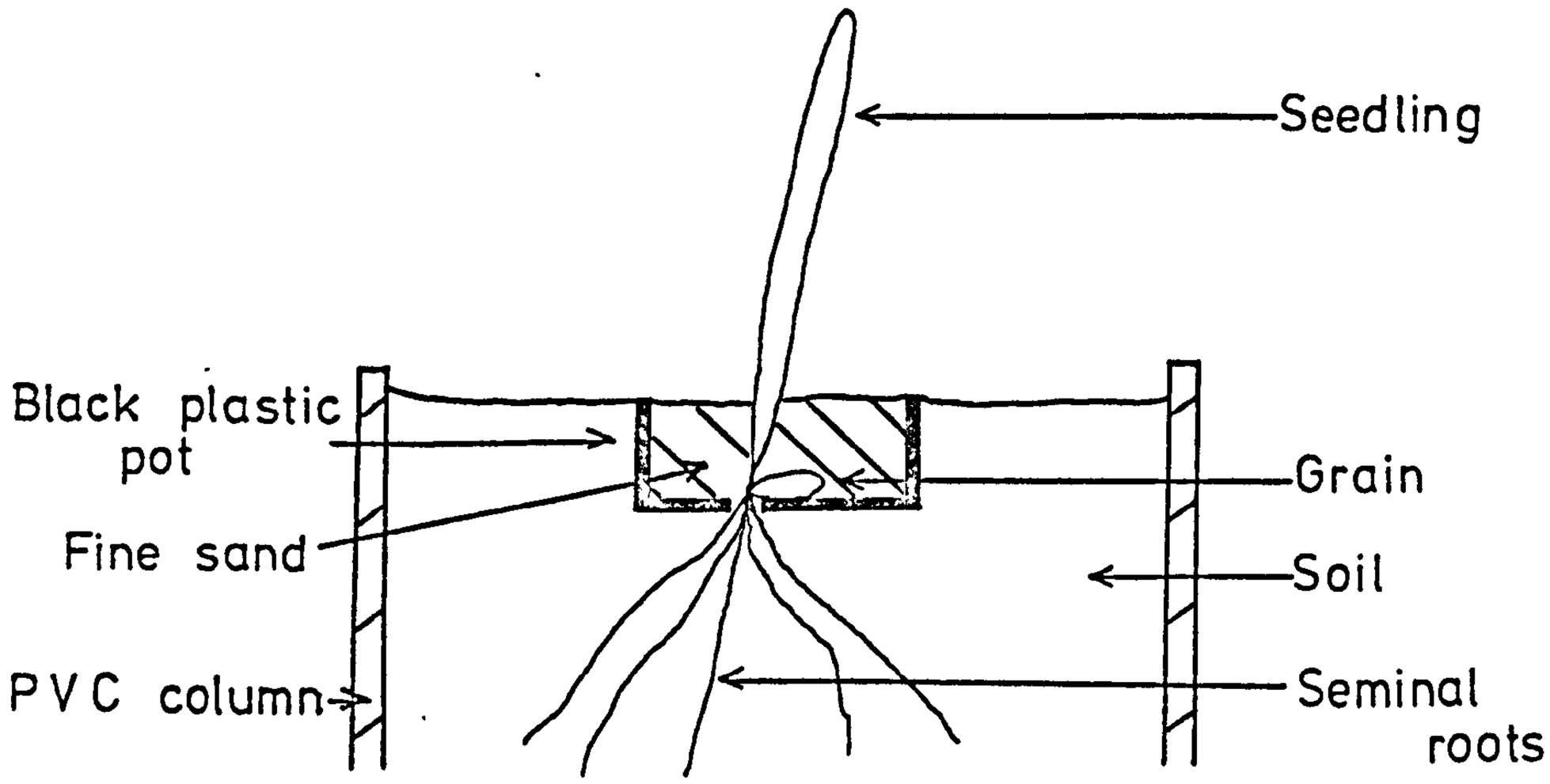
3.2. Experimental method

Surface soil (0 - 10 cm) of a sandy loam (Astley Hall series - main physical and chemical properties shown in appendix 1) was used as the growth medium for the plants. This soil was chosen because roots could be readily washed out and it did not slump when used in pot experiments. The soil was air dried and sieved (< 2mm), mixed with ammonium nitrate and potassium sulphate in solution to give an addition of 50 ppm K and N, and then air dried again.

The spring wheat seed (cv. Maris Dove) was sown in fine, acid washed sand five days before the planned start of the experiment. Only seed of 40 - 45 mg was used to reduce variability in growth during the early stages due to differences in seed reserves. While the seeds were germinating, columns of soil were prepared as follows:

1) Five 5 cm lengths of P.V.C. tubing (7.5 cm diameter) were stuck together with P.V.C. tape (the basal end being previously covered with 1 mm mesh nylon gauze) and filled with 1.5 Kg of air dry soil to give a bulk density of approximately 1.35 g / cm^3. The columns were filled in two stages using a method similar to that described by Schuurman and Goedewaagen (1965) to give columns of soil with a nearly uniform bulk density: this bulk

Figure 3.2. Restriction of nodal root growth using a plastic pot



density was chosen to give minimal slumping when the columns were wetted.

2) A sixth length of P.V.C. tubing was then added and this filled with 250 g of soil labelled uniformly with 25μCi ^{32}P and 8μCi ^{35}S.

3) The column was placed in a bath of water and allowed to wet.

4) After 24 hours, the column was transferred to a tension table maintaining a suction of 50 cm of water and left for 3 days - this treatment gave a gravimetric moisture content of approximately 20 - 22%.

At the start of the experiment, the pregerminated wheat plants were shaken free from the sand and dipped in a beaker of water to remove excess sand from around the roots. Only plants with five seminal roots were selected and were re-planted immediately to avoid drying out of the roots. Plants for treatments 1 and 3 were planted directly into the soil, one per column. In treatment 2, the seedling was placed in a small plastic pot (diameter 2.5 cm) and the five roots threaded through a hole in the bottom (diameter 3mm). This unit was then buried in the column as shown in fig.3.2.

Two columns without plants were also prepared to allow estimates of evaporation from the soil surface to be made. Three additional columns containing plants were prepared (one per treatment) and tensiometers installed through the side of the column centred at depths of $2\frac{1}{2}$, $7\frac{1}{2}$, $12\frac{1}{2}$, $17\frac{1}{2}$, $22\frac{1}{2}$ and $27\frac{1}{2}$ cm.

The experiment was planned to last for five weeks with five weekly harvests. Each treatment was duplicated for every harvest (ie.ten columns per treatment) and the columns were arranged randomly in treatment blocks in the growth room. The light environment of the room had been monitored previously and the columns were sited in

areas with similar light intensity. Air temperature was maintained at 15°C ± 1°C with 16 hour day length.

The columns were weighed daily and water added to treatments 1 and 2 maintaining the moisture content near constant. Harvests were made at 7, 14, 21, 28 and 35 days after planting by cutting off the tops and separating the six rings of the column by removing the P.V.C. tape and slicing through the soil with a thin wire cutter. A sub-sample of soil from each section was kept for gravimetric moisture content measurement (24 hours at 105°C) and the roots washed from the remainder using a spray of water over a 1mm nylon sieve. After washing, very little cleaning was required and they were stored in deionised water / chloroform until required. The following measurements were made on the harvested material:

1) Root length - root samples were spread out on black paper on a tension table. The table was drained and root length measured with a map measuring wheel.

2) Dry weight of shoots and roots - samples were dried at 80°C before weighing.

3) Total K, Ca, Mg, P and S of shoots and roots - ground, dried samples were digested with nitric acid, dry ashed and redissolved in dilute hydrochloric acid (details of digestion methods and measurement of elements given in appendixes 2 and 3).

4) ^{32}P and ^{35}S content of the shoots - counting performed on the digested material (appendix 3).

3.3. Results

3.3.1. Water usage

Water use by the plant was calculated by subtracting an

estimate of bare soil evaporation from the total quantity of water added to the column (treatments 1 and 2) or lost from the column (treatment 3). Average values of 7 mm per day for the first 14 days and 8 mm per day for days 14-35 were determined experimentally for treatments 1 and 2 by evaporation from a damp soil surface and represent the maximum possible water loss by this means. The evaporative correction for treatment 3 was obtained by weighing the two soil columns devoid of plants and determining the daily loss.

Restricting the amount of water available to the plant resulted in significant differences ($P<0.05$) in water use by the plant within 21 days (table 3.1). The table shows that less water passed through non-watered plants than watered and that by 21 days, the plants with only five seminal roots were taking up less than those with all roots allowed to develop. Figures are not presented for the 7 day harvest because of difficulties in estimating the soil evaporation component leading, in some instances, to apparent negative water uptake by the plant. Water extraction was continuously monitored by tensiometers in columns adapted for that purpose and gravimetric moisture content was determined on small samples of soil obtained during the destructive harvesting of the columns. Fig 3.3. shows that except for some limited drying at the top (0 - 5 cm) of the non-watered columns, there was very little drying during the first 14 days. Extraction at depth was evident after 25 days in the non-watered columns and by 28 days, suctions in excess of 60 cm of mercury had developed throughout; drying in the watered columns was, however, still limited to the top soil. The tensiometer measurements also confirmed the adequacy of adding water to the top soil only to make up the daily water loss since no appreciable drying was recorded in the watered columns.

Table 3.1 Cumulative water use by spring wheat

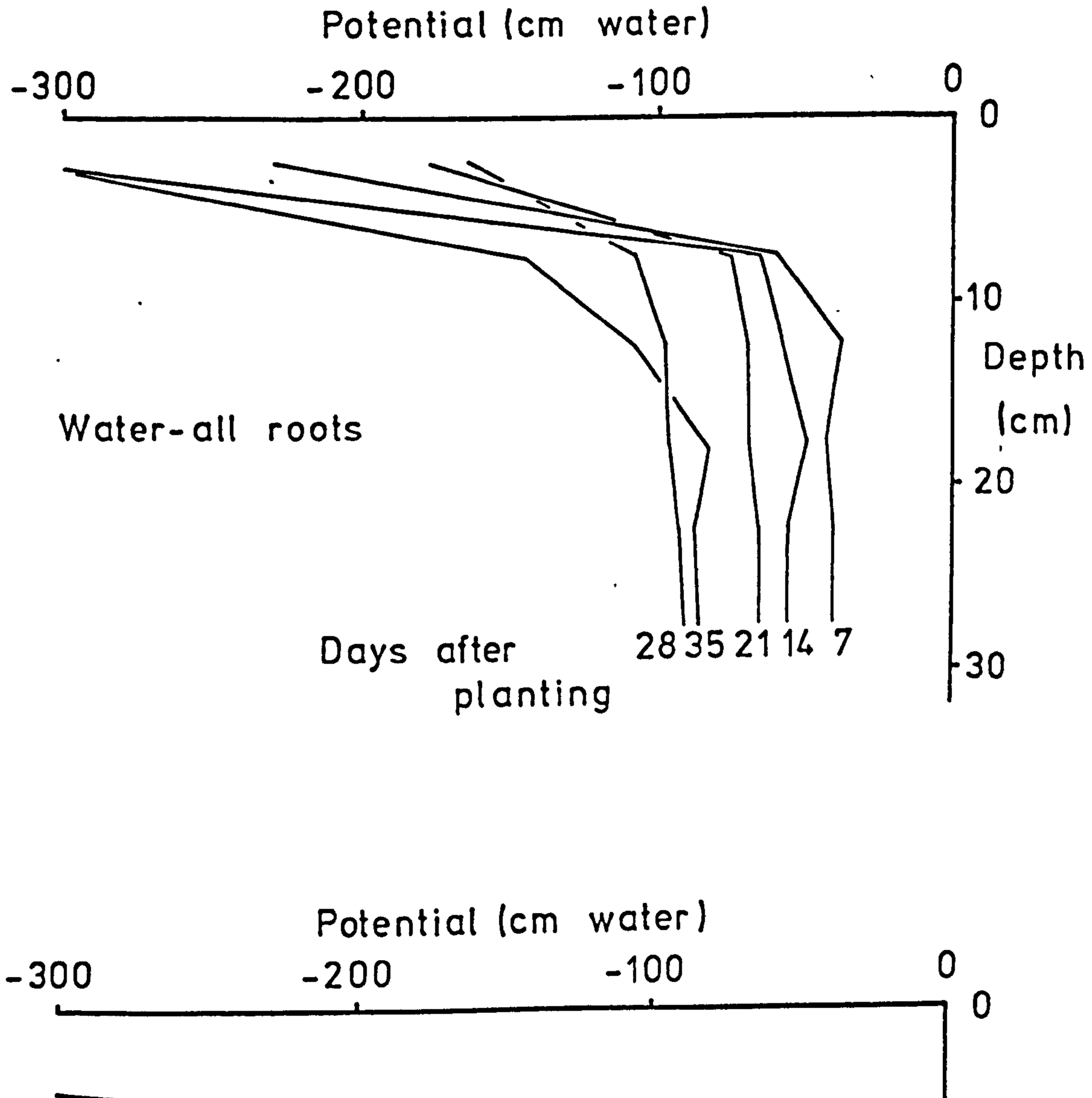
Treatment	Water taken up (g)			
	Days after planting			
	14	21	28	35
Water - all roots	27	76	234	647
Water - seminal roots	10	50	185	432
No water	13	38	79	160

Table 3.2 Growth of spring wheat roots - total root length measurements

Treatment	Root length (m)				
	Days after planting				
	7	14	21	28	35
Water - all roots	0.4	2.8	18.5 (1.0)	55.0 (6.8)	250 (33.8)
Water - seminal roots	0.7	2.4	12.9	47.0	211
No water	0.3	1.7	10.5	20.0	137

Nodal root length is given in brackets

Fig. 3.3. Hydraulic potential / time curves in the soil columns



3.3.2. Root Growth

The growth of the root system is shown in figure 3.4. and table 3.2. Because the seminal root length at day 35 was too large to be determined accurately using the map measuring wheel, data for this harvest are based on regression and extropalation of previous dry weight and length data (r = 0.97; dry weight = 0.034 length + 18).

Significant differences between treatments are visible after 21 days when the nodal roots were first found in the watered columns. The most noticeable effects are the complete absence of nodal roots and the reduction of dry weight and length caused by the non-watering treatment. Watered plants with unrestricted root systems have approximately three times the dry weight and twice the length of roots compared with the unwatered plants at 35 days.

The consequences of physically restricting nodal root growth while maintaining the initial soil water content are also apparent after 21 days. As the dry weights show, almost twice as much root was present at 35 days when nodal roots were allowed to develop. However, despite the large reduction in root dry matter, the reduction in length was much smaller (only 12%). The reason for this is the greater weight per unit length of the nodal roots compared to the seminal roots which arises from the nodal root diameter being over three times the size of the seminal root diameter (table 3.3). These differences between the two watered treatments are confined solely to the absence of nodal root development in treatment 2. If dry weight or length of nodal roots is subtracted from the total dry weight or total root length respectively, then the seminal root systems are the same size - the plant has not expanded the seminal root system to compensate for the loss of nodal roots.

Table 3.3 Root diameters for different types of root

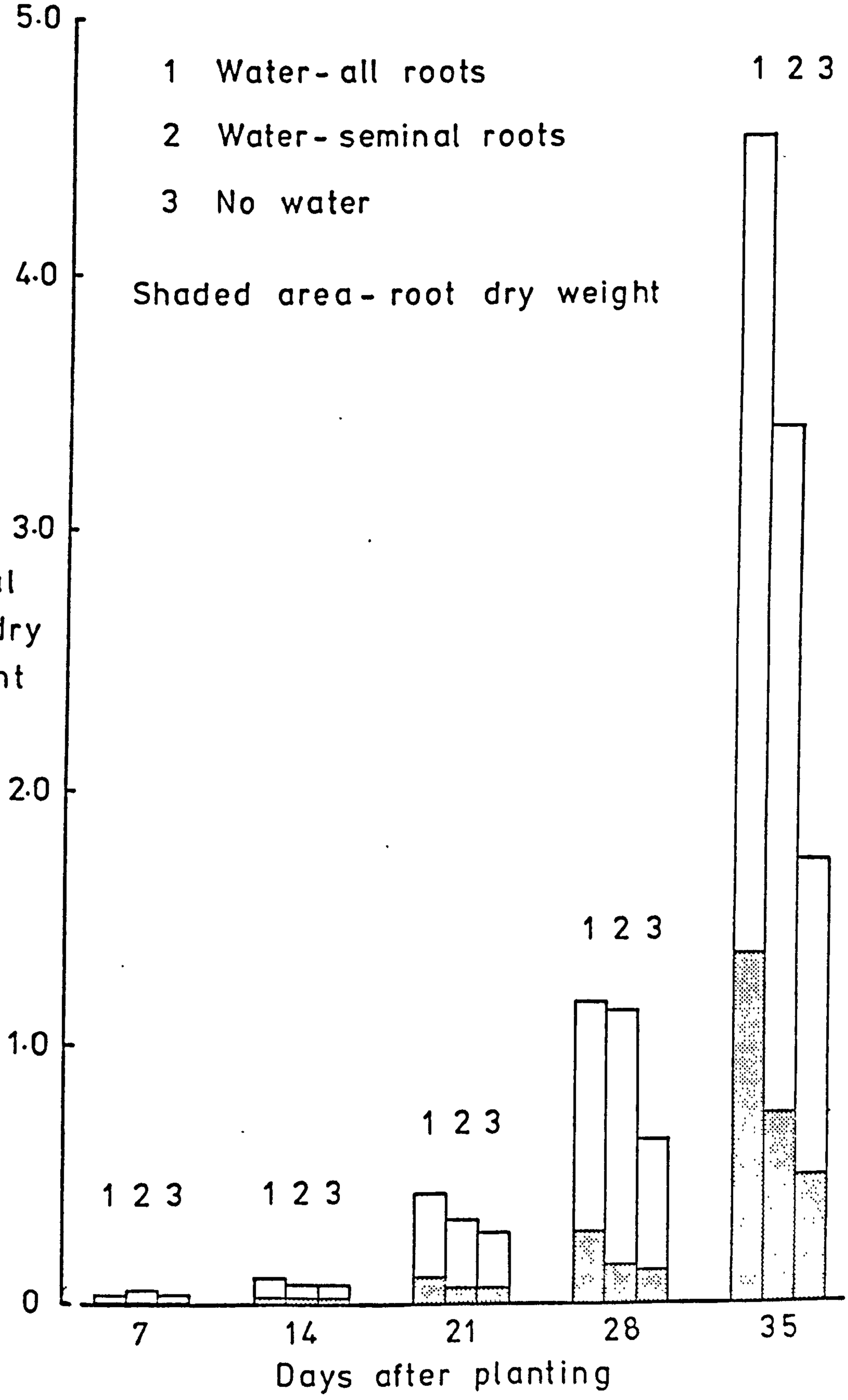
Root type	No. of observations	Av. root diameter (mm)	S.E.
Nodal	10	1.0	0.03
Nodal - primary lateral	10	0.26	0.01
Seminal	5	0.30	0.02
Seminal - primary lateral	5	0.10	0.01

Table 3.4 Example of root fresh weight distribution five weeks after planting

(Example is a watered-seminal root only plant)

Depth (cm)	Percentage of total roots
0- 5	10.8
5-10	13.5
10-15	15.6
15-20	16.9
20-25	16.4
25-30	26.8

Fig. 3.4. The dry weight of spring wheat at weekly intervals after planting



Harvesting the columns in layers also permits the examination of root distribution throughout the profile (fig.3.5). During the first 14 days, the roots of the watered plants are most abundant in the top 0-5 cm and decrease in quantity down the profile; after three weeks, however, the distribution is almost uniform. In the unwatered columns, the initial growth is similar but within 14 days the layer containing the maximum root length is the 5-10 cm layer. This displacement is clear at 14 and 21 days but daily drying of the watered columns has led to a distribution of similar shape in both treatments at 28 days.

Roots were distributed throughout the soil core with a tendency to be more abundant at the soil / P.V.C. interface. Distribution after 28 days was affected by the limited column length; fresh weight obviously so. Much coarser roots are present at the base of the column causing up to 30% of root fresh weight to be confined to the 25 - 30 cm layer. A typical example is shown in table 3.4.

3.3.3. Shoot Growth

Whole plant dry weight shows significant differences between the watered and non-watered treatments at 21 days with differences in root treatments visible only at the final harvest (fig.3.4). Non-watering and physical restriction of root development both result in decreased total dry matter production and shoot dry matter although, for treatment 2, the decrease in total dry matter is largely due to decreased root growth rather than a reduction of shoot growth.

Apportioning dry matter between root and shoot can be expressed by the root : shoot ratio or by root weight as a fraction of total plant weight (table 3.5). Where neither water nor root growth were limited, 25 - 30% of the total dry weight throughout the experiment

Fig.3.5. The percentage of total root length in 5cm depth increments

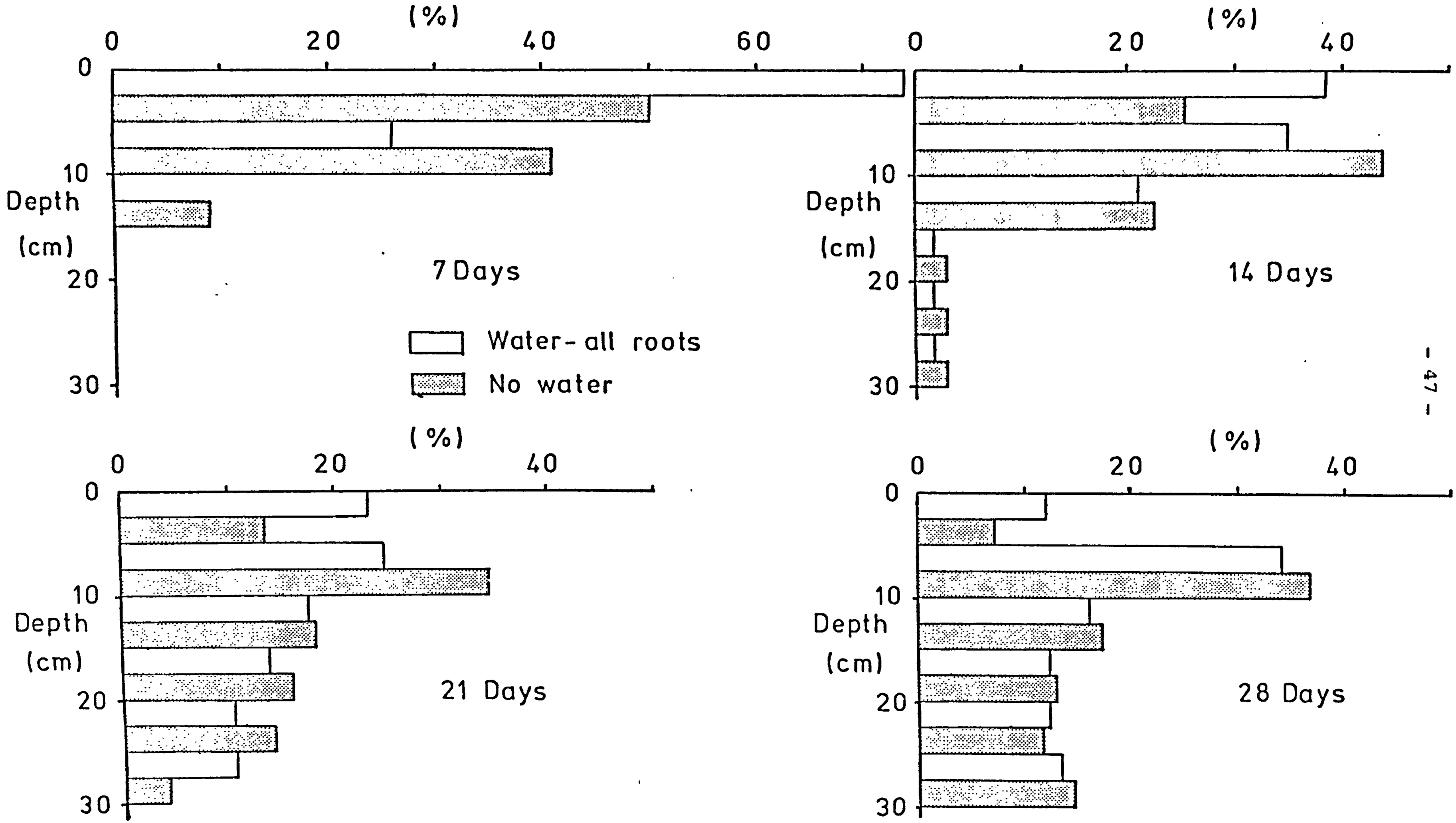


Table 3.5 Root dry weight expressed as a fraction of total plant dry weight at weekly intervals after planting

Treatment	$R_w / S_w + R_w$				
	Days after planting				
	7	14	21	28	35
Water - all roots	0.30	0.29	0.25	0.24	0.29
Water - seminal roots	0.28	0.30	0.18	0.15	0.22
No water	0.36	0.31	0.23	0.19	0.28

was roots. Restricting the water supply resulted in the plant initially having a higher fraction of its dry weight in the roots (harvests 1 and 2) but thereafter the shoot fraction was greater than for watered plants. Treatments 1 and 2 are similar for the first two harvests but as the experiment progressed and nodal roots were restricted, the root dry matter fraction decreases.

One factor not shown by the figures is the larger number of tillers (up to 16) produced by the watered plants; field-grown plants rarely produce more than five or six of which, perhaps, only two survive to give grain.

3.3.4. Nutrient Uptake

The differences in dry matter production are reflected in the plant uptake of nutrients (table 3.6). At the final harvest, non-watering results in a reduction of plant nutrient content by approximately one half but the effects of restricted root growth are not as pronounced and the only significant reductions are in uptake of S, Ca and Mg. This latter result is not surprising when one considers that the main difference between the root treatments was found in root weight and the roots contain about one half the weight of nutrient per unit of total dry weight compared to the shoots ie. if shoot weight is constant, a very large difference in root weight is required before there is an appreciable affect on plant nutrient content. Some leaching of nutrients from the roots during washing and storage may have occurred but this is unlikely to be a major source of error.

The treatment effects are closely related to whole plant growth and when nutrient content is expressed as a percentage of the total plant dry weight(the calculated values are not shown here),

Table 3.6 Total nutrient content per plant for spring wheat at weekly intervals after planting

Nutrient	Treatment	mg nutrient per plant				
		Days after planting				
		7	14	21	28	35
Phosphorus	1	0.14	0.52	2.02	5.10	10.67
	2	0.24	0.43	1.52	5.44	9.94
	3	0.13	0.39	1.50	2.62	4.57
Sulphur	1	0.09	0.32	1.76	3.99	10.36
	2	0.14	0.25	1.22	4.48	7.67
	3	0.09	0.28	1.16	2.19	4.67
Potassium	1	0.56	3.24	16.57	40.30	86.16
	2	1.78	2.91	14.86	51.94	85.55
	3	0.50	2.64	11.70	25.26	48.73
Calcium	1	0.20	0.68	3.08	5.64	19.06
	2	0.37	0.63	2.20	6.69	11.57
	3	0.20	0.60	1.81	4.15	8.18
Magnesium	1	0.07	0.16	0.58	1.64	3.72
	2	0.13	0.14	0.49	1.67	2.90
	3	0.08	0.14	0.40	0.92	2.16

Treatment 1 - Water - all roots

2 - Water - seminal roots

3 - No water

few significant differences between treatments are found although differences between harvests are apparent (presumably influenced by either plant demand or soil restrictions). Treatment effects are limited to the final harvest where the non-watered plants show higher percentages of sulphur, potassium, calcium and magnesium per unit dry weight than watered plants (0.23, 1.89, 0.42 and 0.08 % dry weight for treatment,0.27, 2.83, 0.48 and 0.13 % dry weight for non-watered plants respectively).

To investigate further the relationship between nutrient uptake and root growth, an analysis was performed using Williams' (1948) equation (section 2.7) to calculate inflow. The values used in the analysis were the mean figures for both replicates and an initial root length of 5 cm was assumed. With the exception of two phosphorus and one potassium result, nutrient uptake per unit length of root (table 3.7) decreases with time over the course of the experiment by a factor of 10 -15 and the figures, after the first 3 weeks of growth, are of the same magnitude as those given by Brewster and Tinker (1972). For treatments 1 and 3, phosphorus inflow is comparatively low over the first 7 day period, increases over the second 7 day period and then declines similarly to the other nutrients. This anomaly might be explained by poor contact between roots and soil shortly after the plant was transferred from sand to soil (sand surrounding roots) causing low, initial uptake of those ions supplied principally by diffusion. Some evidence for this interpretation is that the potassium inflow for the same treatments shows a similar trend over the first three weeks of growth.

It is difficult to see precise relationships between inflow and treatment effects on root growth but in general, the effect of non-watering, shown in other respects to be significant after 21 days,

Table 3.7 Nutrient inflow for spring wheat at weekly intervals after planting

Nutrient	Treatment	Inflow - moles cm/root/sec ($\times 10^{14}$)				
		Days after planting				
		7	14	21	28	35
Phosphorus	1	3.8	16.9	9.6	4.9	2.3
	2	24.8	7.5	9.3	8.0	2.2
	3	2.8	16.9	12.4	4.0	1.7
Sulphur	1	28.8	10.3	9.0	3.4	2.6
	2	29.6	4.4	8.0	6.4	1.5
	3	33.8	12.9	9.4	3.6	2.1
Potassium	1	107.5	96.2	67.9	30.0	15.1
	2	289.1	35.4	81.5	59.9	13.1
	3	104.2	117.0	80.0	38.7	16.3
Calcium	1	77.3	28.4	19.8	5.3	7.2
	2	100.8	13.4	17.4	11.8	3.1
	3	89.3	35.5	17.4	10.9	4.6
Magnesium	1	6.4	3.3	2.1	1.3	0.7
	2	14.5	0.3	2.3	1.9	0.5
	3	11.5	3.0	2.2	1.4	0.8

Treatment 1 Water - all roots

2 Water - seminal roots

3 No water

has resulted in lower inflow of phosphorus and calcium, higher inflow of potassium and magnesium and approximately equal inflow of sulphur. Comparison of treatments 1 and 2 shows few differences in inflow. However, at the final harvest, when the length contribution of nodal roots is becoming significant, the inflow is greater for all nutrients where nodal roots have been allowed to develop. This greater inflow could be due to the greater uptake per unit length of nodal roots per se or arise because they are relatively younger than the seminal roots. However, a firm conclusion is difficult to reach because the results for the 28 days harvest all show higher inflow where rooting has been restricted.

Uptake of radioisotopic phosphorus and sulphur from the topsoil (0 - 5 cm) of each column at final harvest (table 3.8) shows a decrease in total activity with soil drying. However, when expressed as specific activity, no differences were apparent between treatments in P uptake but where the soil has been unwatered, uptake of S from the topsoil has been substantially reduced. Since total S per unit dry weight is known to be approximately the same in both watered and non-watered treatments, this means that relatively more sulphur has been supplied from below the topsoil in the non-watered treatment.

3.4. Conclusions

Despite the restricted volume of soil available to the plant, the procedure described was shown by earlier experiments to be suitable for studies during the first few weeks of growth. Continuing the experiment beyond five weeks would have resulted in the death of the non-watered plants and an accumulation of roots at the base of the column with consequent changes in root appearance, and would have rendered nodal and seminal root separation impossible. The profusion of tillers

Table 3.8 The uptake of ^{32}P and ^{35}S from the 0-5 cm layer of soil by spring wheat measured at 35 days after planting

Treatment	cpm per plant		cpm/mg dry wt.	
	^{32}P*	^{35}S	^{32}P*	^{35}S
Water - all roots	155	723	16	27
Water - seminal roots	154	546	17	28
No water	64	84	17	7

* count x 10^{-3}

was obviously different to field - grown plants and represents a limitation to the field application of the results.

The results may be summarised as follows:

Watered v Non-watered:

1) Watered plants showed higher root and shoot dry matter production.
2) The increased growth was accompanied by an increase in total quantities of nutrients taken up although when expressed per unit of dry weight, the differences were unimportant.
3) During the first two weeks of growth, the non-watered plants have a greater fraction of total dry weight as root. As the soil dries out, however, more shoot is produced relative to root. The fraction of dry weight as root for the watered plants remains almost constant throughout the experiment.
4) Drying the soil reduces the water uptake of the plant.
5) Nutrient inflow is generally greater in the non-watered plants but no definite conclusion can be drawn.

All roots v Five seminal roots:

1) The inhibition of nodal roots resulted in decreased root and shoot dry matter production after five weeks. Most of the decrease in total plant dry matter arose from the reduced root growth.
2) Because the nodal roots are thicker than the seminal roots, the doubling of total root weight in treatment 1 only confers a small advantage in additional root length.
3) Water uptake by plants was reduced when the root growth was inhibited.
4) Few differences in nutrient uptake or inflow were observed between the two treatments.

4. FIELD EXPERIMENT

4.1. Introduction

The column experiments conducted in controlled conditions showed that water status of the soil affected root and shoot growth of spring wheat and that plants without nodal roots did not grow as well as plants with a complete root system. The experimental results were limited in application, however, for a number of reasons. The abnormal character of roots developing at the base of the column has already been mentioned and hence the technique is only suitable during the early growth of the plant. Secondly, although each plant had only one and one half times the typical field surface area per plant, the sowing of single plants in columns, meant that light competition was absent and the plants produced a larger number of tillers than those grown in the field.

For these reasons it was obvious that only limited progress could be made indoors in attempting to explore the growth of a typical wheat root system and its ability to take up water and nutrients. Moreover, differences in water and root treatments, while significant, in the short term, may not result in differences in final grain yield.

During 1973 and 1974, a series of small field experiments were conducted on spring wheat in conjunction with Sergeant (1976). The 1973 experiments investigated a soil injection technique using phosphorus-32 to determine root depth and lateral distribution (Bassett et al, 1970) and as a quantitative measure of soil nutrient supply to the plant. The results were acceptable for distribution studies but the quantitative measurements were too variable for nutrient uptake estimates. However, this early work provided useful

experience in installing and maintaining tensiometers, taking soil cores and washing out roots and in the general problems associated with field experiments.

A small field experiment was carried out in 1974 to investigate the number of roots produced by each plant, the effect of drying or wetting the topsoil on root production and the quantity of selected nutrients taken up by the plant. Again, the results were of mixed worth but invaluable experience was gained in the problems of sampling representative plants for analysis and in implementing treatments under field conditions. Many of the uncertainties in the results arose because of the small size of the experimental plots and this limited their interpretation.

At the close of 1974, a number of hypotheses had been formulated as a result of the column and field experiments and sufficient expertise in field work accumulated to enable the testing of them under field circumstances. The Ceres project financed by the A.R.C. provided a unique opportunity to test many of the ideas within the framework of a co-ordinated team, each member co-operating with the others to ensure that no measurement was unnecessarily duplicated or omitted. This approach means that some of the measurements used in this thesis were not made by me but as an essential part of the Ceres project.

The choice of the Ceres project as a basis for the experiments involved a change of crop (from spring wheat to winter wheat) but this was felt unlikely to invalidate previous conclusions. A change to winter wheat also had advantages since one of the treatments considered involved re-planting some areas of the crop in plastic gutters; the long winter period would probably enable the crop to re-establish before rapid growth commenced in the spring.

The experiments were designed to study:

1) The production and growth of winter wheat roots.
2) The uptake of water and nutrients by winter wheat and if possible to estimate the contribution of mass flow and diffusion to plant nutrient uptake.
3) The effects of inhibiting nodal root development on water use, nutrient uptake and final yield.
4) The influence of prolonged soil drying on the ability of roots to extract water.

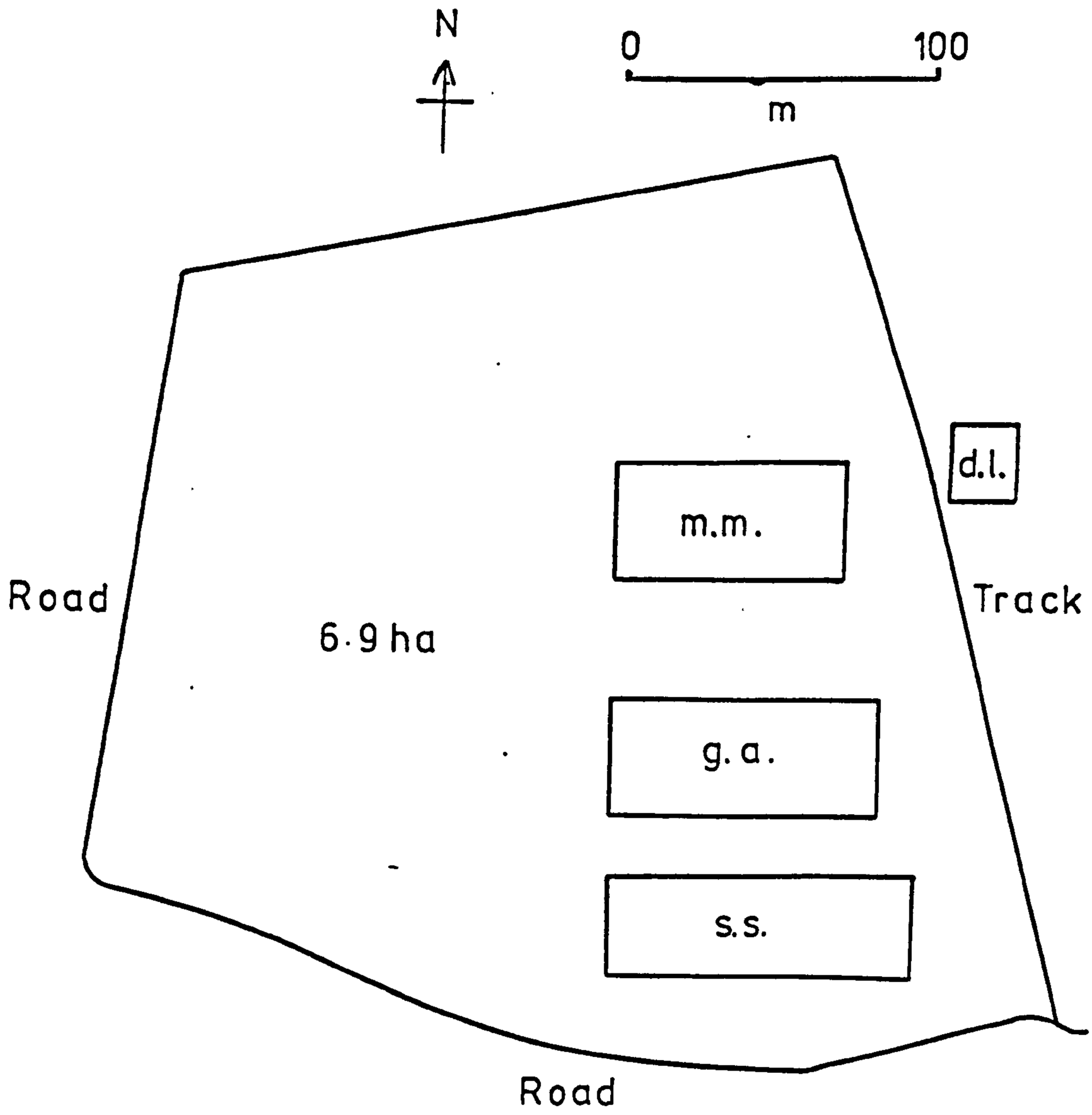
The four chapters immediately following this, present the basic measurements made on the crop and later chapters use these to calculate more complex quantities (eg. the contribution of mass flow to total nutrient uptake) and try to answer the objectives stated above.

4.2. Experimental site

The Ceres experimental site on the University Farm (Nat. Grid. SK.504267) has been described by Biscoe et al (1975a). A plan of the site is shown in fig.4.1 and shows the division of the site into three principal areas. The area allocated to soil water studies was further subdivided into treatment areas as shown in the more detailed plan (fig.4.2).

The soil type is Astley Hall series soil, developed from a sandy fluvio - glacial drift overlying Keuper Marl at about 1 -1½ metre (Thomasson, 1971). Some physical and chemical properties are given in appendix 1 and the soil profile is shown in fig.4.3. The stone content of the soil is variable and the southern end of the field was chosen for the soil water studies because it was less stoney than many areas

Fig. 4.1. Plan of Ceres field experiment



d.l. Data logger
m.m. Micrometeorological measurements
g.a. Growth analysis sampling area
s.s. Soil science experiments

Fig. 4.2. Plan of soil treatment plots

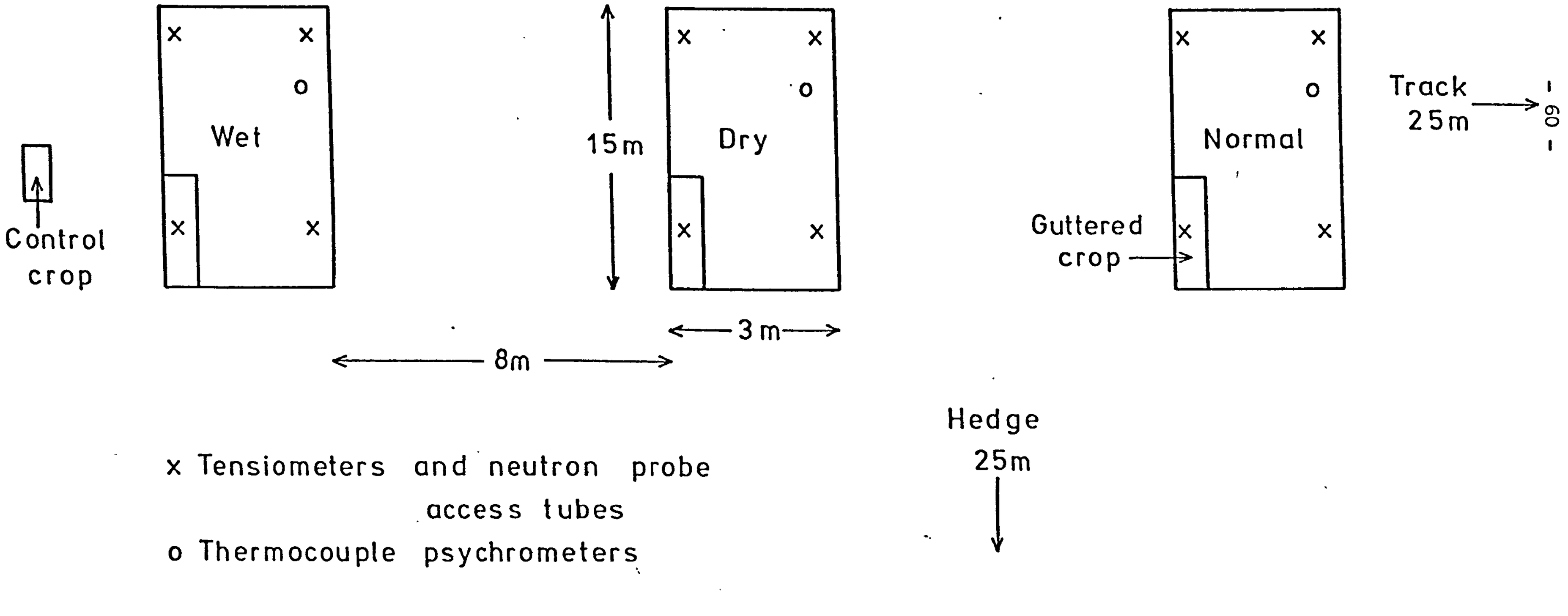
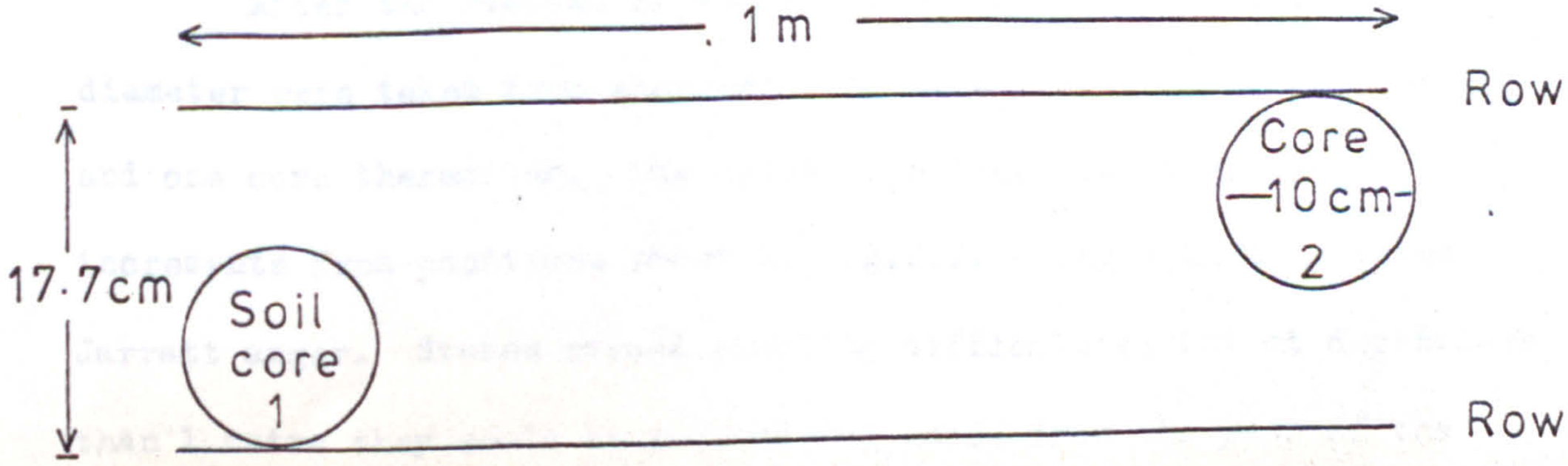


Fig.4.3. Astley Hall series soil profile (Ceres site)

Fig.4.4. Sampling position of soil cores for root measurements



and also had a lower water table (1.2 - 1.5 m in winter). A band of stones, up to 15 cm in diameter, was present at 30 cm - 40 cm and again at 80 cm - 100 cm although this latter band was sometimes missing and more variable in depth. Occasional stone bands were also found at 120 cm - 150 cm and where present frequently led to the abandonment of root excavation before the intended sampling depth had been reached.

4.3. Crop, treatments and field sampling

The crop of winter wheat (cv. Maris Huntsman) was sown on 30th October 1974 according to normal agricultural practice using a seed rate of approximately 120 kg /ha. Because the previous crop had been potatoes no fertiliser was added to the seedbed. A list of cultural operations performed on the crop is included in table 4.1.

Destructive sampling for growth analysis measurements was carried out in area g.a. (fig.4.1) which was divided into four blocks. On the dates shown in table 4.1. one sample comprising all the tops (including hypocotyls) in one metre of row from two adjacent rows was taken for growth analysis. Sampling positions within the block were determined randomly but spaced at least 2 m from sections of row already removed. The material removed from the field was placed in polythene bags and stored at 3°C until growth analysis was performed.

After the removal of the tops, two soil cores 10 cm in diameter were taken from each sampling site inclusive of harvest 10 and one core thereafter. The cores were taken in 10 cm depth increments from positions shown in fig.4.4. using a hand operated Jarratt auger. Stones caused sampling difficulties but at depths less than 1 metre they could be removed, by hand, from the path of the auger. Stones deeper than 1 m could not be removed and this led to

Table 4.1 A summary of operations performed on the winter wheat crop

Date	Operation	Days after sowing
1974 30 Oct	Sowing	0
3 Dec	Harvest 1	34
24	Harvest 2	55
1975 14 Jan	Harvest 3	76
4 Feb	Harvest 4	97
4-10	Installation of neutron probe access tubes and tensiometers	
25	Harvest 5	118
18 March	Harvest 6	139
8 April	Harvest 7	160
10	Cover placed on dry plot	
22	Harvest 8	174
24	Herbicide sprayed	
25	N applied to dry plot	
29	Harvest 9	181
1 May	70 units N applied	
6	Harvest 10	188
13	Harvest 11	195
20	Harvest 12	202
27	Harvest 13	209
3 June	Harvest 14	216
10	Harvest 15	223
17	Harvest 16 (Anthesis)	230
24	Harvest 17	237
1 July	Harvest 18	244
8	Harvest 19	251
15	Harvest 20	258
22	Harvest 21	265
29	Harvest 22	272
5 Aug	Harvest 23	279

the abandonment of further sampling. In the summer, when the soil had dried out and could not be retained in the auger, it was wetted before extraction. Cores were taken to 30 cm and water poured down the hole to wet the deeper layers overnight. Extraction was then recommenced until dry soil was again reached when more water was added. In this manner sampling was able to proceed in the absence of stones to 2m even in dry conditions. The soil cores containing the roots were stored in polythene bags at 3°C until required for analysis.

In addition to the cores for root measurements, an additional core was taken on selected dates from sampling sites 1, 2 and 3 for soil solution extraction. These samples were again taken using a 10 cm diameter Jarratt auger but the soil was bulked in 0 - 30 cm, 30 cm - 60 cm and 60 cm - 100 cm layers and stored at 1°C for short periods of time.

Soil water status was monitored in an area adjacent to the growth analysis area (s.s. on fig. 4.1). The plot referred to as "normal" (fig.4.2) was taken as representative of the whole field and contained four neutron probe access tubes to a depth of 2 m. Tensiometers at 20 cm, 30 cm, 40 cm, 60 cm, 80 cm, 100 cm, 120 cm, 140 cm, and 160 cm were sited within 1 metre radius of the access tubes, and in addition, the plot contained two sets of thermocouple psychrometers at 10, 20, 40, 60 and 80 cm. Neutron scattering measurements with the Wallingford probe (Bell, 1973) commenced on 9th April and were performed every 4 or 5 days throughout the summer. The tensiometers were read every two days except at the week-end and the psychrometers were read when the soil was suitably dry.

Besides the untreated crop (normal) two other soil water treatments were imposed. One plot (referred to throughout as the dry plot) was covered with corrugated plastic sheets mounted on four steel frames to keep out rain (fig.4.5). Each frame carried three

plastic sheets (I.C.I. Novolux, 8ft x 2½ft) one of which was mounted so that it could be readily removed to allow neutron probing to proceed under the covers. The covers were placed over the crop on 10th April and removed on 17th June when the plot was irrigated to bring the soil back to field capacity. On 16th May an estimate was made of the radiation intercepted by the plastic covers using a Kipp and Zonen solarimeter. In both clear and overcast conditions a reduction of 17 - 20% radiation was measured under the covers. This is unlikely to have a major effect on crop growth (Biscoe, pers comm).*

The final plot (referred to throughout as the wet plot) was irrigated weekly from 21st May until 17th June to keep the soil at field capacity. A Wellesbourne designed frame was used to apply the water and was moved to four positions to cover the whole plot. After 17th June no further supplementary water was applied.

In addition to these three water treatments (normal, dry, wet), one corner of each plot was used for an experiment to control nodal root growth. On 4th December, plants in an area 8 rows in width and 2m long were dug up one metre at a time. The plants possessed five seminal roots and these were threaded through holes 3mm in diameter in a 1m length of plastic gutter (fig 4.6) Each 1 metre length of gutter contained 66 holes (approximately 40 plants were dug up per metre) and five much larger holes 1½ cm long in the side of the gutter to allow water to flow away. These larger holes and the ends of each gutter were covered with fine nylon cloth cemented to the P.V.C. to restrict all but the five seminal roots to the inside of the gutter. The gutters plus plants were carefully replanted in the position from which they had been removed. These sub-plots are referred to as the guttered treatments in the text.

* Calculation shows that the maximum loss of dry weight expected is<15% assuming light quality, temperature, water use etc. remain constant. Table 6.I. shows dry matter per m^2 reduced by 23% with no reduction on a per plant basis.

Fig. 4.5. Construction of covers on the dry plot

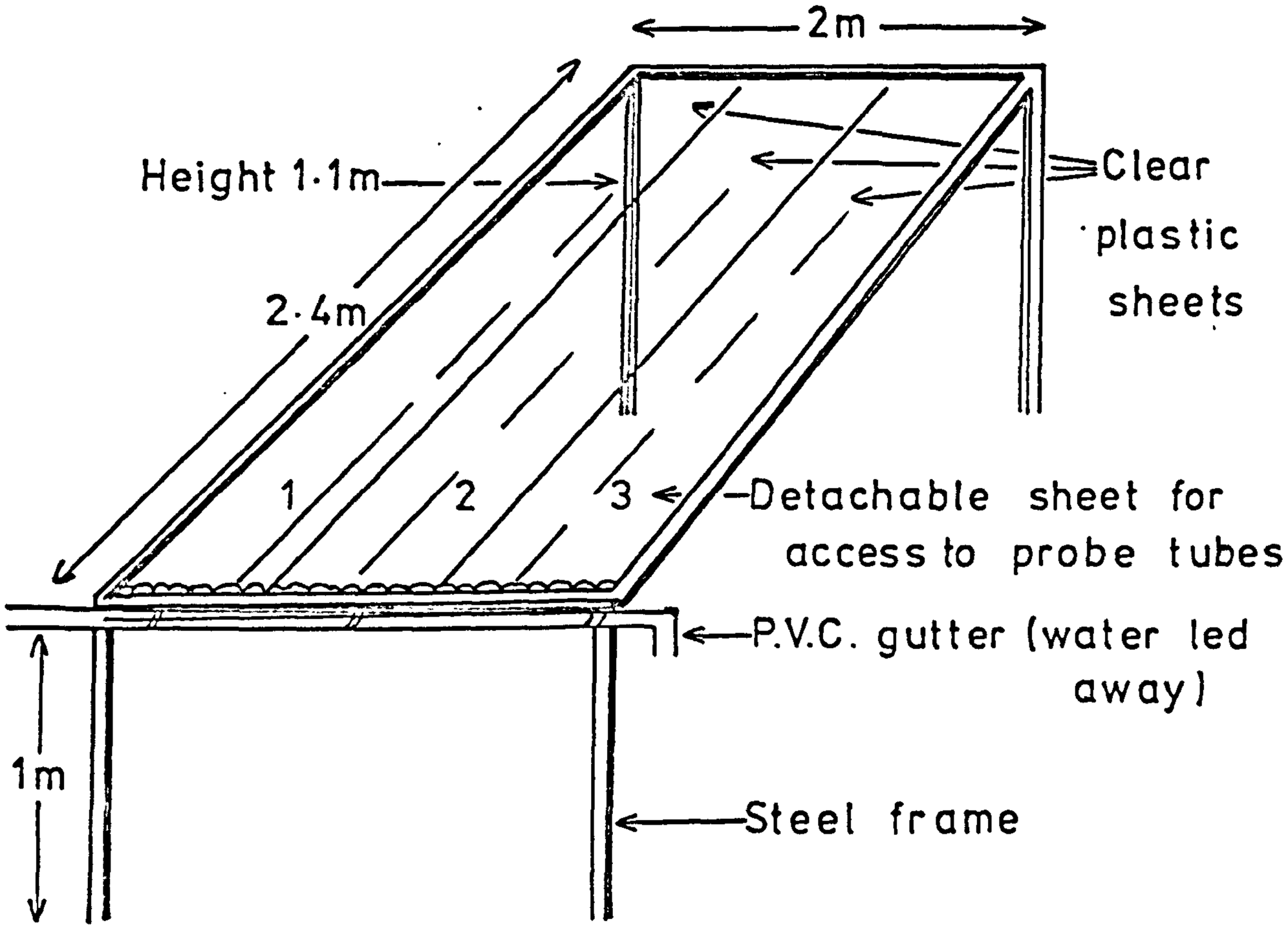
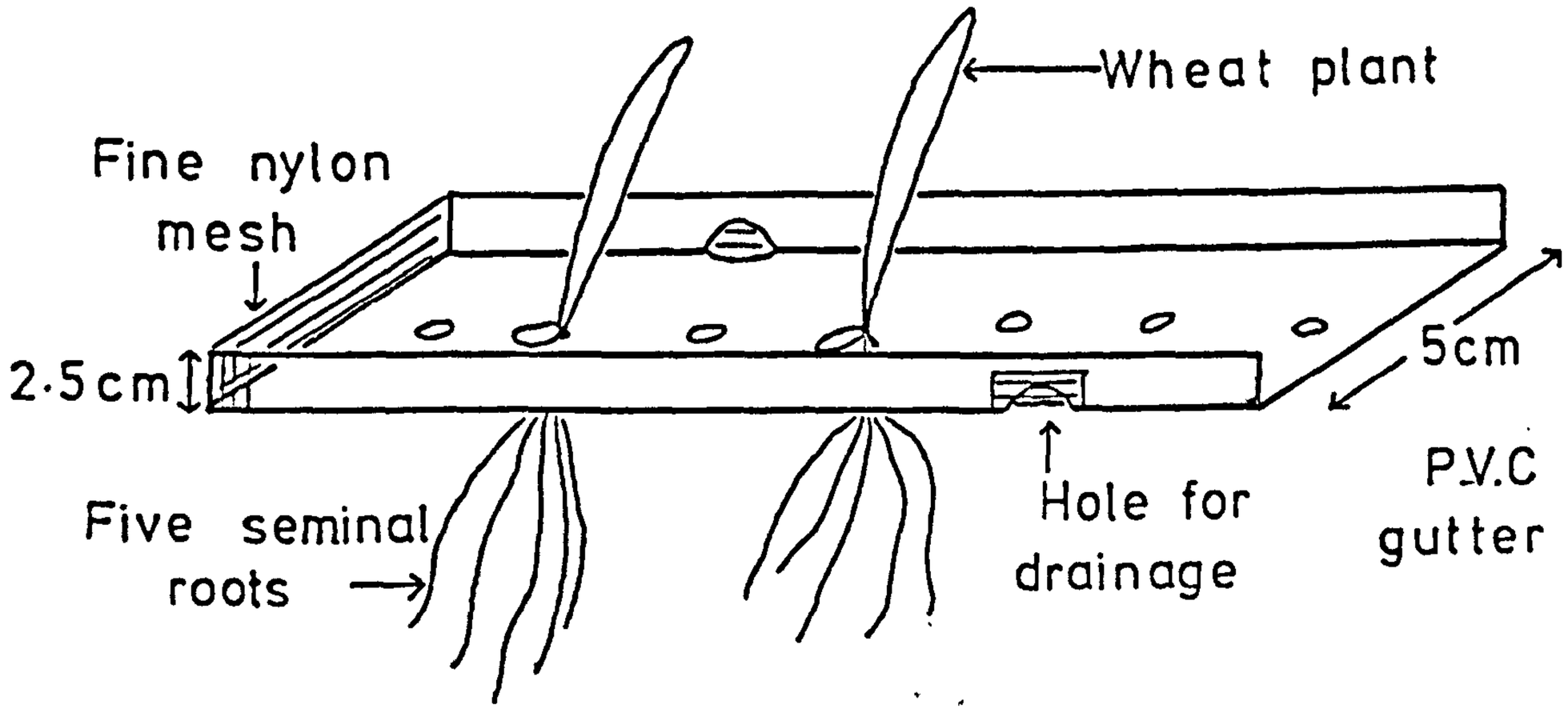


Fig. 4.6. Restriction of nodal root growth using a plastic gutter



To check that digging the plants up was not the cause of later treatment differences, an additional plot 2m long and 4 rows in width was constructed to the west of the s.s. area as a control. In this plot (referred to as the control), plants were dug up, the roots shaken free of soil, exposed to the air and then replanted again after 10-15 minutes directly into the soil.

In summary, area s.s. contained three treatment plots (normal, dry and wet) and each treatment contained a sub-plot (guttered). The three treatment plots contained four neutron probe access tubes and four sets of tensiometers, one of each positioned within the sub-plot. Psychrometers were placed in the main treatment area only.

Plant samples were taken from the treatment plots on 17th June and the final harvest. Flowering first occurred on 18th June but 17th June is referred to throughout as the "anthesis harvest". At anthesis, 20 plants were harvested from each treatment for growth analysis and at final harvest four single metre rows were taken from the main plots, two from each of the guttered plots and two double metre rows from the control plots.

5. GROWTH OF THE WINTER WHEAT ROOT SYSTEM

5.1. Separation of root samples

Soil cores taken for root growth determination were tipped onto either a 1 mm nylon sieve or a 28 mesh (approx. 1mm) brass sieve and washed with a spray of cold water until most of the fine sand, silt and clay had been washed out into a bowl beneath. Stones were removed from the sieve and the remaining gravel and organic matter washed into a large polythene beaker. Roots and plant residues were separated from the gravel by "flotation" using a stream of water and collected on a $\frac{1}{2}$ mm brass sieve.The whole of the material was washed from the sieve into a plastic beaker and stored for not more than a week at 1°C. Soil containing roots was stored at 3°C for upto 6 months with no detectable deterioration of roots but once isolated from the soil, the roots had to be cleaned and measured within a week otherwise they started to rot. When separated from the soil, the roots had the characteristics of fresh roots but once in water, they became flacid and soon began to smell. Addition of chloroform delayed the onset of putrefaction a little but was generally impracticable with large samples stored in open beakers.

The samples were then cleaned. The purpose of cleaning was to separate "white" roots (assumed to be alive) from dead roots and other plant residues and was achieved using two different methods. Samples from below 50 cm generally contained less debris than samples above this depth and also fewer white roots. These samples were poured onto damp green blotting paper on a tension table (Clement,1966) and spread out. On draining the table, the white roots were clearly visible and were picked off into vials using forceps. Samples from above 50 cm were placed in large beakers of water, dispersed and

white roots laboriously picked out with forceps and collected.

After cleaning root lengths of the samples were measured using a version of Rouse and Phillips (1974) instrument. Details of sample presentation and accuracy of the machine are given in appendix 4. Immediately following this measurement, the roots were dried at 80°C and weighed 24 hours later. Many samples were too large to be placed on the root length measurement table and a sub-sample was used for length determination. This was dried separately from the remaining sample, and then the total length was calculated for the original assuming a direct relationship between weight and length.

Root lengths and weights up to harvest 9 inclusive and all treatment plot harvests were measured as outlined. However, after harvest 9 root samples were handled differently because many were large and required considerable sub-division before length determination was possible. Samples from below 50 cm were treated as previously but for samples above 50 cm only dry weight measurements were made; length was estimated using a regression of length and dry weight for the 0 - 50 cm samples of harvests 6,7,8 and 9 (fig 5.1.). The validity of this procedure was checked using ten samples from harvest 18 (table 5.1) where measured and estimated samples agree to within 10% over much of the range of interest although errors of up to 25% were present in some of the large samples. It was concluded that no gross error was introduced using this approach. Errors in root measurements in relation to techniques available are discussed in a later section (section 10).

In addition to the studies of root growth, root number and site of production were also examined. As Milthorpe and Moorby (1974) have pointed out, this is a measurement rarely included in root growth

Fig. 5.1. The relationship between root length and root dry weight

(Samples from 0-50cm, harvests 6,7,8, and 9)

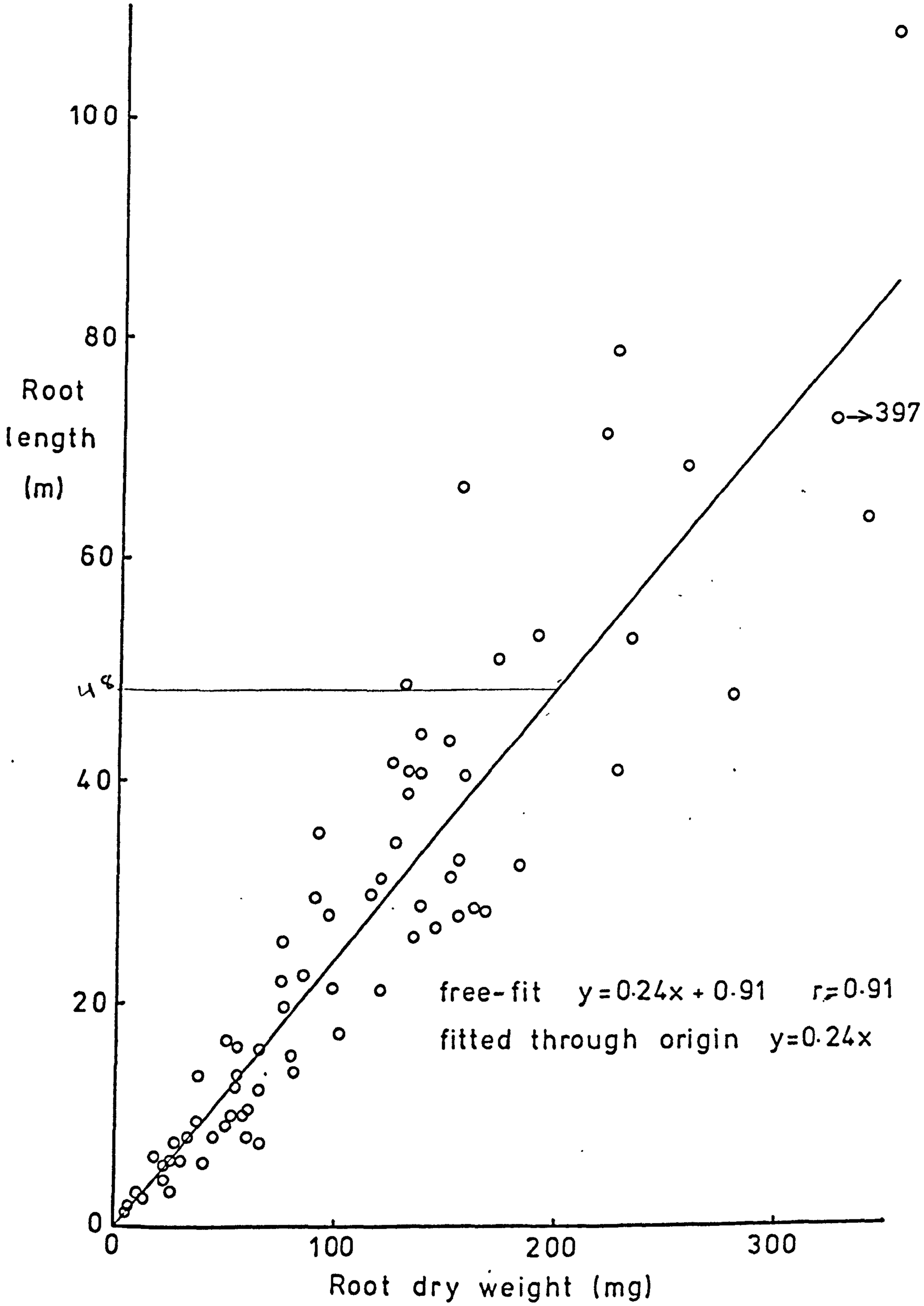


Table 5.1 Comparison of measured root length to that estimated using the regression equation (Samples from Harvest 18)

Sample	Measured length (m)	Estimated length (m)	$\frac{\text{Measured}}{\text{Estimated}}$
1	51.5	66.3	0.78
2	32.9	39.3	0.84
3	9.0	9.4	0.96
4	5.2	4.8	1.08
5	9.9	10.9	0.91
6	10.3	9.4	1.09
7	10.0	10.6	0.94
8	34.7	43.9	0.79
9	19.8	16.4	1.21
10	6.9	8.2	0.84

investigations and little information, particularly on nodal roots, is available. Plants dug up as part of the shoot development programme from area g.a. (fig 4.1.) were washed free of soil and the number of root axes counted. Tiller number, seminal root number and nodal root number were recorded for ten plants and the site of origin of the nodal axes noted.

5.2. Root axis production of winter wheat

In the study of seminal and nodal root production only visible root axes were counted: other axes may have been differentiated within the plant but were not visible to the naked eye. Table 5.2. shows the results obtained by averaging the observations on ten plants at each harvest. Very little variation was found between plants in the rate at which root axes were produced and most of the differences between plants occurred because of varying tiller numbers. All of the plants had produced 6 seminal axes by mid-February and this number remained fairly constant until the beginning of May when, because of its constancy, counting ceased. No plant possessed more than 7 seminal axes at anytime and none less than 5 after day 118.

Nodal root axis count includes the coleoptile node roots produced close to the coleorhiza but these are clearly distinguishable from the earlier seminal roots (fig.5.2). Two root axes were usually produced from this site but occasional plants possessed only one. Nodal axis production proceeds steadily from mid-February until the middle of April (day 174) but despite the increase in axis number it is not until the beginning of April (day 153) that the axes begin to grow and branch profusely. It was observed that branching did not occur until the axis was relatively elongated (5 - 10 cm). Between the end of April and the middle of May (day 202) nodal axis number

Table 5.2 Production of root axes of winter wheat

Date	Days after sowing	No. tillers	No. seminal axes	No. nodal axes	Notes
1974 2 Dec	33		5.0		4th & 5th seminal just visible (length <1 cm). Primary root brnnching
1975 18 Feb	111	3.5	5.6	2.7	Total nodal root length 10 cm No branching
25	118	3.2	6.0	3.1	Total nodal root length 14 cm
4 March	125	4.6	6.1	5.5	Total nodal root length 21 cm
11	132	3.5	6.4	5.9	Total nodal root length 24 cm 35% of nodal roots branching
18	139	3.9	6.4	7.1	Nodal root length now impossible to estimate. 38% of nodal roots branching
25	146	4.1	6.7	8.5	Stems slightly yellow. 33% of nodal roots branching
1 April	153	3.2	6.4	7.8	37% of nodal roots branching
8	160	4.4	6.0	10.6	41% of nodal roots branching
17	167	3.3	6.1	11.6	54% of nodal roots branching
22	174	3.3	6.0	13.3	53% of nodal roots branching
29	181	2.4	6.2	12.3	Tillers are yellowing 70% of nodal roots branching
6 May	188	2.4	6.3	15.0	83% of nodal roots branching
13	195	1.7		20.4	Seminal root number is not varying. Count ceased. 68% of nodal roots branching
20	202	1.6		25.5	All plants show 10 roots on nodes 1-5
27	209	1.1		27.3	All plants show six roots on 6th node
3 June	216	0.8		26.3	
10	223	0.3		24.5	All plants have 10 roots on nodes 1-5 6 roots on node 6 and an average 4.7 roots on node 7

Fig. 5.2. The site of production of root axes

doubles and all of the plants possess 10 axes on nodes 1 - 5 inclusive. The site of production of these roots is difficult to determine because the nodes are very close to each other. The space between nodes 5 and 6 is, however, elongated and axes from node 6 are clearly visible. Counting downwards from the leaves, each node could be numbered and it appeared that nodes 1 - 5 each produced two nodal axes.

At the end of May (day 209) root production was complete and all plants possessed 6 axes at node 6 and at the close of the measurements (day 223) many plants also possessed 6 axes at node 7 although the average was 4.7. The root axes from nodes 6 and 7 were rarely longer than 5 cm and none were branched. Node 7 was typically 1 - 2 cm above the soil surface and node 6 0.5 cm above the surface.

These remarks apply to observations made on the main stems. Because of the paucity of tillers surviving beyond the end of April, few observations were made on tiller root axis production. However, tillers present on 3 June commonly showed 5 (occasionally 6) roots on nodes 1 - 5 (ie. 1 root per node), 6 roots on node 6 and up to 6 roots from node 7. Coleoptile tillers produced up to 6 or 7 roots from nodes 1 - 5.

The death of tillers from mid-April onwards is clearly visible in table 5.2 as are its effects on root production. Between days 174 and 181 nodal root number falls slightly but then increases rapidly while the percentage of branching roots increases steadily but then falls between days 188 and 195. The period of rapid tiller senescence, then, is accompanied by death of nodal roots (only fleetingly visible) but the balance between number per se and number branching might cause a temporary decrease in root weight in the bulk soil. The criterion of tiller death used in this study was the

complete yellowing of the whole tiller and not, as in the shoot development studies, the yellowing of the youngest leaf tip (Gallagher, pers.comm.). This accounts for the difference in live tiller number with time in the two studies but complete yellowing of the shoot is probably necessary before root death results.

5.3. Root axis production of winter wheat on the treatment plots

Plants grown on the wet plot showed identical root production to the normal crop. On the dry plot, plants possessed fewer nodal roots: nodes 1 - 5 possessed 10 roots but 6 and 7 nodes rarely produced roots. The maximum number of roots observed on node 6 was 3 and on node 7, 2. Lack of nodal root production from nodes 6 and 7 seemed to be associated with the increased lodging found with this treatment. These plants were more readily blown about by the wind whereas the thick, stubby nature of roots produced by the normal and wet treatment plants seemed to restrict movement of the stem.

Nodal root production in the guttered plots was similar to the main treatment plots but none were observed to grow out of the guttering. Figure 5.3. taken at final harvest (day 279), shows the effectiveness of the guttering in restricting nodal root growth.

5.4. Root growth of winter wheat

During the growth of the crop, sixteen root harvests were performed as outlined in section 4.3; harvest dates are shown in table 4.1. After length and dry weight had been determined (section 5.1) the results were tabulated and means derived for the four replicates. To enable comparisons between harvests, the results have been presented as values of dry weight or length of roots per unit ground area or unit volume of soil - this overcomes the problem

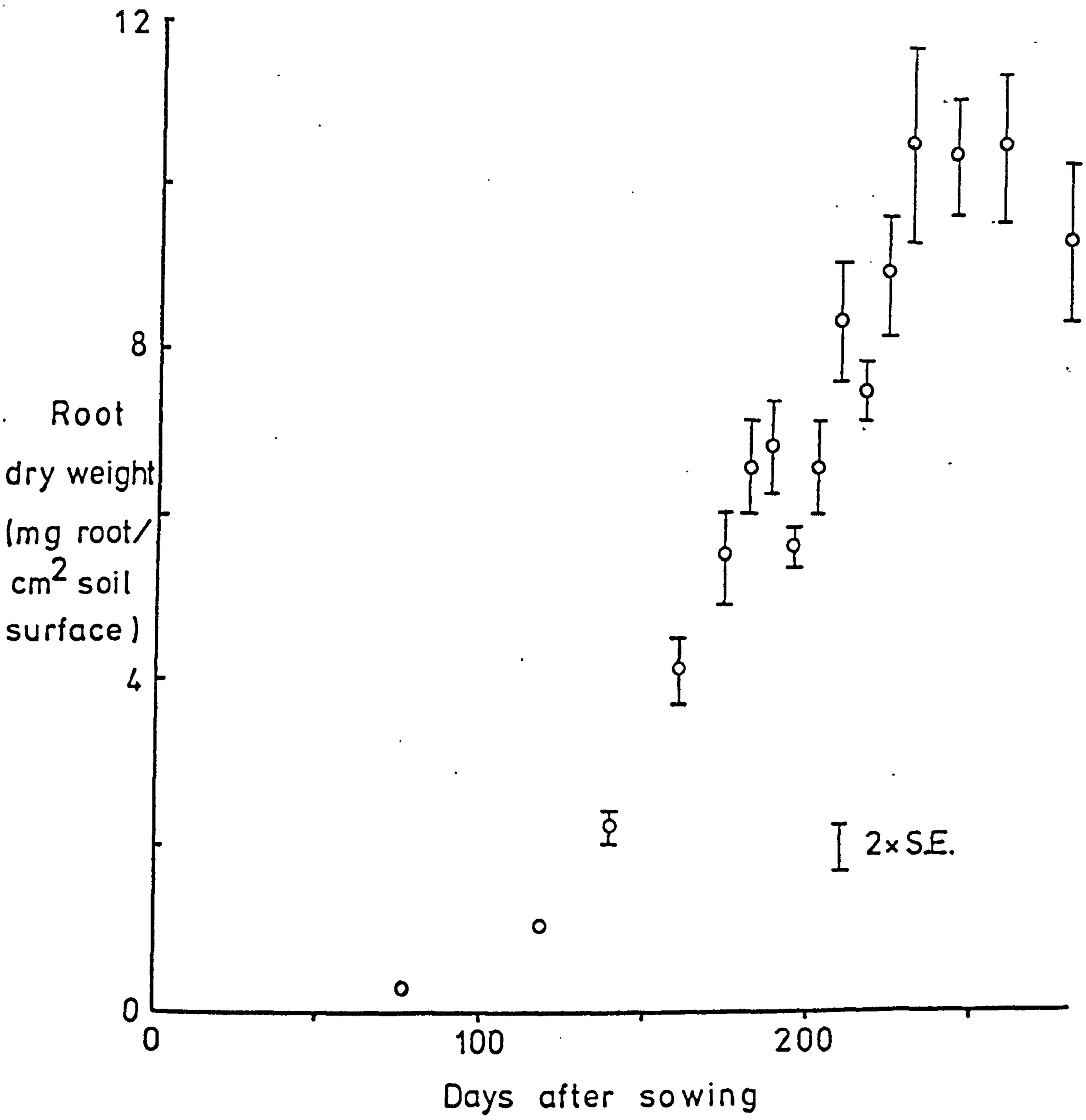
Fig. 5.3. Root growth of guttered plants at final harvest

of different sample sizes.

Figure 5.4.shows the dry weight of root per unit ground area. Since the normal crop root length estimates at 0 - 50 cm after harvest 10 are based on regression, discussion will be restricted mainly to dry weight. Root dry weight is seen to increase exponentially until day 160 and then essentially linearly until day 230 (anthesis). Thereafter root weight remains constant at 10.5 mg root per cm^2 soil surface for 4 weeks (root length 234 cm root per cm^2 soil surface) and then appears to decline to about 9.3 mg root per cm^2 soil surface (root length 205 cm per cm^2 soil surface) at final harvest. This cessation of root dry matter production and decline in root dry weight at or around anthesis has been observed by a number of previous authors working with cereal crops (Mengel and Barber, 1974a;Wel bank *et al* 1974; Biscoe *et al* 1975b).

Two checks to root growth are apparent between days 188 to 195 and between days 209 to 216. The latter is not very severe (a reduction from 8.3 to 7.7 mg root per cm) and considering the errors of measurement is probably non-significant. However, the former is distinct and occurs at a time when a number of factors might be responsible. First, the change in sampling procedure from two cores to one core per replicate might be partly responsible although it is unlikely to be solely responsible. Secondly, herbicide applied on day 176 may have reduced the number of weed roots in the sample. This is again unlikely to be a major cause since the weed infestation of the crop was not large and, where present, was largely grass which remained unharmed by the herbicide. The factor thought most likely is the substantial reduction in tiller number at this time (as mentioned in section 5.2). Evidence to support this is that the weight decrease is restricted to the topsoil where nodal roots of

Fig. 5.4. The growth of the root system



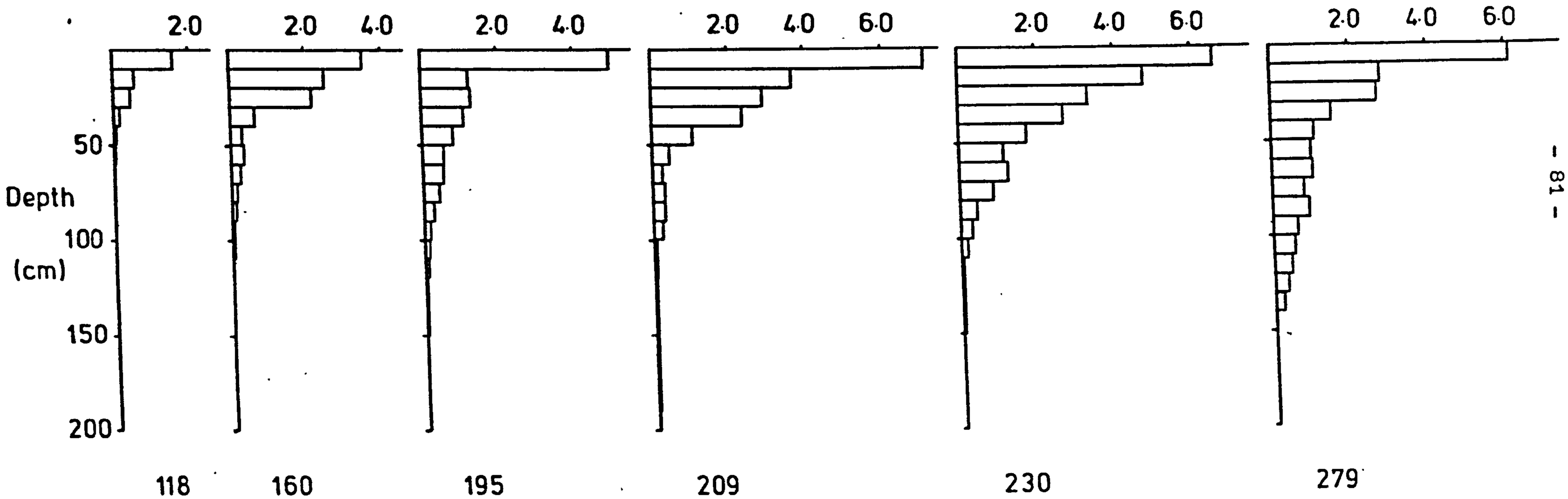
tillers are most likely to be present; roots beyond 30 cm depth are little affected (fig. 5.6).

Harvesting roots in discrete layers enables the distribution of roots throughout the soil profile to be examined. Data from selected harvests are presented in fig. 5. 5. and show that at all harvests the 0 - 10 cm layer contained more length than other layers. In general, the length of root per unit volume of soil decreases in an exponential manner down the profile as described by other workers (Welbank et al 1974).

On 25 February (day 118), roots are present to a depth of 60 cm and gradually extend down the profile to reach 190 cm by 27 May (day 209). Some roots were found in one of the 190 - 200 cm layer replicates on day 209 giving an average extension rate for the period of 1.5 cm per day. The extension rate during the winter growth up to day 118 was 0.5 cm per day. Root extension may have occurred beyond 200 cm But this cannot be stated with certainty because 200 cm was the sampling limit. However, the quantity of roots at this depth did not increase beyond 27 May and roots were unbranched. Maximum root depth is not shown in fig.5.5. because stones in the profile meant that complete root profiles were frequently unobtainable - values in the figure are means of four replicates.

Between 27 May (day 209) and 17 June (day 230) root length in the 0 - 10 cm layer remained almost constant at an L_V (cm root / cm^3 soil) of 6.8. Root growth during this period is restricted to depths below this and total root length almost doubles. The roots appear to produce a framework from which later lateral roots expand. There is a clear indication that growth occurs sequentially down the profile and roots lower in the profile do not produce laterals before much greater branching higher up.

Fig.5.5. Root length profiles under winter wheat - normal crop



For discussion of errors see section IO.I.I. Typical C.V. for topsoil samples was 20-30%; deeper layers 80-90%.

Following anthesis, total length per unit volume of soil in the top layers decreases markedly particularly in the 10 - 20 cm layer where L_V declines from 4.4 to 2.4 at final harvest (day 279). In the same period, however, root length below 80 cm increases by a factor of almost 4 in some layers (100 - 110 cm layer, 0.15 to 0.55cm root / cm soil). Thus while total root dry weight or length tends to decrease after anthesis, some roots are obviously continuing to grow.

The increased qudntity of roots at depth after anthesis can also be seen in fig.5.6. Throughout much of the season, roots in the 0 - 30 cm layers account for approximately 65% of total root dry weight; 30 - 60 cm layer, 20 - 25%; 60 - 100 cm layer, 10 - 15% and 100 - 200 cm layer, 1-4%. After anthesis the proportion of roots below 100 cm increases to a value of 8% at final harvest. Welbank et al (1974) report tnat as much as 80% of the roots recovered at about anthesis were in the top 15 cm of soil. The present study shows a lower percentage than this but the values of L_V shown in fig.5.5. are typical of values quoted elsewhere (Barley, 1970). Root dry weight at anthesis is similar to that measured by Welbank et al (1974)(105 gm^{-2} compared with 120 gm^{-2} for a number of winter wheat varieties) and by Welbank and Williams (1968) with barley but only one half tnat with barley shown by Biscoe et al (1975b).

5.5. Root growth of winter wheat on the treatment plots

Only a limited number of harvests were performed on the treatment plots because of their restricted size. Mean figures of total dry weight and root length per unit soil surface area are given in table 5.3 and the number of replicates used to calculate each mean is shown in brackets. Only one sample was available for harvests on the guttered plots.

Fig. 5.6. The percentage of total root dry weight in selected soil layers

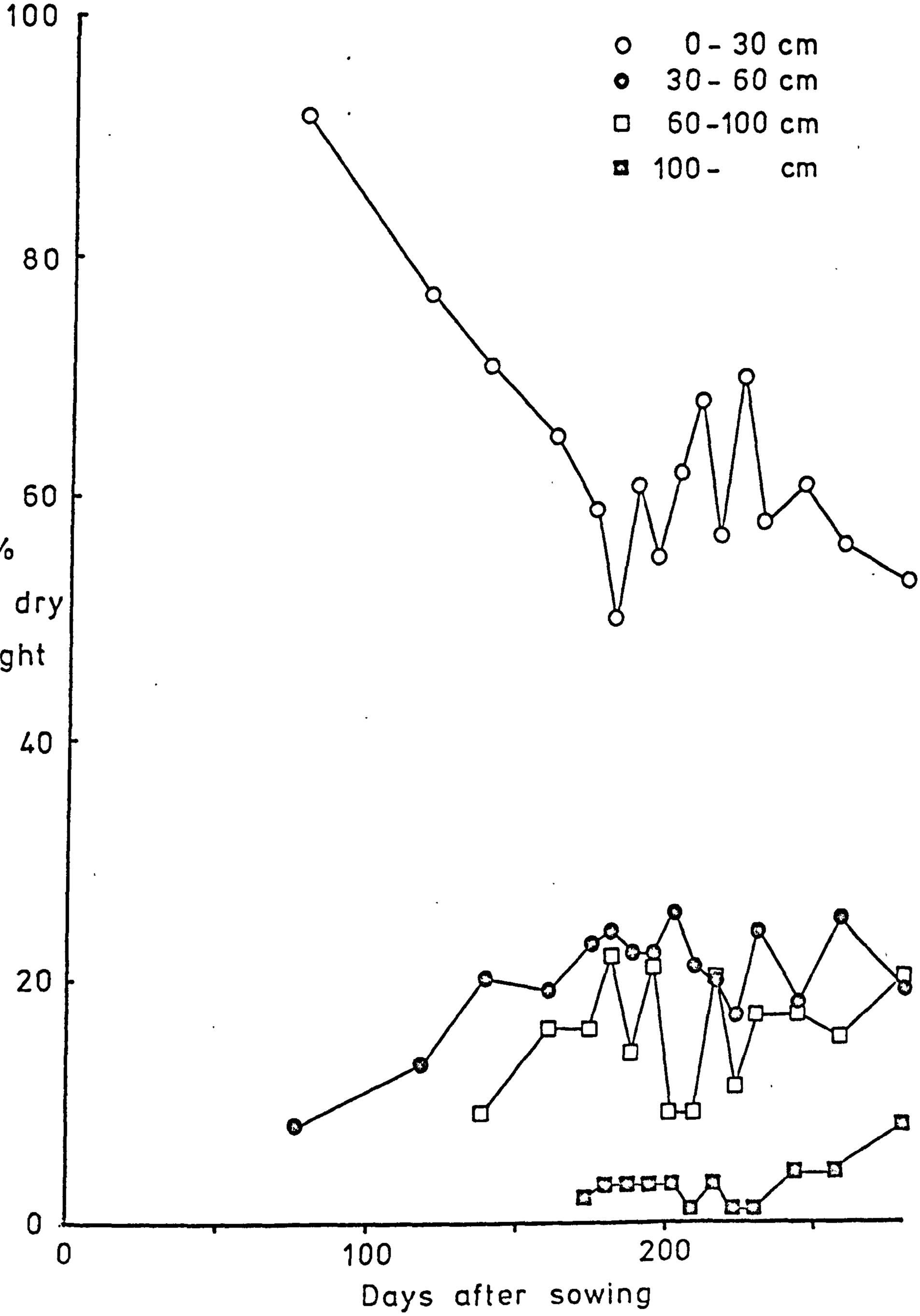


Table 5.3 Root growth of winter wheat on the treatment plots

Harvest Number	Days after sowing	Treatment					
		Normal	Dry	Wet	Normal Guttered	Dry Guttered	Wet Guttered
11	195	1 5.7 2 115	6.4 114 (2)				
13	209	1 8.3 2 186	9.7 130 (1)				
16	230	1 10.5 2 234	9.2 174 (3)	17.6 303 (3)	12.0 223 (1)	5.8 100 (1)	14.5 252 (1)
20	258	1 10.4 2 223	13.4 219 (1)	15.5 322 (1)			
23	279	1 9.3 2 205	15.1 263 (3)	19.4 339 (3)	13.0 231 (1)	9.8 196 (1)	20.0 252 (1)

Line 1: mg root per cm^2 soil surface

Line 2: cm root per cm^2 soil surface

The numbers in brackets are the number of replicates used to calculate the mean.

For discussion of errors, see section IO.I.I.

Keeping the topsoil dry causes an initial higher root dry weight (days 195 and 209) but at anthesis (day 230) dry weight is less than the normal crop. The initial higher dry weight on the dry plots was surprising but when the root length measurements were studied, they were all seen to be lower than those of the normal crop. Two possible explanations of this observation might be that (1) drying the soil causes thicker roots than normal or (2) that production of fine roots is reduced. In general, then, drying the soil reduces root length but its effects on dry weight are dependent on the time of observation. When the soil is re-wetted by irrigation on day 230, root growth re-commences (root length increases from 174 to 263 cm / cm^3 between days 230 and 279) and at final harvest more roots (weight and length) were harvested compared to the normal crop.

Maintaining the soil almost at field capacity resulted in root dry weight and length at day 230 being almost one and one half times that of normal crop. In contrast to the dry plot, however, growth after anthesis is limited and root length increases by only 10% from 303 cm root /cm^3 to 339 cm root / cm^3.

Results from the guttered sub-plots are more difficult to interpret because only one sample was taken at each harvest. In general, root length under the normal plants was the same as for the non-guttered plants at both day 230 and final harvest. This means that the seminal roots must have grown more under these circumstances to compensate for the lack of nodal roots. Between anthesis and final harvest, a small increase in dry weight and length was found but this apparent increase could be accounted for by experimental error; because of stones this particular root sample was very difficult to obtain and a larger volume of soil than usual was extracted.

On the dry plot, root growth of guttered plants at day230 was substantially less (approx. 2/3rds) than the non-guttered. After irrigation, root length increased as with the main treatment plot but seminal root growth did not fully compensate for the lack of nodal roots even at final harvest; they did, however, have the same final harvest length as the normal crop.

The plants on the wet plot show another pattern of growth. At day 230, there was less dry weight and length compared to the non-guttered plants (252 cm / cm^3; 303 cm / cm^3) but after day 230, the roots continued to grow rapidly so that at final harvest there was as much root material under the guttered as the non-guttered plants (352 cm / cm^3; 339 cm / cm^3).

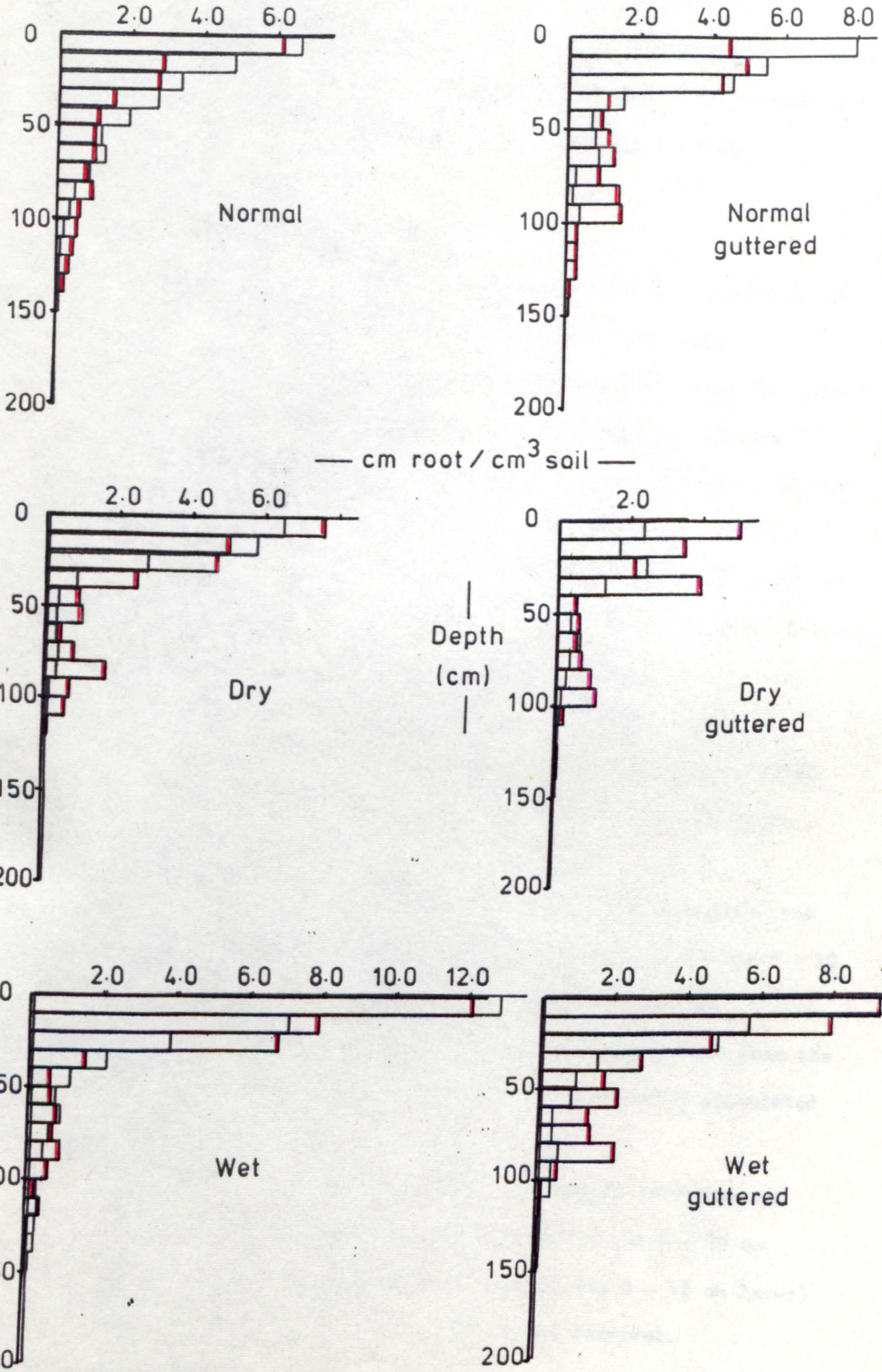
The root profiles (figs. 5.7. and 5.8.) show the distribution of roots in the treatment plots at day 230 and final harvest. On day 230, the normal and dry treatments had similar profiles but the dry plot had less root below 30 cm than the normal plot. The effect of irrigation on the wet plot is clearly visible and root density in the top 30 cm was almost double that of the normal crop (L_V0 - 10 cm is 12.4 cm per cm^3 on the wet plot and 6.3 cm per cm^3 on the normal plot). The percentage of total root weight in the 0 - 30 cm layer is approximately 75% for the wet plot compared with 85% for the dry plot and 60% for the normal plot.

Growing the plants in the gutters had little effect on the distribution profiles of the normal and wet treatments but root growth in the top 30 cm of the dry plot was much reduced when compared to the non-guttered plants. This effect was probably due to the restriction of seminal root branching caused by topsoil drying.

At final harvest (fig,5,8,), root density of the dry guttered plots in the 0 - 30 cm layer had almost doubled since anthesis. This increased root growth in the top layers was in contrast to all other

Fig. 5.8. A comparison of root profiles under winter wheat

Day 280



treatments (except the 10 - 20 cm layer of the wet guttered plot) where root density had decreased. All treatments showed an increase in root density beyond 50 cm between anthesis and final harvest and this was particularly marked in the wet guttered treatment.

5.6. Summary of results

1) Winter wheat (cv Maris Huntsman) produces six (occasionally seven) seminal axes and two coleoptile nodal axes.
2) Main stems produce 10 nodal axes from nodes 1 to 5 (two per node), 6 from node 6 and up to 6 from node 7. Tillers produce 5 nodal axes from nodes 1 - 5 (one per node), 6 from node 6 and up to 6 from node 7. The production of nodal root axes from nodes 1 - 5 was unaffected by soil drying but production from nodes 6 and 7 was reduced and lodging occurred.
3) Total root dry weight increased exponentially until the beginning of April and then almost linearly to reach a maximum of 105 g per m^2 at anthesis. After anthesis total root dry weight declined but continued root growth below 80 cm was clearly visible.
4) Roots extended to 2 m by the end of May with a maximum root density of approximately 7 cm root per cm^3 soil in the 0 - 10 cm layer decreasing exponentially down the profile.
5) Keeping the topsoil dry resulted in less root growth than the normal crop but subsequent irrigation at anthesis stimulated growth.
6) Maintaining a wet topsoil caused substantial increases in root dry weight and length particularly in the 0 - 30 cm layer (L_V 12.5 cm root per cm^3 soil in the 0 - 10 cm layer) and no loss of roots after anthesis was observed.

7) Except where the topsoil was allowed to dry out, additional seminal root growth under the guttered plots by final harvest compensated for the loss of nodal roots.

8) Soil water status has an important influence on the root growth of winter wheat.

6. WINTER WHEAT SHOOT GROWTH

6.1. Sample Preparation

The aerial portion of the crop was sampled on twenty-three occassions between sowing and final harvest at three weekly intervals during the winter and weekly from mid-April (table 4.1.). Field sampling was performed as described in section 4.3. and the plants stored for up to one week at 3°C until growth analysis measurements were made for the Ceres project. The plants were separated into their various components and after measuring size and dry weight, the components were bulked for nutrient analysis in three categories as follows:

Leaves - all yellow and green leaf laminae plus senescent tillers.

Stems - all yellow and green stems and leaf sheaths hypocotyls and peduncles.

Ears - rachis and grain.

The number of plants in each sample was noted and dry weight expressed per plant to facilitate the later calculation of nutrient inflow. The contribution of roots to total plant dry weight was obtained from the root dry weight measurements (fig. 5.4.) using a measured average plant density of 250 plants per m^2: for harvests when roots were not sampled, an estimate of dry weight was obtained by grapnical interpolation.

At anthesis and final harvest, plant samples were removed from the treatment plots (section 4.3.) and used for measurements of dry matter distribution and grain yield. For comparison, grain growth measurements were made on samples of normal crop taken from area g.a. (fig. 4.1.). Twenty stems were used from each treatment at anthesis for plant dry weight, total and fertile spikelet numbers; other

measurements taken are not relevant to this project. Similarly, at final harvest, twenty stems were used for plant dry weight, spikelet number and grain number and dry weight.

6.2. Shoot growth of winter wheat

Figure 6.1. shows changes in total dry weight per wheat plant from days 34 to 279 with changes in component dry weights shown from day 160. Initially dry weight increases exponentially but from about day 200 growth is approximately linear and most of the increase in dry weight (75%) occurs during this linear phase. The change from exponential to linear growth is marked by a short period of slow dry matter production and coincides with the visible signs of tiller death reported previously (section 5.2.). Dry weight increases linearly until day 237, shortly after anthesis, when the maximum stem weight was recorded. Of the total dry weight, stems account for almost 75% but this percentage decreases as the ears commence growth. Leaf dry weight is small compared to the stem, and during the linear growth phase, increases by only one half (0.55g per plant to 0. 78g per plant).

After anthesis the rate of dry matter production is gradually reduced and from day 251, dry weight is almost constant. Some caution is necessary when examining the data after anthesis since the weight on day 258 was anomolously high. However, dry weight measurement made twice weekly in another area of the crop do not show this peculiarly high value and indicate a similar "levelling-off" of plant dry weight.

Total dry weight at final harvest was 1283g per m^2 (shoot plus root weight, 1380 g per m^2) with 533 g per m^2 grain.

Root weight as a fraction of total weight (fig.6.2.) was large in the winter growth period. The first two points are based on less certain data than the remainder and total plant weight showed an

Fig. 6.1. The growth of the shoot

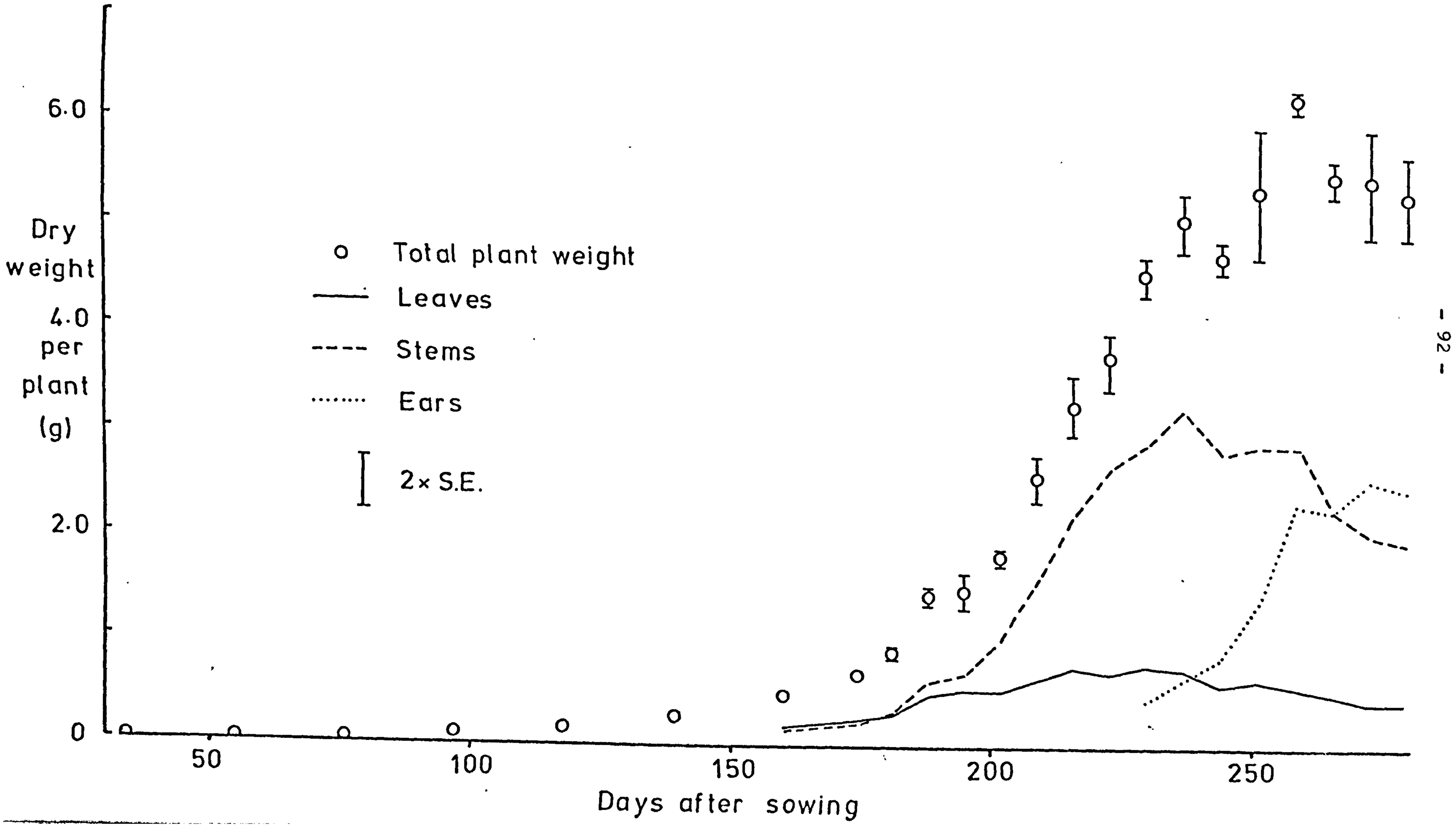
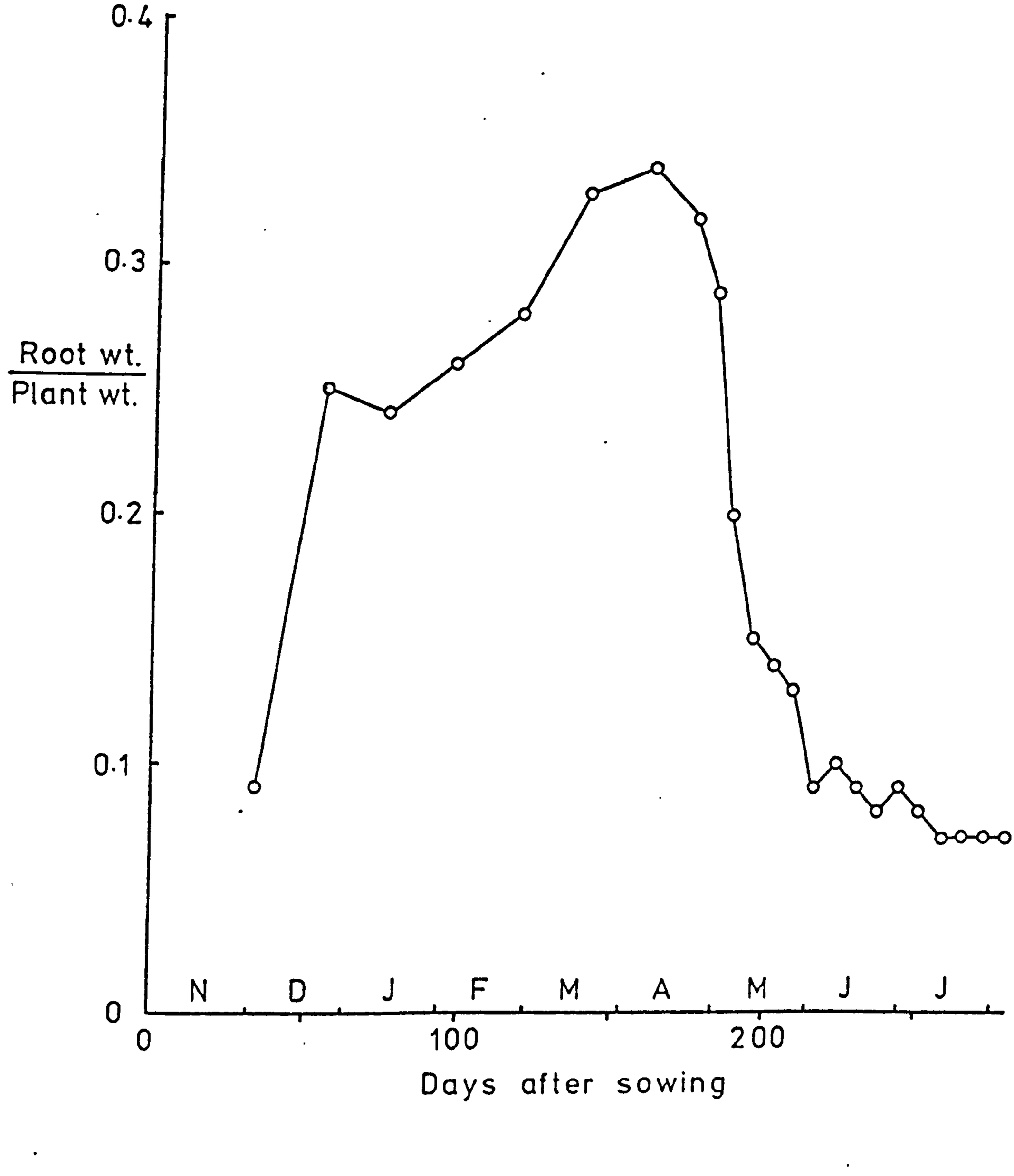


Fig.6.2. The changes in root dry weight as a fraction of total plant dry weight with time



apparent decline in this period. Throughout the winter, root weight is between 0.25 and 0.34 of the total dry weight. Between days 160 and 216 the fraction decreases to 0.09 coincident with the start of the linear phase of shoot growth. After a further small reduction, the fraction remains constant at 0.07. These changes in root weight as a fraction of total weight reflect the changes in assimilate distribution between root and shoot.

6.3. Shoot growth of winter wheat on the treatment plots

Counting the hypocotyls of treatment plot plants gave a substantially lower estimate of plant number per double metre row than the average plant number determined on the g.a. area for the normal crop (table 6.1., column 1). This meant that when plant component weights were calculated on a per plant basis (column 3), plants on the treatment plots (particularly the guttered plots) were heavier than the normal field crop. Counts of ear number per double metre row were similar for all the main plots and also similar, but lower, on the guttered plots (column 2) suggesting that comparison of results on an area basis would not show the normal crop as the smallest. Because of the difficulties in assessing plant numbers from hypocotyls and in extrapolating an average plant number per double metre for the normal crop to this particular area, results have been calculated on an area basis (m^2) rather than per plant.

At anthesis, the total shoot weight of the normal crop (945g per m^2) is greater than the dry (726g per m^2) but less than the wet (1002g per m^2). The guttered crops show similar dry weight ranking but in all treatments, the guttered crops weigh less than the normal and the corresponding main treatment crop. Green leaf weight for all treatments is approximately equal and the main difference between treatments is

Table 6.1 Plant dry weight components and spikelet number at anthesis

Treatment	Plant no. per double metre row	Ear no. per double metre row	Total shoot weight per plant (g)		Dry weight per m^2 (g)					Measurements on 20 ears	
					Ears	Stems	Green leaves	Total shoot weight		Spikelet no.	Fertile spikelet no.
Normal*	89	115	4.15		108	728	109	945		420	281
Dry	61	110	4.22		91	535	100	726		436	287
Wet	80	124	4.45		109	780	113	1002		465	291
Normal Guttered	63	92	4.56		104	605	105	814		469	277
Dry Guttered	54	94	4.47		90	481	108	678		420	297
Wet Guttered	58	103	5.16		101	638	103	842		444	310

*Dry weight data for normal harvest are based on growth analysis measurements amended to exclude yellow leaves and senescent tillers; assumes 250 plants per m^2.

stem weight. Ear weight for the normal and wet treatments and normal and wet guttered plots is very similar but is depressed by about 10% on the dry and the dry guttered plots. There were no significant treatment differences in total and fertile spikelet number per ear.

When the covers were removed from the dry plot at anthesis, the ears were touching the plastic roof and the crop was taller than the surrounding crop. Measurements of peduncle length (normal, 28mm; dry, 109mm; wet, 30mm) showed that the cover had increased extension growth. This was probably only important in the last week before anthesis when possibly air movement under the covers was restricted resulting in a higher temperature around the ear.

Yield components at maturity are shown in table 6.2. The grain weight of the control crop (493g per m^2 - plants dug up and replanted; section 4.3.) is greater than the normal guttered crop (446g per m^2) but less than the normal crop (533g per m^2). Unfortunately, when fertiliser was spread, one wheel of the tractor ran over some of the plants in the control area and this may have reduced yield. For this reason, no definite conclusion can be drawn on the effect of digging up plants but it seems most likely that treatment effects measured on the guttered plots were due to the absence of nodal roots rather than the initial digging up of the plants.

Grain yield is affected by the treatments and the normal crop (533g per m^2) was heavier than the dry (441g per m^2) but less than the wet (576g per m^2). The guttered crops showed the same ranking with wet > normal > dry and in all cases the yield was lower than the corresponding main treatment crop. Measurements made on 20 ears show yields similar to those calculated using all ears and therefore give a good indication of grain yield components (the 20 ears used to assess wet guttered components are not as representative as other treatments).

Table 6.2 Plant dry weight components at final harvest

Treatment	Plant no. per double metre row	Ear no.per double metre row	Dry weight per m^2 (g)				Harvest Index	Measurements on 20 ears						
			Leaf & Stem	Ear	Grain	Total shoot		Grain no.	Shriv-elled grain no.	Grain weight (g)	Grain no.per ear	Grain weight per ear (g)	Mean wt. per grain (mg)	Yield ($g\ m^{-2}$)
Normal	89	115	638	645	533	1283	0.45	654	4	32.80	32.7	1.64	50.3	532
Dry	60	110	559	547	441	1106	0.41	639	26	30.12	32.0	1.51	47.2	467
Wet	74	128	648	693	576	1341	0.44	622	6	30.48	31.1	1.53	49.0	549
Normal Guttered	65	93	492	525	446	1017	0.46	736	4	34.86	36.8	1.74	47.4	456
Dry Guttered	55	94	458	449	363	907	0.41	662	97	27.12	33.1	1.36	41.0	359
Wet Guttered	54	98	503	577	467	1080	0.45	784	4	39.53	39.2	1.98	50.4	544
Control	65	108	532	612	493	1144	0.44	766	3	37.78	38.3	1.89	49.3	493

The reason for the lower yields on the guttered plots compared with the main plots lies in the lower number of ears per unit ground area. Twenty ear measurements show that the number of grains per ear is larger on the guttered plots and that except for the dry guttered plot, which has a large number of shrivelled grain (15% of the total), the mean weight per grain is the same throughout. The larger number of grains per ear for the guttered crops is, then, reflected in a similarly larger grain weight per ear. This advantage of having bigger ears is not manifest in a larger grain yield per m^2 , however, because of the lower number of ears per m^2.

The smaller number of ears per unit area compared with the main treatment crops arises directly from the lower plant density since the number of ear-bearing tillers per plant is the same in both guttered and main treatment crops (approximately 1.3 tillers per plant for normal and 1.7 tillers per plant for wet and dry). In short, although the ground area per plant is greater for the guttered plots, no additional tillers were produced, only larger ears.

The differences between the normal, dry and wet crops can also be explained largely in terms of ear numbers per m^2 since the number of grains per ear and the mean weight per grain are almost identical for each. This applies particularly to the yields of normal and wet crop but the reduction in dry crop yield is aided by the larger number of shrivelled grains. Similarly differences between the guttered crops result from the number of shrivelled grains on the dry treatment producing a lower mean weight per grain and hence a lower yield than on the normal and wet guttered crops. The yields of normal guttered and wet guttered crops are similar when all ears per double metre are used, but from the 20 ear measurements the wet guttered yield is larger because the grain numbers and mean grain weights are both higher.

Yield reduction of both dry and dry guttered crops was evident despite their irrigation at anthesis. This leads to the conclusion that some elements of yield, in particular the number of grains that will fill, may be influenced by soil water status prior to anthesis.

6.4. Summary of results

1) Total plant dry weight of the field crop increased until approximately four weeks before final harvest (day 251) and gave a final harvest weight of 5.35g per plant and 533g per m^2 grain.

2) Maintaining the soil water content near field capacity until anthesis resulted in higher grain yield than the normal crop.

3) Allowing the soil to dry without replenishment of water prior to anthesis resulted in reduced straw and grain yields.

4) Restricting nodal root growth resulted in lower straw and grain yields than the normal and corresponding main treatment crops and arose from the lower number of ears per unit ground area.

5) The dry and dry guttered plants had greater numbers of shrivelled grains (15% of the dry guttered grain) than the normal and wet treatments and this was the main factor reducing their yield.

6) Grain yield was affected by the pre-anthesis soil water status.

7. SOIL WATER REGIMES

7.1. Introduction

Soil water status was monitored using tensiometers, thermocouple psycnrometers and a neutron probe; their distribution in the plots has been described in Section 4.3.

Tensiometers were constructed after Webster's (1966) design and installed in tne field by augering a hole 1cm in diameter to the required depth and pushing the tensiometer into it to give a tight fit. Tne porous pod and nylon tube of the tensiometer were then filled with water and connected to a mercury manometer ensuring that all air was purged between the pod and the mercury column. More detailed descriptions of the technique are given by Williams (1971) and Fry (1975).

Provided that the tensiometers were carefully installed without large gaps between the pod and soil, they could be used without much maintainance tnroughout the season. Readings were taken in the early morning to avoid errors due to diurnal variation in temperature (Fry, 1975). Using this technique, soil matric potentials to - 0.8 bar could be measured but for lower water potentials, thermocouple psychrometers were used. The thermocouple psychrometers (P -51 Wescor type) were installed by augering to the required depth with a Jarratt auger. Ten cm increments of soil were placed in separate polythene bags, the psychrometers inserted into the side of the hole and the hole refilled with the original soil. When the soil was known to be drier than - 0.8 bar, the psychrometers were read with a Keithley microvoltmeter modified to provide a cooling current and an internal electronic reference of 0°C. Soil temperature was measured shortly before the psychrometric reading using an additional built-in copper - constantan thermocouple (mV / 0.04 $\simeq$ °C). The thermal equilibrium of the thermocouple psychrometer was checked and any

small e.m.f. zeroed out before passing a cooling current of 5m A for 15 seconds. The plateau output was recorded and corrected to 20 °C from the relationship (Brown, 1970)

Corrected reading at 20 °C = Reading / (0.376+0.032 T)

where T is the measured psychrometer temperature in degrees C.

The water potential as measured by the thermocouple psychrometer is the sum of the matric and osmotic potentials. For this soil, the osmotic potential component was small as indicated by the electrical conductivity of saturation extracts (about 0.5 mmhos / cm). At saturation and -15 bars water potential, the volumetric water contents of the topsoil are approximately 36% and 12% respectively. Considering all solutes to remain in solution, the osmotic potential would be equivalent to only - 0.54 bar at - 15 bars water potential measured by the thermo-couple psychrometer.

Volumetric soil water content was measured with a modified Wallingford probe (Bell, 1973). Aluminium access tubes (4 cm i.d., 0.3 cm wall thickness) were installed to 180 cm by augering a hole slightly smaller than the tube, reaming with a hollow steel pipe and then driving the tube into the slightly undersized hole with a sledge-hammer. The top of the tube was cut off with a hacksaw 5cm above the soil surface and a rubber bung inserted to close the tube. To reduce soil surface damage during installation, all operations were performed while standing on a board placed around the hole. Horizons were monitored with the probe at 10 cm intervals starting at the base of the profile.

Calibration of the instrument and the errors associated with the method have been fully discussed by Williams (1971).

The main sources of error are:

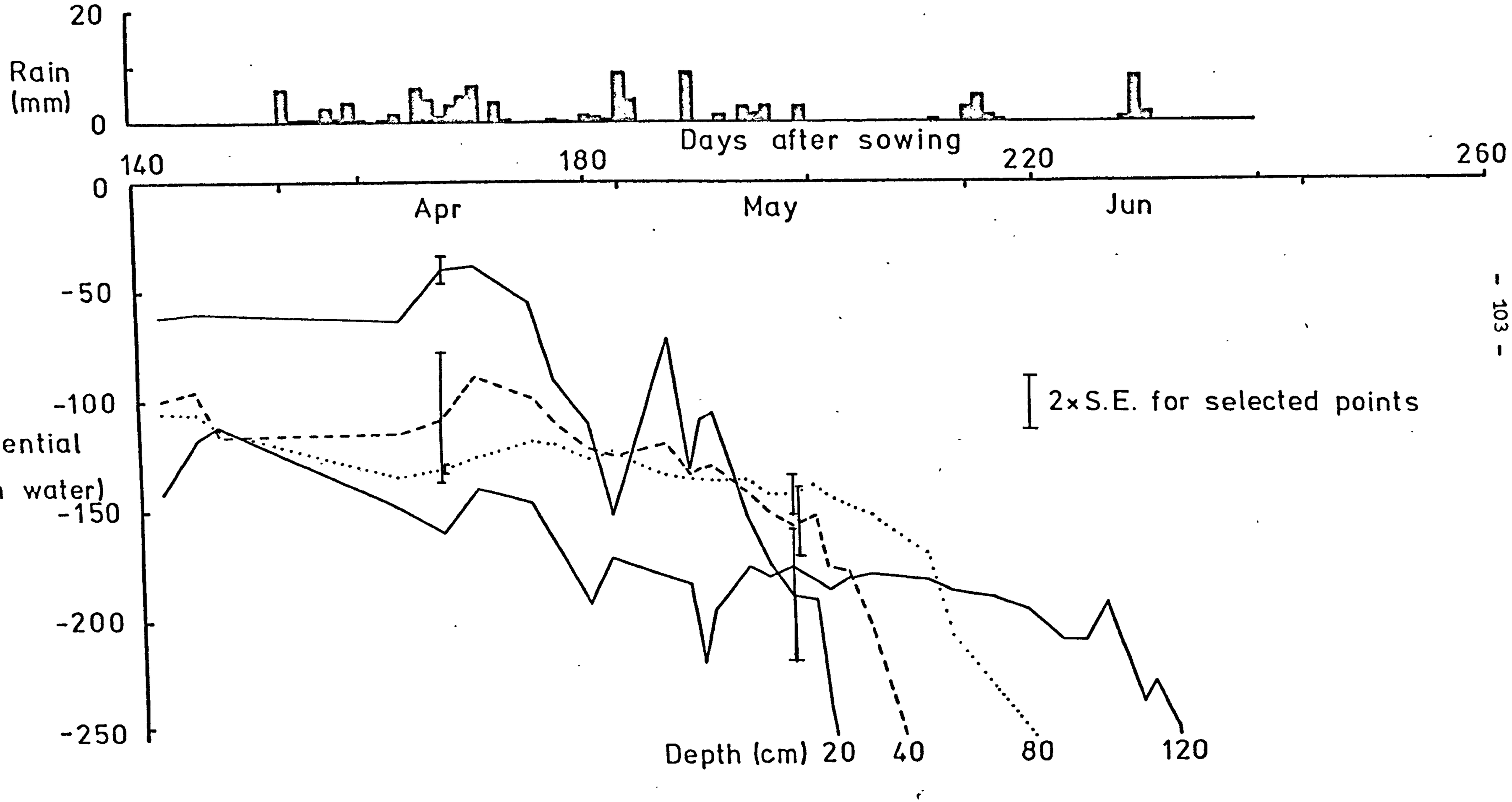
1) Systematic	a) Calibration curve	-	± 4mm in estimated soil storage change up to maximum soil water deficit.
	b) Installation	-	some voids around the access tube are inevitable.
	c) Soil surface damage	-	reduced by using boards during installation.
	d) Seasonal instrument drift	-	counts were performed in a water tank before and after probing to check on any drift.
2) Random	a) Random count error	-	by counting for 16 seconds all readings are within ± 1% of the volumetric water content with 99.7% certainty.

7.2. Hydraulic potentials

The hydraulic potentials (defined as the sum of matric and gravitational potentials and expressed in units of cm of water) derived from the tensiometer readings have been referenced from the soil surface and have been used to describe the direction of water flow within the soil profile.

Hydraulic potential / time curves are shown in figure 7.1. (mean of three readings). To reduce the confusion caused by including all measurements, only selected depths are shown and potentials have been terminated at - 250cm water since at this potential, the potential changes rapidly until the tensiometer fails due to entrance of air into the pod.

Fig.7.1. Hydraulic potentials of horizons under winter wheat - normal crop

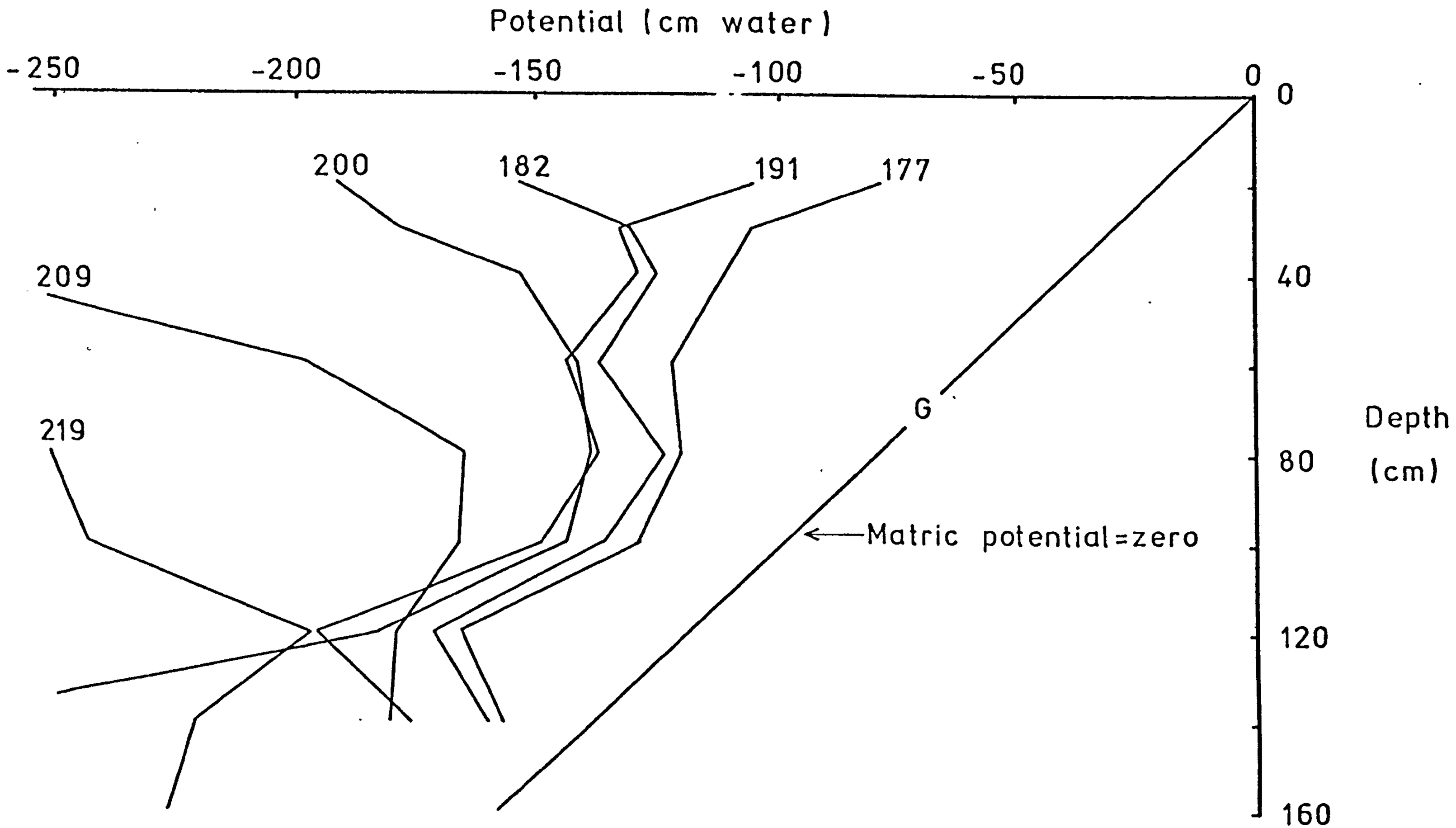


After installation, the hydraulic potentials remained almost constant at each depth until day 163 when rain wetted the profile and potentials increased. A steady hydraulic potential gradient, associated with drainage through the profile occurs until day 182 when the hydraulic potential at 20 cm becomes lower than at 40 cm. This means that evaporation is occurring and water movement must be upward from 40 cm to 20 cm depth. Rain on days 183, 184 and 189 rewetted the topsoil and the hydraulic potential at 20 cm became higher than at 40 cm indicating downward water movement through the profile again. Then at day 194, the potential at 20 cm again became lower than at 40 cm which in turn became less than at 80 cm as the upward movement of water in response to evaporation reached greater depths in the soil. Rainfall after day 194 was small and, until day 255, insufficient to reverse the hydraulic potential gradient between 40 cm and 20 cm.

Profiles of hydraulic potential for selected days are presented in figure 7.2. Day 177 shows potentials decreasing with depth and hence a drainage situation. By day 182 the potentials at 20 cm and 30 cm were less than at 40 cm as these upper layers dry because of evaporation. However, rain rewetted the surface soil and day 191 again shows a downward movement of water. After this time rainfall was low and the three remaining profiles at days 200, 209 and 219 demonstrate the gradual movement down the profile of the depth at which the hydraulic potential gradient is reversed; 60 cm - 80 cm at day 200 to 80 cm on day 209 and 120 cm on day 219.

When the hydraulic potential in one soil layer becomes lower than that of the layer immediately below, water is induced to move upwards from that lower layer either through the soil or via plant roots. The depth to which water is under the influence of an upward acting hydraulic gradient may be used to define an "effective rooting depth" of the crop

Fig. 7.2. Hydraulic potential profiles under winter wheat - normal crop



(Mc Gowan, 1973). This is not necessarily the same as the actual rooting depth. Indeed, it has already been shown (section 5.3.) that on day 182, roots are present to at least 100 cm whereas the effective rooting depth is only 30 - 40 cm. For spring sown cereals, however, effective and actual rooting depths are frequently similar (Mc Gowan, 1973).

7.3. Water potentials

Thermocouple psychrometers continued the measurements of water potential below - 0.8 bar and it is primarily those readings which are discussed in this section. Matric potential was calculated from the tensiometer readings by subtracting the gravitational potential from the hydraulic potential, and is comparable with the water potential measurements of the psychrometers (the osmotic component of water potential is small - section 7.1.)

Water potential / time curves are shown in figure 7.3. (mean of two readings except at 80 cm which is only one reading). The almost complete absence of rain between days 200 and 250 allowed a continuous drying pattern to be monitored. Water potentials decreased to nearly -20 bars at all depths by day 254 when showers and a heavy rainfall rewet the topsoil and the potential at 20 cm increased to - 1 to - 2 bars. This rainfall was only sufficient to rewet the 20 cm layer. Subsequently the potentials at greater depths also gradually increased and correspondingly a slight increase in water content was found (eg 0.4% at 80 cm) in the water content profile measurements.

Throughout the period when the profile was drying (days 224 - 264 on fig.7.3.) the potential at 20 cm was lower than at 40 cm, which, in turn was less than at 60 cm. However, the 80 cm layer always had a lower potential than the 60 cm Layer and was frequently less than the 40 cm layer. No definite reason for this observation can be suggested and it may simply

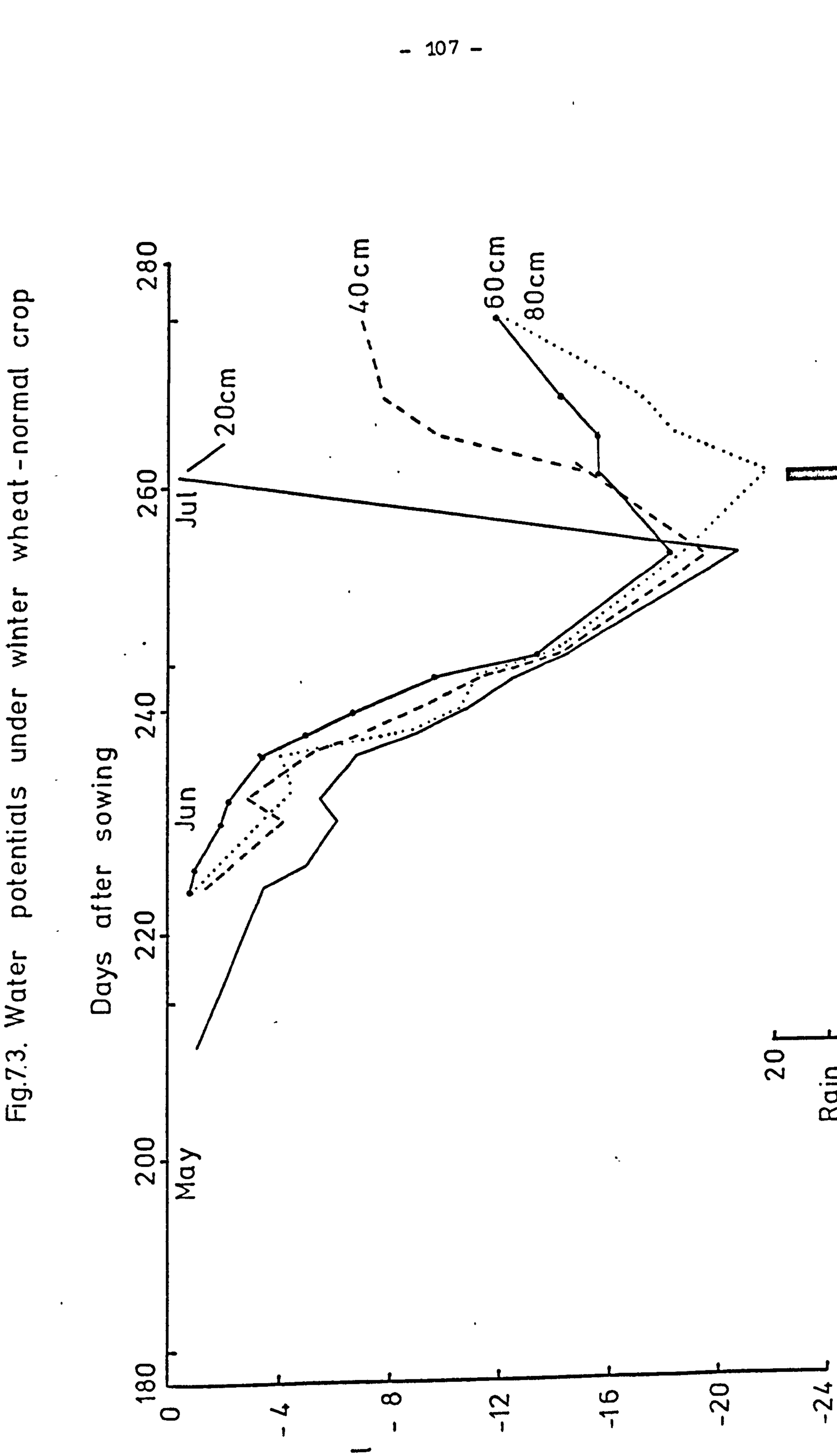


Fig.7.3. Water potentials under winter wheat-normal crop

arise because of the error associated with an unreplicated reading.

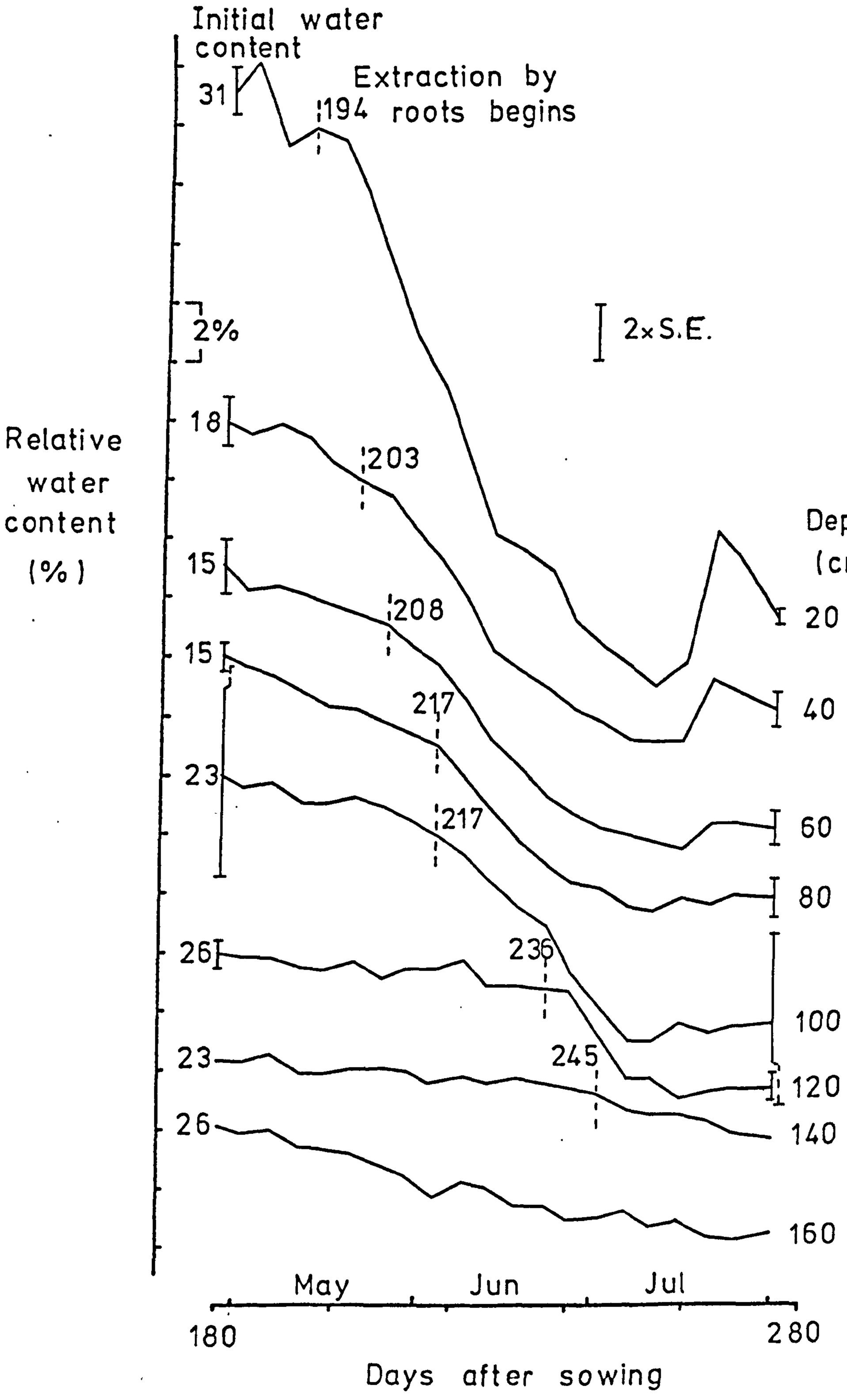
7.4. Water content changes

Since the water profiles were monitored in 10cm intervals, a change in water content of 1% by volume is equivalent to 1mm depth of water.

To calculate how much water has passed through the plant, it is first necessary to separate drainage from evaporation. As a layer of soil drains, the water content falls gradually and because of a simultaneous decrease in hydraulic conductivity, the rate of water loss from that increment also decreases. When evaporative loss commences from that layer, the rate of water loss increases and there is a discontinuity in the water content / time curve associated with root water extraction. The identification of these discontinuities and their use in separating drainage from evaporation has been described by Williams (1971) and McGowan (1973).

Water content / time curves under winter wheat are presented in figure 7.4. (mean of three readings). Only selected layers are shown and the curves have been vertically displaced on the water content scale with the initial water content shown against the first point. The 20cm layer shows an initial gain of water, then a loss and subsequently another small gain resulting from frequent rain showers. Starting at day 194 there is a phase of rapid soil drying and extraction of water by roots which is maintained until rewetting by rain occurs about day 255. The discontinuity at 40 cm is not so clear but discontinuities for the 60 cm, 80 cm and 100 cm depths are readily discernable. Where no obvious start to evaporative loss was found, the profile data were examined and an estimate made; for example, although the 40 cm discontinuity is not clear, upward movement from this layer is likely to occur before movement from 50 cm and this allows a reasonable estimate of the start of root water

Fig. 7.4. Water content / time curves under winter wheat - normal crop



extraction to be made.

The continuous drying profiles are interrupted about day 255 and water content increases in all layers to 100 cm. This coincides with a period of heavy rainfall but soon after all layers start to re-dry again (particularly the 20 cm and 40 cm layers). As depth increases, it is apparent that the change in water content during the growing period is less for each successive layer. At 140 cm, only a very small quantity of water is extracted by roots and at 160cm, all of the water lost between days 180 and 275 can be attributed to drainage.

Although the recognition of discontinuities is partly subjective, it allows the identification of the day when water was first extracted from that layer and provides another independent means of determining an effective rooting depth. For comparison, the effective rooting depths determined by tensiomoters and those by the neutron probe are shown in figure 7.5. At all times the rooting depth indicated by tensiometers is some 10 - 20 cm ahead of that indicated by the neutron probe. This is frequently observed in such comparisons (McGowan, 1973; Fry, 1975) although the reason for the finding is not entirely clear. Nevertheless, the comparison is favourable and indicated an average downward rate of the drying front of 2cm / day for the neutron probe and 2.4 cm / day for the tensiometers.

7.5. Hydraulic and water potentials on the treatment plots

Before anthesis, the wet plot was irrigated weekly to maintain soil water content close to field capacity and only for two short periods did the hydraulic potential fall below -250 cm water at 20 cm depth. On the dry plot, hydraulic potentials at all depths to 120 cm (fig.7.6.) started to decrease before the corresponding depth on the normal plot. This was the expected result since the cover on the dry plot intercepted 63.1mm

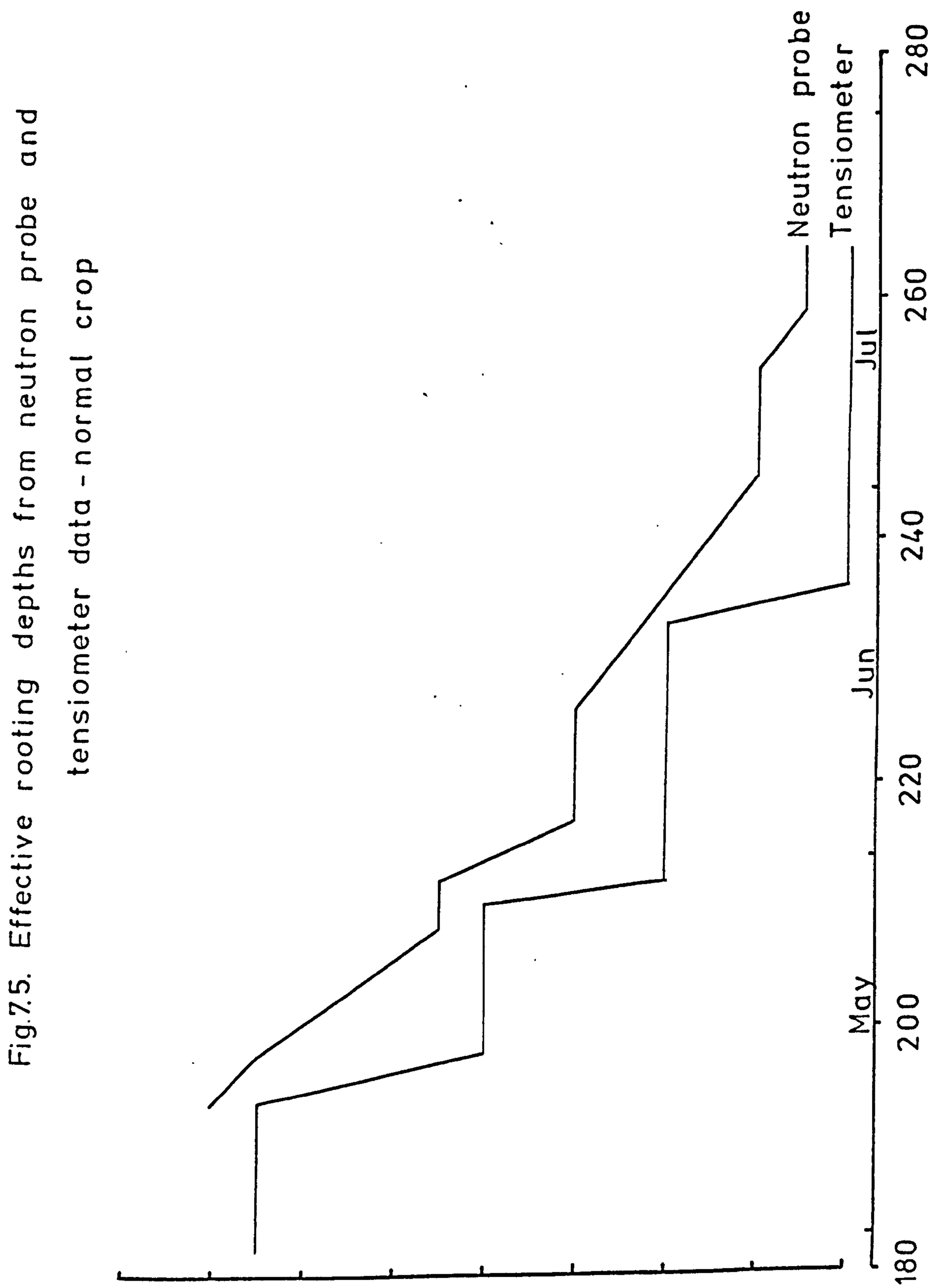


Fig.7.5. Effective rooting depths from neutron probe and tensiometer data - normal crop

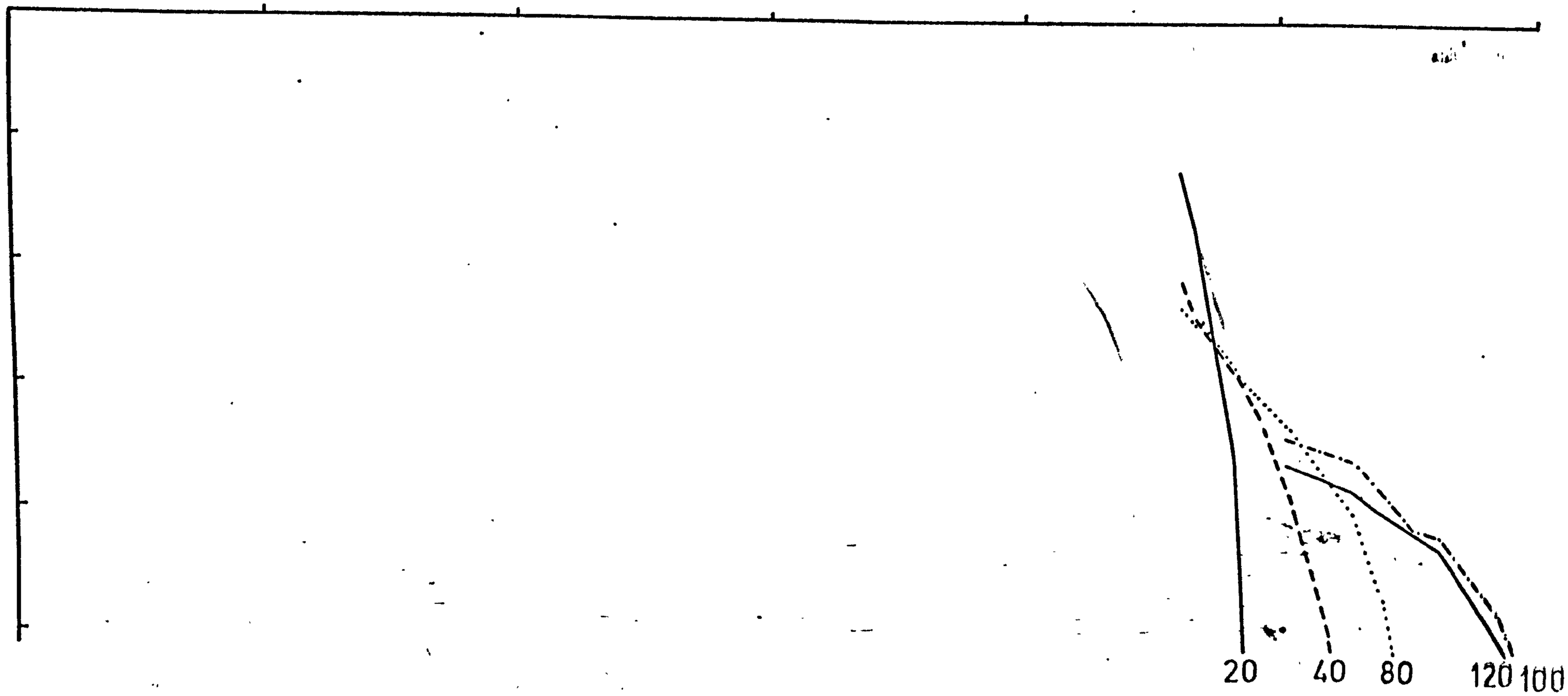
rain during April - May - water which continually rewetted the topsoil of the normal crop. By day 230, the steady drying of the soil on the dry plot resulted in a water potential of - 13.4 bars at 20 cm depth compared with - 6.1 bars on the normal plot.

The main interest in these measurements lies after day 230. At this time both wet and dry plots were irrigated to field capacity and then exposed to the prevailing weather conditions. Figures 7.6. and 7.7. show that potential decreased quickly at 20 cm on both plots but reached - 250cm water on the wet plot before the dry. Hydraulic potentials at 40cm, 60cm (not shown) and 80cm decreased similarly on both plots and reached - 250cm water on the same dates. Below 80cm, potentials reached - 250cm water on the dry plot before the wet plot and the potential profiles show that root water extraction from depths below 80cm proceeds first on the dry plot. This is seen even more clearly when effective rooting depth is examined (fig.7.8.). It is plain that the plants on the previously dry plot take up water down to 140cm by day 247 while those on the wet plot are extracting only to 100cm.

The effective rooting depth is not so deep on the treatment plots as on the normal plots and water potentials never fell below - 1.7 bars at 20cm depth.

Hydraulic potentials at any depth generally decreased later on the guttered plots than on the corresponding main treatment: this is shown by the shallower effective rooting depth on most days (fig.7.9.) This figure also shows that the dry-guttered plants were extracting water from below 80 cm before the wet-guttered plants ie. the manner in which the plants responded to irrigation was similar on the guttered and non-guttered plots.

wet



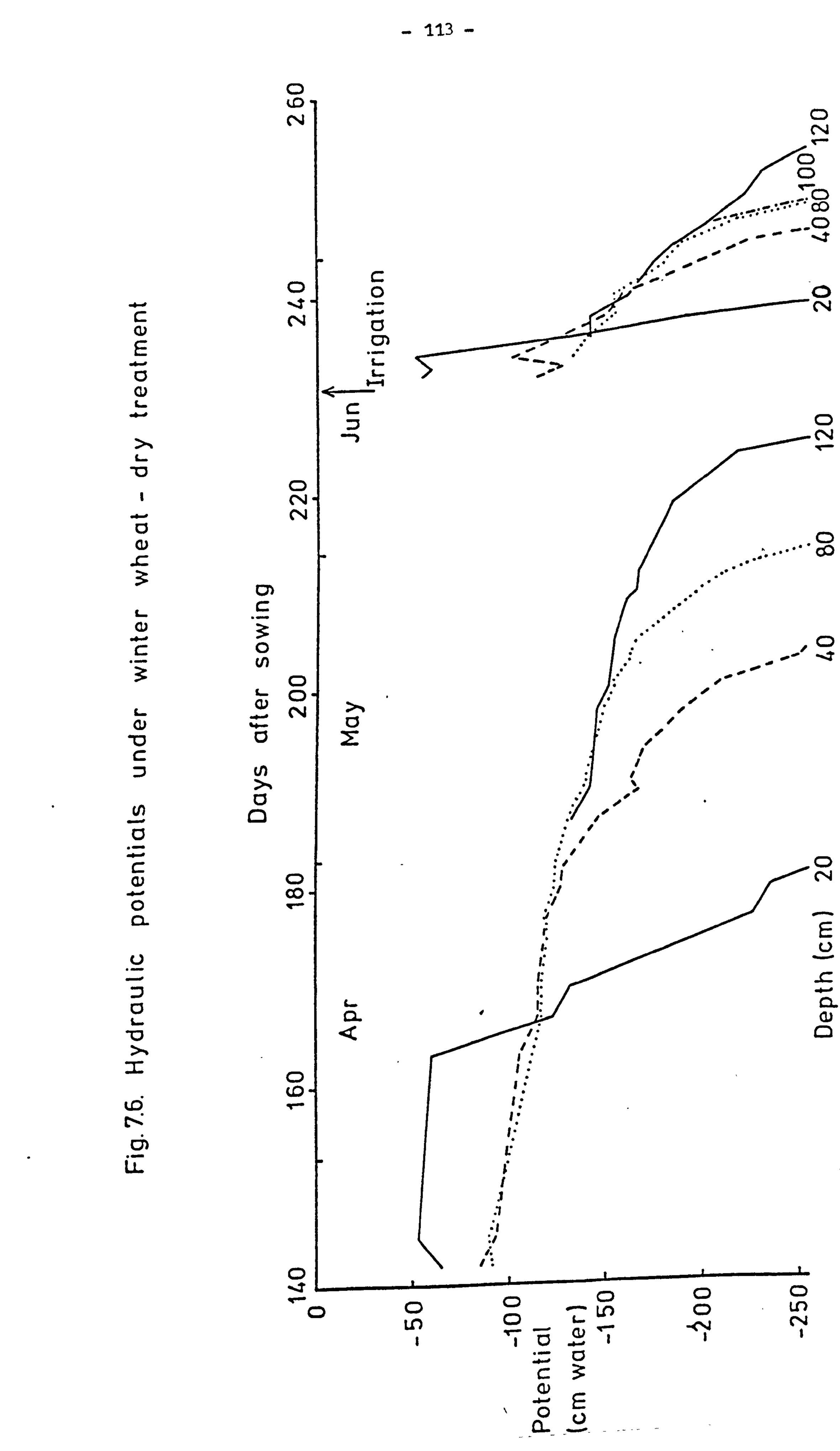


Fig. 7.6. Hydraulic potentials under winter wheat - dry treatment
Days after sowing
Apr
May
Jun
Irrigation
Depth (cm)
Potential (cm water)
20
40
80
100
120
140
160
180
200
220
240
260
0
-50
-100
-150
-200
-250

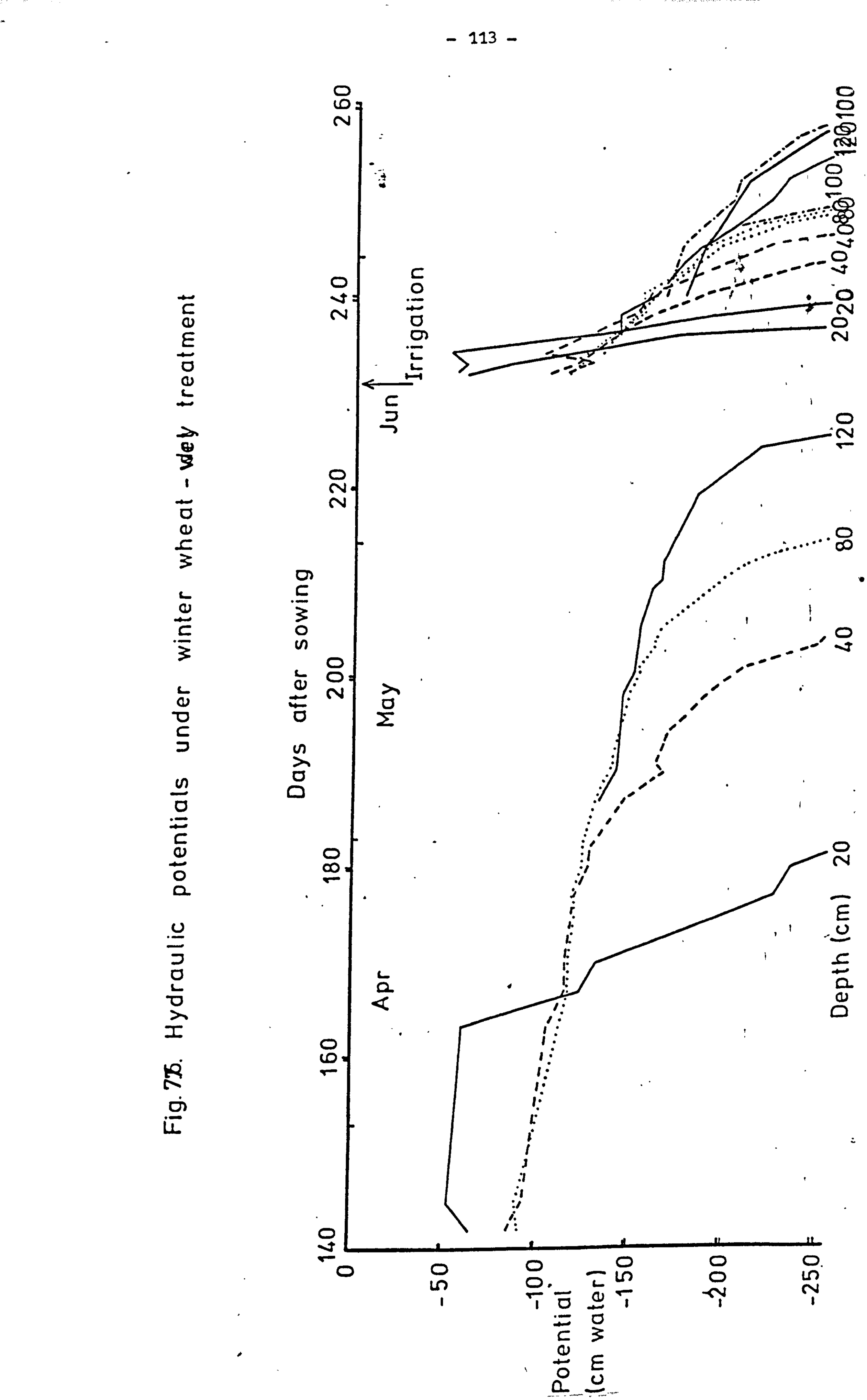
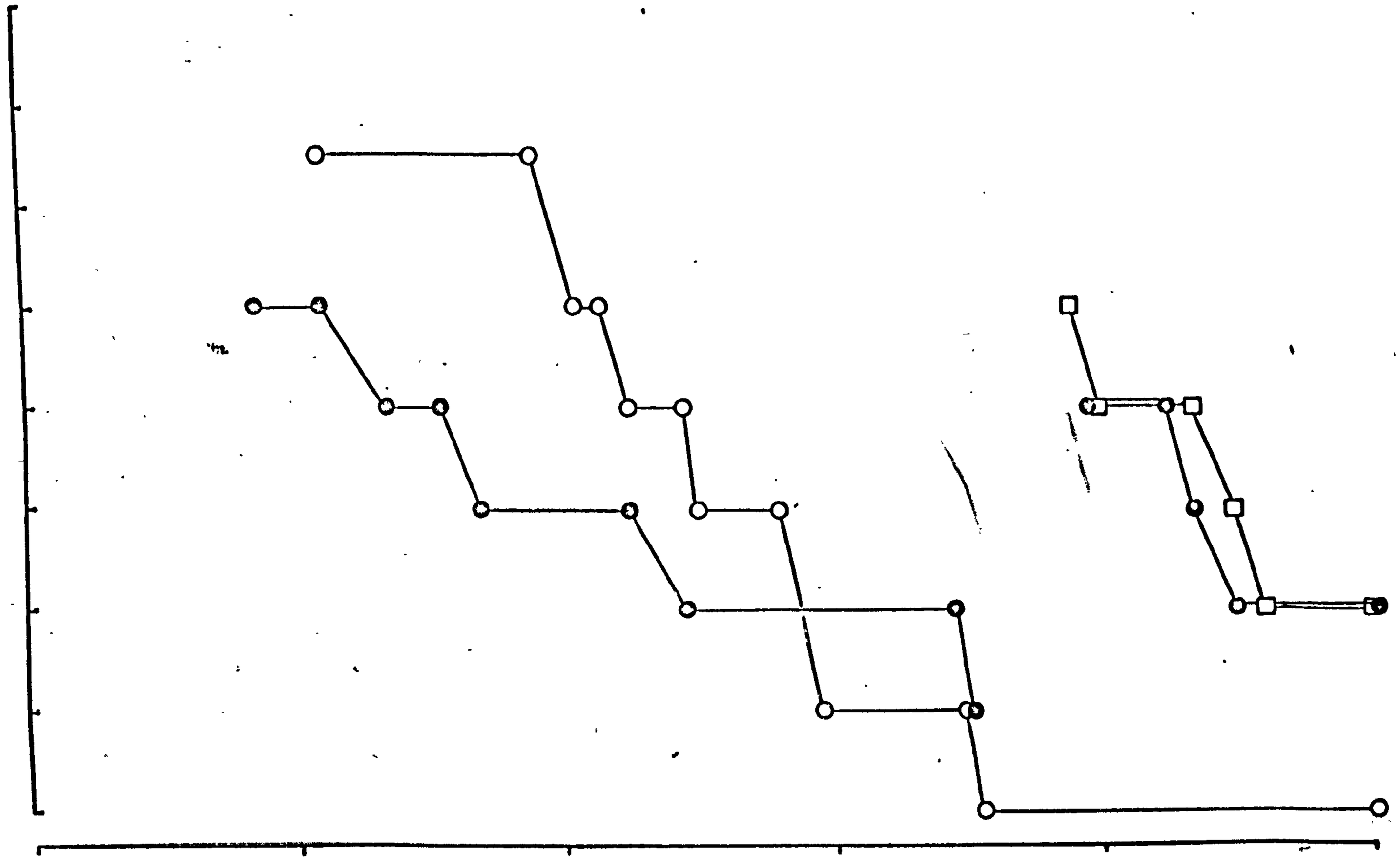


Fig. 7b. Hydraulic potentials under winter wheat - wet treatment

guttered



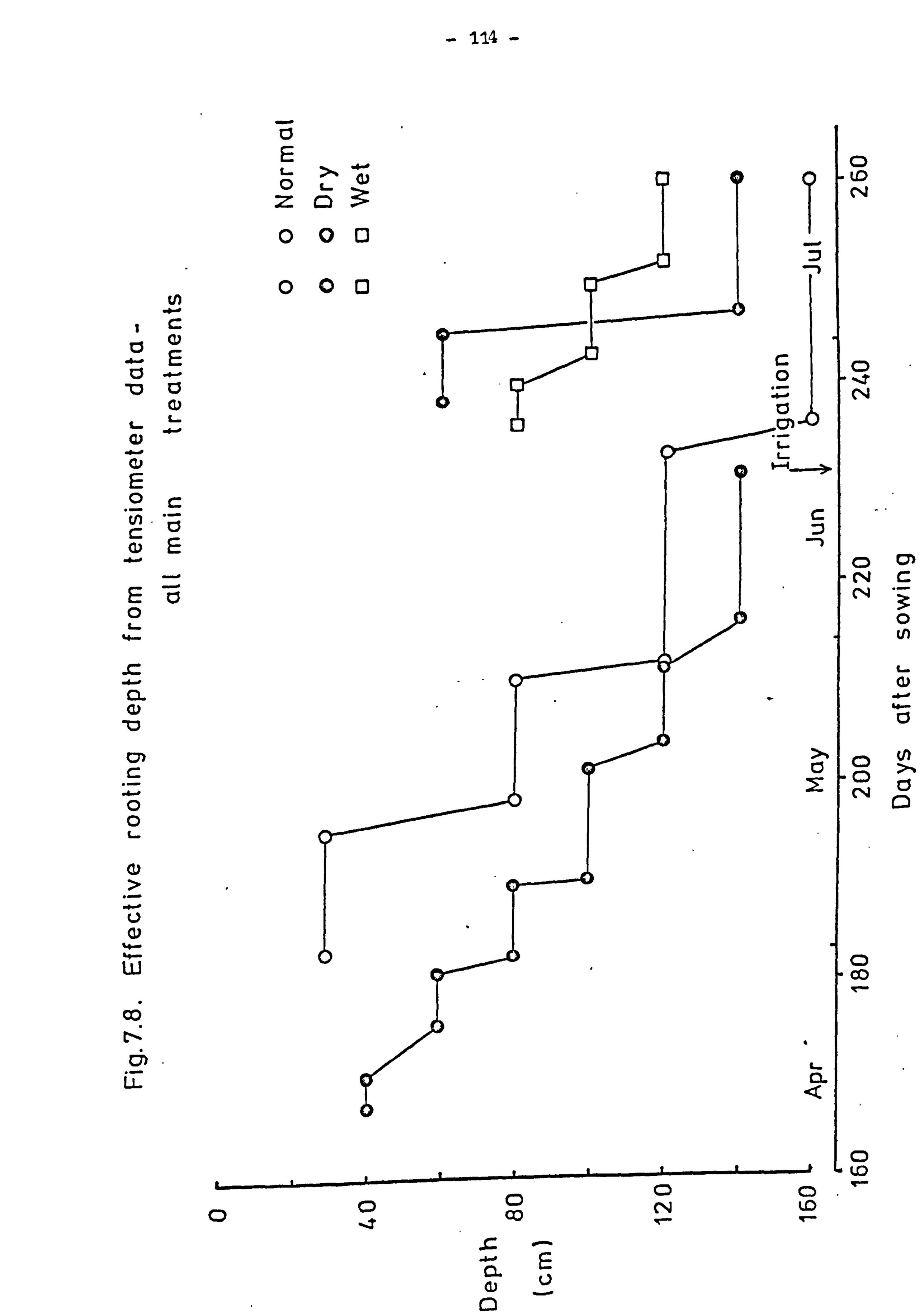


Fig.7.8. Effective rooting depth from tensiometer data - all main treatments

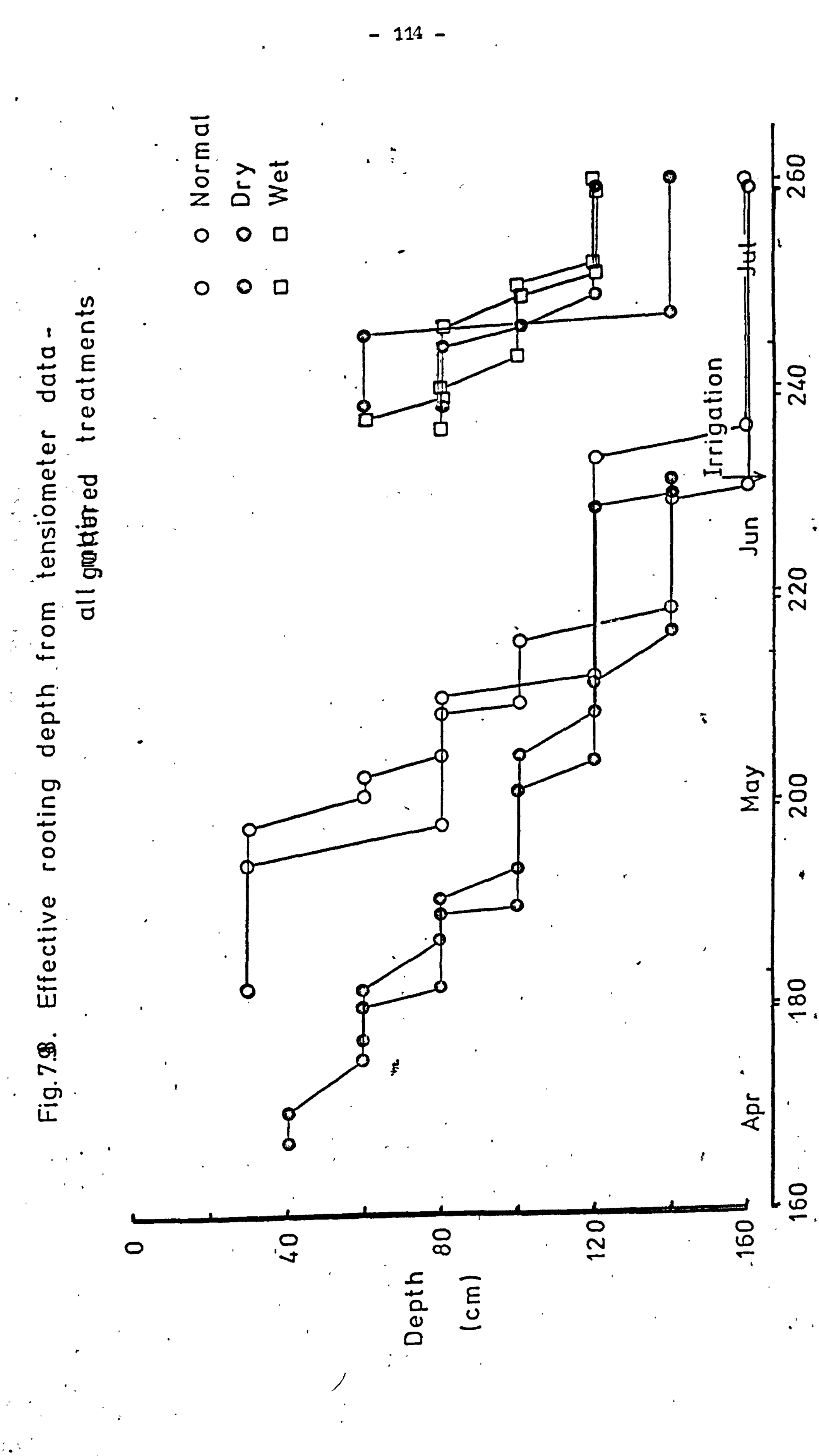


Fig. 7.8. Effective rooting depth from tensiometer data- all treatments

7.6. Water content changes on the treatment plots

Water content/time changes will not be discussed in any detail since the handling of the neutron probe data has been described earlier: the main interest is not in the water content / time curves themselves but in the quantities of water extracted by the roots. This inflow of water to the plants will be described in section 9.2.

The effective rooting depths estimated by tensiometer and neutron probe data are generally similar and the previously observed extraction of water at depth on the dry plots compared with the wet plots was also evident from the neutron probe results.

7.7. Summary of results

1) The absence of rain after the beginning of June allowed the continuous monitoring of water uptake by the plant using tensiometers, thermocouple psychrometers and a neutron probe.

2) Interpretation of the tensiometer and neutron probe data allowed independent estimates of the depth of water extraction (effective rooting depth). The two estimates were generally close and the depth of extraction reached 140 - 160 cm shortly after anthesis.

3) Before anthesis, effective rooting depth was greater on the dry plot than the normal but could not be assessed on the wet plot.

4) After irrigation of the wet and dry plots at anthesis, hydraulic potentials in the top soil layers decreased similarly but drying at depths greater than 80 cm occurred earlier on the previously dry plot.

5) The guttered plots showed similar responses to the main treatment plots but their effective rooting depth was generally less.

6) Water potential at 20cm on the normal plot decreased to - 20 bars on day 254 but increased after this because of rain. At anthesis the water potential on the dry plot was - 13.4 bars at 20cm (compared with - 6.1 bars on the normal plot) but after irrigation, potentials were

never less than - 1.7 bars on either previously wet or dry plots.

8. NUTRIENT COMPOSITION OF WINTER WHEAT

8.1. Sample preparation

The dried plant material used for growth analysis of the aerial crop was bulked into leaf, stem and ear (section 6.1.) and ground with either a Glen Creston hammer mill or a Christy - Norris mill.' Samples of the ground material were digested using the procedures outlined in appendix 2 and analysis for Na, K, Ca, Mg, P, S and N performed as described in appendix 3. The results presented in the text are the means of the four replicate plant samples taken at each harvest.

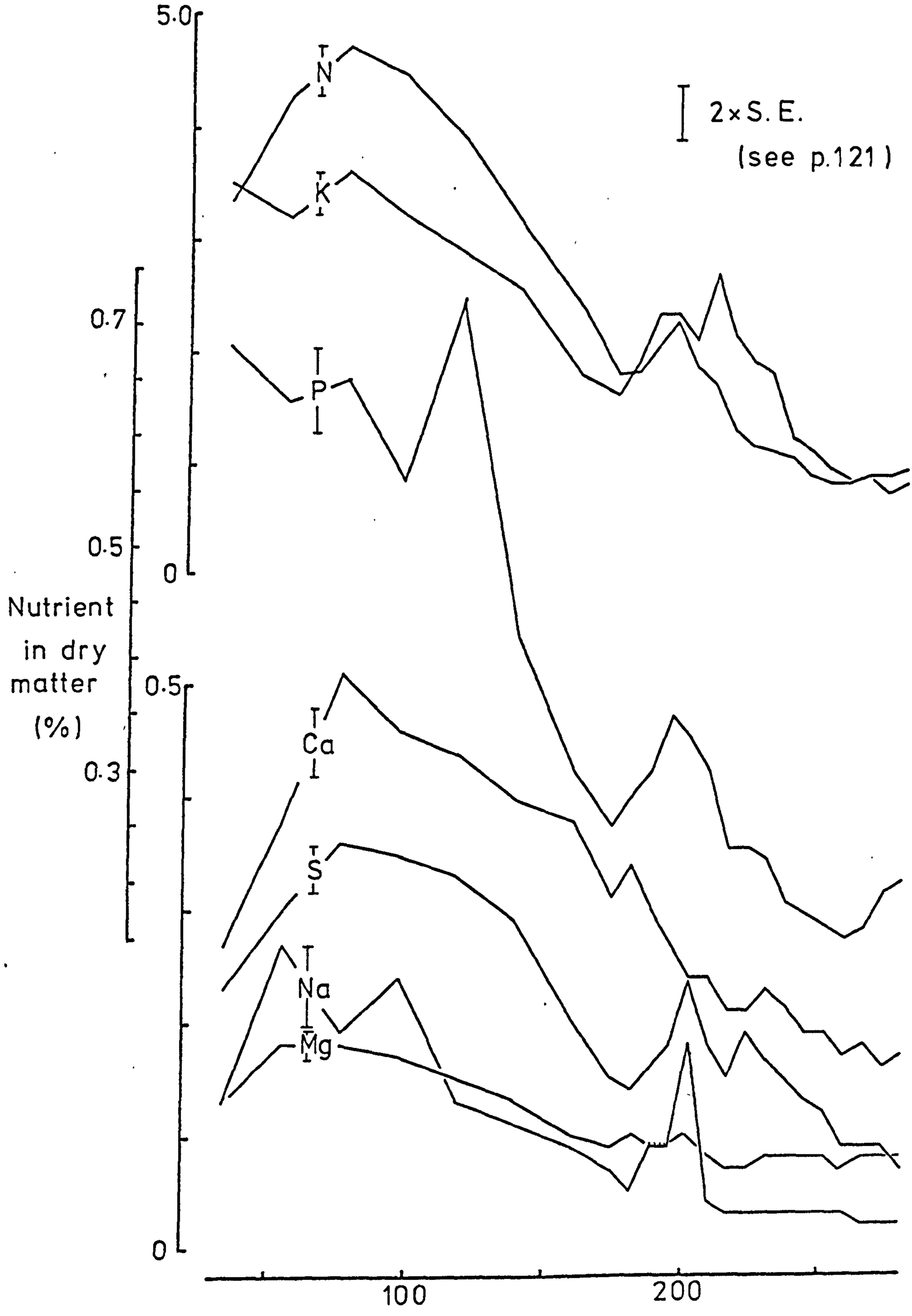
Root material was also analysed but because of the relatively small size of the samples, replicates were bulked before digestion. If some nutrients leached out during storage and washing of the roots, the quantity was unknown.

8.2. Percentage composition of the plant

8.2.1. Whole plant

In general, the percentage of all nutrients decreased over the growing period (fig.8.1.) but a number of phases within the generalised pattern can be recognised. Initially, the percentage of all nutrients rises and the maximum values are recorded (with the exception of phosphorus) about day 76. This increase has not been reported by other authors working with field-grown wheat because samples have not usually been analysed so early in the crop's life. Mengel and Barber (1974b) working with corn have,however, observed a similar increase. The reason for the increase is not certain but as mentioned in section 6.2. shoot weight is remaining fairly constant in this period and the translocation of nutrients from the seed plus uptake by the roots may produce the observed result. The decrease in nutrient percentage that follows is

Fig. 8.1. Nutrient composition of winter wheat with time



caused by the slower rate of nutrient assimilation compared to carbon and may be divided:

a) Period until anthesis. The decrease is greatest for sodium which falls to a value at day 230 one sixth that at day 76. Nitrogen percentages also fall appreciably(to one fifth) with phosphorus decreasing to one third and potassium, calcium, magnesium and sulphur to one half their value at day 76.These decreases are marked by an interruption between days 181 and 202 when small increases are observed for most nutrients (all except calcium and magnesium). One reason for this increase might be a suddenly increased rate of nutrient assimilation relative to carbon, but this seems unlikely. An alternative explanation is that this is the time of visible tiller senescence (commented on in sections 5.2. and 6.2.) and could result from translocation of nutrients from the tillers to the main stem occurring faster than the carbon assimilation of that stem.

b) Period after anthesis. Percentages of sodium and magnesium during this period are almost constant but for other nutrients they continue to decrease. The decrease is most noticeable for potassium and sulphur which at final harvest are one-half the anthesis value while calcium percentage decreases to two-thirds its anthesis value. Nitrogen and phosphorus decrease by a small amount after anthesis but three weeks before final harvest the phosphorus percentage apparently increases again.

8.2.2. Stem

The percentage of nutrients in the stems with time (fig.8.2.) follows a similar pattern to that described for the whole shoot. This decrease in percentage throughout the season has been commented on by other workers (Knowles and Watkin, 1931); Gasser and Thorburn, 1972) and is a common feature of wheat growth. Nitrogen shows the largest

decrease in stem composition but potassium and phosphorus also fall by large amounts. As with the whole shoot percentages, the decrease is interrupted between days 181 and 202.

8.2.3. Leaf

The inorganic nutrients are generally more concentrated in the leaves than stems during crop growth. After an initial increase of nutrient percentage in the leaves (except phosphorus), the familiar decrease is observed with a short lived interruption about day 181. Composition after this time does not show a general pattern and may conveniently be separated:

a) Period from day 181 until anthesis. The percentage of all leaf nutrients, particularly sodium and nitrogen, increases between days 181 and 202. After this, calcium, magnesium and sulphur continue to increase while the remainder decrease.

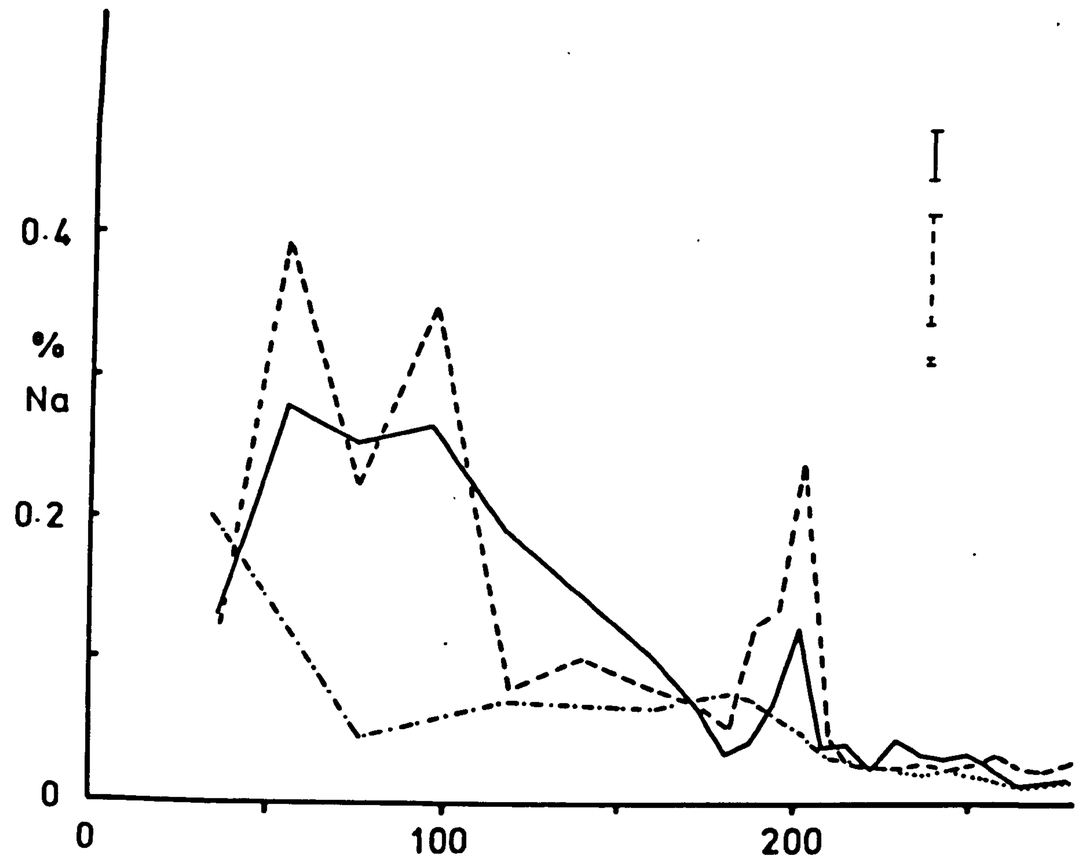
b) Period after day 230. Calcium, magnesium and sodium composition remain almost constant while potassium, phosphorus, nitrogen and sulphur decline.

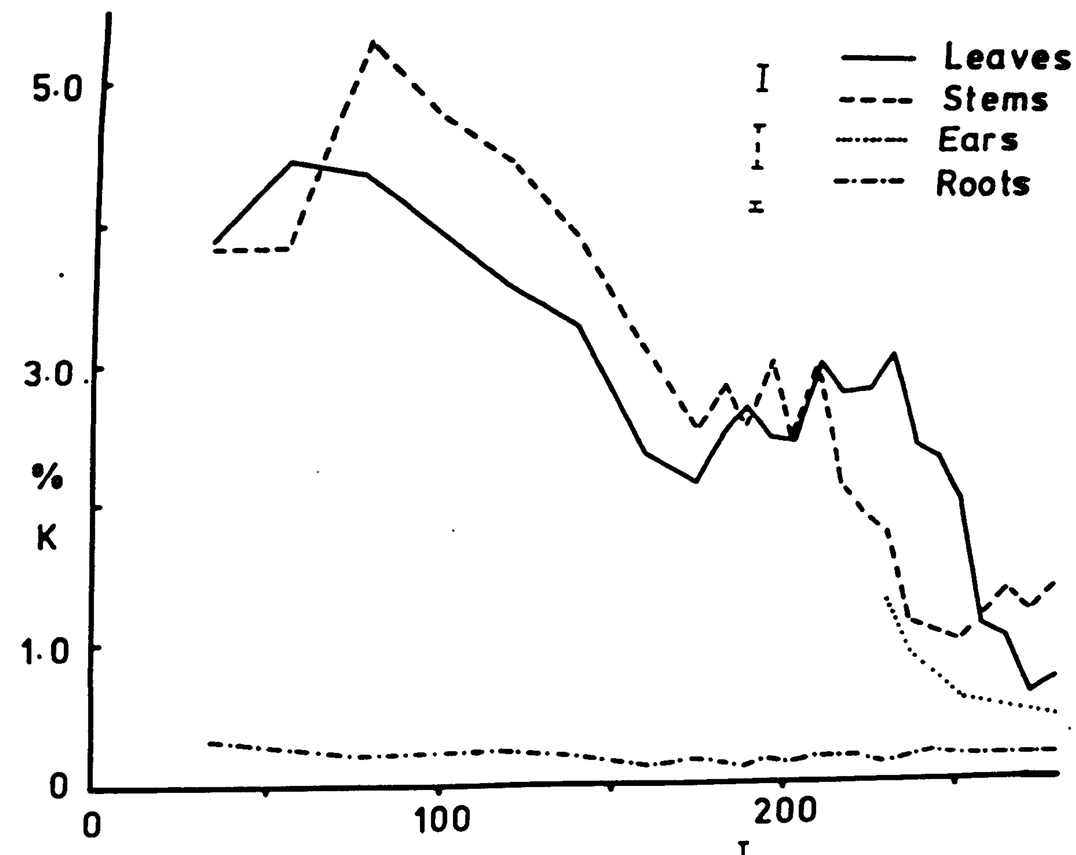
Unfortunately, previous workers have not analysed the leaves separately from the stems but have bulked their material as "straw". The increases in calcium and magnesium composition and their maintainance at levels higher than (calcium) or comparable with (magnesium) those early in the crop's life would be masked by this procedure.

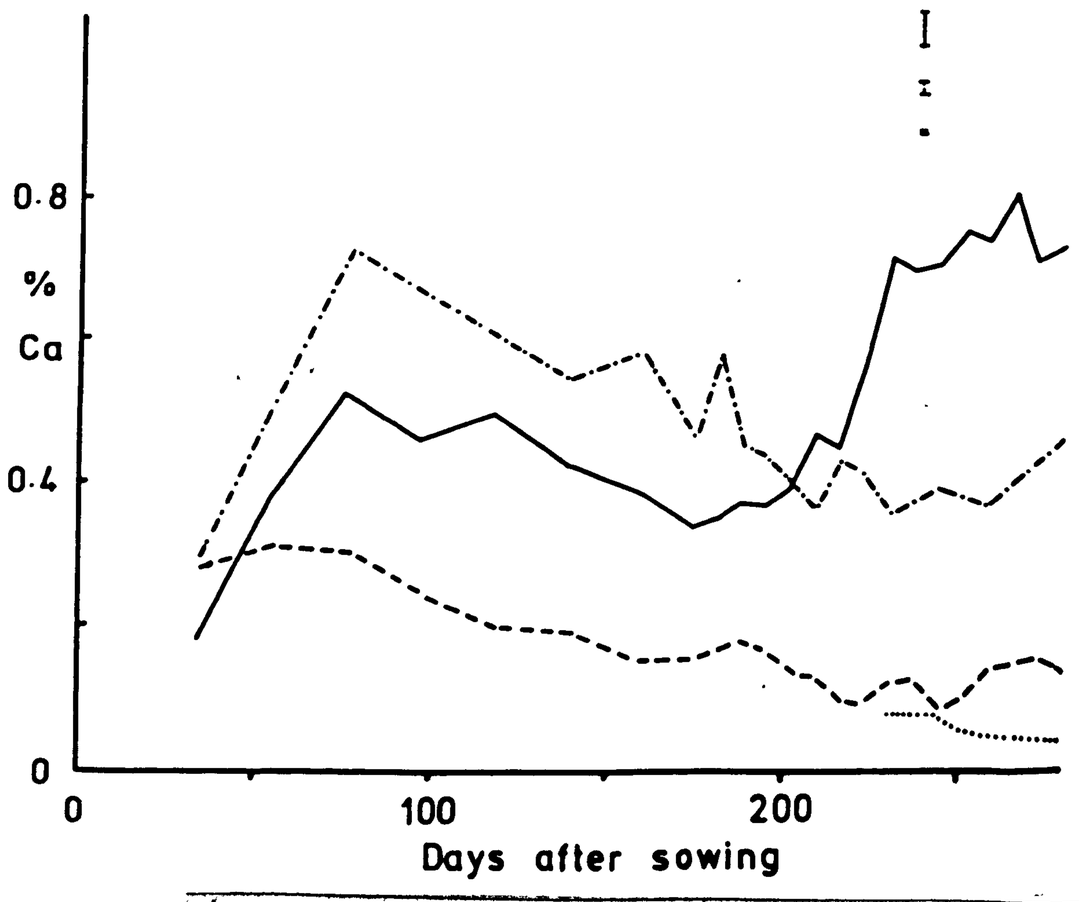
8.2.4. Ear

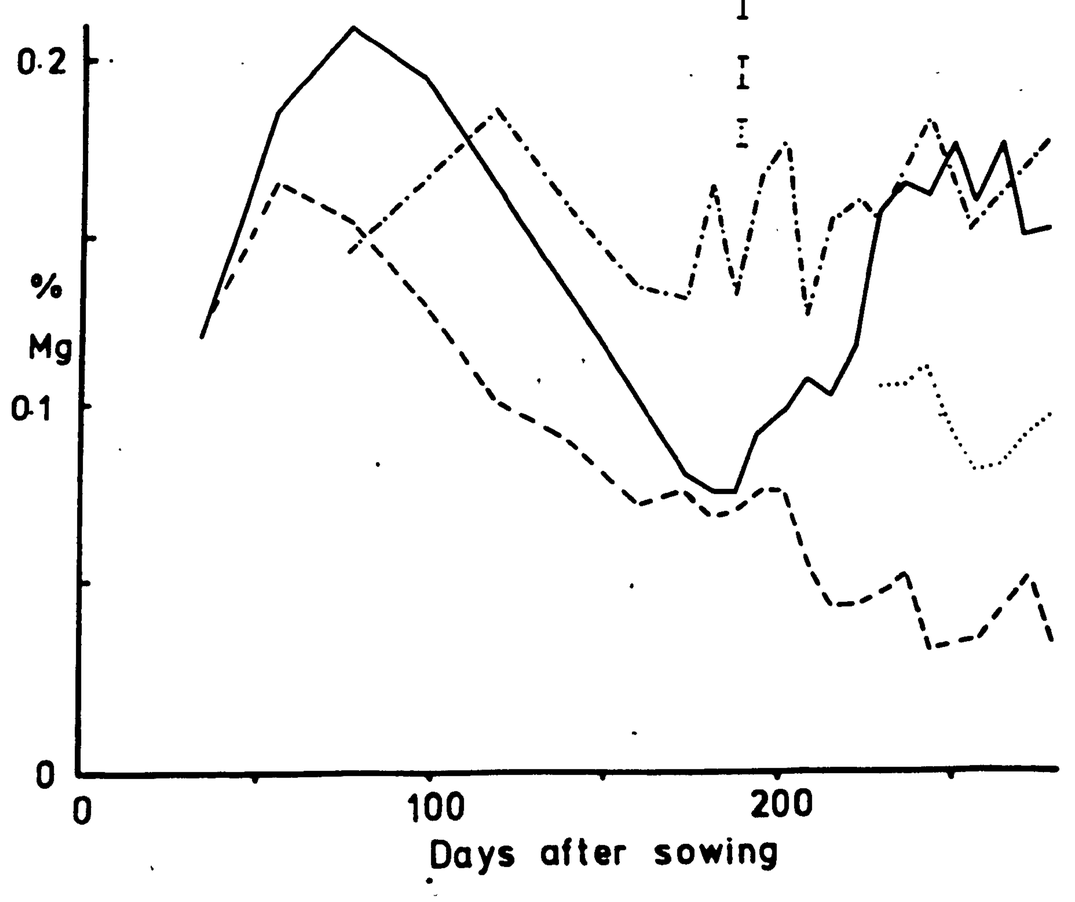
Figure 8.2. shows that the nutrient percentages of the ear decrease from their maximum values at anthesis. Potassium and sulphur percentages decline throughout the grain - filling period but sodium, magnesium, phosphorus and nitrogen all increase again (phosphorus to its anthesis

Fig. 8.2.a. Percentage nutrient composition of plant organs - Na, K, Ca, Mg





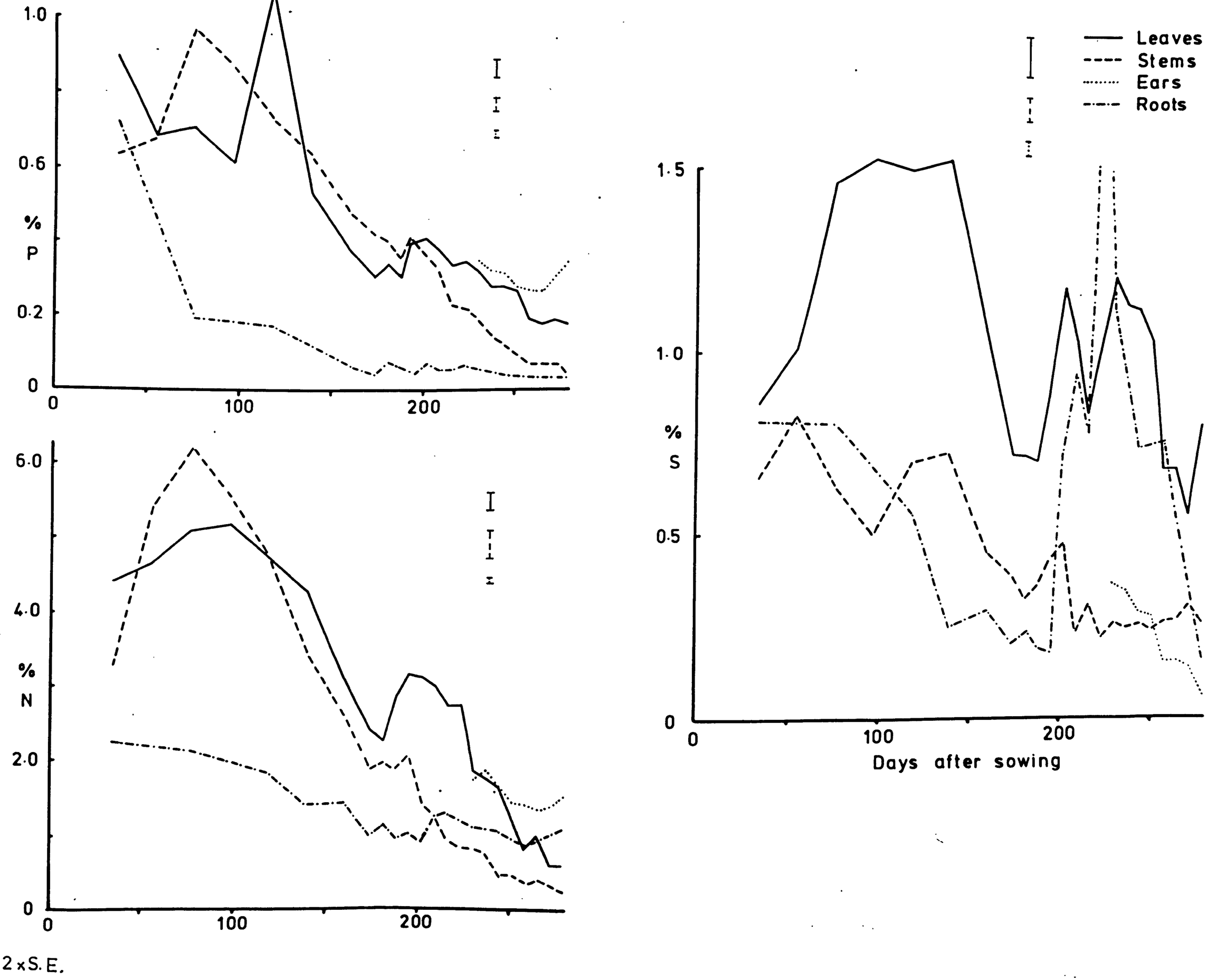




2xS. E.

For simplicity the error quoted is a mean over the whole season. It is an overestimate for early harvests but a slight underestimate for later harvests.

Fig.8.2.b. Percentage nutrient composition of plant organs - P, S, N



value) during the final two weeks before harvest. This observation contrasts with the results of Knowles and Watkin (1931) where after an initial decrease, nitrogen, phosphorus and calcium composition remained constant - no later increase was found.

8.2.5. Root

The most striking feature of these measurements is the low percentage of potassium in the roots relative to other plant organs. This may have arisen because of leaching out during root washing and storage although if this were a major source of error, it is surprising that other ions do not show a comparable reduction. In addition, the values are similar to those of other nutrient cations in the roots (0.2% K compared with 0.35% Ca, 0.12% Mg and 0.05% Na).

With the exception of sulphur, the percentages do not all show the same downward trend as the shoots and after an initial sharp decrease remain almost constant. The percentages of sodium, potassium and nitrogen are, for most the time, less than those in any part of the shoot but about day 200 they became comparable to percentages in the stem. Root nitrogen then exceeds the stem value.

Calcium and magnesium percentages are generally similar to leaf values and always higher than the straw percentage. Sulphur composition is initially low compared with other organs but rises rapidly about day 200 to a relatively high figure (7%); it then decreases again almost as rapidly to reach its original value at final harvest.

8.3. The weight of nutrients in the plant

8.3.1. Whole plant

Table 8.1. presents the weights of nutrient per plant throughout

Table 8.1 Nutrient content per plant throughout the life of the crop

Days after sowing	mg/plant						
	Na	K	Ca	Mg	P	S	N
0	0.01	0.26	0.01	0.05	0.20	0.003	1.11
34	0.06	1.50	0.12	0.06	0.29	0.10	1.44
55	0.09	1.03	0.12	0.06	0.20	0.09	1.37
76	0.11	1.99	0.28	0.10	0.36	0.20	2.58
97	0.22	3.06	0.43	0.16	0.53	0.33	4.18
118	0.19	4.43	0.67	0.23	1.09	0.51	5.93
139	0.28	6.73	1.05	0.34	1.11	0.77	8.24
160	0.41	8.73	1.82	0.50	1.47	0.96	11.63
174	0.47	11.19	2.13	0.65	1.74	1.00	12.34
181	0.48	17.51	3.10	0.91	2.57	1.28	16.55
188	1.23	32.81	4.27	1.25	4.27	2.27	28.98
195	1.39	35.01	4.09	1.41	5.19	2.75	34.02
202	3.26	38.60	4.45	1.76	6.14	4.32	34.05
209	1.16	69.64	6.35	2.01	7.89	4.56	44.38
216	1.05	70.66	6.95	2.24	7.73	5.08	41.97
223	1.09	72.04	7.79	2.60	8.67	6.96	43.08
230	1.35	82.23	10.72	3.64	10.02	7.62	50.14
237	1.45	62.38	11.11	4.29	9.37	7.74	54.26
244	1.34	52.00	8.77	3.58	8.06	6.36	41.79
251	1.58	51.54	10.01	4.16	8.76	6.72	44.44
258	1.83	53.51	10.73	4.48	9.68	5.89	51.42
265	1.23	48.19	9.77	4.31	8.92	5.18	48.77
272	1.14	40.37	8.65	4.62	10.53	4.88	48.67
279	1.31	42.12	8.99	4.45	10.62	3.68	49.58
2×S.E.	0·34	8.10	1·02	0·40	1·16	0·64	5·54

the growth of the crop. The main feature of the results is that until anthesis (day230) a nett uptake of all nutrients occurred but at this time uptake of potassium ceased. Witnin two weeks of anthesis, uptake of all other nutrients stopped and for the remaining 5 - 6 weeks until final narvest, nutrient content remained either constant or fell. Similar observations have been made by Knowles and Watkin (1931) and Chambers (1953). The cessation of nutrient uptake at or about anthesis is in contrast to the accumulation of dry matter which continues until about day251(section 6.2.) and is the more remarkable when one considers that water uptake persists until final harvest (section 7.6.).

Substantial losses of potassium, sulphur and calcium occurred from tne plant in the seven weeks between anthesis and final harvest (table 8.2.). At final harvest only 50% of plant potassium and sulphur and 80% of calcium remained. Losses of this magnitude have been reported previously for potassium (50% by Knowles and Watkin, 1931; approx 30% by Chambers, 1953) and calcium (30% by Chambers 1953) but none of these workers analysed for sulphur. Table 8.2. also shows that the time over which these losses occurred was not identical for each nutrient. Four-fifths of the potassium lost disappeared during the first two weeks after anthesis with only a small amount in the remaining five weeks. Calcium was lost between days 258 and 272 (four to six weeks after anthesis) wnile sulpnur was lost continuously from day 237 (one week after antnesis) until final harvest.

Tne cause of these nutrient losses is not well understood but possible reasons are:

a) Loss of plant material during sampling.

b) Leaching by rain.

c) Translocation to the roots and efflux into the soil.

Some loss of senescent tillers and leaves is inevitable when sampling.

Table 8.2 Relative weights of potassium, calcium and sulphur in the plant after anthesis

Days after sowing	Relative weight		
	K	Ca	S
230 (Anthesis)	100	97	99
237	76	100	100
244	63	79	82
251	63	90	87
258	65	97	76
265	59	88	67
272	49	78	63
279	51	81	47

However, the total weight of leaves relative to stems was small in this period and could only account for a very small proportion of the measured losses.

Although leaching by rain is a possibility and Raybould (1976) has shown that sulphate concentration in rainwater is increased after passing through a wheat canopy, no rain fell during the period of rapid potassium loss or during the initial losses of sulphur. Using the data for sulphate concentration in rainfall and through canopy rain and assuming a 50% loss of rain as stemflow (Raybould, 1976), the maximum possible loss of sulpnur by rainwater leaching is 508 µgS / plant compared with a measured plant loss of 3040 µgS / plant (ie. 17%).

The most probable mechanism for nutrient loss, therefore, is translocation back to the roots and thence to the soil. This mechanism has been suggested previously by Knowles and Watkin(1931) but possible leaching loss by rain was never fully explored. Circumstantial evidence for return of potassium directly to the soil is provided by the measurements of Nair and Talibudeen (1973). Their data show that the potassium concentration in soil solution under winter wheat increased between anthesis and maturity particularly in the early stages of grain-filling. Rainfall data in the same period show that rainfall was less than 10mm and hence this increase in soil potassium concentration is unlikely to result from leaching. In the same publication, nitrate concentration in solution measurements are reported and these do not show increases in concentration until close to final harvest.

While suggesting that loss via the roots is the predominant mechanism for the decrease in potassium, calcium and sulphur content after anthesis, it must also be mentioned that no evidence of accumulation or depletion of these nutrients in the roots was observed (fig.8.2.) during this period.

Although percentage composition is generally decreasing throughout the crop's life, the weight of nutrients in individual organs increases until anthesis. Since total plant nutrient content is stable after anthesis (except potassium, sulphur and calcium), the nutrients in the growing grain must be supplied by translocation within the plant. To describe the relative importance of each organ as a sink for nutrients during the life of the crop, and particularly in the post-anthesis period, nutrients in individual organs have been calculated as a percentage of the total nutrient content (figure 8.3.).

8.3.2. Stem and Leaf

The contribution of stem and leaf nutrients to total follows this general pattern:

a) Shortly after germination the stems contain most (70%) of the nutrients but this percentage falls (to 20% - 30%) as more leaves are produced by the plant.

b) During the winter period the crop is prostrate and the leaves contain most of the nutrients (60% - 70%).

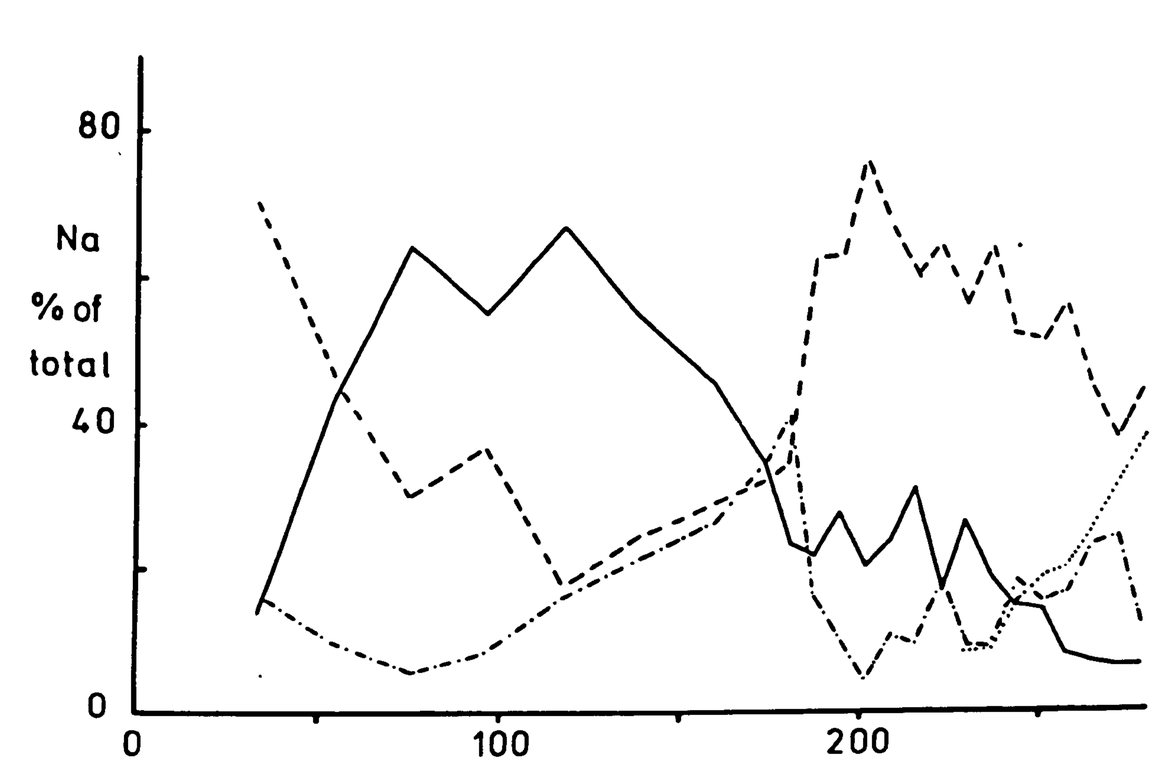
c) As the stems start to elongate (about day 160) their share of total nutrients increases to 50% - 60%) and by anthesis, stem weights of sodium, potassium, magnesium and phosphorus are higher than leaf weights, sulphur and nitrogen are similar, and only calcium remains lower.

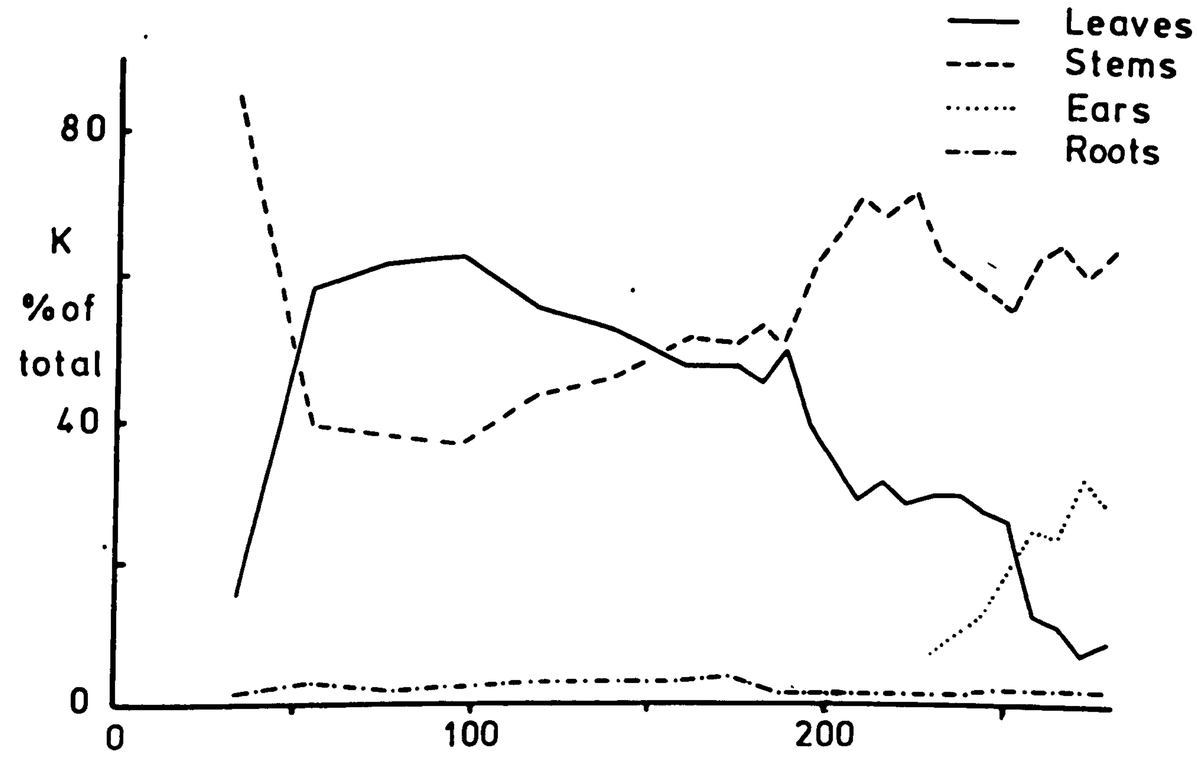
d) After anthesis leaf and stem contribution to total nutrient content generally decreases. For example, stem phosphorus decreases from 70% to 10% of total and stem nitrogen from 50% to 10%. However, stem potassium, calcium and sulphur remain at an almost constant percentage despite the rapid efflux of these ions from the plant in this period.

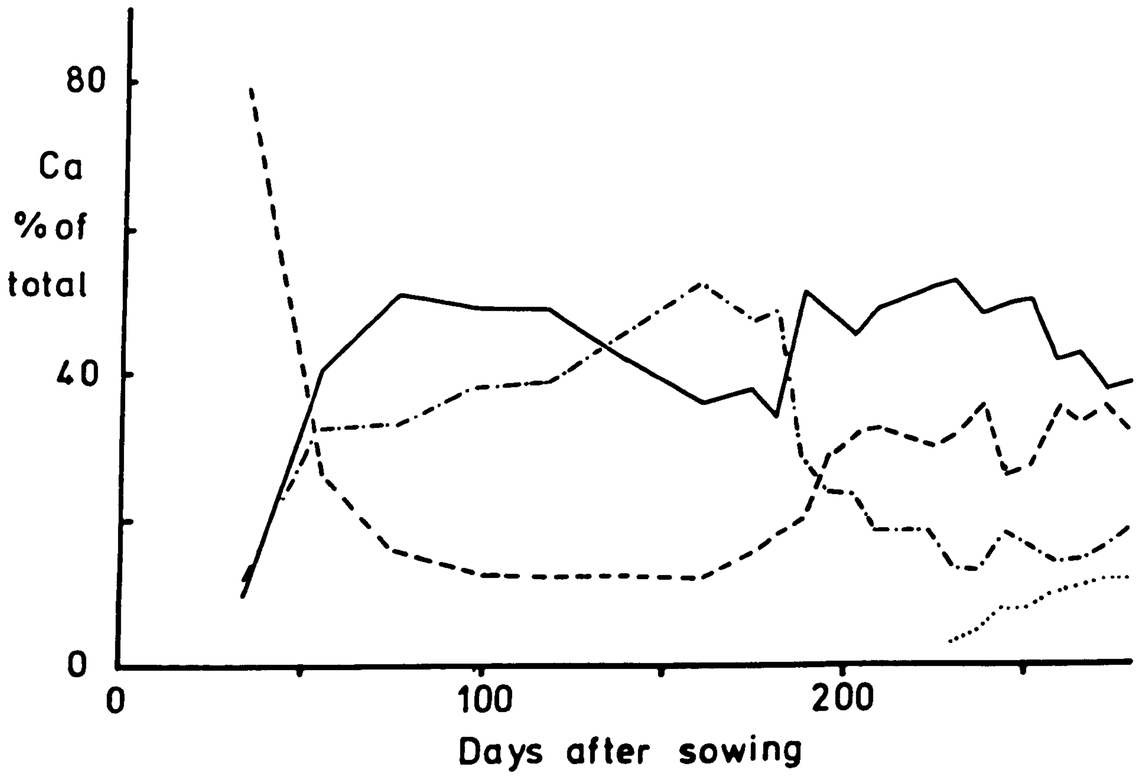
8.3.3. Ear

After anthesis the nutrient content of the leaves and stems decreases.

Fig. 8.3.a The relative distribution of total nutrient content in plant organs - Na, K, Ca, Mg







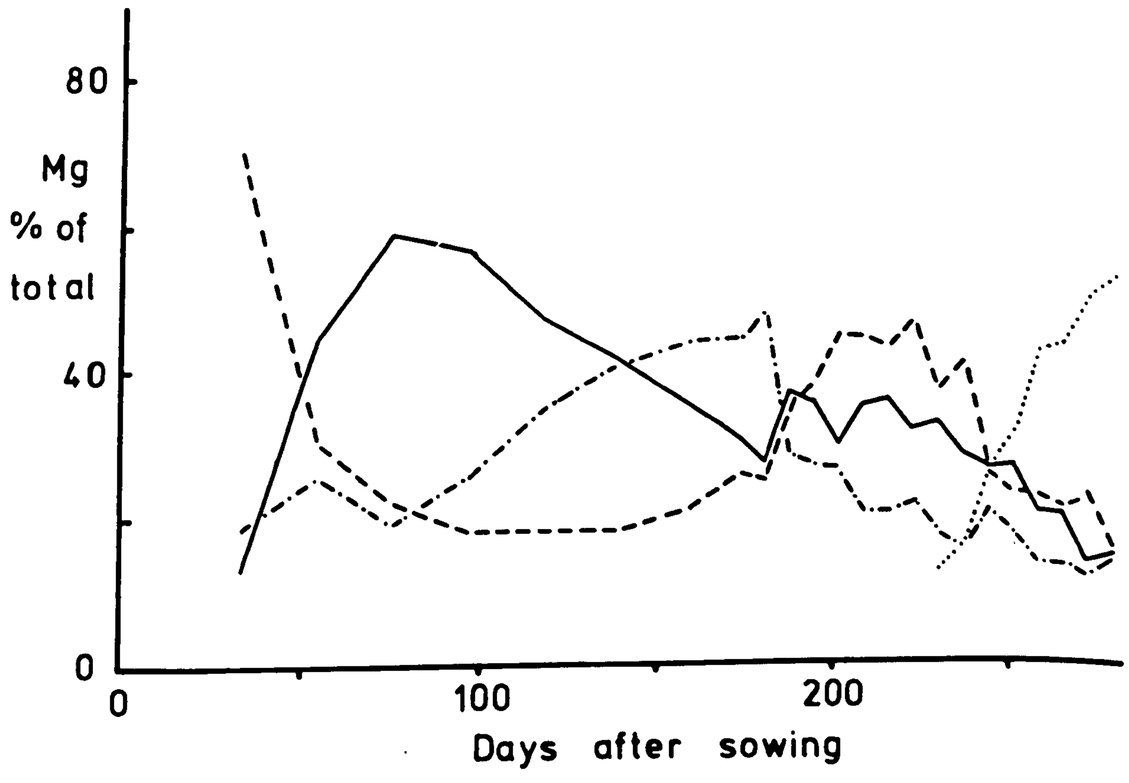
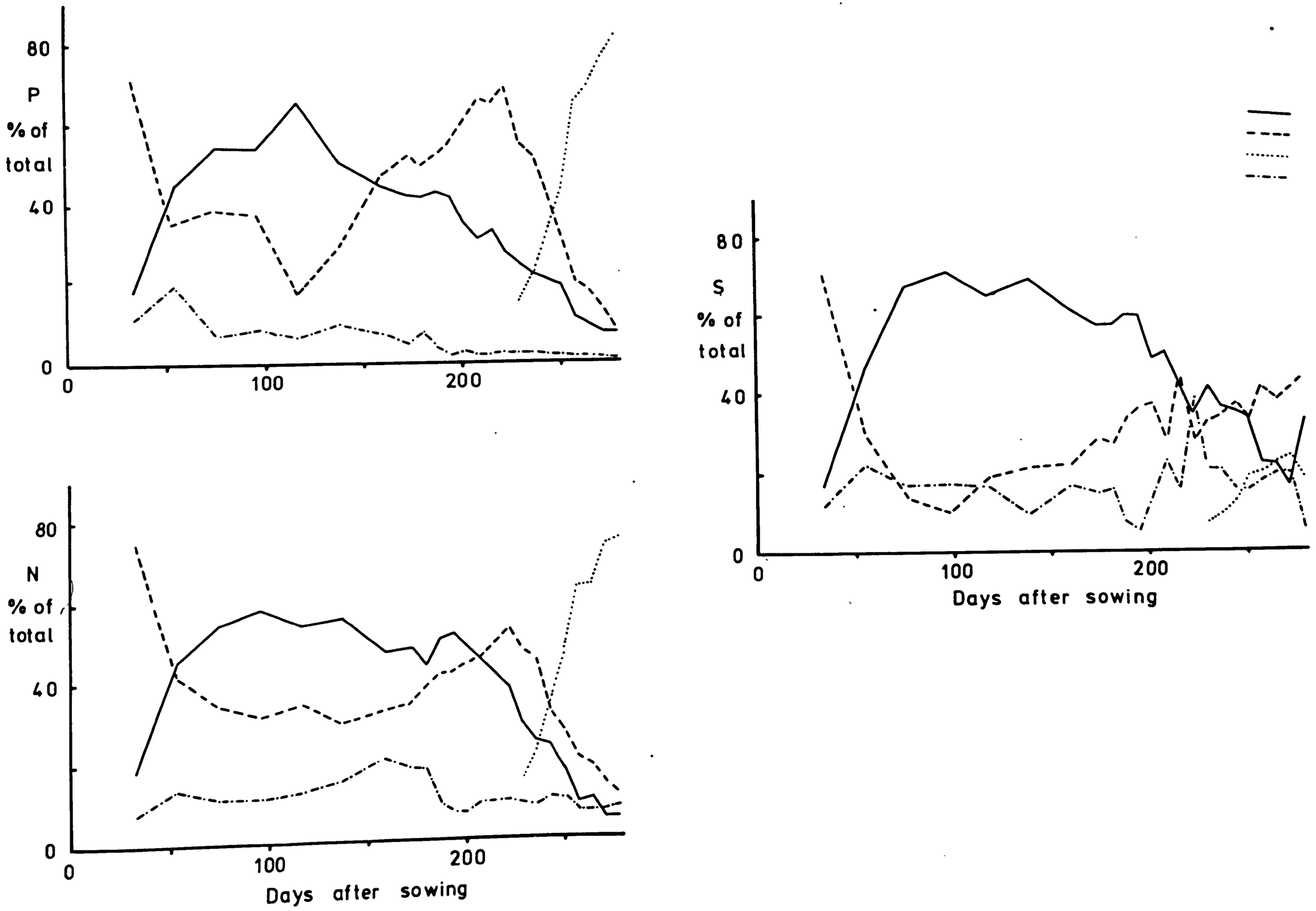


Fig. 8.3.b. The relative distribution of total nutrient content in plant organs - P, S, N



grain-filling commences and nutrients are translocated to the ears. In this period, nitrogen in the grain increases from 15% - 75% of total plant nitrogen, phosphorus from 15% - 85%, sodium from 10% - 40% and magnesium from 10% - 55%. It is noticeable that the increases in potassium (5% - 30%), calcium (2% - 12%) and sulphur (5% -20%) are not as marked as increases in other nutrients.

Such measurements suggest high rates of movement within the plant and although much of the nutrient is translocated to the grain between days 244 and 258, an average rate of translocation during the period anthesis to final harvest may be calculated. Table 8.3. shows the average rate of nutrient and carbon translocation to the ear and comparable rates determined by other workers. Translocation from leaves and stems does not appear to occur simultaneously from both organs and generally nutrient content of the leaves is reduced most rapidly in the early grain-fill period. Stem nutrient weight falls steadily until 3 - 4 weeks before final harvest but then decreases rapidly as the crop matures.

8.3.4. Root

Whilst the contribution of root nutrients to total varies throughout the life of the crop, it is generally about 10% - 20%; until day 160 root calcium and magnesium contribute 30% - 50% of the total and after day 160 phosphorus contributes less than 5%. The exception to the generality is potassium which never exceeds 3.5% of the total and this may arise because of potassium leaching during root washing or because of the low potassium composition relative to the other plant organs (section 8.2.5.).

Comparison with other results is difficult because of the paucity of data but Mengel and Barber (1974b) report that corn roots contained approximately 15% of the total plant nutrients. These data were for plants

Table 8.3 Rates of nutrient translocation to the ear (calculated as an average between anthesis and harvest)

Nutrient	µg/nutrient/ear/day			
	Results in this thesis (Maris Huntsman)	Knowles and Watkins (1931) (Victor)	Jennings and Morton (1963a and b) (Gabo)	Duffus and Rosie (1976) (Julia - barley)
Sodium	7.9			
Potassium	119	100		25*
Calcium	14.9	32		7*
Magnesium	39.8			7*
Phosphorus	146	275	45*	21*
Sulphur	3.3			
Nitrogen	610	439	630*	294*
Carbon	5780+			

* Assumes 30 grains/ear and ear consists only of grain.

\+ Assumes 40% of C in grain is translocated material (Biscoe, pers. comm.).

grown in solution culture but, except for potassium the figures are comparable to the present field grown wheat.

8.4. The nutrient composition of plants on the treatment plots

Only a limited number of plant samples were available for nutrient analysis because of the relatively small size of the plots. Unfortunately, the plant samples taken for analysis at anthesis were disposed of before the measurements were made reducing even further the number of possible comparisons.

Figure 8.4. compares the nutrient composition of the dry with the normal plots on two occas ions before anthesis and at final harvest. To avoid confusion, only results for potassium, phosphorus and nitrogen have been shown - results for the other nutrients show the same general pattern as these three. As with the normal crop, the percentage of each nutrient decreases with time. In general, the percentage nutrient composition of the dry plot plants was greater than the normal, particularly for nitrogen and potassium. The percentage of phosphorus remains almost constant for all treatments and this was the only nutrient to show this behaviour. The effect of restricting root growth to seminal roots only is not clear since in some instances the guttered plants have higher nutrient percentage composition and in other cases have lower than the corresponding main treatment.

Table 8.4. shows the composition of all treatments at final harvest. Generally the composition of all treatments was similar with a tendency for the dry plot plants to have a higher nutrient percentage than the wet or normal. There was no consistent effect produced by guttering.

Because the differences in percentage nutrient composition are small, the total quantities of nutrient present in the plants of the different treatments are largely a reflection of difference in plant dry weight.

Fig.8.4. Nutrient composition of winter wheat on the treatment plots

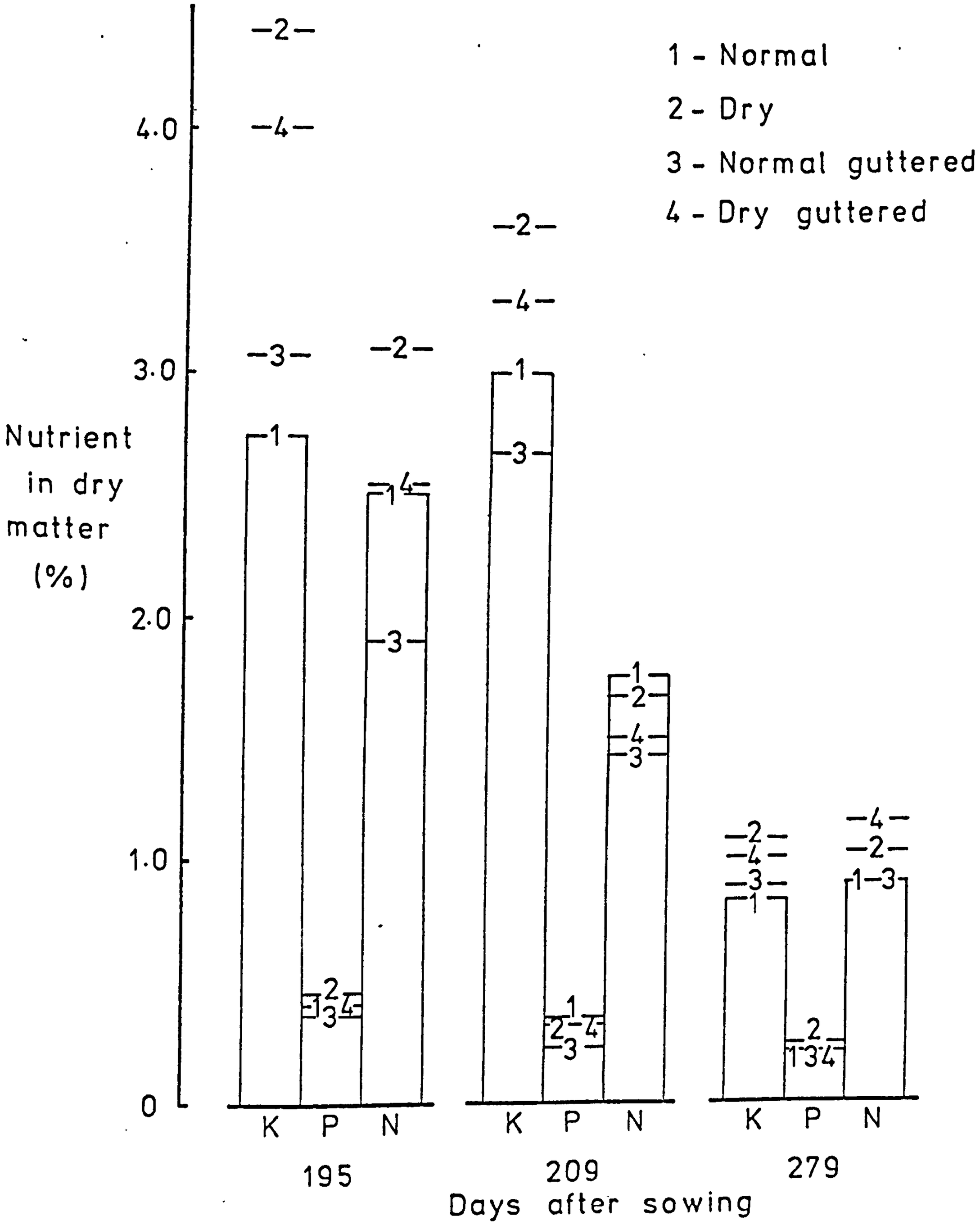


Table 8.4 A comparison of the percentage nutrient composition of normal and treatment plot plants at final harvest (day 279)

Treatment	% nutrient in shoot						
	Na	K	Ca	Mg	P	S	N
Normal	0.020	0.83	0.15	0.08	0.21	0.21	0.91
Dry	0.026	1.08	0.13	0.08	0.19	0.31	1.02
Wet	0.035	0.99	0.10	0.09	0.23	0.21	0.78
Normal Guttered	0.018	0.89	0.11	0.08	0.22	0.22	0.90
Dry Guttered	0.026	1.18	0.15	0.08	0.21	0.30	1.15
Wet Guttered	0.022	0.99	0.10	0.08	0.21	0.23	0.85

For probable errors see p. I2I.

Table 8.5 A comparison of the percentage nutrient composition of normal and treatment plot grain at final harvest (day 279).

Treatment	% nutrient in grain						
	Na	K	Ca	Mg	P	S	N
Normal	0.02	0.42	0.03	0.11	0.40	<0.004	1.72
Dry	0.02	0.41	0.03	0.11	0.37	*	2.12
Wet	0.02	0.46	0.02	0.11	0.34	*	1.33
Normal Guttered	0.03	0.49	0.02	0.11	0.39	*	1.69
Dry Guttered	0.02	0.48	0.04	0.12	0.35	*	2.42
Wet Guttered	0.01	0.47	0.03	0.10	0.35	*	1.42

*Cannot be measured accurately using stated technique.

For this reason, these data have not been presented.

When the nutrient composition of the grain is examined (table 8.5.) it is seen to be remarkably constant. The previously observed differences in total plant composition have largely been removed (except for nitrogen). Dry plot grains (main and guttered) have a higher nitrogen composition than normal grains which in turn is larger than that of wet plot grains. The reason for this must lie in relatively greater translocation of nitrogen to the grain compared with carbon on the dry plots.

8.5. Summary of results

1) The values of nutrient percentage composition recorded were comparable with those of Knowles and Watkin (1931) and Chambers (1953) although differences in soil type and fertiliser application make detailed comparisons impossible.

2) After an initial increase in nutrient percentage composition (possibly caused by the slow mobilisation of seed reserves to the growing stem), the overall pattern was for shoot nutrient percentage to decrease throughout the growing period as carbon assimilation proceded faster than nutrient assimilation.

3) The general decrease in shoot nutrient percentage was interrupted between days 181 and 202 when small increases were observed. It is suggested that this may be a result of redistribution of tiller nutrients to the main stem since this corresponds with the time of tiller death.

4) The nutrient composition of the leaves was generally higher than the stems. Root nutrient composition was comparable with other organs except for potassium.

5) Nutrient weight in the plant increased until shortly after anthesis and then remained constant or fell.

6) Large losses of plant potassium and sulphur (50%) and smaller

losses of calcium (20%) occurred between anthesis and final harvest. Estimates of nutrient losses by rainfall leaching were shown to be small and efflux via the roots seemed the most probable explanation.

7) Since nutrient accumulation ceased about anthesis, nutrients present in the harvested grain must have been translocated from other organs within the plant.

8) Shoot percentage composition on the treatment plots was similar for all treatments although the dry plots (main and guttered) had generally higher composition (particularly of nitrogen and potassium) than the normal and wet plots.

9) The guttered plot plants did not show any consistent differences when compared with the corresponding main treatment.

10) Grain nutrient composition was almost constant for all treatments except nitrogen. Dry plot grains had a higher nitrogen percentage than normal or wet.

9. WATER AND NUTRIENT UPTAKE

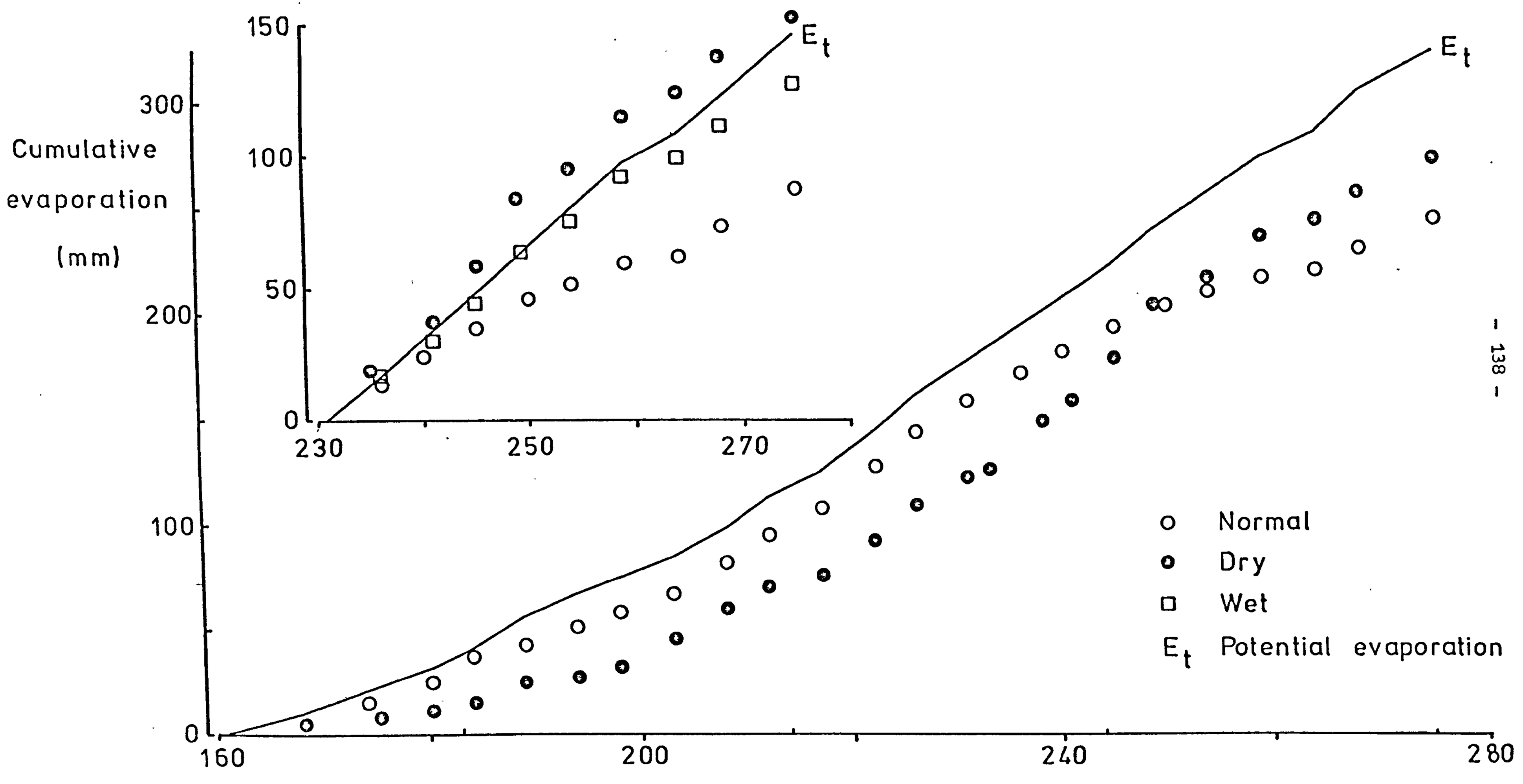
9.1. Water uptake

The identification of discontinuities in water content /time curves previously described (section 7.4.) can be used to calculate water use by a growing crop. The effective rooting depth was found for each probe date and the loss of water for each soil layer within the rooting depth calculated. This calculation, summed over the whole rooting depth, gives the total water loss from the soil and, together with the rainfall received during that period, is an estimate of evaporation from the crop.

Continual rewetting of the topsoil in the normal crop during April and May meant that until 12 May (day 194), the neutron probe data could not be used to accurately distinguish drainage from evaporation over short time periods. To estimate evaporation from 9 April (day 161) until 12 May two micro-meteorological techniques were used. Over the whole period these values (Bowen ratio by profile, 51.7mm; Bowen ratio by difference, 48.8mm; Biscoe, pers.comm.) were close to the gross loss (evaporation and drainage) of 55.1mm estimated by the neutron probe. The Bowen ratio by profile estimate of evaporation has been used in the period days 161 -194. From day 194 until the final measurement, the neutron probe data were used in the manner previously described.

Figure 9.1. shows the cumulative evaporation from the normal, dry and wet plots compared with potential evaporation calculated using Penman's equation (M.A.F.F. 1967). Cumulative measured evaporation on the normal plot is always less than cumulative potential evaporation (E_t). Between days 188 and 230, the rates of measured and potential evaporation are similar during any time interval, and cumulative totals over the same period are almost identical (E_t, 122mm; normal crop evaporation, 118mm). After anthesis (day 230) potential and measured rates became less similar (shown in insert) and between days 259 and 264, evaporation almost ceased.

Fig. 9.1. Cumulative evaporation from April until August



(a similar check to E_t was also apparent in this period but it was not as marked). This gradual fall in evaporation was caused by the drying out of the soil; water potentials of -20 bar were recorded throughout the soil profile on day 254. Heavy rainfall on day 260 re-wet the topsoil and evaporation re-commenced at a rate approaching the potential.

Evaporation from the wet plot was measured only from anthesis because drainage losses prior to this time were impossible to separate from evaporation. The insert (fig.9.1.) shows that evaporation was greater from the wet than the normal plot in any interval but similar to potential, indicating that soil water availability was not limiting.

Evaporation from the dry plot may be separated into two stages:

a) Before anthesis. Cumulative water loss from day 161-230 was less than the normal plot but between days 198 and anthesis it was almost the same (E_t, 103mm; normal, 102mm; dry 90mm). The apparently lower evaporation during April and early May may have been caused by the cover above the crop reducing wind movement or because some rain was blown in under the cover and has not been included in the water balance. During the period days 161 - 198, 60mm of rain fell compared with(E_t - measured evaporation) of 43mm.

b) After anthesis. The total quantity of water evaporated by the dry crop between anthesis and the final measurement was greater than by the normal or wet crop, and at times, rates of evaporation were considerably nigher than potential. The dry crop was taller than the surrounding crop at anthesis so evaporation from this crop can reasonably be expected to be higher. However, the height advantage was lost within 10 days after anthesis and during this period measured evaporation was close to potential. The main anomaly is in the period from day 241 to 249 when actual evaporation was 50% - 60% higher than potential. Such a large difference is difficult to explain especially since similar losses were not found

from the wet plot, although they were 9% - 14% above potential. This period was a time of rapid drying in the surrounding soil when both soil and plant water potentials decreased - this would result in large quantities of advected energy being available to evaporate water from any moist areas in the crop. From day 254 to final measurement, evaporation is almost the same on both (dry,57mm; wet,52mm).

Table 9.1. shows the quantity of water taken up from individual soil layers. Rainfall has been included in the 0 - 30cm values of water loss. The smaller quantity of water lost by the dry plot until day 195 is clear; subsequently the normal and dry plot evaporation rates are similar until anthesis, but the zone of water extraction was not. The plants on the dry plot extract a much greater fraction of their water from depths below 30cm and uptake commences from each succeeding layer before the normal plot.

After anthesis, the main interest is in the response to irrigation of the dry and wet plots. The total evaporative loss from the dry plot until day 250 is higher than the wet plot but the difference between the two is almost entirely accounted for by uptake below 30cm. It has been commented previously (section 7) that the effective rooting depth on the dry plot increased rapidly after anthesis and this is now seen to be complemented by a larger water loss from depth.

Evaporative losses from the guttered plots have not been presented here because they are based on a single measurement. The information presented in section 7 indicates that guttered and main treatment plots reacted similarly to the treatments imposed although the magnitude of the response was generally lower on the guttered plot.

9.2. Water inflow

It has already been shown that the sizesof root systems on the

Table 9.1 Water loss from individual soil layers

Days after sowing	Uptake - litres (mm) water per m^2														
	Normal					Dry					Wet				
	Total	0-30	30-60	60-100	100+	Total	0-30	30-60	60-100	100+	Total	0-30	30-60	60-100	100+
161-167	7.0	7.0				3.8	3.8								
167-174	8.5	8.5				4.0	4.0								
174-181	10.5	10.5				4.4	4.4								
181-188	13.5	13.5				6.8	6.8								
188-195	13.0	13.0				9.5	9.3	0.2							
195-202	14.0	14.0				14.7	6.7	3.8	3.5	0.7					
202-209	17.6	14.8	2.3	0.5		19.8	14.8	3.2	4.7	1.1					
209-216	22.6	18.0	3.8	0.8		19.0	5.5	3.3	5.3	0.9					
216-223	25.6	14.0	6.3	5.3		19.0	4.2	6.5	6.0	2.3					
223-230	24.6	13.3	4.8	6.5		21.4	3.6	6.5	8.3	3.0					
231-237	19.1	10.8	3.5	3.5	1.3	24.0	17.0	7.0			19.0	18.0	1.0		
237-244	17.6	5.5	2.8	5.3	4.0	30.0	18.8	5.0	5.0	1.2	22.0	16.0	6.0		
244-251	13.1	3.3	2.0	3.5	4.3	34.0	13.4	9.5	8.5	2.6	27.5	16.7	5.5	5.0	0.3
251-258	11.2	8.8	0.8	0.8	0.8	20.0	8.5	5.0	5.3	1.2	17.0	7.8	3.5	4.2	1.5
258-265	10.8	10.0	0.0	0.0	0.8	20.0	15.5	1.3	2.2	1.0	17.0	14.5	0.0	1.3	1.2
265-272	12.1	10.3	1.3	0.0	0.5	17.0	14.3	0.4	1.5	0.8	17.5	15.6	0.0	0.7	1.2

treatment plots were affected by the treatment imposed (section 5). Determination of water inflow (uptake per unit length of root per unit time) should indicate to what extent the observed differences in water uptake could be related to differences in root length or to other factors.

Assumptions and approximations in the calculation of inflow are:

1) All rain falling reached the soil surface and was taken up through the roots ie all the evaporative loss was via the plant.

2) There was no movement of water from one soil layer to another.

3) The root lengths used to calculate average inflow for the whole root system were the lengths in the effective rooting depth.

4) Root length in each individual soil layer was obtained by "smoothing" the data either by eye or, where appropriate, by linear regression.

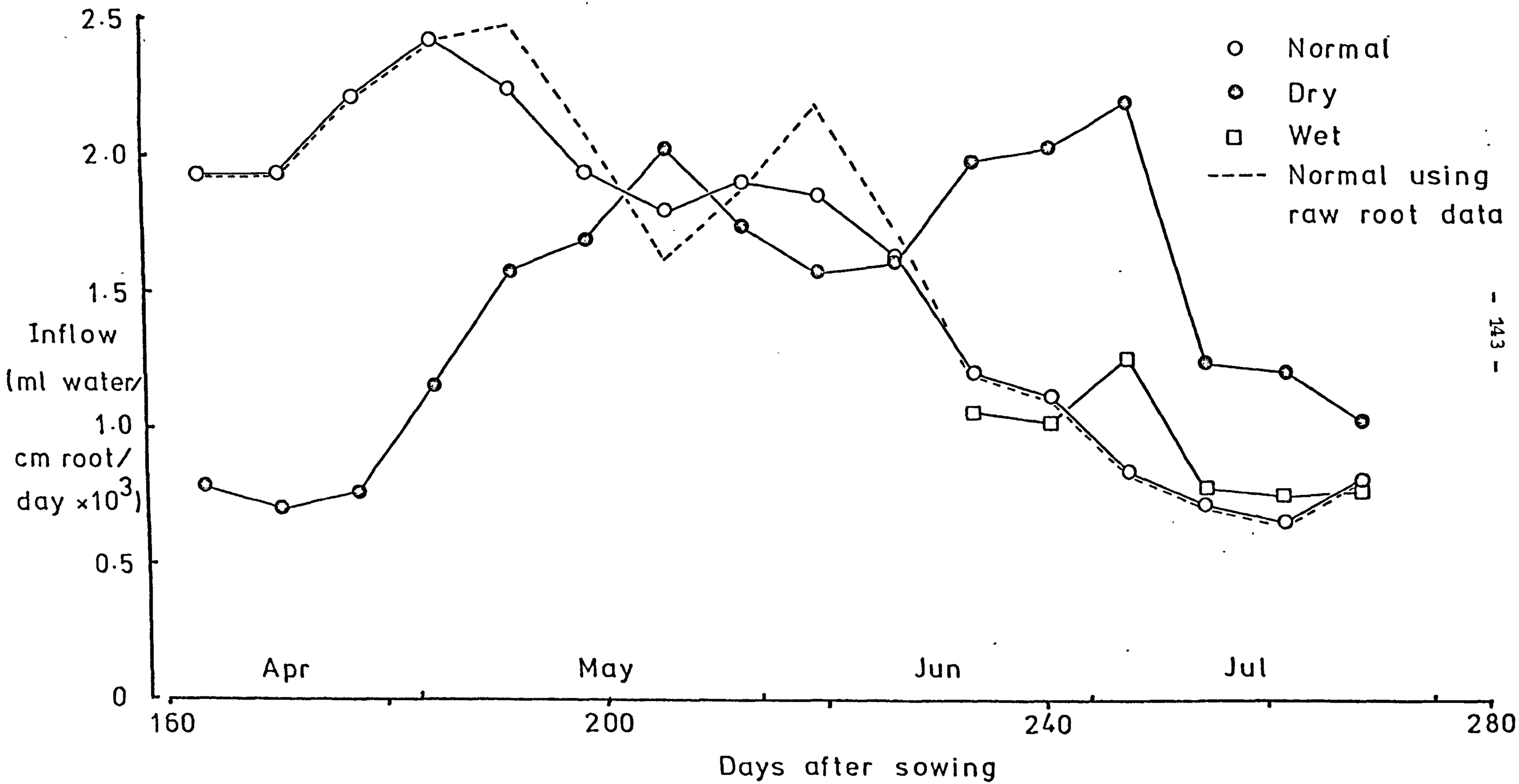
5) Because of the necessary amendment to the root length data an exponential root growth was not valid and Williams' (1948) equation (section 2.7.) was modified to:

$$I_w = \frac{W_2 - W_1}{t_2 - t_1} \times \frac{1}{[(L_2 + L_1)/2]}$$

where W = cumulative water loss (ml)

Figure 9.2. shows inflow for the three treatments calculated for the effective rooting depth. The inflow of the normal crop calculated using the raw effective root length values is also shown and indicates that smoothing the length data has introduced no great error into the calculation (at least for the normal crop). Inflow of the normal crop decreases over the growing period from a maximum of 2.5×10^{-3} ml water per cm root per day to a minimum of 0.66×10^{-3} ml/cm/day close to final harvest. The values determined are similar to those found by other

Fig. 9.2. Water inflow to winter wheat

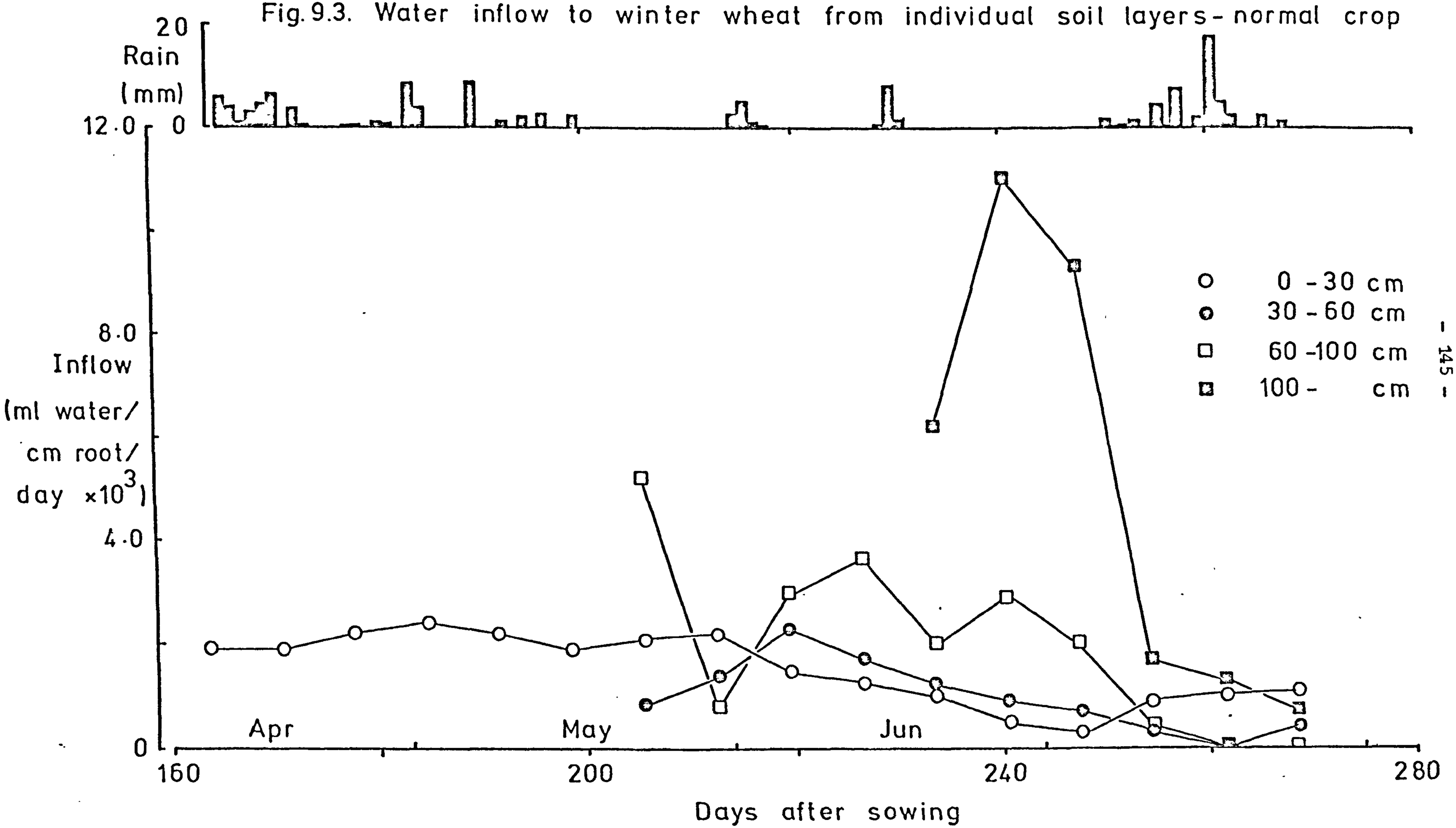


workers (table 2.2.) and the observed reduction in inflow over a growing season has also been measured previously (Taylor and Klepper, 1971).

Dry plot inflow is initially lower than the normal but between days 200 and 230 is almost the same. This low initial inflow may be a real effect although it is unlikely that the drying treatment should affect uptake so soon after its imposition; it is more likely that the water balance is in error because of rain blowing in under the cover. After irrigation at anthesis, the dry plot inflow is almost double the normal, a result which arises not only because of larger evaporative losses but also because root length is smaller. These reasons also explain the larger inflow of the dry compared to the wet plot.

Inflow in separate soil layers in conjunction with the information on soil water status (section7) show the combination of factors giving rise to the average inflow over the whole profile. Forthe normal crop (fig.9.3.), water uptake occurs first from the 0-30cm layer and inflow is almost constant until the soil becomes drier when water uptake commences from the next two layers (about day 202). During this period rates of water extraction have increased (table 9.1.) but so has root length and the resultant is an almost constant inflow. As the topsoil dried, water use from depths greater than 30cm occurred and inflow in the top 30cm decreased. Inflow in each successive layer was reduced as drying proceeded but at any given time inflow increased down the profile. The high inflow to roots in the layer below 100cm during the period immediately after anthesis is noticeable. Root length below 100cm is approximately 1% -2% of total length at this time but supplies 20% of the water used. The ability of a few roots at depth to supply a substantial proportion of the water requirement during a drying phase has been mentioned by Zadontsev and Bondarenko (1970);and Allmaras et al

Fig. 9.3. Water inflow to winter wheat from individual soil layers - normal crop



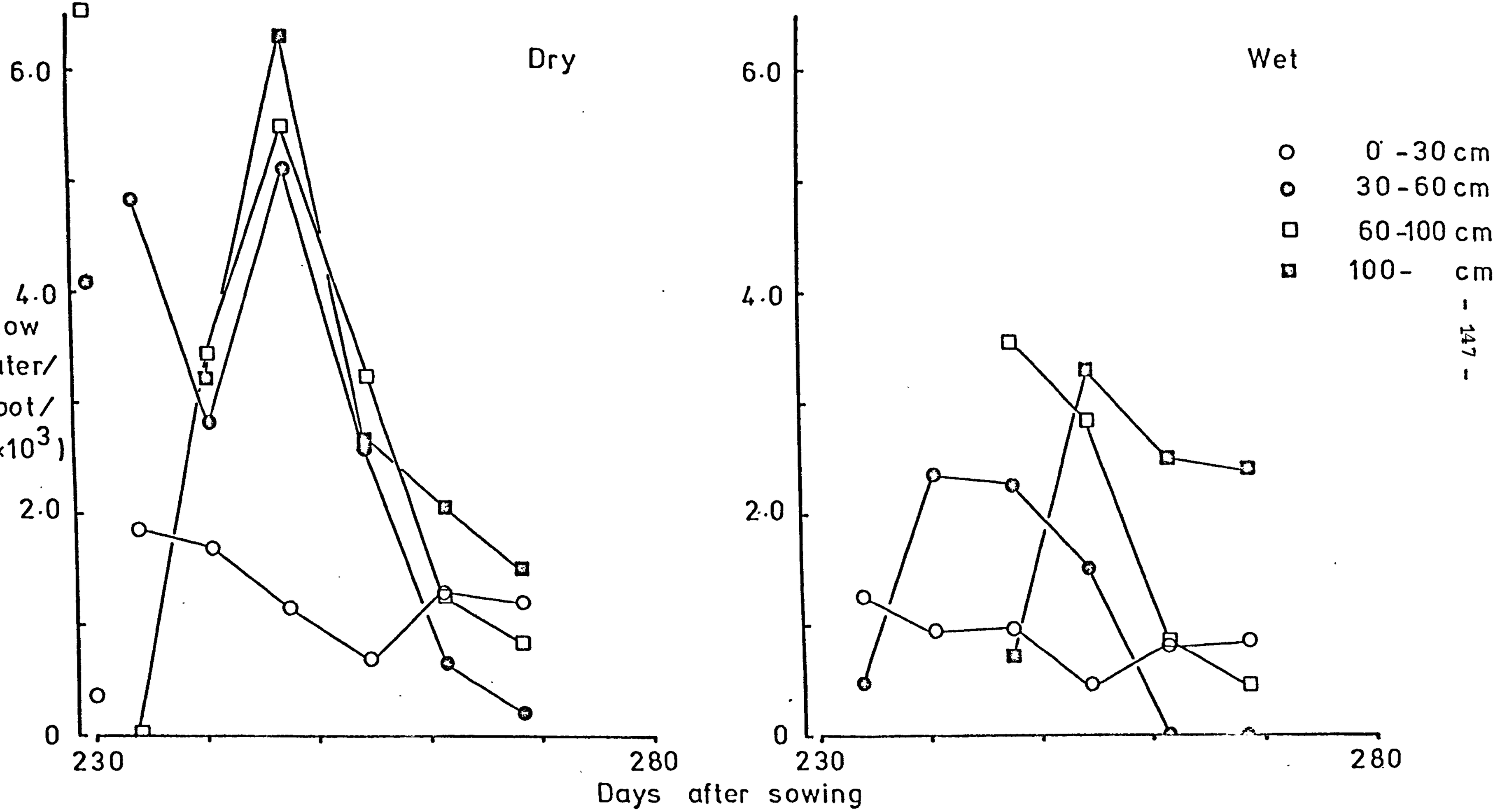
(1975); the high inflow results from plant demand for water being met by reserves of water at depth at high potential (water potentials below 100cm had not fallen substantially at this time).

After day 250, the general pattern outlined no longer holds and inflow in the 0 - 30cm layer increases while inflow in other layers, particularly the 100cm layer, is reduced. Rainfall re-wet the topsoil and the resultant 0 - 30cm inflow increase arises because water is now available to be taken up or because it directly evaporated from the soil surface. The simultaneous reduction of inflow from below 100cm could be due to two factors, either a) drying of the soil around the root reducing water availability, or b) because water is available at the surface uptake by the plant diminishes from depth. These two possibilities were tested using a simple resistance analogue of plant / water relations and as shown in appendix 5, explanation (b) was found to hold. If no rain had fallen, the model predicts that inflow below 100cm would have been maintained close to its previous value (Wallace, pers.comm.).

Inflow from individual layers in the dry plot prior to anthesis is not shown but because the plot was covered, exploitation of stored soil water started before that on the normal plot. This resulted in dry plot inflow being generally lower in the topsoil (0 -30cm) but higher at depths below 30cm compared to normal values on the same day. After irrigation at anthesis, inflow from the 0 - 30cm layer and 30 - 60 cm layer increased (fig.9.4.) while uptake from below 60 cm ceased. Between days 231 and 250, water loss from below 30cm on the dry plot is greater than on the wet plot (table 9.1.) and together with a smaller root length, this resulted in a higher inflow.

Inflow from the 0 - 30cm layer on the wet plot after anthesis is generally higher than on the normal plot because although root length is greater, so is soil water availability.

Fig.9.4. Water inflow to winter wheat from individual soil layers - dry and wet treatments



Both wet and dry treatments first show a reduction of inflow as the 0 - 30cm layer dries out, and then an increase after rainfall. On these plots, water uptake below 100cm continues but inflow from other layers is reduced and becomes less than the topsoil layer at the final measurement.

9.3. Nutrient uptake

In the discussion that follows it has been assumed that all the nutrients present in the plant (section 8) came from the soil via the roots. This assumption is reasonable for most nutrients but it is known that atmospheric sulphur can contribute to plant sulphur content when soil sulphur reserves are low (Jensen, 1963). The present soil was known to contain adequate sulphur (approximately 36 ug - S per g topsoil as acetate extractable sulphate) but previous studies on the same site have shown that the various processes encompassed by "dry deposition" could supply almost the whole of a winter wheat crop's sulphur requirements during a growing season (Fowler and Unsworth, 1974).

An attempt was made to estimate the contribution of atmospheric sulphur to total plant sulphur: columns containing ^{35}S labelled soil were buried in the field to the west of the treatment plots and plants sown in them. The loss of sulphur from the plant after anthesis made analysis of the results difficult and, unfortunately, the experiment contributed little to the required result. Plant sulphur content, then, has been assigned to root uptake although a contribution (estimated at 10% - 15% prior to anthesis) from the atmosphere is conceivable.

In calculating nutrient inflow, no account has been taken of the possible influence of root hairs or endotrophic mycorrhizal associations (see section 2.7.).

9.4. Nutrient inflow

Nutrient inflow between sampling dates until anthesis was first calculated using Williams (1948) equation (section 2.7.). The calculated inflow was, however, very irregular with time (fig.9.5.) because of sudden fluctuations in the measurements of both root length and nutrient content. To overcome this, polynomial equations (maximum degree 5) were derived for the transformed (logarithmic) root length and nutrient content data, and the fitted curves used to calculate inflow at particular times. These "instantaneous" inflows (Hunt,1972) are given in table 9.2.

For all nutrients, inflow was highest in the young plant (day 34) and thereafter decreased until day 160. This decrease in inflow with time has been observed previously both in the laboratory (section 3) and in the field (Brewster and Tinker, 1970; Mengel and Barber, 1974b) and is due to a more rapid increase in root length than nutrient uptake. Between days 34 and 160, the reduction in inflow is only a factor of 3 or 4 - much lower than found by Mengel and Barber(1974b) with corn where nitrogen inflow decreased to one-twentieth of that measured in the young crop.

After about day 160, nutrient inflow increases for all nutrients and continues to increase for most nutrients until anthesis; such a result has not been reported previously and will be discussed in Section 10. Potassium and nitrogen inflows clearly show (fig.9.5.) the increased inflow after day 160 and also a small decrease shortly before anthesis; a similar pattern was found for sodium and magnesium. Calcium, phosphorus and sulphur all give a steady increase in inflow until anthesis (table 9.2.). It is interesting that all these inflows are maintained at a comparatively high rate right up to anthesis but that nett uptake then ceases within seven days (table 8.1.)

Fig. 9.5. Inflow of potassium and nitrogen - normal crop

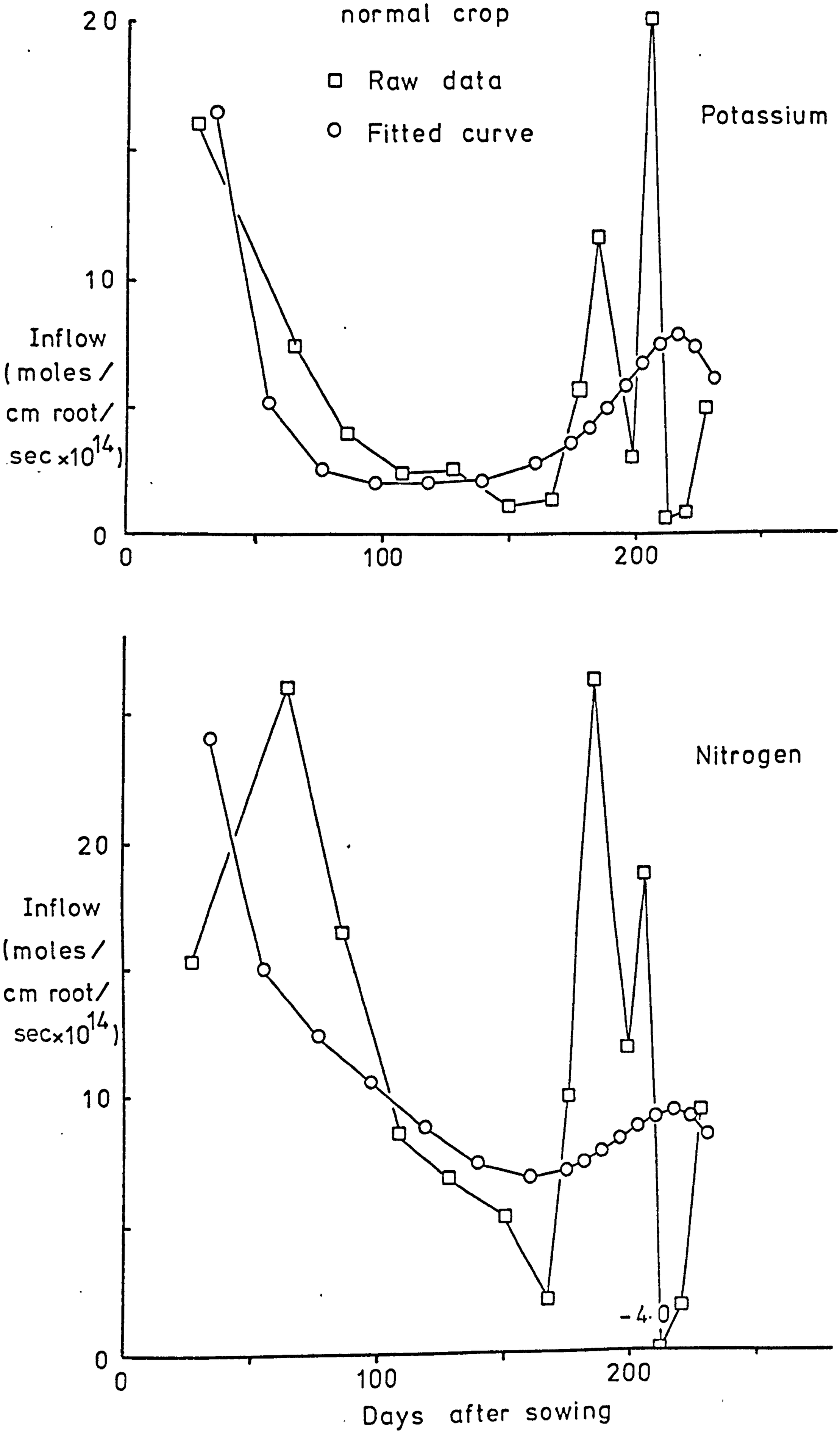


Table 9.2 Nutrient inflow to winter wheat from sowing until anthesis

Days after sowing	Inflow - moles/cm root/sec (x 10^{14})						
	Na	K	Ca	Mg	P	S	N
34	1.03	16.54	1.96	0.55	1.60	3.00	24.04
55	0.60	5.20	0.82	0.44	0.91	1.14	15.01
76	0.46	2.59	0.56	0.35	0.71	0.43	12.40
97	0.36	2.02	0.49	0.27	0.60	0.27	10.63
118	0.26	1.96	0.44	0.20	0.50	0.25	8.83
139	0.19	2.15	0.40	0.17	0.44	0.25	7.41
160	0.14	2.75	0.38	0.18	0.45	0.27	6.86
174	0.13	3.60	0.39	0.21	0.52	0.32	7.09
181	0.12	4.21	0.41	0.24	0.58	0.36	7.39
188	0.12	4.96	0.44	0.28	0.66	0.41	7.80
195	0.12	5.82	0.48	0.32	0.77	0.48	8.29
202	0.12	6.71	0.55	0.37	0.90	0.58	8.80
209	0.12	7.45	0.63	0.41	1.05	0.73	9.22
216	0.11	7.78	0.75	0.44	1.22	0.93	9.41
223	0.10	7.40	0.90	0.43	1.20	1.20	9.18
230	0.09	6.12	1.08	0.37	1.55	1.55	8.38

The range of values obtained for inflow are of the same order of magnitude as those reported by Brewster and Tinker (1972), with potassium and nitrogen approximately ten times phosphorus inflow. Sulphur inflow was comparatively large during initial growth - a result commented on earlier in the column experiment and possibly related to the very low grain sulphur content (table 8.5.). Suitable measurements were not available to estimate inflow after anthesis when potassium, sulphur and calcium showed large efflux from the plant to the soil. Apparent transitory losses of sodium observed up to anthesis have been masked by the calculation procedure but may be a real effect.

9.5. Mass-flow and diffusion contribution to nutrient uptake

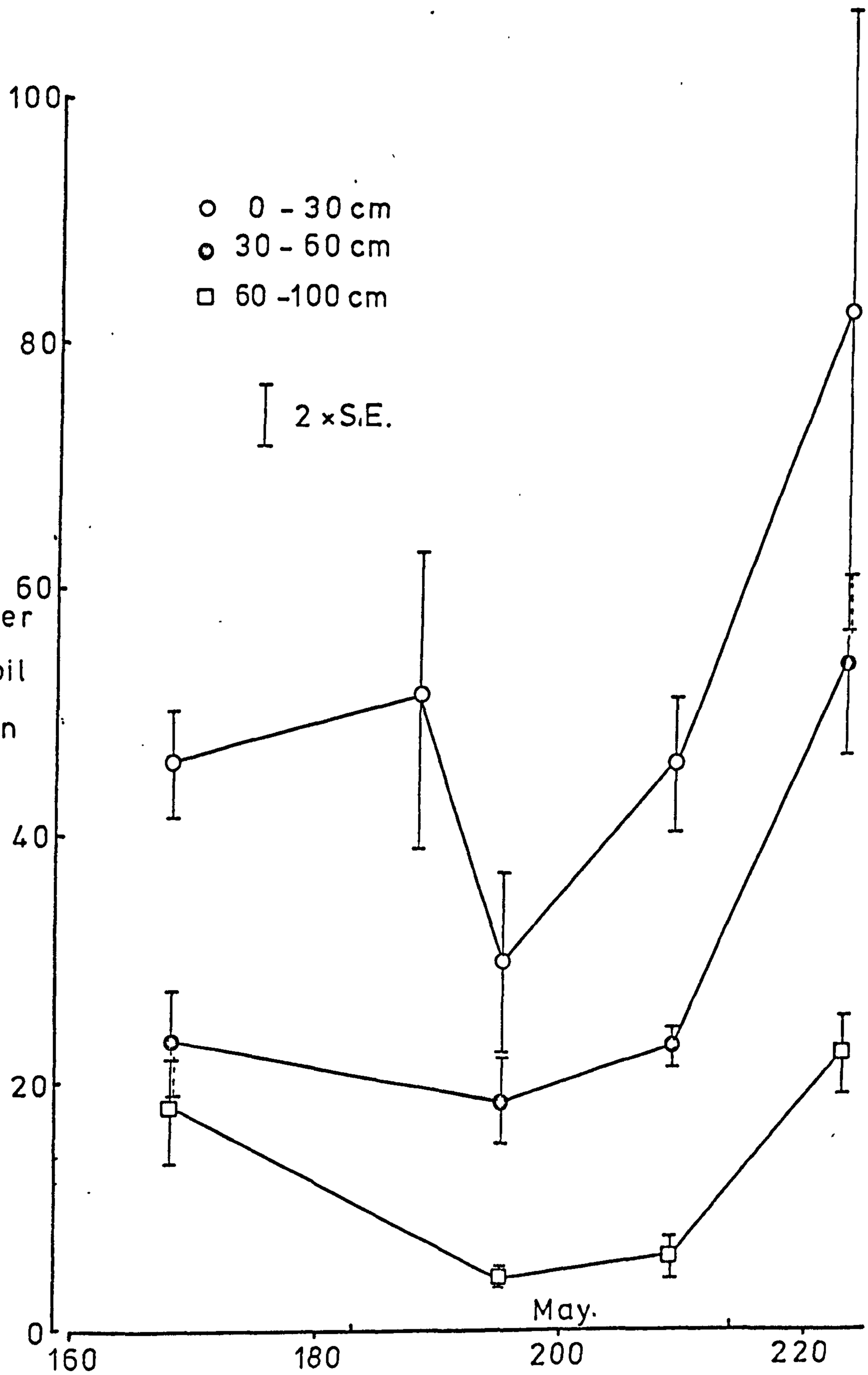
Soil cores were taken from the field on days 168, 188, 195, 209 and 223 for soil solution extraction (section 4.3.) The soil was sieved (< 4mm) and 600g soil at field moisture mixed with 150g coarse sand (18 - 25 mesh). This was packed into a Perspex tube (28mm i.d.) and soil solution displaced using 70% glycerol solution (Moss, 1963). One drop of toluene was added and the solution stored at 1°C; analyses were performed as described in appendix 3.

Figure 9.6. shows the concentration of potassium in solution with depth and time and indicates the variability and standard error associated with such measurements (mean of three analyses). Apart from sodium and nitrogen(nitrate and ammonium ions) which showed large variations in concentration on many occasions, the coefficient of variation was generally no more than 20 - 25% of the mean. Appendix 6 contains mean soil solution concentrations for all nutrients.

Mass flow was calculated in weekly intervals from day 160 until anthesis making the following assumptions:

1) Soil solution concentration in each interval was the average

Fig. 9.6. Potassium concentration in soil solution



concentration between the two dates ie. for period 188 - 195, nutrient concentration is as day 191.5. Exceptions to this are periods 160 - 167 (which is treated as day 168) and 223 - 230 (which is treated as day 223).

2) All rain reaches the soil surface, wets only the 0 - 30cm layer and is all evaporated via the plant.

3) No water movement from one soil layer to another occurred.

Measured uptake and possible contribution from mass flow (calculation A) are compared in figure 9.7. Plant uptake of potassium, phosphorus and nitrogen is seen to be higher than that predicted by mass flow alone while sodium, calcium, magnesium and sulphur uptake is lower. Between days 160 and 230, mass flow accounts for only 37% potassium, 5% phosphorus and 44% nitrogen uptake but could supply 15 times the sodium, 9 times the calcium, twice the magnesium and three times the sulphur found in the plant. These conclusions are in general agreement with the outline of soil processes supplying individual nutrients stated by Barber, Walker and Vasey (1963) for a corn plant. In any period, mass flow is never capable of supplying the observed uptake of potassium, phosphorus and nitrogen but always capable of supplying the other nutrients.

The first assumption used to calculate these results is the best possible (given the variation of soil solution concentration) but it is unlikely that all the rain fell to the soil surface and was evaporated via the crop (assumption 2). For this reason, the results were re-calculated to achieve a figure for minimum mass flow, assuming that in each rainfall event, 1mm of the total was lost by other means (interception and / or direct loss from the soil surface). This gave mass flow B on figure 9.7. and indicates that to assume all the rainfall was evaporated via the crop could not introduce any gross error. The real contribution of mass flow probably lies somewhere between these two estimates.

Fig. 9.7.a. The contribution of mass flow to measured nutrient uptake - Na, K, Ca, Mg

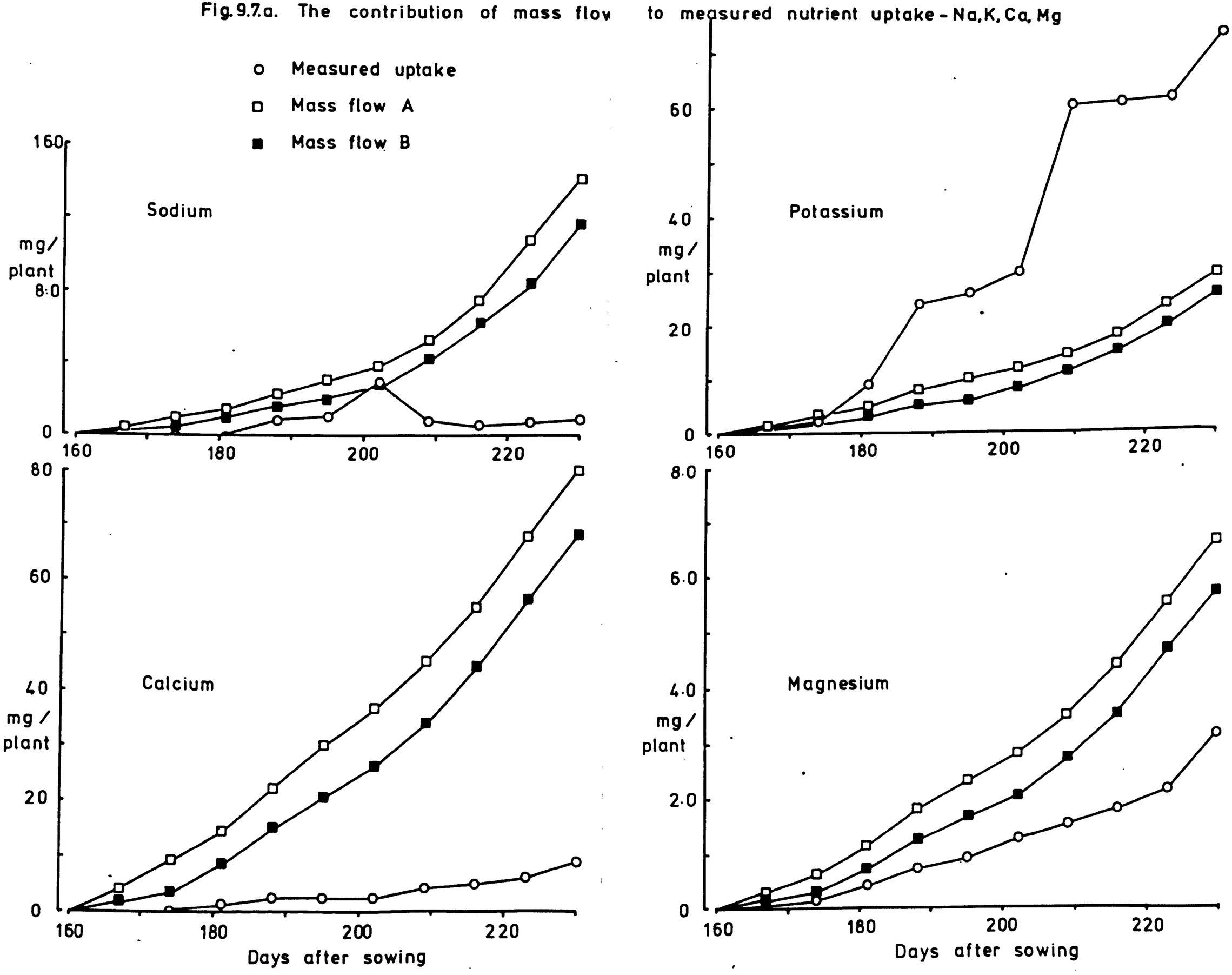
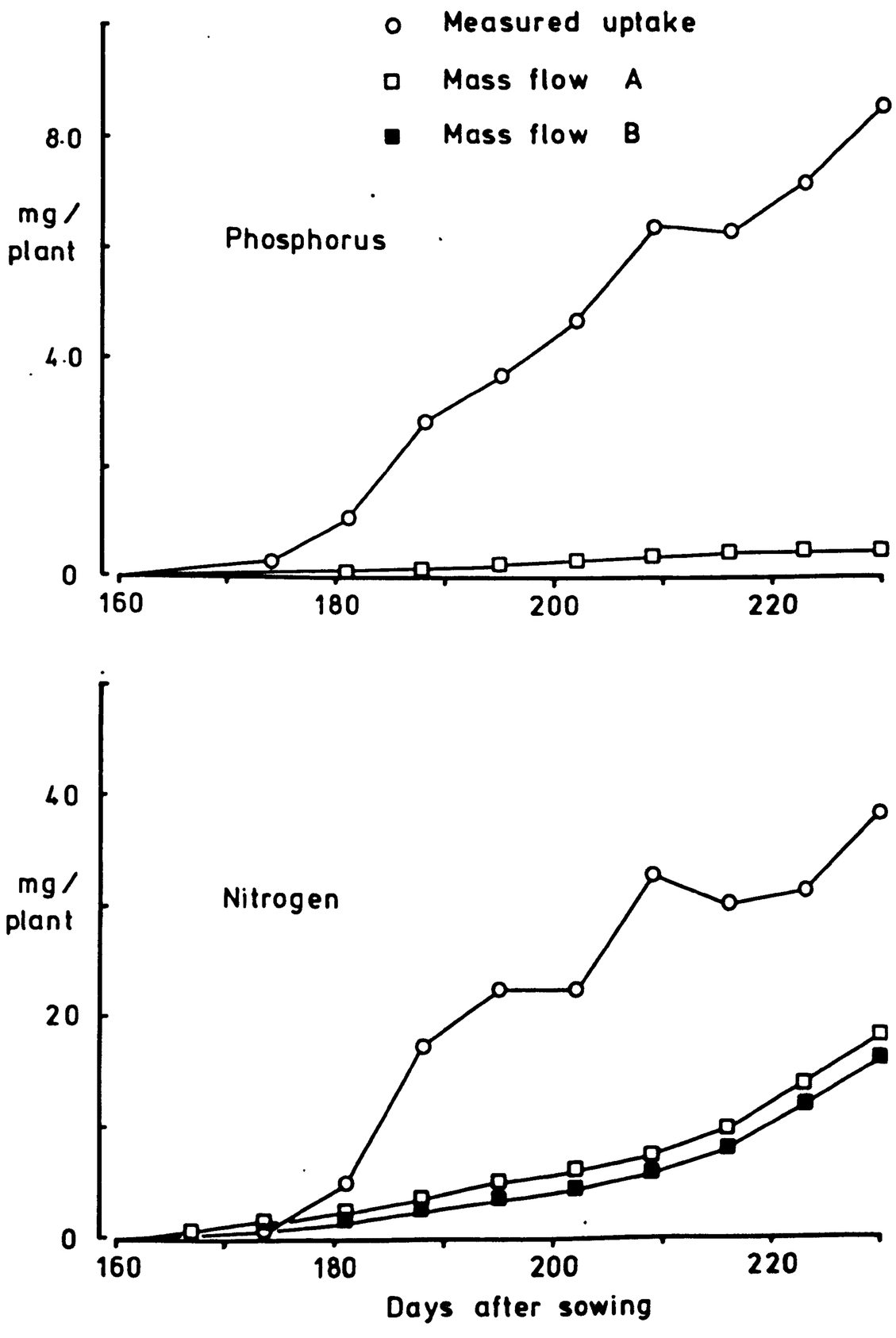
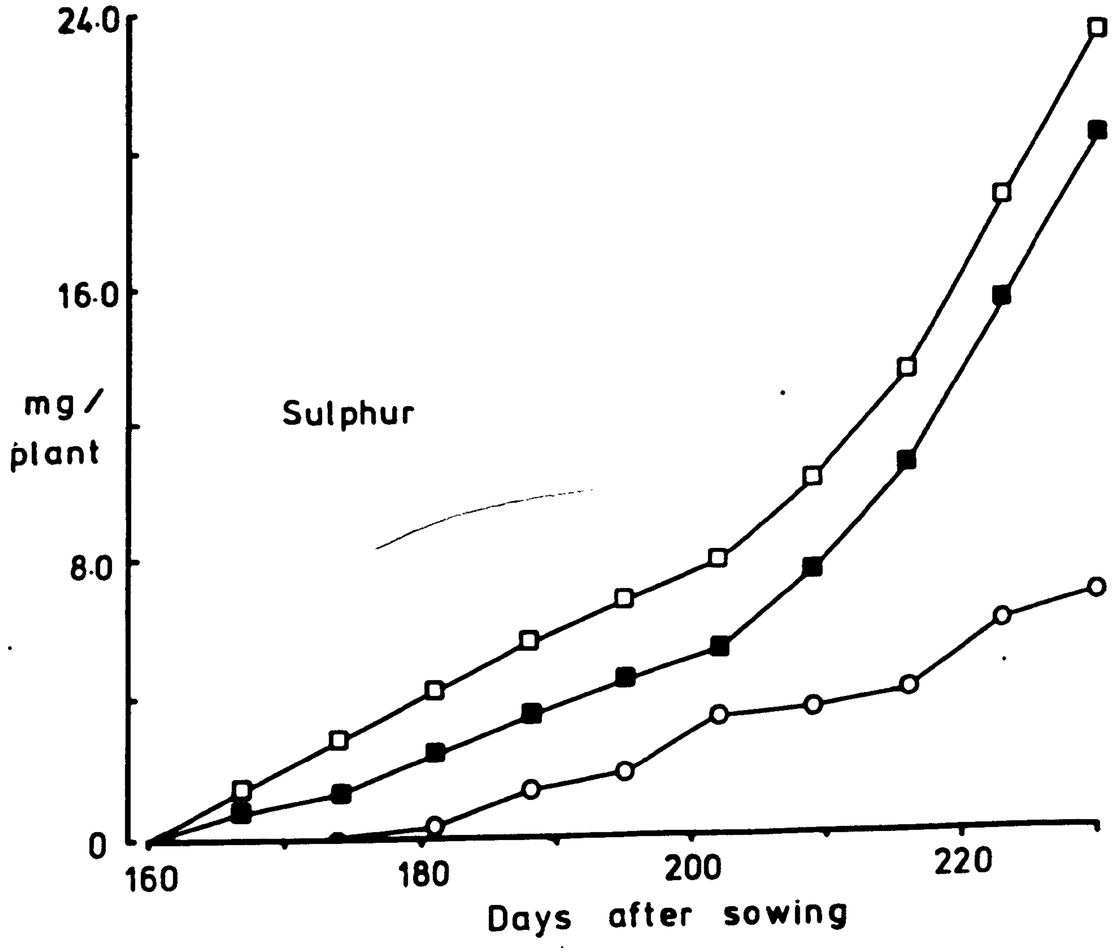


Fig.9.7.b. The contribution of mass flow to measured nutrient uptake - P, S, N





The apparent diffusion contribution to nitrogen uptake was larger than expected and would arise if nitrate or ammonium concentration in soil solution had been under estimated. Large variation in nitrogen concentration has already been noted and perhaps results f rom the general drying from mid-May onwards leading to an uneven distribution of the spring top dressing of "Nitram". Nevertheless, recalculation of measurements made by NaNagara, Phillips and Leggett (1970) of nitrogen uptake by corn suggest that between 20% and 60% of plant nitrogen could be supplied by diffusion.

9.6. Summary of results

1) Cumulative evaporation from the normal crop was less than potential over the growing season but almost equal during the period of rapid growth (mid-May to mid-June). Rates of potential and wet plot evaporation after antnesis were similar but dry plot evaporation exceeded potential during some periods - reasons for this are suggested.

2) Inflow of water generally decreased with time as the soil became drier.

3) When water uptake during a dry phase occurred from layers below 30cm, inflow at any one time was generally higher at depth.

4) Rainfall or irrigation caused reduction or cessation of uptake at depth, and uptake from the topsoil to recommence at a higher rate. This resulted in higher inflow in the 0cm - 30cm layer compared with the pre-watered figure. Drying the soil had no measurable effect on the ability of the roots to extract water except through its effect on availability.

5) Uptake and inflow of water after anthesis from depths below 30cm were higher on the dry plot than the wet. It is suggested that this uptake occurred because topsoil root length on the dry plot was lower

than on the wet, and hence the quantity of water readily available was also lower. To meet evaporative demand, uptake had to occur from depths below 30cm resulting in deeper effective rooting and a higher inflow.

6) Nutrient accumulation ceased at anthesis.

7) Nutrient inflow initially decreased with time but after day 160 increased and, for some nutrients, continued to increase until anthesis.

8) Between days 160 and 230 mass flow was capable of supplying all the sodium, calcium, magnesium and sulphur the crop accumulated but only 40% of potassium and nitrogen and 5% of phosphorus.

10. DISCUSSION AND CONCLUSIONS

10.1. Experimental results

The field experiment was designed to investigate four major questions (section 4.1.). Each of the chapters 5 - 9 carries a summary of results but these have not been discussed in relation to each other or to all the original stated objectives. This section deals with the implications of the summarised results to these objectives.

10.1.1. The production and growth of winter wheat roots

The six (occasionally seven) seminal axes produced by the plant were in accordance with the general observations of other workers (Percival, 1921; Troughton, 1962). Five of the axes were produced within 6 weeks of sowing. This is a longer time than reported by most workers but their work was carried out indoors at higher temperatures than those experienced by the plant in the field immediately after germination. Two nodal axes were produced from the coleoptile node in mid-February and axis development from stem nodes also started about that time. By anthesis, each main stem possessed approximately 20 stem nodal axes; ten axes had grown from stem nodes 1 to 5, six from node 6, and up to six from node 7. Although few observations of site of nodal axis production are reported in the literature, Milthorpe and Moorby (1974) state similar numbers of axes for each node. Except for nodes six and seven, the number of axes produced was unaffected by soil drying. However, the laboratory experiment (chapter 3) has already shown that if drying is imposed early in the crops' life, production from lower nodes can also be reduced. Such extreme drying early on is uncommon in the field but Locke and Allen (1924) have measured similar effects with field grown wheat.

Root production from tillers was difficult to study because of the

lack of growing tillers after the end of April. The results obtained supported the statements of Peterson (1965) with basal nodes producing a single axis and higher nodes (six and seven) producing up to six axes.

Figure 10.1. provides a schematic representation of the sites of root production. Different orders of root may differ in their contribution to the total uptake of nutrients or water (Clarkson and Sanderson, 1971; Granam, Clarkson and Sanderson, 1974). The numbers of axes produced will, therefore, have an effect on the morphological and physiological characteristics of the total root system.

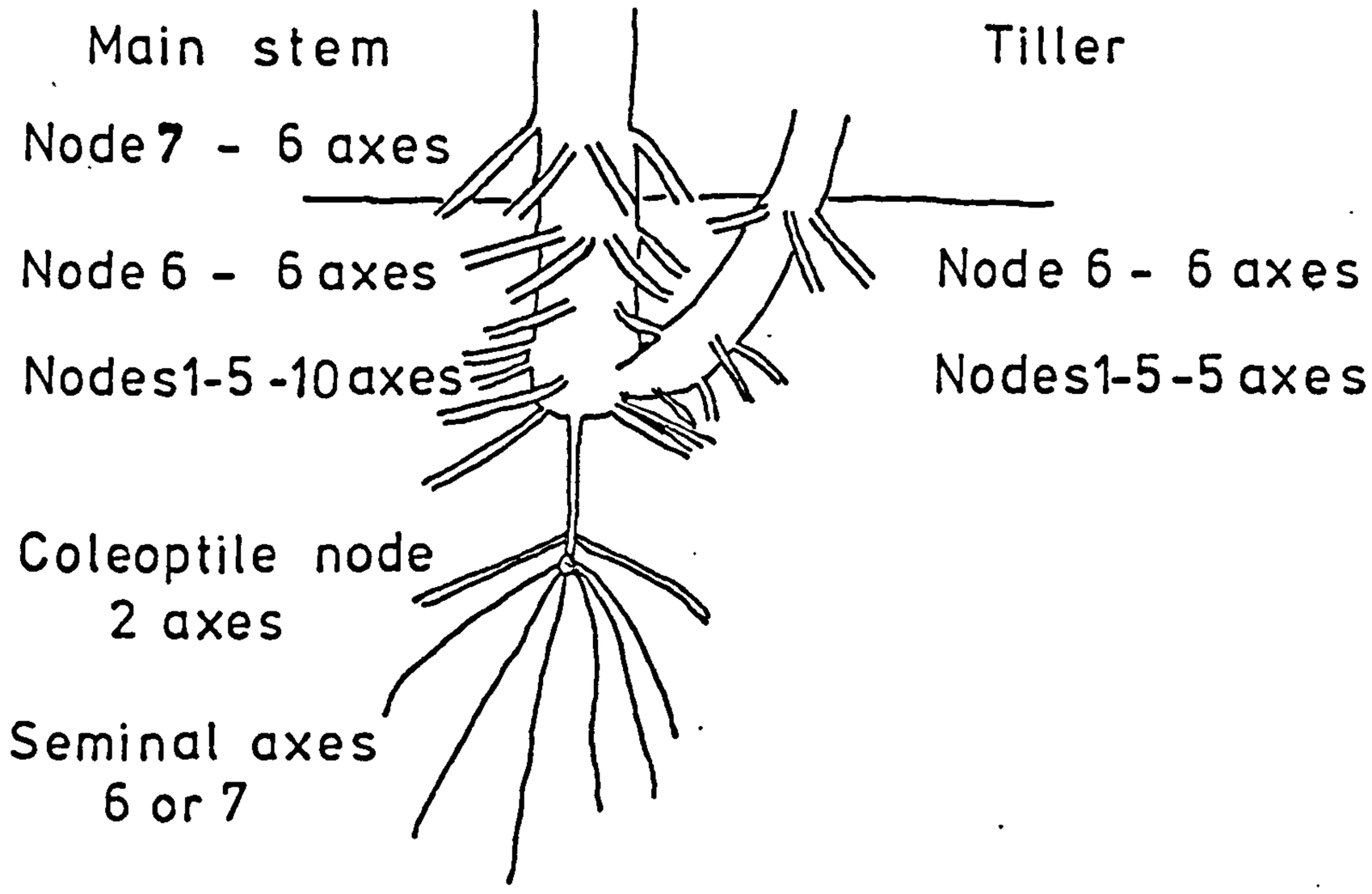
The study of root growth is hampered by the difficulty of extracting roots from the soil. Methods for examining root growth have been discussed previously (section 2.4.). The method chosen in this study was to auger soil samples and then to wash out the roots. Numerous workers (eg. Clarkson and Sanderson, 1971; Russell, 1971; Pearson, 1974) have expressed objections to this particular method, but few have attempted to quantify the errors involved. It is relevant at this point to discuss errors since many of the treatment differences reported in this thesis are dependent on the root data.

Estimated errors are:

a) Augering in the field. No smearing of roots against the side of the auger was observed and the use of a hand-operated (as opposed to a powered) auger has advantages in this respect. If the auger does not go straight down but hits stones and takes out a hole larger than 10cm in diameter, this would introduce a large error. For example, a hole of 11 cm diameter would have 20% more soil; 12cm diameter, 44% more soil.

The 10 cm increments of soil excavated are accurate to within 1cm - unimportant for the summed profile but providing up to 10% error for each individual value.

Fig.10.1. Sites of root axis production



b) Storage in the cold room. No deterioration of roots was observed. Size of errors unknown but likely to be small.

c) Washing and cleaning. Cereal roots do not exhibit a continuous range of diameters but fall into discreet bands related to the order of root (Hackett, 1968). The information presented in table 2.1. suggests that the main axes (diameter 0.5mm) and primary laterals (diameter 0.2mm) will give much of the root length. Although the sieve used for washing had a 1mm mesh, it is unlikely that roots would pass straight through. Water pressure was kept to a minimum during washing and no pulverisation of roots was observed nor were roots seen in the bowl beneath the sieve.

Cleaning the roots is likely to be a major source of error though impossible to specify especially for topsoil samples. The picking out of "live,white roots" from other organic material is subjective and two people working together may easily disagree on what is a "white" root. The relative distribution of roots within a profile as assessed by two workers may well be similar but large differences in absolute values might exist.

An estimate of the error in these two stages was obtained by mixing four known lengths of root with four samples of soil containing no roots. These were then rewashed, cleaned and the length remeasured (table 10.1.) Agreement was good but cannot be applied directly to estimate the error for a field sample because fine roots may have been lost during the initial washing to obtain the "known" sample.

d) Root dry weight and length measurement.

Dry weight could be measured to 0.2mg - an unimportant error for topsoil samples but introducing up to 20% error in samples lower in the profile. The error associated with length measurements is shown in table A.4.1. (appendix 4) to be about 5%. In practice, 10% seems more

Table 10.1 A test of the root washing and cleaning procedure using samples of known length

Sample	Initial Length (m)	Final Length (m)	Final / Initial
1	4.2	4.25	1.01
2	3.6	3.9	1.08
3	2.9	3.45	1.19
4	3.25	2.95	0.91

likely particularly as roots tend to mat together. Using a regression of dry weight and length for root samples early in the season to estimate length from dry weight measurements later in the season was shown (section 5.4.) to introduce no gross error (approximately 10% for most samples). Root character (eg. average root diameter) may change with age but no serious deviation from the linear regression was found.

These are the errors involved in obtaining a single root measurement for a 10cm increment of soil. Table 10.2. shows the variability of root distribution with space and the standard error associated with the mean for a typical root harvest. Root dry weight in the topsoil layer can vary by a factor of two (usually no more than three) but as depth increases so does variability, and factors up to ten below 60cm are not uncommon. The coefficient of variation was generally 20 -30% of the mean in the topsoil layers and over the summed profile but could be up to 100% in the deeper, subsoil layers. Such large variability at depth is probably due to a combination of soil heterogeneity and the problems of sampling fewer roots. Compared with the errors involved in measuring plant nutrient content (less than 5%) or determining plant water uptake (about 10%) the errors are large.

Despite the experimental difficulties, the dry weight and length measurements obtained were of similar magnitude to other results for cereals (Barley, 1970; Welbank et al, 1974). The total root dry weight of 105 g per m^2 at anthesis was similar to the average of 120 g per m^2 obtained by Welbank et al (1974) for a number of winter wheat varieties. Altnough this does not vindicate the experimental method (Welbank used the same technique), the measure of agreement is encouraging. Total root dry weight and length decreased after anthesis (see also Welbank

Table 10.2 A typical root harvest showing the degree of sample variability (day 209).

Sample depth (cm)	Root dry weight (mg)				Mean (mg)	S.E. (mg)	Coefficient of variation (%)
	1	2	3	4			
0-10	177	181	256	312	232	32.4	28
10-20	125	65	141	150	120	19.1	32
20-30	79	88	125	88	95	10.2	22
30-40	108	34	47	124	78	22.2	57
40-50	50	23	31	34	35	5.7	33
50-60	35	15	35	25	28	4.8	35
60-70	13	18	27	16	19	3.0	33
70-80	21	22	24	5	18	4.4	49
80-90	27	13	16	3	15	4.9	67
90-100	16	19	2	2	10	4.5	93
100-110	6	2	1	2	3	1.1	81
110-120	2	1	1	1	1		
120-130	1	<1	<1	1	<1		
130-140	1	<1	1	2	1		
140-150	1	<1	<1	<1	<1		
Total	662	481	708	764	654	61.2	19

and Williams, 1968; Mengel and Barber, 1974a; Biscoe et al 1975b) but new root growth at depths below 80 cm occurred.

Root growth was affected by topsoil moisture status - dry topsoil decreasing length and wet topsoil increasing length. Root dry weight on the dry plot was, however, similar to normal dry weight until shortly before anthesis suggesting the production of heavier (thicker) roots in dry topsoil. A similar result for lettuce roots (Rouse,1974) has also been reported. The application of irrigation at anthesis allowed the growth of roots throughout the soil profile and total root weight increased.

10.1.2. Uptake of water and nutrients

Between mid - May and anthesis, water uptake occurred at a rate close to potential evaporation. A prolonged period of soil drying from mid - May until mid - July was experienced and by mid - July measured crop evaporation rate was substantially lower than potential rate. After rain in mid - July, evaporation continued at a rate close to potential. Taylor and Klepper (1971) and Allmaras et al (1975) have all shown water inflow decreasing within a soil layer as drying proceeds, and the present results confirm these observations.

In contrast to water uptake, nutrient accumulation ceased at or around anthesis. This has also been noted by Knowles and Watkin (1931) and Chambers (1953) working with wheat but not by Mengel and Barber (1974b) with corn. Although nett accumulation of nutrients ceased at anthesis, the present experiment does not allow a definite conclusion on whether uptake itself stopped or whether the balance between uptake and efflux was zero. Considerable losses of potassium and sulphur (50%) occurred between anthesis and final harvest with a smaller loss(20%) of calcium. The most probable mechanism of loss is efflux via the roots into the soil

(Knowles and Watkin, 1931). A consequence of nett uptake ceasing at anthesis was that all nutrients in the harvested grain must have been translocated from other parts of the plant. Comparable rates of translocation have been determined by other workers (eg. Jennings and Morton, 1963a and b) (table 8.3.). Much of the work performed to formulate uptake behaviour has been carried out with young plants (see review by Brewster and Tinker, 1972). The results presented here together with those in chapter 3 agree with the general pattern and values reported for such plants. Where older plants have been used under field circumstances (Brewster and Tinker, 1970; Mengel and Barber, 1974b) they have been spring-sown crops and this may result in a different inflow pattern.

Nutrient inflow decreased after emergence until day 160 but then increased continually until, or slightly before anthesis. This latter increase in inflow has not been found by other workers (Brewster and Tinker, 1970; Mengel and Barber, 1974b) and possible explanations were sought.

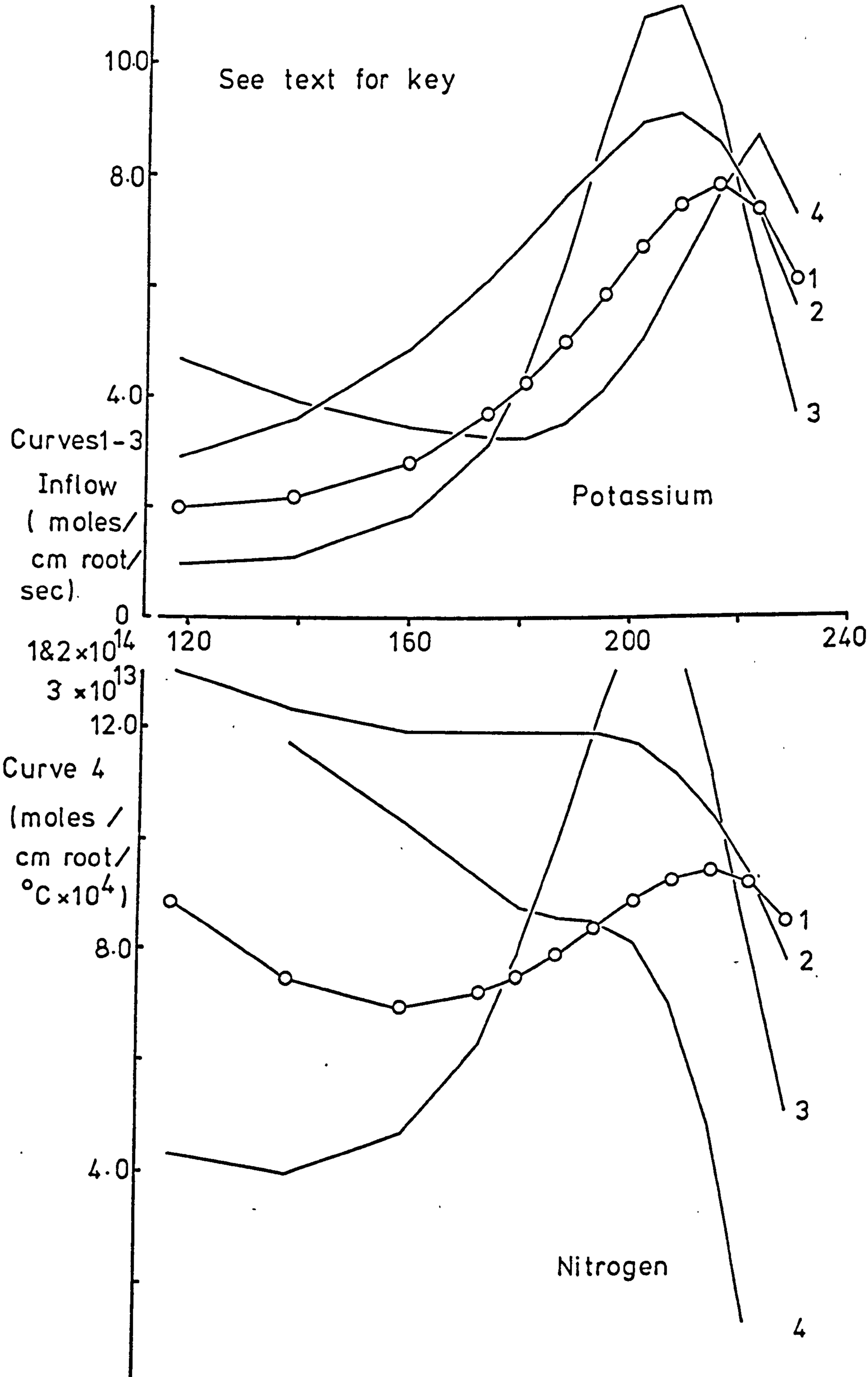
The growth analysis equation used (Williams, 1948) to calculate inflow contains three components, namely, nutrient content, root length and time. Assuming nutrient content and time to be the most accurately measured variables, the inflow was recalculated making the following alterations:

1) Only roots taking up water absorbed nutrients ie. using the "effective root length" (curve 2).

2) Only roots less than seven days old absorbed nutrients (curve 3).

Figure 10.2. shows the potassium and nitrogen inflows calculated using these assumptions; curve 1 was determined as described in section 9.4. In general, sodium and nitrogen behaved similarly for each assumption while the remainder behaved as does potassium. Except using assumption 2 for nitrogen and sodium, the shape of the inflow curve after day 160 remained unchanged, indicating that no gross mistake arose from using

Fig.10.2. Inflow of potassium and nitrogen



total root length in the initial calculation. Neither would the error inherent in using a regression technique to estimate topsoil root length after day 181 significantly change the shape of the curve.

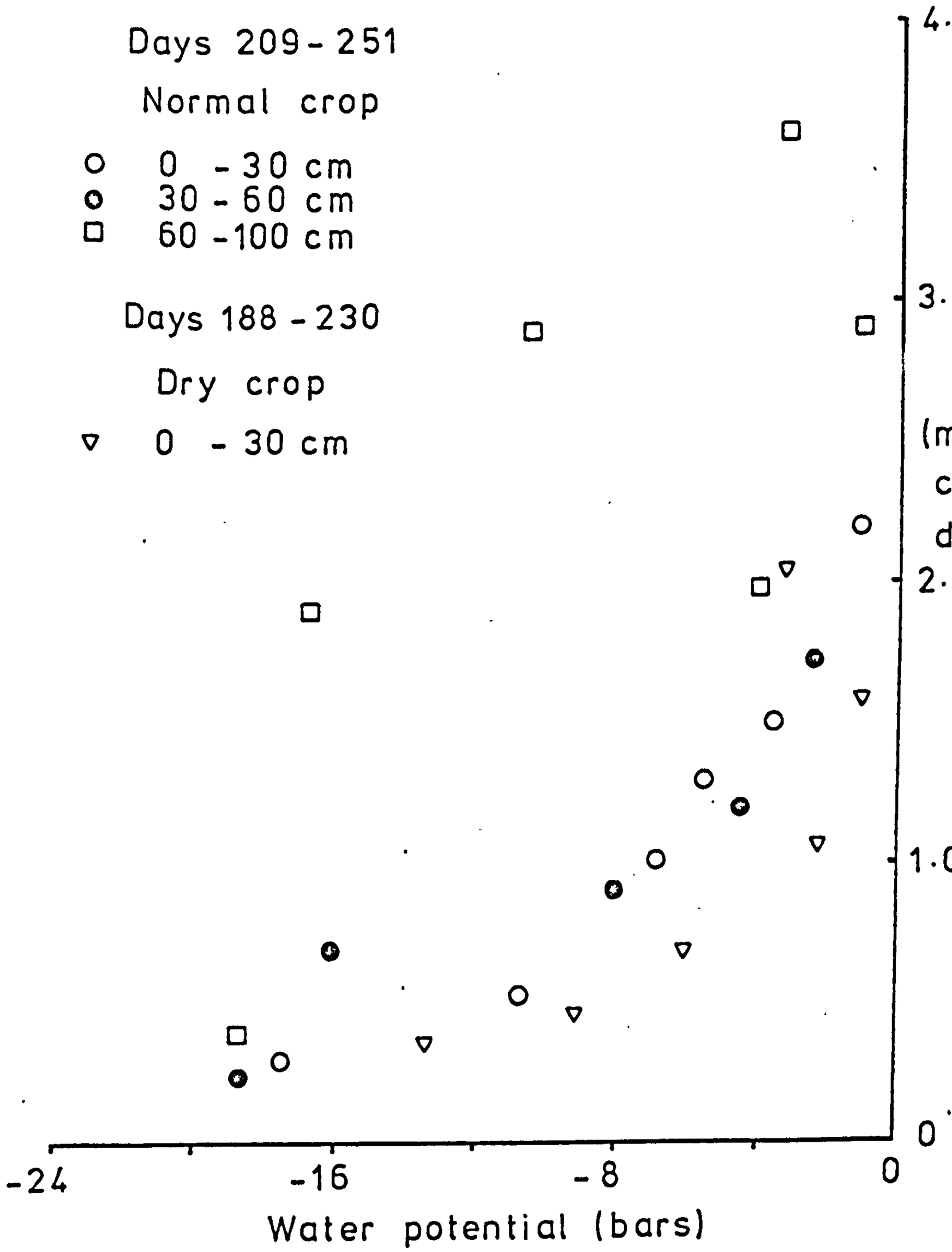
Power et al (1964) have shown that soil temperature has an effect on phosphorus availability to plants and Boatwright, Hayden and Sims (1976) have also shown that nutrient uptake by wheat from solution is influenced by temperature. The contribution of soil and plant factors controlling uptake manifest in the inflow value might, then, be temperature dependent.

Temperature would exert its influence through the day length component of William's equation since a plant at 10°C would not experience the same "physiological time" as a plant at 20°C (Nuttonson, 1955). Assuming that plant nutrient uptake ceases at 0°C, the inflow calculation was repeated using accumulated degrees Celcius (daily mean measured at 20cm depth) instead of time. This gave curve 4 on figure 10.2. - note that it is in units of moles / cm root / °C and is on a scale different from curves 1-3.

For the majority of nutrients the shape of inflow time curve was unaltered but nitrogen and sodium did show a continual reduction in inflow when a temperature correction was applied. Although temperature may influence inflow, it would not seem to be the sole contributing factor to the increased inflow after day 160. A possible alternative explanation is that nutrient inflow increases in response to a demand from within the plant. Water inflow responds to evaporative demand (E_t) which is controlled by a number of measurable variables. It has been shown (section 9.1.) that water uptake(the sum of water inflow from all soil layers) is equal to this demand over much of the period of interest (day 188-230). No similar mathematically derivable potential exists for plant nutrient demand and, until available, no further progress can be made in explaining the observed inflow behaviour.

Figure 10.3. shows the relationship between water inflow and water

Fig.10.3. The relationship between water inflow and water potential during periods of soil drying



potential for selected soil layers during a drying phase when root length in the 0.60 cm layer is not changing rapidly. Clearly soil water potential is not the only factor affecting inflow as is shown by the 60 - 100cm layer. However, the figure also indicates the type of analysis possible for water uptake data obtained from field results - considerably more advanced than the understanding of factors influencing nutrient inflow.

Mass flow was capable of supplying the whole of plant sodium, calcium, magnesium and sulphur content during the period day 160-230 but only 40% of potassium and nitrogen and 5% of phosphorus. These results are comparable with the general outline described by Barber, Walker and Vasey (1963). The balance of soil processes before day 160 may be different but transpiration of water is impossible to estimate accurately during the winter. Had the calculation of mass flow been based on two nutrient analyses at day 160 and final harvest, it would have been concluded that mass flow could supply all the plant's potassium and 85% of nitrogen. This gives credence to the statement of Knowles and Watkin, (1931) that, "Observation of yield, coupled with analysis of the final plant, cannot be expected to give any guidance as to the manurial requirements of the crop" - nor, indeed, to the processes occurring.

10.1.3. Effects of innibiting nodal root growth

As Locke and Allen (1924) showed, grain can be obtained even when nodal roots are absent. The Huntsman crop possessed very few tillers and yield was reduced by about 20% when nodal root growth was innibited. It has been suggested that nodal roots are particularly important in supplying tiller nutrients and water (Krassovsky, 1926) and so where tillers are an important factor in producing ears, grain yield might

be reduced more markedly (Sallans, 1942).

Compensatory growth of barley roots when one part of the system was removed has been described by Crossett, Campbell and Stewart (1975). Except where dry soil conditions pertained, seminal root growth compensated for the loss of nodal roots.

Nutrient and water uptake of plants without nodal roots was not examined in detail because of the limited quantity of material available.

10.1.4. The influence of prolonged soil drying on the ability of roots to extract water.

The continuous drying of the normal crop from mid - May until mid - July followed by rain allowed measurements of water uptake and inflow in addition to those on the dry plot. As the soil dried, uptake from successively deeper soil layers occurred and the summed inflow from each layer was at a rate to supply the evaporative demand. Inflow in each layer generally decreased with time. However, when rain fell or the soil was irrigated, the inflow increased again from the topsoil layer and decreased at depth. This observation clearly indicates that if water is sufficiently available in the topsoil to meet evaporative demand, then water extraction will occur preferentially from that layer.

Support to such a hypothesis is also given by the dry plot results. Dry plot irrigation at anthesis caused immediate water uptake by roots at the surface at a much faster rate than previously. Because topsoil root growth had been limited on this plot (thereby reducing water availability in the topsoil), extraction from depths below 30cm occurred more rapidly than on the wet plot.

10.2. Concluding remarks and ideas for future work

10.2.1. Methods of studying roots

The main limitation to work of this kind, particularly in the field, is the problem of obtaining reliable root data. An example of the difficulty is provided by the results of Connor (1975) where measurements of roots produce only a crude outline of root dry matter production. Much effort has been channelled into devising techniques which eliminate the necessity of destructive sampling. Radioisotopic techniques devised at the Letcombe Laboratory (eg. Ellis and Barnes, 1973; Mercer et al, 1975) enable the estimation of relative root distributions but are clearly of limited use in studies of the present type.

An alternative approach is the use of a root observation laboratory (Taylor et al, 1970). If the soil / glass interface problems can be overcome, this might provide the means to measure and observe root benaviour. The development of a "mini - rhizotron" (Böhm, 1974) seems the most desirable way forward and would enable treatment effects on root growth to be conveniently studied. This is impracticable at present because of the large plot size and labour requirement involved in destructive methods.

10.2.2. The desirability of field work

Much of the work performed by other workers has been with young plants and good agreement between theoretical models of soil processes sypplying nutrients with measured uptake has been obtained (Bhat and Nye 1974b). The problems of measuring nutrient uptake in the field and the development of a theoretical basis for such measurements has received attention recently from a number of workers (Passioura, 1963; Na Nagara et al, 1976) The approach adopted is similar to that in many laboratory experiments (eg. Nye, 1968a) and may well provide a useful link between the more precisely controlled laboratory experiment and the complex interactions

of the field.

The present study indicates the difficulties in extrapolating results from young plants to field plants. In particular, the increase in inflow between days 160 and 230 and the complexity of processes occurring at the root surface after anthesis, have received little attention. However, the need to progress beyond single root experiments has been well expressed by Barley (1970) who stated the resistance to nutrient uptake would be determined by the size and shape of the root system as well as the soil processes of nutrient supply.

The field results reported in this thesis were obtained for one crop in one season. Additional study is required to check that the observed increase in inflow during the spring is not simply a product of one season but a recurring phenomenom. A comparison between the nutrition of a spring and autumn sown cereal may be useful in understanding the soil / root / plant interaction but is impracticable if large numbers of destructive root harvests are to be performed.

The response of wheat varieties to fertiliser placement is probably also worthy of study although many of the commonly grown cereals in this country have been bred from a limited number of parents ie. differences in temperate cereals may be small. Weed competition with cereals for nutrients and water has been little studied but would pose a number of technical problems (such as separating different root systems) before earnest work could commence.

10.2.3. Possibilities in crop breeding

Hurd (1968) and Subbiah et al (1968) have shown that wheat varieties differ in root morphology and this may have important consequences for water and nutrient uptake. Studies of numbers and orders of root produced are necessary before improvements in root qualities are possible

(Passioura 1974) although breeding in this country has produced varieties with similar morphology (Lupton et al, 1974). For example a study by Raper and Barber (1970a) with two varieties of soy bean showed one variety to have a much larger root system than the other. It was concluded that the bean with the smaller root system would be at a disadvantage when competing against the other. However, when nutrient inflow was calculated (Raper and Barber, 1970b), the smaller system was physiologically more effective and, under some circumstances, would be at an advantage.

This example illustrates the difficulty of using one parameter to define the activity of a root system and suggests that future work on the interaction between the root and its environment might be fruitful. With the high cost of fertiliser, the need to provide an efficient absorbing surface is apparent and improvements in both root morphology and physiological activity are desirable.

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Table A.1 Chemical properties of Ceres site soil (Astley Hall series)

Depth (cm)	pH	% Carbon	% Nitrogen	C.E.C. me/100g soil	Exchangeable ions (me/100g soil)			
					Na	K	Ca	Mg
0-10	6.8	2.26	0.27	8.69	0.90	0.75	8.5	0.54
10-20	7.0	2.23	0.23	8.52	0.33	0.63	9.2	0.52
20-30	7.1	2.05	0.22	7.44	0.31	0.55	9.8	0.44
30-40	7.3	1.07	0.11	5.28	0.32	0.42	5.1	0.31
40-50	7.2	0.76	0.08	4.38	0.20	0.24	3.2	0.22
50-60	7.2	0.63	0.07	3.34	0.11	0.18	2.7	0.21
60-70	7.1	0.36	0.04	3.28	0.21	0.17	2.6	0.25
70-80	6.4	0.25	0.04	3.32	0.14	0.20	2.4	0.21
80-90	5.7	0.28	0.02	4.49	0.28	0.44	3.2	0.34
90-100	5.8	0.26	0.03	5.29	0.30	0.33	4.1	0.40

Note that in the topsoil (0-30 cm) the sum of the exchangeable ions is higher than the measured C.E.C. This is probably because of the presence of free Ca and Mg present in recently applied dolomitic limestone.

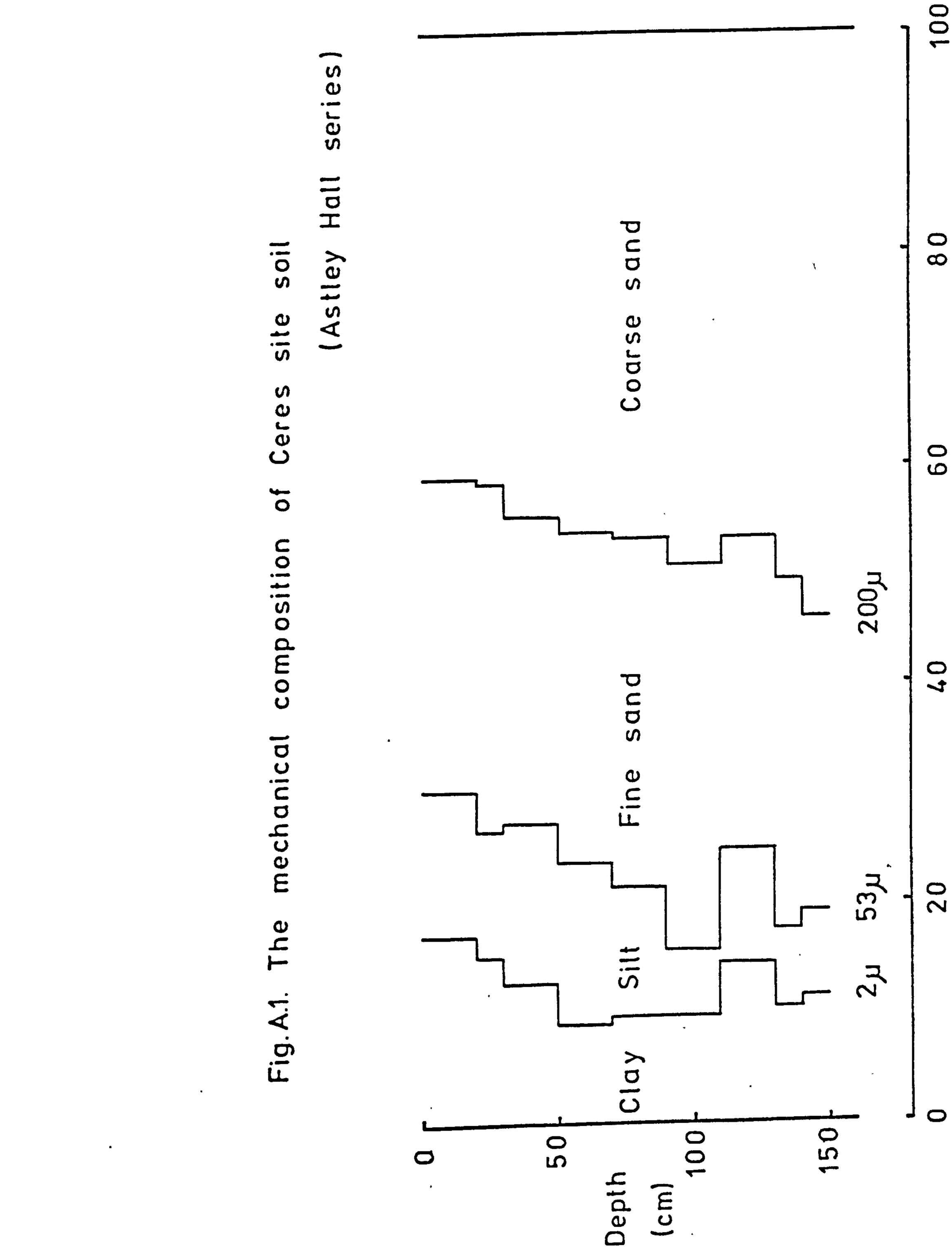


Fig.A.1. The mechanical composition of Ceres site soil (Astley Hall series)

APPENDIX 2

Preparation of plant material for analysis

For the determination of sodium, potassium, calcium, magnesium, phosphorus and sulphur, the following digestion procedure was based on Cunningham (1962). Analytical grade reagents were used throughout.

1) In a 50ml tall beaker place approx. 500mg dried, ground plant material. Add 1ml de-ionised water and 5ml conc. nitric acid. Cover with a watchglass and leave overnight.
2) Wash watchglass adding washings to beaker and evaporate slowly to dryness.
3) Place in a cold muffle furnace and heat for 4 hours at 450°C.
4) Cool. Add 4ml 6N hydrochloric acid and evaporate to dryness to dehydrate the silica.
5) Add 1ml IN hydrochloric acid plus 10-15ml de-ionised water and warm on a hotplate until all the salts are dissolved.
6) Filter through a Whatman No.42 paper into a volumetric flask (usually 100ml). Rinse the beaker and replace on the hotplate then add these washings to the filter.
7) Make up the volumetric flask to the mark with de-ionised water.

This procedure differs from Cunningham's original method in that no additional magnesium was added prior to dry ashing because magnesium was to be determined in the digests. Sufficient alkaline earth elements were present in the digested material to prevent volatilisation of phosphorus at 450°C.

For the determination of nitrogen, the following procedure was employed:

1) Weigh 500 mg dried, ground plant material into a small kjeldahl flask. Catalyst tablets (2g $NaSO_4$; 0·01g Se and 0·1g Cu) were

added with 6ml low N conc. sulphuric acid and 2 drops octyl alcohol.

2) Place the flask and contents on a heater and warm gently for one hour.

3) Gradually increase the heat and heat vigorously for 3 hours.

4) Cool and add distilled water. Wash into a volumetric flask (usually 50ml) and make up to the mark.

APPENDIX 3

Chemical determinations

1) Sodium and potassium:

Sodium and potassium were determined using an EEL flame photometer. A ppropriate dilutions of the digested material were made to measure in the range 0-10 ppm Na and 0-10 ppm K.

2) Calcium and magnesium;

These were determined on an EEL240 atomic absorption spectrophotometer. 10^3 ppm strontium was added to the diluted solutions before measurement in the range 0-20 ppm Ca and 0 -0.5 ppm Mg.

3) Phosphorus:

Phosphorus was determined as the blue molybdophosphate complex has described by Fogg and Wilkinson (1958). The solutions were read at 810nm on an SP500 spectrophotometer in 1cm glass cells.

4) Sulphur:

Sulphur was determined as barium sulphate and dissolved in 2% ammonium EDTA containing 2000 ppm K. The barium was measured on an EEL 240 atomic absorption spectrophotometer at 553.6nm and converted to sulphur concentration. Full details of the technique are given by Cunningham (1962).

When determining sulphate in soil extracts, 1ml seed solution containing 50 ppm sulphate had to be added before precipitation would commence.

5) Nitrogen:

a) Total nitrogen - A suitable volume of digest (eg,5ml) was pipetted into a Markham still, 6ml 50% sodium hydroxide solution added and ammonia distilled into 5ml 2% boric acid until 25ml of solution had distilled over. Titration with N/140 sulphuric acid was performed on a Pye Unicam autotitrator to pH 5.25.

b) Nitrate - Nitrate in soil solution was determined with chromotropic acid (CTA) and the intensity of the yellow CTA $-NO_3$ complex measured on an EEL colorimeter using an Ilford OB 10 filter. Full details of this method are given by Sims and Jackson (1971).

c) Ammonium - Ammonium in soil solution was determined using Nessler's reagent reading at 405nm on an SP500 spectrophotometer in 1cm glass cells (Vogel, 1961).

6) Phosphorus-32:

The digested material was pipetted into a 10ml sample vial and Cerenkov radiation counted on an ICN Tracerlab counter.

7) Sulphur-35:

Samples of 0,1ml EDTA-$Ba^{35}SO_4$ were pipetted onto a glass coverslip (diameter 1.5cm). dried under a tungsten lamp and placed on an aluminium planchette. This was counted on a Nuclear Chicago proportional counter (2% pentane in argon at 7½% psi). Correction was made for the effect of salts by pipetting 0.1ml of low salt ^{35}S solution onto the coverslip, redissolving the EDTA-$Ba^{35}SO_4$. drying and recounting. The original count was then corrected by the measured efficiency of the second.

APPENDIX 4

The Root Length Measuring Machine

The machine used in the present study was a modified version of the instrument described by Rouse and Phillips (1974).

1) Sample presentation:

a) Place a piece of fine nylon bolting cloth on a tension table (Clements 1966) and cover with a thin layer of water.

b) Pour out the roots on to the cloth and spread out using a pair of forceps. If sufficient water is present, the roots can be easily separated and distributed randomly over the area.

c) Drain the tension table until the excess water is removed and the roots held firmly against the cloth. At this stage, the cloth should still be slightly damp but there should be no marked water meniscus between roots and cloth. If too much water is left, water menisci around the roots can cause problems when focusing the detector and adjusting the light intensity to provide accurate readings.

d) Slide the cloth and attached roots onto the instrument measurement table removing any air bubbles trapped between the cloth and glass by raising the cloth and lowering slowly until a continuous water film exists over the whole area. Occasionally additional water has to be added to achieve this condition and this is best added from a wash bottle directly to the glass surface; if the water is added on top of the cloth it will not pass through to wet the glass underneath.

2) Setting of optics:

Rack the microscope barrel down until the objective is nearly touching the cloth. Look down the eyepiece and rack up until the threads of the cloth can be clearly distinguished. If the barrel is now racked up by a small amount, the cloth becomes out of focus and fine roots should appear as faint black lines when placed under the lens. Replace the photo detector tube on top of the eyepiece and adjust the light so that counts are registered on the digital display as roots are passed under the microscope lens.

The correct combination of focus and light intensity is critical and may take a little time to find. However, once adjusted, the machine should work for a considerable time without further alteration.

Some difficulties have been encountered when excess water is present between the bolting cloth and the glass table. Under these conditions, the excess water accumulates at the edges of the cloth raising its level and bringing it into focus. If one then adjusts focus to remove this source of count, the fine roots at the centre of the cloth are no longer counted.

3) Calibration and accuracy of reading:

The machine has been designed so that a direct reading is possible, i.e. 425 on the digital display means that there is 425 cm of root on the table.

To test the performance of the machine, five known lengths of fine black nylon thread were used. Samples of thread were cut into lengths (10-30 mm) and distributed randomly over a piece of cloth. Five estimates of each sample were made; each sample was rearranged between estimates.

Table A.4.1 Comparison of measured and root-instrument estimated lengths of thread

Measured length (m)	Estimated length (m)					Mean estimated length (m)	Standard error	Largest error for a single reading
	1	2	3	4	5			
1.00	1.02	1.03	1.05	1.06	1.03	1.04	0.01	6.0%
2.00	2.03	2.11	1.97	2.08	1.97	2.03	0.03	5.5%
4.00	3.92	4.19	4.16	4.10	4.16	4.11	0.05	4.8%
6.00	5.93	6.01	6.09	6.10	6.16	6.06	0.04	2.7%
8.00	7.93	8.22	8.12	8.00	8.25	8.10	0.07	3.1%
10.00	10.04	10.15	10.17	10.19	10.28	10.17	0.04	2.8%

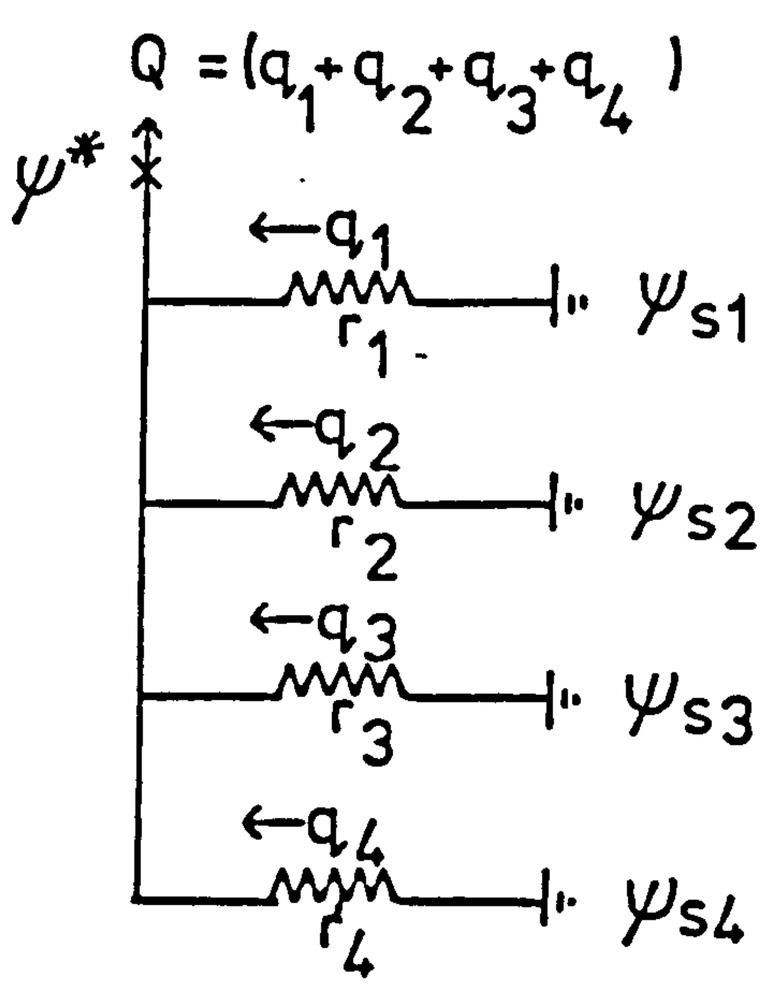
The results are shown in Table A.4.1. All five estimates were within 5% of the known length and the largest error associated with a single reading was 6%. The instrument, in contrast to the original of Rouse and Phillips, shows no decrease in accuracy up to 10 m,probably because the present measurement table is larger. Adding further thread to the cloth would undoubtedly cause a decrease in accuracy and it is inadvisable to measure samples larger than 10 m.

Cloth 120 T) supplied by Brocklehurst Fabrics Ltd., Macclesfield, Cheshire.

APPENDIX 5

Simulation of water extraction by wheat roots using a simple resistance model.

By dividing the soil profile into four layers, 0-30cm, 30-60cm, 60-100cm and 100-160cm, the simple resistance model shown in the figure below was used to simulate root water extraction.



where ψ_s = mean soil water potential

ψ^* = water potential at base of the wheat stem.

q = flow of water

r = resistance to water flow.

Q = total water extraction

Subscripts 1 - 4 refer to soil layer

<u>ie</u> $$r_1 = (\psi_{s1} - \psi^*)/q_1$$

If at time t_1, values of q_1, q_2, q_3, ψ_{s1}, ψ_{s2}, ψ_{s3} and ψ^* are known, the resistances r_1, r_2 and r_3 can be calculated. Assuming that these resistances remain constant, at time t_2, q_1, q_2 and q_3 can be calculated and q_4 determined by subtraction of Σ q_1, q_2 and q_3 from Q.

Since the measured water flow rates are weekly averages, the value of ψ^* must also be an average. This was estimated from the available data but it was not directly measured. Estimated values are :

Time	ψ^* (bars)
24 Jun - 1 Jul	- 22
1 Jul - 8 Jul	- 24
8 Jul -15 Jul	- 20 (or - 25 if no rain had fallen)

Using these values the following comparison of measured and estimated uptake was obtained.

Period 1/7/75 to 8/7/75	Soil layer (cm)			
	0-30	30-60	60-100	100-160
Measured extraction rate (ml/plant)	13	8	14	17
Predicted extraction rate (ml/plant)	12	7	15	18
Period 8/7/75 to 15/7/75				
Measured extraction rate (ml/plant)	35	3	3	3
Predicted extraction rate (ml/plant)	35	3	2	4
Predicted extraction rate assuming no rain had fallen (ml/plant)	8	6	9	21

The model predicts that if no rain had fallen during the period commencing 8th July, then inflow from 0-30 cm would not have increased and inflow from below 100 cm would not have decreased so rapidly.

My thanks to Wallace (1976) for performing this calculation.

Appendix 6. Concentration of nutrients in displaced soil solution

Days after sowing	Depth (cm)	Moisture content (w/w) %	µg Na/ml soil solution		µg K/ml soil solution	
			Mean	S.E.	Mean	S.E.
168	0-30	20.5	12.7	0.4	45.8	4.3
	30-60	11.3	30.6	3.3	23.3	4.3
	60-100	9.4	36.1	5.4	17.8	4.2
188	0-30	16.6	14.7	2.7	51.0	11.9
195	0-30	17.5	14.6	3.1	29.7	7.2
	30-60	12.8	19.0	19.5	18.5	3.5
	60-100	11.1	22.6	2.3	4.2	0.7
209	0-30	13.6	19.1	2.1	45.8	5.5
	30-60	10.9	34.0	14.5	22.8	1.6
	60-100	10.5	44.4	2.2	5.8	1.8
223	0-30	9.9	27.5	6.0	82.2	25.6
	30-60	8.3	44.6	10.5	53.7	7.2
	60-100	7.2	40.7	3.5	22.2	3.2

Days after sowing	Depth (cm)	µg Ca/ml soil solution		µg Ma/ml soil solution	
		Mean	S.E.	Mean	S.E.
168	0-30	128	11	9.4	0.2
	30-60	96	8	7.1	0.3
	60-100	131	31	11.4	2.4
188	0.30	149	13	13.3	2.1
105	0-30	131	7	7.5	2.4
	30-60	78	10	4.3	0.7
	60-100	99	12	6.6	0.7
209	0-30	119	3	11.0	0.6
	30-60	78	5	6.4	0.8
	60-100	142	22	11.2	0.3
223	0-30	137	3	12.9	1.9
	30-60	111	11	8.2	0.8
	60-100	109	16	9.7	1.6

Days after sowing	Depth (cm)	µg P/ml soil solution		µg S/ml soil solution	
		Mean	S.E.	Mean	S.E.
168	0-30	0.72	0.04	43.3	2.7
	30-60	0.14	0.04	50.9	10.9
	60-100	0.08	0.0	71.3	17.4
188	0-30	1.25	0.74	22.6	1.4
195	0-30	1.34	0.26	19.4	2.8
	30-60	0.14	0.0	13.8	1.2
	60-100	0.08	0.0	45.9	5.8
209	0-30	0.66	0.3	30.3	2.9
	30-60	0.19	0.1	47.6	10.1
	60-100	0.06	0.0	104.2	12.5
223	0-30	0.25	0.11	31.7	6.6
	30-60	0.14	0.0	66.7	20.2
	60-100	0.04	0.0	71.1	4.9

Days after sowing	Depth (cm)	µg NO_3^-/ml soil solution		µg NH_4^+/ml soil solution	
		Mean	S.E.	Mean	S.E.
168	0-30	87	30		
	30-60	89	4		
	60-100	144	45		
188	0-30	103	103	2.3	0.5
195	0-30	104	49	1.7	0.1
	30-60	76	29	3.2	1.4
	60-100	83	62	1.3	0.2
209	0-30	40	26	4.1	1.2
	30-60	26	5	54.9	25.4
	60-100	57	12	2.2	0.4
223	0-30	148	30	28.3	7.5
	30-60	83	16	28.0	23.0
	60-100	0	0	30.0	14.2