DRAINAGE AND WATER UPTAKE TERMS IN THE WATER BALANCE

A thesis submitted
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LIST OF SYMBOLS

Unless otherwise specified, the units of values given in the text are as stated below:

A	Plane area (cm^2).
B	Matching factor.
C	Fractional count rate from neutron moisture meter.
D	Total number of root axes per plant.
E_o	Potential evaporation rate (cm day^{-1}).
E_p	Transpiration rate (cm day^{-1}).
E_s	Rate of evaporation from the soil surface (cm day^{-1}).
$E_t=E_s+E_p$	Rate of evapotranspiration (cm day^{-1}).
G'	Rate of surface runoff (cm day^{-1}).
H	Hydraulic head (cm).
H_e	Hydraulic head of water at the root surface (cm).
H_x	Hydraulic head of water within the bulk of the xylem vessels (cm).
I	Amount of irrigation and/or precipitation (cm).
I'	The rate of irrigation and/or precipitation (cm day^{-1}).
J	The inflow to the xylem per unit length of absorbing root member (cm^2 sec^{-1}).
K	Hydraulic conductivity of soil (cm sec^{-1}).
K_o	Hydraulic conductivity of saturated soil (cm sec^{-1}).
$K(\theta)$	Hydraulic conductivity of unsaturated soil at a particular water content θ (cm sec^{-1}).

K_p	Axial conductance of a segment of a root member calculated from vessel radius using the Poiseuille equation (cm^3 sec^{-1}).
K_t	Conductance of a ceramic tube (cm^3 min^{-1} bar^{-1}).
K_α	Axial conductance of a segment of a root member (cm^3 sec^{-1}) derived from outflow data.
K_β	Radial conductance of a segment of a root member (cm sec^{-1}).
K_Π	Osmotic conductance of a segment of a root member (cm sec^{-1}).
L_A	Root length per unit area of ground surface (root abundance) (cm^{-1}).
L_v	Root length per unit volume of soil (rooting density) (cm^{-2}).
L_H	Hair-bearing root length per unit volume of soil (cm^{-2}).
M	Plant density (cm^{-2}).
N	The number of root axes per unit area of horizontal plane at a specified depth (cm^{-2}).
P	Hydrostatic pressure (dyne cm^{-2}).
Q	Flow rate in a specified tube (cm^3 sec^{-1}).
R	Resistance opposed to the flow of water into and within the xylem of a set of roots (cm sec).
$R_\alpha = \frac{1}{K_\alpha}$	Axial resistance of a segment of a root member (cm^{-3} sec).
$R_\beta = \frac{1}{K_\beta}$	Radial resistance of a segment of a root member (cm^{-1} sec).
R_e	Reynold's number.
S	Amount of water stored in soil (cm).

S'	Rate of change of amount of water stored in the root zone and plant cover (cm day^{-1}).
U	The vertical flux of water in the soil at a specified depth (cm day^{-1}).
V	Rate of flow of water across unit cross section of the soil or apparent velocity of flow of water within a tube (cm sec^{-1}).
W	Gravimetric water content (dimensionless).
W_s	Dry weight of soil (g).
Z	Depth of root zone (cm) or other specified depth.
$f = \frac{K_\alpha}{K_p}$	Discrepancy factor.
g	Acceleration due to gravity (cm sec^{-2}).
h	Suction head (cm).
h_m	Height of mercury column (cm).
h_s	Suction head in the bulk of the soil (cm).
h_w	Height of water column (cm).
h_x	Suction head within the xylem vessels (cm).
h_Π	Osmotic head (cm).
k_α	Axial conductance of a set of roots (cm^3 sec^{-1}).
k_β	Radial conductance of a set of roots (cm^2 sec^{-1}).
l.	Litre.
n	Number.
q	Rate of water uptake per unit length of root (cm^2 day^{-1}).
r	Radial distance from axis of tube, or tube radius (µm).
r_1	Root radius (cm).

$r_2 = 1/(\pi L_v)^{\frac{1}{2}}$	Half distance between roots (cm).
r_A	Mean radius of a tube for tubes of radius r_{e_1}, r_{e_2}, ... r_{e_n} in a set of parallel tubes (μm) as defined by Eq. (51).
r_H	Radius of a tube equivalent to a series of vertical tubes each of radius r_{A_i} (μm) as defined by Eq. (54).
r_e	Radius of a tube equivalent to a set of parallel vessels within a single root member (μm) as defined by Eq. (42).
s	Standard deviation.
t	Time (sec).
w	Width (cm).
z	Depth (cm).
Λ_p	Resistance to flow of water within the plant.
Λ_s	Resistance to flow of water within the soil pores (cm sec).
η	Viscosity of water (poise).
ν	Reduction in volumetric water content due to withdrawal of water by roots (dimensionless).
$\lambda = \frac{d\nu}{dt}$	Rate of withdrawal of water by roots (day^{-1}).
ρ	Density of water (g cm^{-3}).
ρ_b	Bulk density of soil (g cm^{-3}).
θ	Volumetric water content of soil.
θ_o	Volumetric water content of soil at saturation.
θ_b	Volume of water remaining in the soil after drying at 105°C per unit volume of soil ('bound water').
θ_e	Volumetric water content of the soil at air entry.

κ	Specific axial conductivity of a segment of a root member (cm sec^{-1}).
Π	Osmotic pressure (bar).
γ	Porosity of the soil (dimensionless).
ψ	Leaf water potential (bar).

SUMMARY

In Part I of the thesis the drainage flux in a red brown earth is estimated from Darcy's law, using both field and laboratory measurements of the hydraulic conductivity $K(\theta)$ and field measurements of hydraulic gradient. The moisture characteristic of the subsoil from 80 to 110 cm depth in the red brown earth is also studied. In Part II of the thesis the influence of the resistance offered by roots to the flow of water is examined in relation to the withdrawal of water from subsoils by crops. Axial and radial conductance of roots are measured for wheat (*Triticum aestivum* L., cv. Halberd). For comparison, data on the axial and radial conductance of pea roots (*Pisum sativum* L., cv. White Brunswick) are also obtained. The data on conductance are used to assess the resistance offered by the roots to the flow of water.

In Part I the variability of K in the deeper subsoil of a red brown earth is described. The conductivity at saturation K_0 measured in the laboratory on intact soil cores showed a similar degree of variation to that found in the field. The variability arose both from spatial variability in the properties of the soil and from errors of measurement. Further results suggested that, given the variability of the soil, calculating hydraulic conductivity from the moisture characteristic gave sufficient accuracy for hydrological work in the field. It is recommended that a sufficient number of samples

be taken to obtain a reliable estimate of the mean moisture characteristic and of the matching factor used to calculate hydraulic conductivity. Hysteresis should be kept in mind when planning studies involving a comparison of hydraulic properties of soil in the field and in the laboratory; and especially when attempting to deduce the distribution of soil water suction in the field soil from the moisture characteristic measured in the laboratory.

In Part II of the thesis, laboratory measurements of the axial conductance K_α of segments of main axes of the seminal roots of wheat showed that the relation between conductance and metaxylem vessel radius generally did not differ significantly from a fourth power relation. However, at the dough stage the exponent was significantly (P, 0.05) less than the theoretical (Poiseuille) value. At any given value of a tube radius r_e, equivalent to a set of parallel vessels within a single root member, the axial conductance K_α at the first and second harvest was less than that at the third harvest. For nodal root axes K_α also increased between the second and third harvests. Possible causes of these variations are outlined. The axial conductance K_α of segments of pea root axes did not differ significantly from that of first order laterals at given values of r_e, and the conductances did not differ significantly between stages of growth. The exponent of the relation between r_e and conductance did not differ significantly from the theoretical (Poiseuille) value.

The radial conductance K_β was measured using a potometer method for unbranched zones of axes of seminal roots of wheat. For these zones $\overline{K}_\beta = 5.5 \cdot 10^{-9}$ cm sec^{-1}, s = $7.9 \cdot 10^{-9}$ cm sec^{-1}. The corresponding values for unbranched zones of main axes of pea roots were $\overline{K}_\beta = 1.4 \cdot 10^{-9}$ cm sec^{-1}, s = $2.1 \cdot 10^{-9}$ cm sec^{-1}.

In the main field experiment, conducted in 1973, an increase in seeding rate from S_1 = 27 plants per m^2 to S_3 = 595 plants per m^2 decreased the number of nodal roots per plant. However the mean number of nodal roots per tiller at both flowering and dough stages increased. Increasing plant density increased the dry weight of tops at the dough stage. An attack of rust late in the season affected the relation between seeding rate and grain yield. Irrigation slightly increased mean weight per grain, and weight of grain produced per square metre.

Nodal roots penetrated less than 40 cm deep in 1972, a relatively dry season, when preliminary observations were made on wheat sown at an intermediate seeding rate. In the wetter year (1973) some nodal roots penetrated to 90 cm or more at all seeding rates.

The number of root axes at zero depth was ranked $S_3 > S_2 > S_1$, however at 30, 60 and 90 cm depth the numbers did not differ significantly between seeding rates at either flowering or dough stages. The total number of root axes per m^2 decreased markedly from 0 to 30 cm depth at each seeding rate. The number of root axes per m^2 at 30 and 60 cm depth increased after flowering at each seeding rate.

The radius r_A of a tube representative of the individual tubes of radius r_{e_1}, r_{e_2}, ...,r_{e_n} in a parallel set decreased with depth from 30 to 90 cm at both stages of growth. Also, r_A tended to decrease from flowering to the dough stage, probably because the soil had become drier.

The rooting densities L_V at flowering were in the sequence, $S_3 = S_2 > S_1$, at 0 to 10 cm depth, but L_V did not differ between seeding rates from 10 to 75 cm depth. The root length per unit ground area L_A ranged from 242 cm^{-1} at S_1 to 348 cm^{-1} at S_3. The percentage of the total root length bearing root hairs increased with depth, increasing from 4 to 11 percent at 0 to 5 cm depth to 41 to 75 percent at 75 to 100 cm depth. Changes in the hair bearing length of root per unit volume of the soil L_H with depth were small compared with changes in L_V.

At flowering on the non-irrigated treatment the soil water suction had increased to 15 bar or more to 70, 100 and 80 cm depth at S_1, S_2 and S_3 respectively. More water tended to be extracted from the soil in the interval between 25 and 75 cm depth between stem extension and flowering at S_2 and S_3 than at S_1.

Estimates were made of the pressure drop required to produce a flow along the metaxylem vessels corresponding to a transpiration rate of 1.0 cm day^{-1}. Assuming Poiseuille flow, at the dough stage the pressure drop required to elevate water to the base of the stem from 90 cm depth was 20, 12 and 13 bar at S_1, S_2 and S_3. When allowance was made for observed discrepancies from Poiseuille flow, the pressure drop increased slightly at flowering and decreased slightly at the dough stage. The pressure drop required for a flow of 1 cm day^{-1} from 60 cm depth or below in the drier year (1972) at the intermediate seeding rate was higher than that needed in the wetter year (1973) both at flowering and dough stages.

The pressure gradients needed for a flow of 1 cm day^{-1} in the basal unbranched zone of the axes of pea roots appeared to be similar to the gradients needed in the main axes of wheat roots.

The pressure drop across the roots within a specified depth interval was less than 1 bar at E_p = 1 cm day^{-1}, except at 90 to 100 cm depth, where the pressure drop may have been as high as 3 to 4 bar. The resistance in the axial direction was dominant whenever the roots withdrew water exclusively from below 30 cm depth.

At the lowest seeding rate (S_1) the resistance offered by the soil to the flow of water to the roots in the deeper subsoil appeared to be insufficient on its own to account for the low observed rates of uptake of water.

Between stem extension and flowering the mean apparent rates of water uptake per unit length of root $\overline{q}$ were 1.3 . 10^{-3}, 1.7 . 10^{-3} and 1.8 . 10^{-3} cm^2 day^{-1} at S_1, S_2 and S_3 respectively. The local apparent rate of uptake $q_{,z,t} = \lambda/L_{\backslash,z,t}$ (cm^2 day^{-1}) reached maximum values of 3.0 . 10^{-3} at S_1, 3.7 . 10^{-3} at S_2 and 4.8 . 10^{-3} at S_3. Maximum values of q calculated assuming that water was abosrbed only by the hair bearing length of root were $6.8 \cdot 10^{-3}$ at S_1, $1.2 \cdot 10^{-2}$ at S_2 and $1.1 \cdot 10^{-2}$ at S_3. These values are similar to earlier estimates obtained by Walter and Barley (1974) for wheat roots in the field at Roseworthy, South Australia.

STATEMENT

This thesis contains no material that has been accepted for the award of any other degree or diploma in any University and, to the best of my knowledge and belief, it contains no material previously published or written by another person, except when due reference is made in the text.

P. Ponsana

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GENERAL INTRODUCTION

1.0 GENERAL INTRODUCTION

The instantaneous water balance for an agricultural field may be expressed as

$$I' - (S' + G' + U + E_s + E_p) = 0 \qquad (1)$$

where I' is the rate of water ~~input~~ supply to the soil by precipitation and irrigation (cm day^{-1}); S' is the rate of ~~change~~ increase in storage in the root zone and in the plant cover (cm day^{-1}); G' is the rate of surface runoff (cm day^{-1}); U is the vertical drainage flux (positive downwards) of water in the soil at the bottom of the root zone (cm day^{-1}); E_s is the rate of evaporation from the soil surface (cm day^{-1}); and E_p is the rate of transpiration (cm day^{-1}).

I' and S' can be measured relatively simply and with reasonable accuracy. For a level cropped area G' can either be ignored or otherwise can be avoided by means of grading and banking. E_s is small compared with E_p, when the top few centimetres of soil are dry, and the leaf area index - LAI - $\geq$ 2 (Cowan and Milthorpe 1968a; Denmead 1973).

U and E_p are generally the most difficult variables to measure in the water balance equation. Although it is sometimes ignored U may be large, and where drainage is ignored, or where no account is taken of its variability, large errors can arise in the estimation of E_p from Eq. (1).

In addition to estimating E_p we wish to know the way in which the resistances offered by the soil Λ_s and by the plant Λ_p to the flow of water affect its withdrawal from the soil. An instantaneous water balance equation can also be used to estimate the rate of withdrawal of water from the soil by plant roots λ at any given depth, z. Here it will be necessary to measure the gradient dU/dz; the vertical distribution of λ may then be related to the distribution of Λ_s and to the resistance to the flow of water offered by the roots themselves.

The studies in this thesis are divided into two parts. Part I deals chiefly with the accuracy of estimates of U based on Darcy's law. Part II deals with the resistance offered by roots to the flow of water to the base of the stem. Briefly, the axial and radial conductances of a set of roots taken at various depths in the field are measured. These conductances are then used to obtain an estimate of the pressure drop required to produce a given flow within the roots in the axial and radial directions.

PART I.   DRAINAGE

2.0 INTRODUCTION

The classical approach to the estimation of drainage is based on Darcy's law. Darcy's law states that the (constant) rate of flow of water in a saturated soil V (cm day^{-1}) is directly proportional to the difference in hydraulic head ΔH between the ends of the column considered and inversely proportional to the length of the column (z). For vertical flow Darcy's law can be expressed as:

$$V = -K_o \frac{\Delta H}{\Delta z} \qquad (2)$$

where H is the hydraulic head in centimetres of water, z is the depth (cm) and V is the flow rate (cm day^{-1}) both positive downwards. The parameter K_o is generally designated the hydraulic conductivity (cm day^{-1}).

Darcy's law has also been found to apply in unsaturated soil (Richards 1931). The important point here is that K is no longer constant for the particular soil but becomes a function of the volumetric water content θ. The variability of K can be high at a given value of θ, because of spatial differences in pore size distribution. In addition to this K is extremely sensitive to θ. Values of $K(\theta)$ may change from 10^{-3} to 10^{2} cm day^{-1} for a change of 0.1 in θ. The coefficient of variation of θ in the field for a uniform soil at high values of θ is about 10 percent (Rogowski 1972). Error in the estimation of θ can contribute considerably to the error in assessing conductivity.

Values of hydraulic conductivity have a log normal frequency distribution, and they are commonly plotted as log K (Nielsen *et al.* 1973). Rogowski (1972) suggests as a criterion for uniformity in a soil that the anti-log of the standard deviation of $\log_e$ K should not exceed 2. It follows that 68 percent of the measured values should lie between $2\overline{K}$ and $\overline{K}/2$, where $\overline{K}$ is the geometric mean. Because of spatial variability in K and its sensitivity to θ, it is difficult to evaluate U with acceptable precision.

The present experiment is designed to determine the conductivity function $K(\theta)$ and its statistics for a deep soil layer by measurements in the field, and to compare these values with $K(\theta)$ calculated from the moisture characteristic. Field and laboratory measurements of pore size distribution, expressed as the moisture characteristic, will also be compared.

The first section of Part I reviews literature dealing with the estimation of U. Emphasis is placed on the measurement of $K(\theta)$ and problems associated with the measurement and the use of the moisture characteristic. The second section deals with experimental work on evaluation of K using field and laboratory methods.

2.1 LITERATURE REVIEW

2.1.0 Drainage

During infiltration, or after its cessation, water may percolate below the root zone. We will call this process of percolation beyond the root zone 'drainage'.

2.1.1 Factors affecting drainage

When the soil is saturated with water, redistribution following infiltration occurs due to the gradient in the hydraulic head. After the water on the surface of the soil has disappeared drainage still continues. The rate of drainage is influenced by clay content, type of clay mineral, organic matter content, and aggregate porosity (Jamison and Kroth 1958). Drainage is influenced by profile characteristics, the depth of the water table (Richards 1941), and by the depth of the soil profile (Wilcox 1959).

The depth of the root zone affects the amounts of water lost by both evapotranspiration and drainage; Holmes *et al.* (1968) found that drainage under *Pinus radiata* in South Australia was less than under nearby shallow rooted pastures. These is some evidence that plants also affect drainage by changing the hydraulic conductivity of the soil (Emerson 1955; Barley and Sedgley 1959).

2.1.2 Drainage estimation in the water balance equation

Methods of estimating the drainage term in a water balance study can be considered under two broad headings; firstly, drainage can be estimated from direct measurements of the hydraulic properties of the soil, or, secondly, drainage can be assessed indirectly from empirical relationships of drainage with other soil properties, as, for example, the mean soil water content of the wetted zone.

2.1.2.1 Direct measurement of U

There are two principal direct methods, namely the hydraulic gradient (Darcy's law) method, and the measurement of drainage using lysimeters.

According to Darcy's law, expressed in the form

$$V = -K(\theta)dH/dz \qquad (3)$$

if $K(\theta)$ is known, the instantaneous rate of drainage at a given depth can be evaluated by measuring the hydraulic gradient and the water content at that depth. This method has the advantage that the hydraulic gradient and the water content at a particular depth need only be known over the particular range of values found during drainage. This method has been widely used. Day and Luthin (1956) tested the method in long soil columns in the laboratory. They determined $K(\theta)$ from rate of outflow using a steady state infiltration method. The hydraulic gradient was measured with tensiometers and the water content was inferred from a laboratory moisture characteristic. They used these values of $K(\theta)$ to estimate U in succeeding runs. The calculated drainage exceeded the drainage measured as outflow from the base of the columns. They considered that this was due to non-uniform packing, and to errors in the measurement of the hydraulic gradient. Hysteresis in the moisture characteristic, and possible changes in the properties of the column with time also need to be considered. Ogata *et al.* (1960) estimated drainage below the root zone of lucerne (*Medicago sativa* L.) using a measured hydraulic gradient and field and laboratory values of K(θ). Rouse and Wilson (1971) obtained a K(θ) function from the water characteristic using a pore size distribution model (Millington and Quirk 1959). Rose and Stern (1967), van Bavel *et al.* (1968b), and La Rue *et al.* (1968) measured K(θ) in the field and then computed drainage under a crop. Roulier *et al.* (1972) and Brust *et al.* (1968) used K(θ) obtained from laboratory measurements to estimate field U. In only a few of these works was computed drainage compared with a direct measurement of actual drainage. Roulier *et al.* (1972) found that calculation of U from K(θ) obtained with a transient flow laboratory method overestimated field measurement using the hydraulic gradient method by a factor of two or three. They considered that this error was due to structural disturbance during sampling. They proposed the use of a matching factor determined by field measurement. Brust *et al.* (1968) had rather limited success using the double tube method (Bouwer 1961) to obtain a matching factor for K(θ) calculated from the moisture characteristic. Van Bavel *et al.* (1968b) compared measurements of U made with weighing lysimeters with values of U calculated from field measurements of K(θ) on an adjacent site and from the hydraulic gradient measured in the lysimeters. They used techniques similar to those used by Rose *et al.* (1965), to be described later, but differing in the important point that the suction head h was measured directly with tensiometers instead of being inferred from measured values of water content and the moisture characteristic. Their results were not satisfactory; failure to account for variability in $K(\theta)$ was offered as a possible explanation.

In some of the above experiments values of drainage were obtained by measuring the change in total water content of the profile over a time interval, often with the neutron moisture meter (NMM).

U can also be measured directly by means of lysimeters equipped with a suction plate (Cole 1958), or a grid of suction tubes (Black *et al.* 1968). While this method has considerable advantages it is costly. Where measurements are not replicated, as often happens due to cost, the method does not give a measure of the variability of U. The problem of obtaining a realistic hydraulic head at the lower boundary of the lysimeter can sometimes be overcome by a pumping and recording system, where a water table exists (Holmes and Colville 1970). However, where suction plates are used an arbitary boundary condition has to be applied.

Common practice is to pack the lysimeter with disturbed soil. This is satisfactory for some soils but in many cases it results in a different root distribution and causes a different evapotranspiration component. Besides these within-soil problems the disturbance of surface geometry and the occurrence of hot spots and wind funnels in the field (Rose *et al.* 1972) points to the need for more replication than is commonly used.

2.1.2.2 Indirect measurement of U

Examples of indirect measurement of U are the empirical equations of Richards *et al.* (1956) and Davidson *et al.* (1969). Richards *et al.* (1956) described drainage for an uncovered plot as a function of time as:

$$U = -abt^{-(b+1)} \tag{4}$$

where U is drainage (cm day^{-1}), t is the accumulative time from the cessation of infiltration (day) and a and b are constants. Later Wilcox (1959) modified this equation by eliminating t as:

$$U = ab(\frac{\theta}{a})^{(b+1)/b} \tag{5}$$

This equation implies that U is a function of θ where θ is the mean volumetric water content for the wetted profile. Wilcox (1960) estimated U under the crop on the assumption that the rate of drainage in the cropped plot was the same as the rate in an uncropped plot at an equal mean water content. However, he concluded that the method was not suitable for routine work because of the difficulty of obtaining precise measurements of θ using current techniques. van Bavel *et al.* (1968b) used the Wilcox method to estimate U in fairly uniform soil under sorghum (*Sorghum vulgare* Pers.). θ was measured with the NMM. They found that for the first two days the estimation of U was reasonably accurate. Miller and Aastad (1972), using gamma ray attenuation to measure water content, found that, following an irrigation which did not completely wet the whole profile, a discrepancy occurred at small times and that this arose from a lag in distribution.

More recently Black *et al.* (1969) suggested integrating the equation

$$\frac{d\theta}{dt} = \frac{d}{dz}[K\theta \frac{dH}{dz}] \qquad (6)$$

from the soil surface z = 0 to depth Z assuming that unit hydraulic gradient prevails, that is that h is uniform within interval from z = 0 to Z, and that no evaporation occurs at the soil surface during drainage. Given this assumption, it follows that

$$L\frac{d\overline{\theta}}{dt} = -K(\theta)\Big|_{Z=-L} \qquad (7)$$

where $\overline{\theta}$ is the mean volumetric water content from 0 to depth L, and K is the conductivity at $\overline{\theta}(t)$.

Davidson *et al.* (1969) assumed an exponential relationship between K and θ as

$$K(\theta) = K_o e^{a(\theta - \theta_o)} \qquad (8)$$

where a is a constant

Substituting Eq. (8) in Eq. (7), assuming that θ is invariant with z and equal to $\overline{\theta}$ to depth L, and integrating from 0 to t and θ_o to θ yields

$$\theta = \theta_o - a^{-1}\log_e(1 + aK_o tL^{-1}) \qquad (9)$$

Differentiating Eq. (9) with respect to t and multiplying through by L gives the drainage rate at depth L as

$$U = \frac{K_0 L}{L + aK_0 t} \tag{10}$$

The predictive value of Eq. (10) was tested in three different field soils. They found that the agreement with actual drainage depended on the uniformity of the profile, the most uniform soil giving the best agreement. Nielsen *et al.* (1972) used a similar analysis to estimate U in the field. They found that the calculated drainage agreed with the measured values better than calculations based on a $K(\theta)$ function derived from Eq. (1) with matching factor (Millington and Quirk 1961). However, for this analysis to be used, $K(\theta)$ must be evaluated for all horizons within the depth of interest. This presents considerable problems, the degree of which depends on the techniques used and the variability of the soil.

2.1.3 The hydraulic parameters of the soil

Processes that involve the movement of water in the soil, infiltration, redistribution and drainage, depend on the two basic hydraulic parameters of the soil, the hydraulic conductivity function $K(\theta)$ and the water characteristic $h(\theta)$.

2.1.3.1 Measurement of K_0

Talsma (1960), Bouwer (1962), and Boersma (1965) have reviewed techniques for measuring K_0 in the field. These include the auger hole method (Diserens 1934), the piezometer method (Kirkham 1946), the double-tube method (Bouwer 1961, 1962), the shallow well pump-in method and the permeameter method (Boersma 1965). Although these methods avoid disturbing the structure of the soil during core sampling, most of them require specialised equipment, and problems may still arise from disturbing the soil during preparation of the site or installation of the equipment. In addition to error due to these technical difficulties, soil variability from site to site presents a particularly serious problem with these methods because of the large number of measurements required to obtain a reliable estimate of K_0. As mentioned earlier, Brust *et al.* (1968) had only limited success using the double tube method to obtain a measured value of K_0. It is possible that the discrepancies in their results can be explained by a failure to account for variability in K_0.

Laboratory methods for the measurement of K_0 have recently been reviewed by Klute (1965). The different methods have been designed basically to measure the rate of flow of water V across unit cross section of a saturated soil core under a known hydraulic gradient $(\frac{\Delta H}{\Delta z})$. K_0 is then obtained from Eq. (2). Numerous methods have been developed: constant head, falling head (Klute 1965), or steady upward flow in a vertical column (Wit 1967). The method chosen depends on the hydraulic conductivity of the soil, for example the constant head method is useful when K_0 is high, while the falling head method is used mainly when K_0 is low (Klute 1965).

The following technical problems arise in the laboratory measurement of K_0 on undisturbed soil cores: disturbance during core sampling (Reeve 1957a, b; McIntyre 1974), the effects of the concentration and chemical nature of the solution used (Reeve 1957a; Smith and

Stallman 1954; Foster 1954), swelling and slaking of aggregates, biological activity blocking pores (Allison 1947), entrapment of air, and leaking along the interface between the soil and the container (Reeve 1957a). Disturbance of the soil core during sampling is difficult to avoid for many soils. McIntyre (1974) has discussed this topic in detail and outlines procedures for coring. Thin-walled sampling tubes should be used with an area ratio of less than 15.0 percent, where the area ratio is the ratio of the cross sectional area of the sampler wall at its maximum thickness to the cross sectional area of the core. This criterion limits wall thickness to 2 mm for a 7.6 cm diameter sampler. Lubrication of the sampler with oil or silicone is recommended for sampling clays. Insertion of the sampling tube under a steady pressure at a uniform rate of 15 to 30 cm sec^{-1} is advised. The water content of the soil to be sampled should be toward the wet end rather than the dry end of the range of available water.

2.1.3.2 Laboratory measurements of hydraulic conductivity in unsaturated soil $K(\theta)$

Here we are concerned with the transfer of water within the soil when the suction head is greater than zero and $\theta \leqslant \theta_0$. Methods have been developed based on steady state or steady rate conditions. These have been discussed fully by Staples (1967), and only several of the most popular methods will be described here.

i) Transient methods

The outflow method was first developed by Gardner (1956). This method uses a specially designed pressure membrane apparatus.

Firstly, the water content of a soil core is brought to equilibrium with an initial pressure. On increasing the pressure to a higher value, water is forced out and the outflow is measured as a function of time. On attainment of equilibrium the process is repeated until the required range is covered. This method is commonly referred to as the multi-step method. The multi-step method has been further developed by other workers: Miller and Elrick (1958); Ritjema (1959); Kunze and Kirkham (1962); Jackson *et al.* (1963); and Peck (1969). Several assumptions are made to simplify the analysis of the results: for example, constant diffusivity is assumed within the range of water contents encountered at each step. The method is time-consuming and demands considerable expertise. For highly structured soils it is difficult to match the curves derived from outflow data with the theoretical curves. Jackson *et al.* (1963) concluded that the method might produce unreliable results because of the effects of variable diffusivity in the soil, plate resistance, and resistance at the boundary between the porous plate and the soil.

In 1965 Doering introduced another version of the outflow method, the one-step method. This differs from the multi-step method in that only one equilibration is required. Calculations are simpler than for the multi-step method. Doering found that $K(\theta)$ values from the one-step method agreed with those from the multi-step method over a range of suction heads from 0.1 to 10 bar*. Miklich and Richards (1965)

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* One bar is equal to 10^6 dyne cm^{-2} or $\frac{1.0 \times 10^6}{\rho g} \simeq 1.0 \times 10^3$ cm of water suction head.

compared results from the outflow methods with those from a steady state method. They found that the one-step method resulted in values for K(θ) which were unreliable over the range 0 - 0.5 bar suction. This could have been caused by sample disturbance, plate resistance or poor contact between the core and the plate.

ii) Steady state method

Richards (1931) first used a steady state procedure for a layer of soil placed between two porous plates to measure the conductivity. Suction head gradients across the layer are maintained until the distribution of water content is steady. Many versions of the steady state procedure have been used by different workers: Elrick and Bowman (1964), Topp and Miller (1966), Watson (1966), Nielsen and Biggar (1961), Youngs (1960, 1964) and Collis-George *et al.* (1966). The method is soundly based but is not suited to routine measurement. Difficulties associated with entrapped air and changing plate resistance require skilled attention.

iii) Calculation from the moisture characteristic

To avoid problems associated with the measurement of unsaturated conductivity, use is often made of equations which allow the hydraulic conductivity to be calculated from other more readily measured parameters. These equations are based on Poiseuille's and Darcy's laws, and evaluate the contribution of pores of different sizes to flow. Many empirical equations have been introduced. Some of these, for example the Kozeny equation and the Purcell equation (Marshall

1959), are useful in material with pores of fairly uniform size. However, in media such as soils, pore sizes are far from uniform. For such media equations for calculating $K(\theta)$ have been developed based on a description of pore size distribution as expressed in the moisture characteristic.

The equation of Childs and Collis-George (1950), subsequently modified by Marshall - M - (1959) and Millington and Quirk - MQ - (1959), is based on the assumption that pore size is randomly distributed and that the dominant resistance to flow is due to the smaller pores in each sequence. Values of hydraulic conductivity calculated using these methods have been compared with experimentally determined values by Nielsen *et al.* (1960), Jackson *et al.* (1965), Kunze *et al.* (1968), Brust *et al.* (1968), Green and Corey (1971), Jackson (1972) and Roulier *et al.* (1972). Nielsen *et al.* (1960), Jackson *et al.* (1965) and Kunz *et al.* (1968) found that the M and MQ models gave higher values of K than measured values. However, both the M and MQ methods are easy to use, and for many soils yield satisfactory values of conductivity when they are matched at a known value of θ with a value of K. The ratio of measured to calculated K_o is the most commonly employed matching factor. Recently Green and Corey (1971), and Jackson (1972) modified the M equation for ease of calculation with the matching factor, expressed as:

$$K(\theta) = K_o \frac{\left[\sum_{j=i}^{n} (2j + 1 - 2i) h_j^{-2} \right]}{\left[\sum_{1}^{n} (2j + 1 - 2i) h_j^{-2} \right]}, \quad i = 1,2,\ldots,n \qquad (11)$$

where n is the number of pore classes corresponding to selected equal divisions in the θ scale of the water characteristic; i denotes the last pore class at the wet end, for example, i = 1 identifies the class corresponding to θ_o and i = n is the class at the lowest water content considered; j denotes a given class of water-filled pores, and h_j is the suction head (cm) equivalent to the midpoint of that class. The denominator (11) represents the saturated condition; i is set equal to 1 and the term is summed for j = 1 to n. The numerator represents an unsaturated condition with pores water-filled say from i = 3 to n. In this case i in the numerator is set at the value 3 and the term is summed over the range J = 3 to n.

The moisture characteristic is required only over the range of θ for which K(θ) is of interest. Green and Corey (1971) and Jackson (1972) illustrated that the M and MQ equations, using a matching factor, agreed with measured K(θ). Roulier *et al.* (1972) suggested that the matching factor to be used should be obtained in the field or within the range of θ relevant to the particular problem. For example, in a drainage problem matching should be done near the wet end of the range. Where the problem is concerned with the dry end of the moisture characteristic matching at a large suction head would be preferable. On the other hand, there is evidence that, even when matching factors are used these equations may sometimes yield unsatisfactory results (Brust *et al.* 1968; Roulier *et al.* 1972). Discrepancies appear to be due to either error in the matching factor itself associated with sampling or measurement, or, alternatively, due to hysteresis in the water characteristic.

2.1.3.3 Field measurement of K(θ) in unsaturated soil

The hydraulic conductivity of unsaturated soil can also be measured in the field by the use of Darcy's law. The required data are the rate of flow of water through the cross sectional area of interest, the water content, and the hydraulic gradient at the depth of measurement.

For a fallow soil, when the upper boundary is the soil surface (reference plane at depth 0) and the lower boundary is a plane at depth Z, for a period of time, t_1 to t_2, Eq. (1) can be expressed in the integral form as:

$$\int_{t_1}^{t_2} (I' - E_s - U_Z)dt - \int_{t_1}^{t_2} \int_{0}^{Z} \frac{\partial \theta}{\partial t} dz \, dt = 0 \qquad (12)$$

From Darcy's law, U_Z, positive downwards, is:

$$U_Z = K(\theta) \left(\frac{\partial h}{\partial z} + 1\right), \; z = Z \qquad (13)$$

Substituting Eq. (13) in Eq. (12) and rearranging we obtain:

$$K(\theta)_Z = \left\{ \int_{t_1}^{t_2} \left(I' - E_s - \left(\int_{0}^{Z} \frac{\partial \theta}{\partial t} dz\right)\right) dt \right\} \left\{ \left(\frac{\partial \bar{h}}{\partial z} + 1\right)_Z T \right\}^{-1} \qquad (14)$$

where $K(\theta)_Z$ is hydraulic conductivity (assumed to be constant) over the interval $T = t_2 - t_1$ (days) between the measurements and $\frac{\partial \bar{h}}{\partial z}$ is the arithmetic mean of the gradient in suction head at depth Z at times t_1 and t_2. When the term on the right hand side is measured, Eq. (14) may be used to calculate K(θ) at any depth. If $t_2 >> t_1$, error is introduced by using the arithmetic mean $\frac{\partial \overline{h}}{\partial z}$.

Under fallow error may arise in the estimation of E_s and I'. For this reason the determination of K(θ) is best made with the soil surface covered (Rose *et al.* 1965). For the covered plot Eq. (14) is written as:

$$K(\theta)_Z = -\{\int_{t_1}^{t_2}\int_0^Z \frac{\partial\theta}{\partial t}\, dzdt\}\{(\frac{\partial\overline{h}}{\partial z} + 1)_Z T\}^{-1} \qquad (15)$$

Then if the depletion of water from 0 to the depth Z between t_1 and t_2, and the mean hydraulic gradient at Z are known, K(θ) can be calculated.

Richards *et al.* (1956) attempted to measure K(θ) using Eq. (14) in uniform sandy loam following a heavy irrigation. Change in water content $\Delta S = \int_{t_1}^{t_2}\int_0^Z \frac{\partial\theta}{\partial t}\, dzdt$ (cm) was measured gravimetrically. Values of $\frac{d\overline{H}}{dz}$, the hydraulic gradient, were obtained from tensiometers, and E_s was estimated from Cl^- accumulation at the surface. K(θ) was calculated for the top 50 cm. When this experiment was repeated by Ogata and Richards (1957) but with a covered plot technique the scatter of the values of K(θ) was significantly reduced. Nielsen *et al.* (1964) also used a covered plot instrumented with tensiometers. Values of ΔS were obtained from measured values of h and the water characteristic obtained on cores in the laboratory. This method has the disadvantage that errors can arise from hysteresis and from sampling. Rose *et al.* (1965) attempted to measure K(θ) over a wide range of soil water contents. The neutron moisture meter was used to measure θ as a function of z and t and hence the depletion ΔS. h was obtained from θ using a laboratory moisture characteristic. Their results were scattered widely. They attributed this to site variability, but error could also be due to hysteresis and to errors in the estimation of E_s. The method has the advantage that the measurement of K(θ) is made on a large undisturbed bulk of soil. However, the NMM is not suitable for the absolute measurement of θ in a strongly developed profile because of its large radius of influence (Holmes and Jenkinson 1959; McHenry 1963). Also there are problems associated with its calibration (Greacen and Schrale 1975). For satisfactory use in this type of experiment two checks must be made:

a) that absolute values of θ are measured with sufficient accuracy at Z, and

b) that the NMM gives an accurate measurement of ΔS.

No attempt was made in the work reported above to test the accuracy of the NMM technique.

Besides error associated with the use of the NMM, error in tensiometer readings due to temperature change has been demonstrated by Richards and Neal (1937), Richards *et al.* (1938), Richards (1949), and Hainse and Kelly (1950). Diurnal fluctuation in the reading of field instruments was shown to be pronounced near the soil surface but less marked with depth. This effect depends mainly on air entrapped in the instrument, and on the thermal properties of the upright connecting tubes to which the porous cup is attached (Hainse and Kelly 1950). To minimize these effects Richards *et al.* (1949) and Kelly (1950) suggested reading the manometer at the same time each day, and preferably early in the morning when temperature effects are minimal.

van Bavel *et al.* (1968a) used the NMM and tensiometers to measure θ and ΔS and $\frac{dH}{dz}$ in a fairly uniform soil profile in order to obtain a field measurement of $K(\theta)$. They concluded that scatter in their values of $K(\theta)$ within the profile and between sites was due to soil variability.

2.1.4 The moisture characteristic

The moisture characteristic is the relationship between the volumetric water content θ and the suction head h. The relation between θ and h is not monotonic, without change of pitch but depends on whether the soil is wetting or drying. The equilibrium water content for a given suction head is greater on drying than on wetting. This dependence on the equilibrium content of soil water on the direction of the wetting and drying process is called hysteresis. The two complete curves of the characteristic, from saturation to dryness and *vice versa*, are called the main branches. When a partially wetted soil begins to dry, or when a partially dried soil is rewetted, the relation of h and θ is described by an intermediate curve as it moves from one main branch to the other. Such intermediate curves are called scanning curves. In the past, hysteresis has often been disregarded in the theory and practice of soil physics. In field situations, the hysteresis effect may be important in the case of composite processes in which wetting and drying occur simultaneously or sequentially in various parts of the soil profile. This complicates studies of the moisture characteristic and its use for calculating $K(\theta)$.

The extent of hysteresis has been shown to depend on the contact angle between the wetting fluid and the porous medium (Cassie 1948; Collis-George 1955; Biggar and Taylor 1960), on the amount of entrapped air (Foster 1951; Holmes 1955; Davidson *et al.* 1966), on the swelling and shrinking of soil (Holmes 1955; Emerson 1955; Hillel and Mottes 1966) and on the geometry of the pores (Hillel 1971).

Normally the moisture characteristic is obtained by wetting a soil core to saturation at zero suction head after which the soil is drained to equilibrium under different suctions. At each suction the water content is determined after equilibrium is reached. The resultant plot of θ against h is called the drying curve. This drying curve may not apply to the field; for example, during infiltration the soil does not usually wet up to zero suction, except near the top of the profile or above a layer of low permeability.

In addition to hysteresis, the weight of overburden also presents a problem in using a moisture characteristic determined in the laboratory. This is important as part of the overburden pressure is carried by the soil water. A method for allowing for overburden pressure has been discussed briefly by Rose *et al.* (1965). This is particularly important when dealing with swelling soils (Philip 1972; Smiles 1974).

In addition to the above effects, the moisture characteristic is sensitive to alteration of structure (Richards and Fireman 1943; Elrick and Tanner 1955; Perier and Evan 1961; Salter and Williams 1965). The effects of structure are more strongly pronounced at the wet end of the range of available water when $h \leqslant 1$ bar. In drainage investigations, where the wet end of the range is all important, it is imperative that sampling procedures do not change the pore-size distribution.

For analytical laboratory work, determination of the moisture characteristic is made from numerous measurements over the full range of water contents. For field studies, where variability is usually high, equations have been developed that may allow a satisfactory moisture characteristic to be obtained with reduced experimental effort. Visser (1966) has proposed an empirical equation:

$$h = -a(\gamma - \theta)^b/\theta^c \qquad (16)$$

where a, b and c are constants, and γ is the porosity. The practical use of this equation is hampered by the difficulty of evaluating the constants. Gardner *et al.* (1970) have used

$$h = a\theta^{-b} \qquad (17)$$

where a and b are constants. They point out, however that this equation fits only a limited range of the characteristic curve. To give a better description of the wet end of the range, the region of interest in the present study, an equation has been proposed by Rogowski (1971) based on the air entry value or saturated water content and one other point at the drier end of the range.

Rogowski (1971) proposed the empirical relation:

$$\theta = \theta_e + \alpha \log_e(h - h_e + 1) \qquad (18)$$

where $\alpha = (\theta_{15} - \theta_e) \log_e (h_{15} - h_e + 1)$, h_e is the suction head (cm) at air entry, θ_e the volumetric water content at air entry, h_{15} the suction head corresponding to a suction of 15 bar and θ_{15} the volumetric water content at h_{15}.

Rogowski has shown for a restricted range of soils that Eq. (18) provides a calculated water characteristic of sufficient accuracy for field work. Its usefulness for a particular soil, however, can only be established by testing.

2.2 EXPERIMENTAL PROGRAMME

2.2.1 Introduction

The present study is aimed at investigating a method of assessing the drainage term in a water balance study on a red brown earth. The method is based on Darcy's law and uses measured values of hydraulic conductivity and a measured hydraulic gradient at the lower boundary of the zone considered.

2.2.1.1 Site and soil

The experiments were conducted at the CSIRO field station at Parafield, South Australia, in 1972. The soil was a red brown earth (Stace *et al.* 1968), classified as Dr. 2.3.3 (Northcote 1971) and formed on an alluvial argillaceous deposit. The profile was well developed with 30 cm of loamy sand overlying a medium red brown clay B horizon at 40-60 cm depth. Below this depth there was a clay loam with occasional limestone nodules and pipes.

2.2.1.2 Material and methods

i) Field establishment and measurement

A level 6 m X 6 m area, surrounded with earth banks 20 cm high, was used as the experimental plot. The banks enabled irrigation by flooding, and prevented lateral run-off of water. The soil inside the dam was levelled to within ± 1 cm. Four NMM access tubes (mild steel) were installed to a depth of 1.6 m at the corners of a 3.5 X 3.5 m^2 area in the middle of the plot (Fig. 1). Probe-tensiometers were installed for the measurement of suction head. The manufacture and installation of this type of tensiometer has been described by Forrest (1974). The sensing elements were ceramic tubes, 7 cm long, 0.46 cm O.D., 0.27 cm I.D. (Coors Porcelain Co., Golden, Colorado, U.S.A.). Each ceramic tube was sealed with "Araldite" (an epoxy resin) into the end of a stainless steel stand-pipe 0.64 cm O.D. X 22 G. of required length, allowing 5 cm of tube to project as the sensing element. The exposed end of the ceramic tube was plugged with araldite (Fig. 2). The response time of the tensiometer was determined by the method of Richards *et al.* (1937) and Richards (1949). Their equation can be expressed as:

$$K_t = \frac{57 \text{ X } A}{t} \tag{19}$$

where K_t is the conductance of the ceramic tube at 20°C (cm^3 min^{-1} bar^{-1}), A is the cross-sectional area of the mercury column in the attached manometer in cm^2, and t is the response time, that is, the time taken in minutes for the suction to decrease to half of the initial value after immersing the ceramic cup in water. For the tensiometers used A = 0.196 cm^2; the measured response time was 10 seconds, giving a value for the conductance of the ceramic cup of 67.2 cm^3 min^{-1} bar^{-1}.

Vertical access holes for the tensiometers were made in the soil with a solid steel probe, 0.64 cm O.D., to 2.5 cm less than the required depth. This was then withdrawn and a second probe of the same diameter but with a leading spike, 0.32 cm O.D., 5 cm long was then inserted to the required depth. The leading spike creates an undersize hole for the ceramic cup; this second probe was then withdrawn and the tensiometer was pushed to the required depth. The depth of the tensiometers was established by means of an Erthel level, four replicates being installed randomly at 11, 16, 26, 50, 80, 110 and 140 cm depth below the soil surface. The arrangement is shown in Fig. 2b.

After the first day of flood irrigation on January 16, 1972, the tensiometers were primed by inserting one end of a fine plastic "spaghetti" tube leading from a squeeze wash bottle into the tensiometer cup and filling the system with de-aired water; mercury U-type manometers (I.D. 5 mm) were used as pressure gauges. The tensiometer installation is shown in Fig. 2B.

Irrigation water was obtained from the metropolitan supply. The electrolyte concentration was not measured but generally exceeds 300 p.p.m. After three days of irrigation the readings of soil water suction became steady. Following this period of irrigation the soil was covered with black polyethylene sheet to prevent evaporation. The sheet was then covered with ≈ 2 cm of loose dry soil to avoid excessive heating due to the black polyethylene and to improve contact between the soil surface and the plastic. Good contact between the soil and the plastic was necessary to minimize condensation. Air temperature in a Stevenson screen at a height of 1 m above the ground and soil temperature at depths of 5 cm and 20 cm were recorded continuously with a mercury in steel Cambridge temperature recorder, Model M 105, and soil temperature at 60

Fig. 1. Layout of 1972 field experiment at Parafield, South Australia.

●	NMM access tubes
X	tensiometer
0	thermistor
⟟ ⟟	Cambridge soil thermometers at 5 cm and 20 cm depth
☒	Stevenson screen with temperature recorder and air thermometer at 1 m

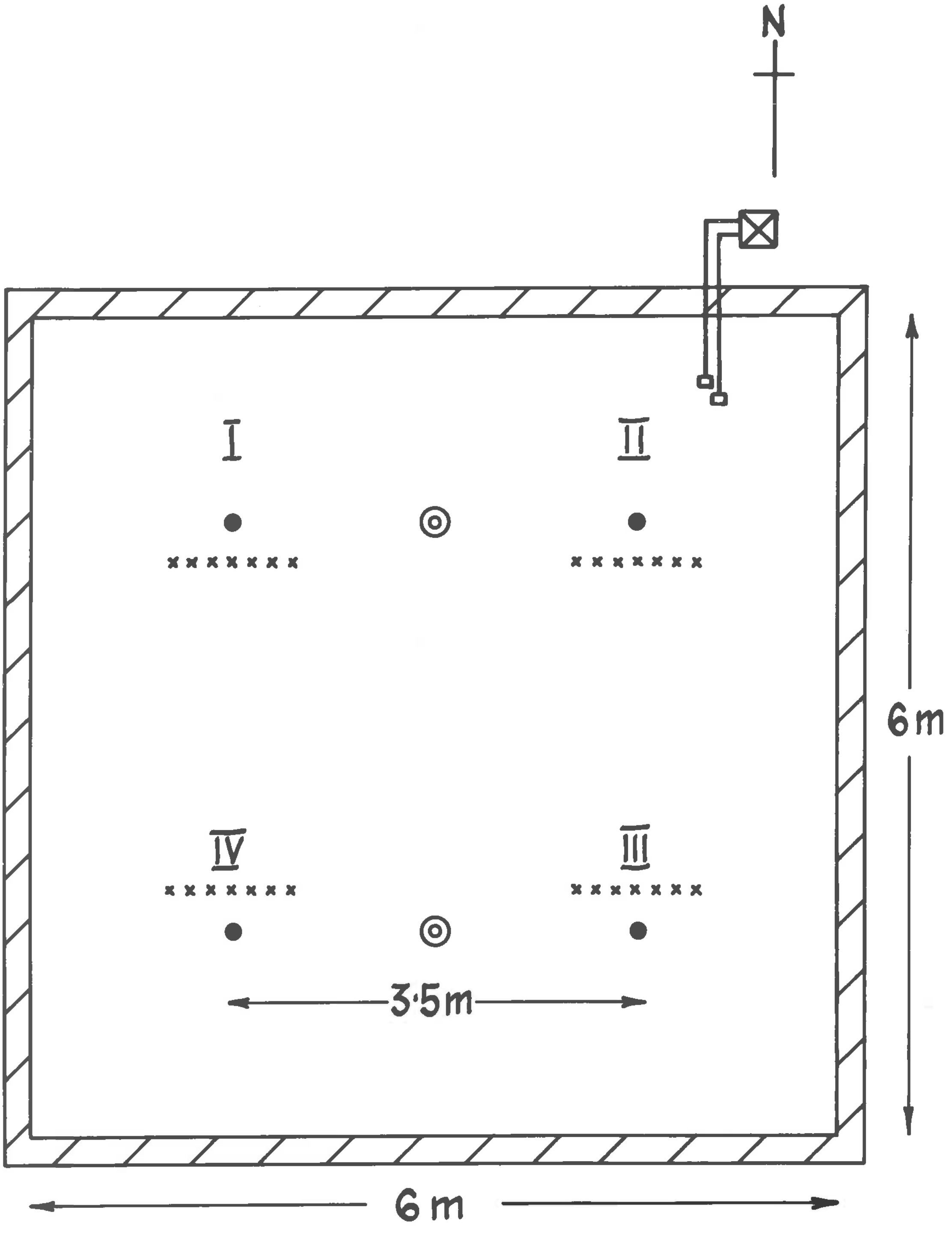
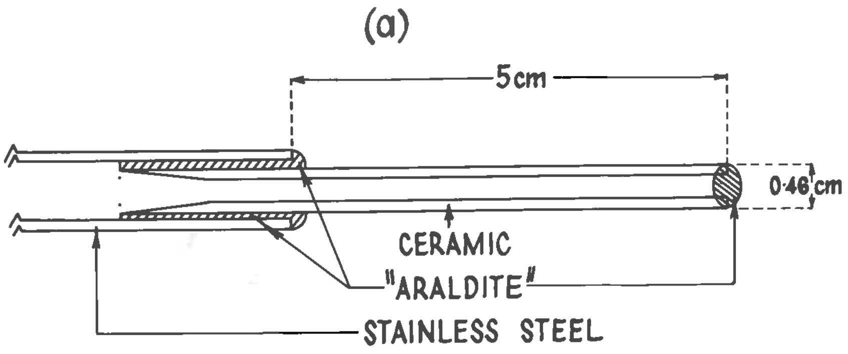
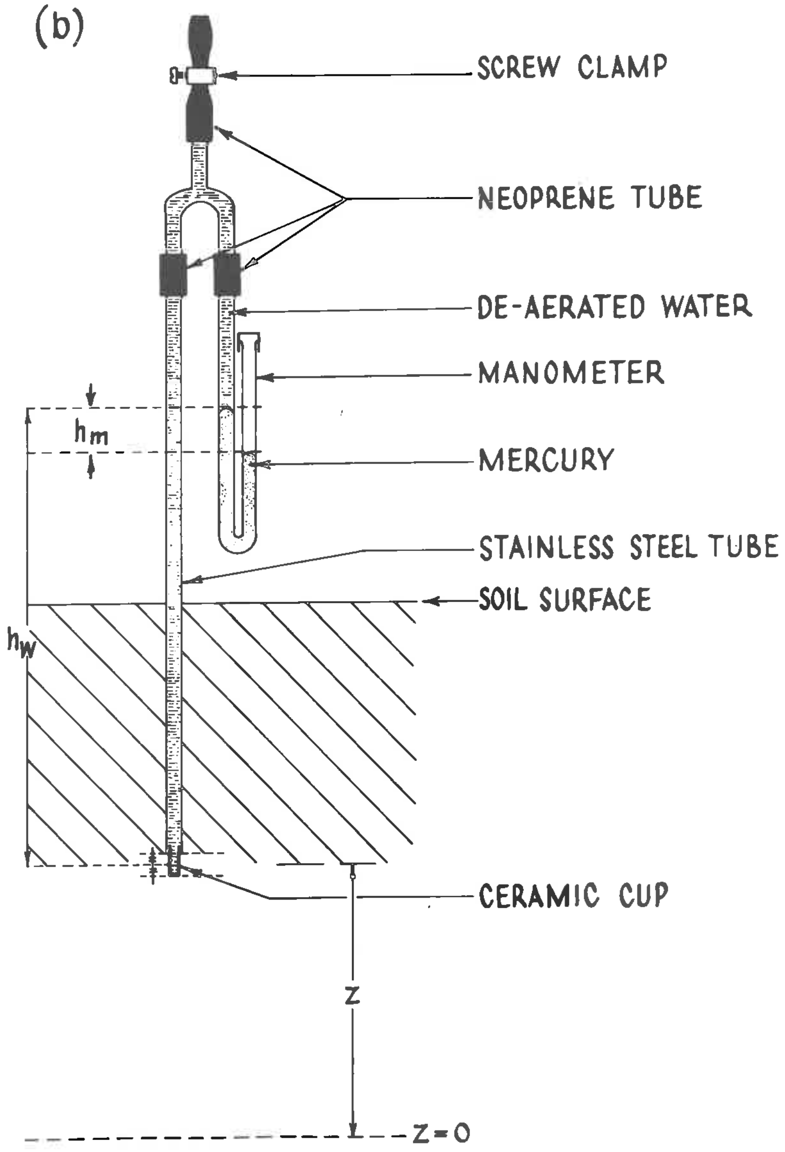

N
I
II
III
IV
3·5m
6m
6 m

Fig. 2. a) Detail of tensiometer construction

b) Tensiometer installation


(a)
5cm
0·46 cm
CERAMIC
"ARALDITE"
STAINLESS STEEL


(b)
SCREW CLAMP
NEOPRENE TUBE
DE-AERATED WATER
MANOMETER
h_m
MERCURY
STAINLESS STEEL TUBE
SOIL SURFACE
h_w
CERAMIC CUP
Z
Z=0

and 90 cm depth was measured with thermistors set in a 0.64 cm stainless steel tube and read with a Wheatstone bridge.

Soil water content θ was measured daily during the drainage period with a NMM (Type NE8402, 30 mc Am-Be source) at 20 cm depth increments, using a 1-minute counting period at each depth. The technique of using the NMM has been described by Gardner and Kirkham (1952) and Holmes (1956). A calibration curve for the soil at this site had been obtained previously using the packed drum technique (Hughes and Forrest 1971). This involved correcting for bulk density and bound water, values of which were known for each layer of the profile (Greacen and Schrale 1975).

In addition to measurement of θ with the NMM, θ was measured by core sampling at 4 and 28 days after cessation of irrigation. Core samples were taken with a 4.30 cm I.D. tube sampler (Stace and Palm 1962), driven hydraulically at a steady rate of approximately 15 cm $\sec^{-1}$. The soil core was gently pushed out of the tube and allowed to lie on a wooden plank; it was cut immediately into 10 cm long segments to 120 cm depth. The segments of each core were then weighed wet, dried at 105^{o}C for 48 hours, and the oven dry weights recorded. θ was calculated from

$$\theta = \frac{W\overline{\rho}_b}{\rho} \qquad (20)$$

where $\overline{\rho}_b$ is the bulk density of the soil (mean for each depth for all soil cores), ρ is the density of water taken as unity in c.g.s. units, and W is the gravimetric water content of the soil.

Tensiometer readings were made at three hourly intervals over a period of three days to examine possible diurnal fluctuations due to temperature, and then on a daily basis at 0630 hrs throughout the test period. From Fig. 2 the hydraulic head, H, at tensiometer depth in the soil with respect to the datum z=140 and atmospheric pressure = 0 is

$$H = h_w - 13.6\, h_m + z \qquad (21)$$

where H is the hydraulic head (cm); h_w and h_m the height of the water column and the difference in mercury levels in the manometer (cm), respectively, and z is the elevation with reference to datum level at 140 cm depth. The suction measured at the tensiometer cup together with a measured value of θ gave an *in situ* field value for the moisture characteristic.

ii) Laboratory measurements

At the conclusion of the drainage measurement, 6 cylindrical core samples 7.6 X 7.6 cm were taken at 86 to 93.6 cm depth from around each access tube. To avoid disturbance of the soil structure during sampling at this depth, it was found necessary to remove the overlying soil firstly by a mechanical auger and then finally with a light hand auger (10 cm O.D.). The cores were then taken with a lubricated, thin-walled tube (7.6 cm I.D. wall thickness 1.5 mm, area ratio 10 percent), driven hydraulically at a steady rate. The ends of the soil cores were then trimmed with a sharp straight knife and both ends were covered with lids and sealed with P.V.C. tape. Subsequently the cores within the sealed samplers were taken to the laboratory and kept in a controlled temperature room (20^{0}C). Laboratory measurements of K_0 and the moisture characteristic were made on these soil cores.

a) Measurement of K_0

Measurements of K_0 were made using a steady state upwards flow method. The equipment shown in Fig. 3 had components similar to those of the permeameter described by Klute (1965).

The sampler containing the soil core was held by end caps having 'o' ring seals to prevent leaking of water. Each end cap was fitted with a high porosity plate, and the two caps were connected across the soil core with long bolts. The soil, already in a wet condition, was wet to saturation from below at a suction head of 30 cm of water. To avoid dispersion of the soil, 0.05N $CaCl_2$ solution was used as the permeating fluid. No attempt was made to remove air entrapped in the sample. A supply at constant head was obtained by means of a Mariotte tube. Outflow was measured in a 50 ml burette held in a near horizontal position to give a near constant head at the point of outflow; a hydraulic gradient of 2 was used. Measurements of accumulated outflow were made over a period of several hours after K_0 became constant. Since the cores were not truly saturated the value of θ was measured at the completion of the test, care being taken that no water drained from the sample on dismantling the permeameter. In all, measurements of K_0 were made on twelve undisturbed soil cores.

From Fig. 3 it can be seen that

$$K_o = \frac{VL}{\Delta H} \qquad (22)$$

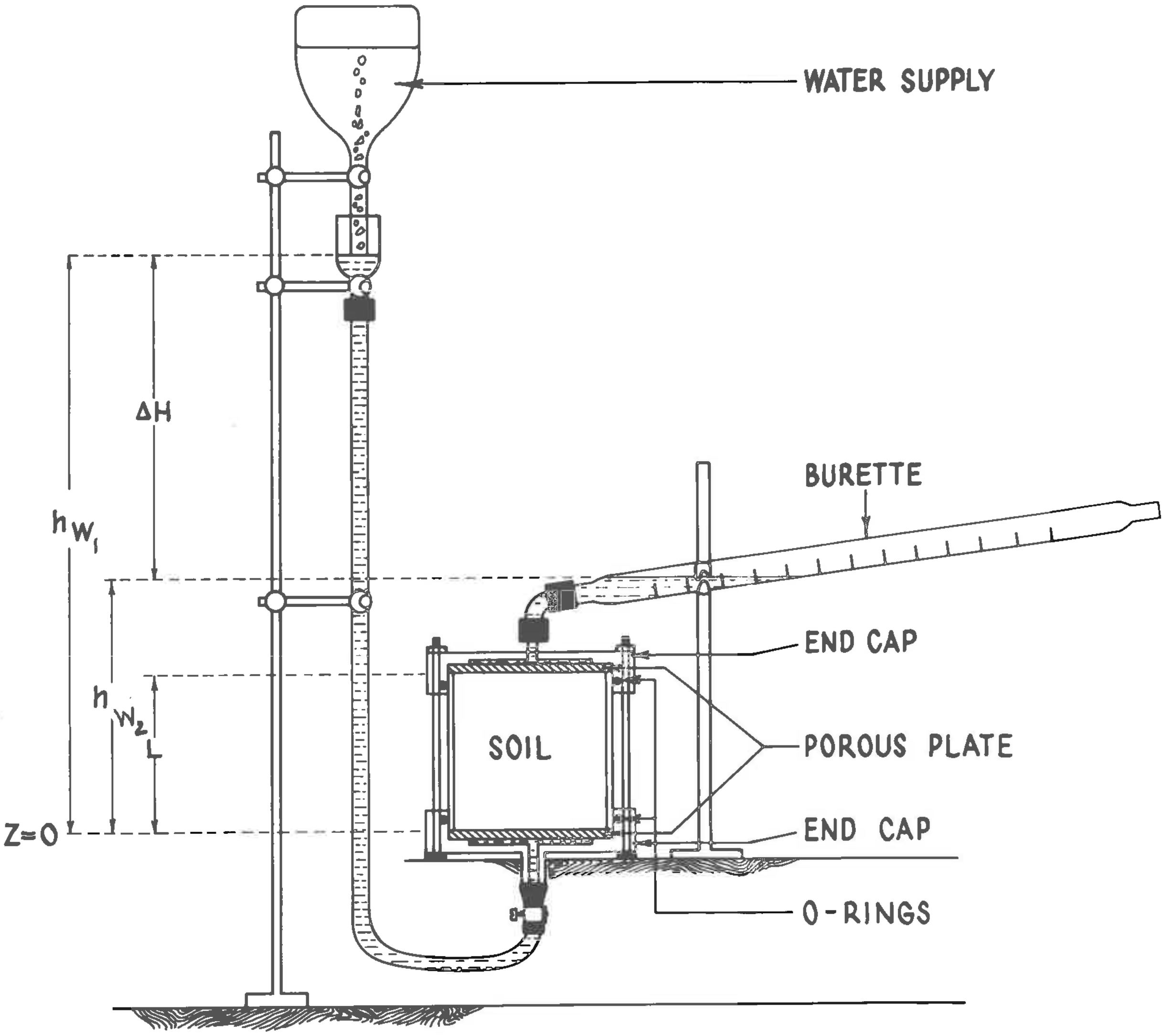
where V is the flux (cm sec^{-1}), L is the length of the soil core, and $\Delta H = h_{w_1} - h_{w_2}$, the difference in hydraulic head between the lower and upper ends of the soil core (cm).

b) Measurement of the moisture characteristic

Cores taken near the access tubes were also used to determine the moisture characteristic. The measurements were made using a set of 10 cm diameter sintered glass funnels as suction plates, with their outlets connected by plastic tubing to graduated 10 cc pipettes. The porosity grade of the sintered glass had an air entry value just greater than 0.3 bar suction, this value being greater than the maximum suction measured in the field throughout the experiment.

During infiltration soil water suction at the depths measured by the tensiometers never fell below 0.03 bar (Section 2.3.2). The drying curve appropriate to this wetting history was determined by wetting the soil initially at 0.03 bar suction. Subsequently the same soil cores were wet at zero suction and the drying curve determined at suction heads of 0, 0.03, 0.1 and 0.2 bar. Twelve undisturbed soil cores were used to determine these two moisture characteristic curves.

<u>Fig. 3.</u> Apparatus used in measurement of saturated hydraulic conductivity.


WATER SUPPLY
BURETTE
END CAP
POROUS PLATE
END CAP
O-RINGS
SOIL
ΔH
h_{W_1}
h_{W_2}
L
Z=0

2.3 RESULTS AND DISCUSSION

2.3.1 Change in water content of the soil following cessation of infiltration

Values of water content θ were calculated from the NMM readings using the laboratory calibration-regression and correcting for the content of bound water at each depth (CSIRO Division of Soils Tech. Memo. No. 60/1971, and computed by the programme described in CSIRO Division of Soils Tech. Memo. No. 16/1971). For the particular red brown earth, θ is given by

$$\theta = 0.78C\sqrt{1.50/\rho_b} - \theta_b - 0.059 \qquad (23)$$

where C is the fractional count rate, that is the count rate expressed as a fraction of the count rate in water, θ_b is the volume of water per unit volume of soil after drying at 105°C ("bound water"), and ρ_b is the bulk density at the depth of measurement. Values of bound water for this soil profile were obtained from earlier measurements (Greacen, pers. comm.). The term $\sqrt{1.50/\rho_b}$ corrects C to the fractional count rate that would be obtained for the same value of θ in a soil of density 1.50 g cm^{-3}.

Values of bulk density, shown in Fig. 4, were obtained from the core samples taken for the determination of soil water (Section 2.3.3). These values agreed with those obtained from the 7.6 cm cores that were taken with special care for the K_0-measurement at the lower boundary (Section 2.3.4.2). From 0 to 55 cm depth bulk density was close to 1.65 g cm^{-3}. It decreased markedly to 1.505 at a depth of 75 cm, increasing slightly to 1.52 at the lower boundary at 140 cm depth.

Mean water content profiles from the NMM readings and from core sampling on days 4 and 28 after infiltration, are shown in Fig. 5. The soil water profiles show strong vertical heterogeneity. Drainage was restricted by the 36 to 66 cm layer. This restriction to flow is associated with the high clay content of the layer. Above and below this layer the water drained freely.

Stolzy and Cahoon (1957) and van Bavel (1961) showed that due to neutron escape the NMM does not give an accurate measurement of the water content of the topsoil. They recommended using direct measurements for this layer. In the present investigation the water content was maintained at a high value ($\theta \simeq 0.30$) to the surface by the plastic cover. At this volumetric water content the radius of influence of the NMM is 20 cm (Olgaard, 1965), so that for a reading at 20 cm depth, the NMM would give an accurate measurement of the water content of the top 20 cm. Measurement of θ by the NMM at 20 cm gave approximately the same value for the surface layer as did direct sampling (Fig. 5).

As the gradient in θ increased, as in the 30 to 80 cm depth interval, the error of θ measurement from the NMM increased. This is almost certainly due to the fact that the NMM samples a relatively large volume of soil around the neutron probe so that the value of θ

obtained is some unspecified average of the water content of the soil within the radius of measurement. This explanation is supported by the work of Holmes and Jenkinson (1959) and McHenry (1963). Below the depth of 85 cm the gradient in the water content profile is negligible and the neutron meter readings agree with the direct measurements. This problem of vertical heterogeneity has been discussed by Holmes and Jenkinson (1959); it presents a serious disadvantage for the measurement of water content with the NMM where large gradients exist in θ. While the above problem concerns mainly the measurement of actual values of soil water content, it also applies, but to a lesser degree, to the measurement of change in water content. Water depletion within the profile as measured by the NMM was compared with change in water content measured gravimetrically by direct sampling. Water content was measured by direct sampling on days 4 and 28 following irrigation. The change in water content from direct measurement from 0-120 cm, for this period, was 2.03 (± 0.31) cm compared to 2.01 (± 0.23) cm measured by the NMM.

Hydraulic conductivity is calculated from values of U and H; it appears that the NMM is measuring $\Delta\theta$ accurately even in a heterogeneous profile. Since K is extremely sensitive to θ (Nielsen *et al.* 1972), a more serious error in estimating hydraulic conductivity is that associated with finding the absolute value of θ.

2.3.2 Hydraulic head profile during drainage

Diurnal fluctuations of air temperature and soil temperature and the influence of these factors on tensiometer readings were examined

Fig. 4. Vertical distribution of bulk density at Parafield 1972.

The solid line connects the means for 28 samples at each depth.

The dotted lines show the standard deviation.

The horizontal lines indicate the layer for which K(θ) was determined in the field.

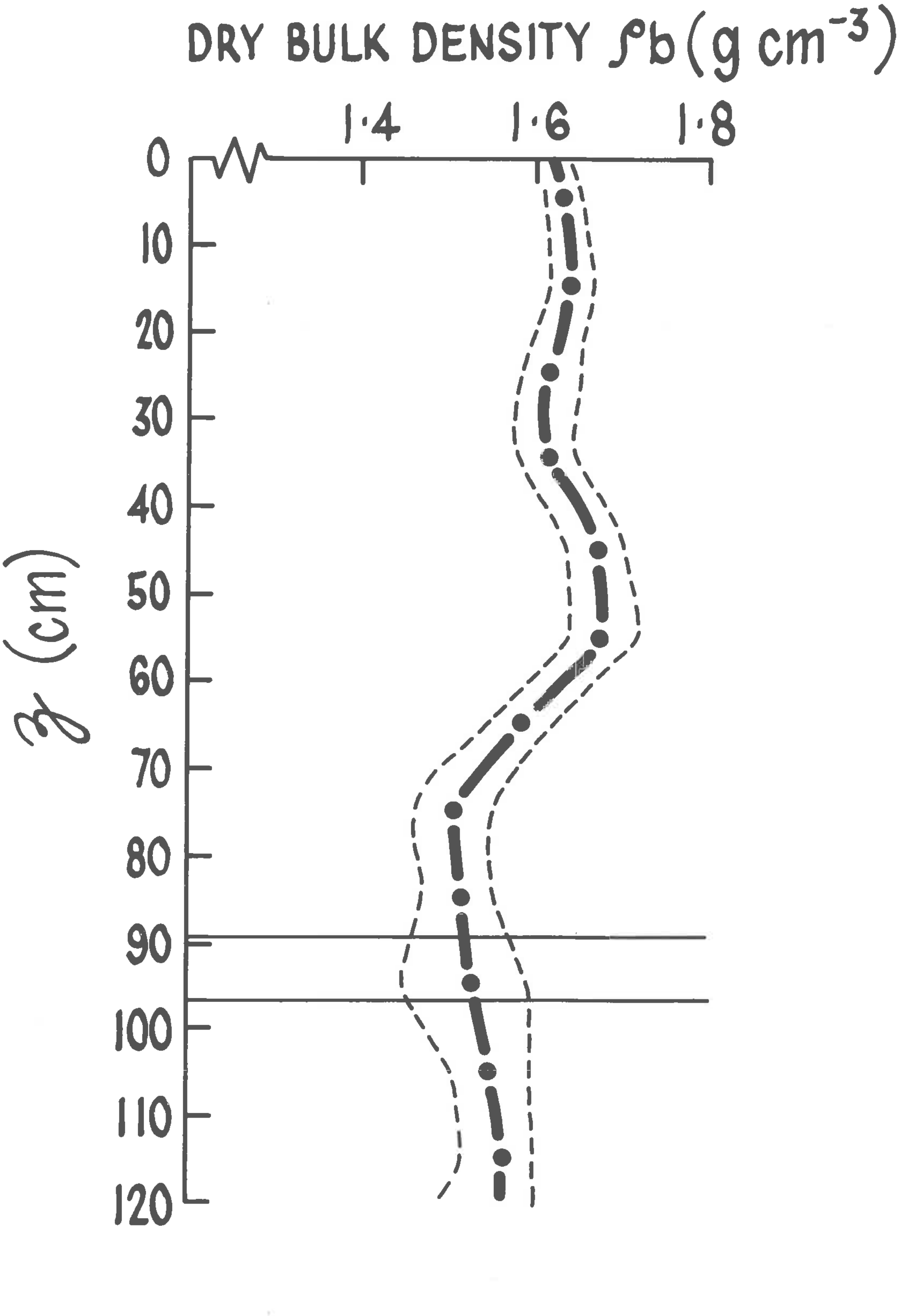
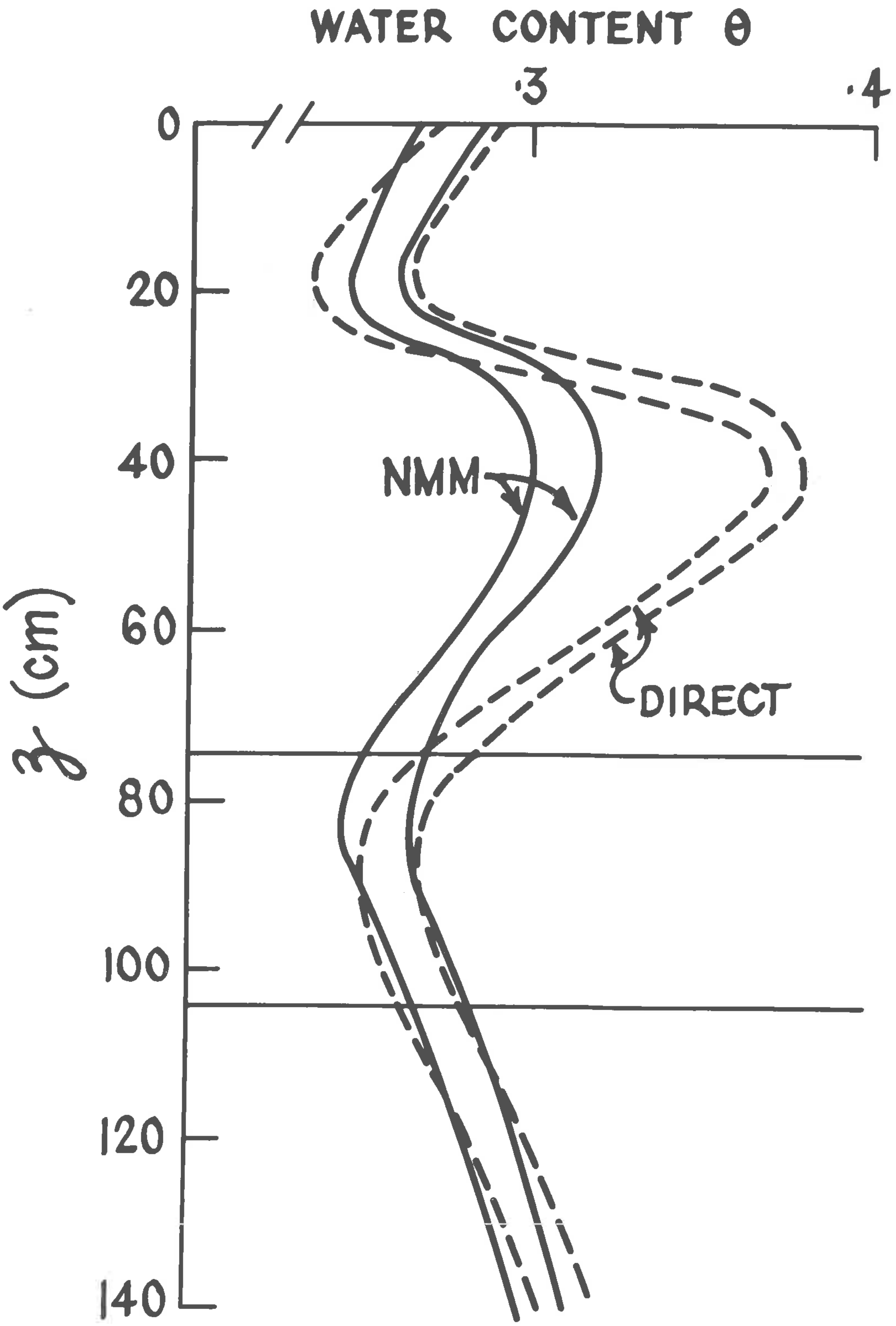

DRY BULK DENSITY ρb (g cm⁻³)
1·4
1·6
1·8
0
10
20
30
40
50
60
70
80
90
100
110
120
z (cm)

Fig. 5. θ, z relation for red brown earth at Parafield.

– – – – Direct sampling

——— NMM

In each case the R.H. curve shows the distribution on January 21, 1972; and the L.H. curve shows the distribution on February 14, 1972.


WATER CONTENT θ
·3
·4
0
20
40
60
80
100
120
140
z (cm)
NMM
DIRECT

over a three-day period during the experiment. The results were similar on the three days. The data for one day only, January 19, 1972, are shown in Fig. 6a, b. The soil deeper than 60 cm was not affected by diurnal air temperature fluctuation (Fig. 6b). This agrees with results obtained by West (1952) over an eight year period in New South Wales. Soil temperature at 60-90 cm depth was approximately 21°C. Air temperature at the experimental site on January 19, 1972 ranged from 11°C to 37°C.

The mean suction head h for the 4 tensiometer locations at each depth is shown in Fig. 6a. Diurnal temperature fluctuation affected the tensiometer readings strongly at 5 and 10 cm from the surface, but it affected readings only slightly below this depth. The effect of diurnal temperature fluctuation on tensiometer readings was similar to that described by Hainse and Kelly (1950) but less pronounced, although the air temperature fluctuation was in the same range.

Air temperature rose in the late morning, from 0700 to 1500 hr. Over the same period h remained steady until 1000 hr, and then rose until 1800 hr, after which it became steady again. The increase in h was probably caused by an expansion of the tensiometer stand pipe with increase in temperature, the expansion lagging 3 hours behind air temperature. Failure of h to fall again with decrease in temperature was due to the value of h in the bulk of the soil increasing during the course of drainage. If a straight line is drawn to connect the value of h at 0700 hr on one day to that at 0700 hr on the next day, the deviation from the straight line is at no time more than 4 cm from 20 cm depth downwards, even though the difference between the minimum and maximum air temperature during the day was 26°C. Air temperature affected tensiometer readings simultaneously in the same direction and to a similar extent in the deep layers as at 10 cm. For this reason the effect of air temperature on the measured hydraulic gradient at 75 to 105 cm depth at any one position was negligible.

Hydraulic head was obtained from the mean of the four tensiometer readings at each depth interval after the cessation of irrigation. The z, H function is shown in Fig. 7. The values of the hydraulic gradient, $\frac{dH}{dz}$, were not unity, as would be expected for a uniform soil, but varied throughout the profile. Fluctuations in the value of H at 5 cm depth can be explained by condensation on the under surface of the plastic sheet due to diurnal fluctuation in temperature. Below this depth the gradient $\frac{dH}{dz}$ was always such that water moved downwards during the experimental period.

2.3.3 Hydraulic conductivity of the lower boundary-layer

Values of the hydraulic conductivity were obtained from the measurements at each of four positions over the range 30-120 cm suction head. These values were calculated from:

$$K(\overline{\theta}) = -\overline{U}\,\frac{\Delta z}{\Delta H} \qquad (24)$$

where $K(\overline{\theta})$ is the conductivity at the mean water content over the time intervals shown in Fig. 7 for the 74 to 104 cm layer, and $\overline{\theta}$ is the mean volumetric water content for the 74 to 104 cm layer. $\overline{U}$ is the mean flux

Fig. 6. a) Variation in suction head h at various depths over one day (January 19, 1972).

x	5 cm	●	74 cm
o	10 cm	■	104 cm
Δ	20 cm	□	134 cm

b) Variation in air-soil temperature over one day (January 19, 1972).

Δ	air temperature
□	soil temperature 5 cm
●	soil temperature 20 cm
x	soil temperature 60 cm
o	soil temperature 90 cm

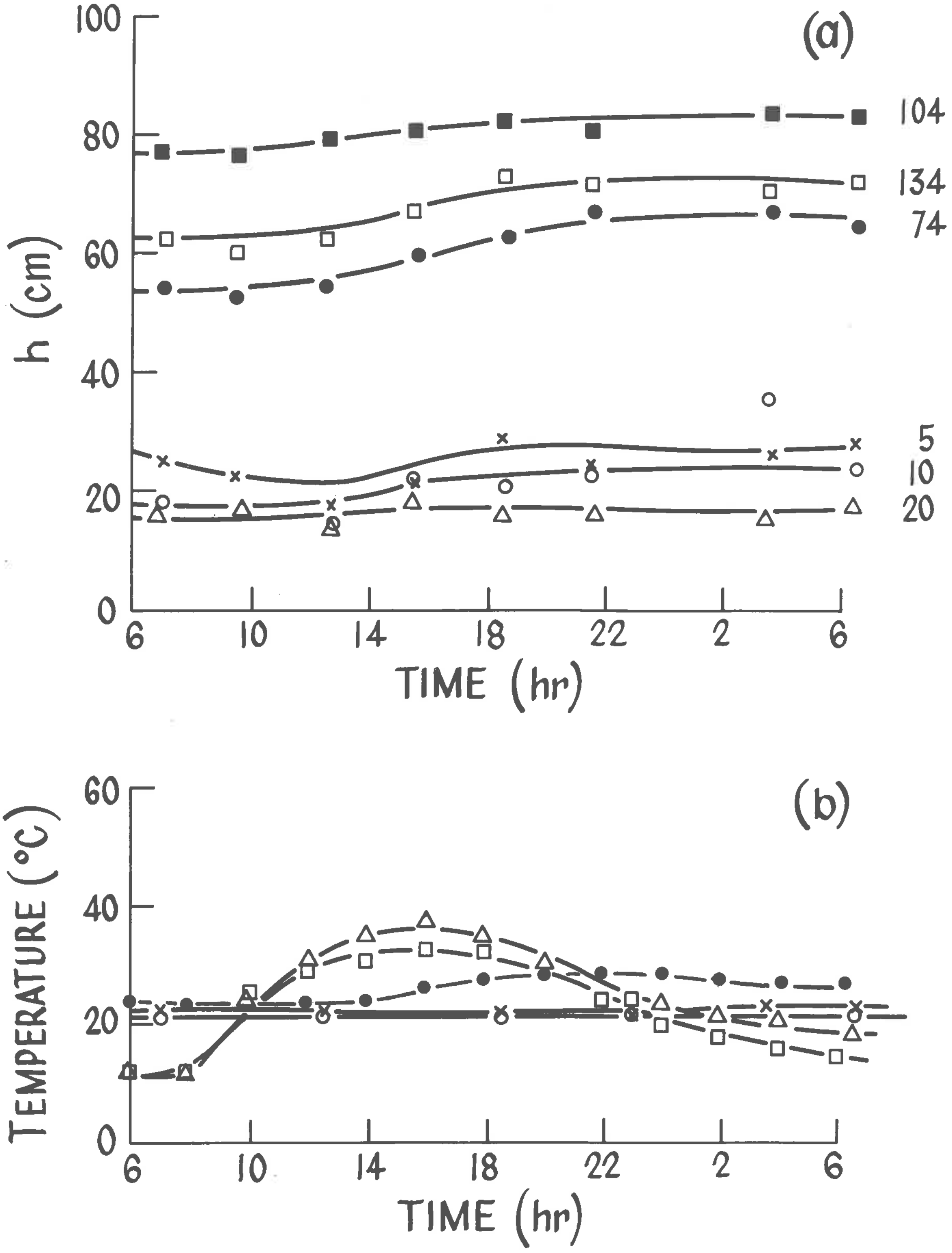
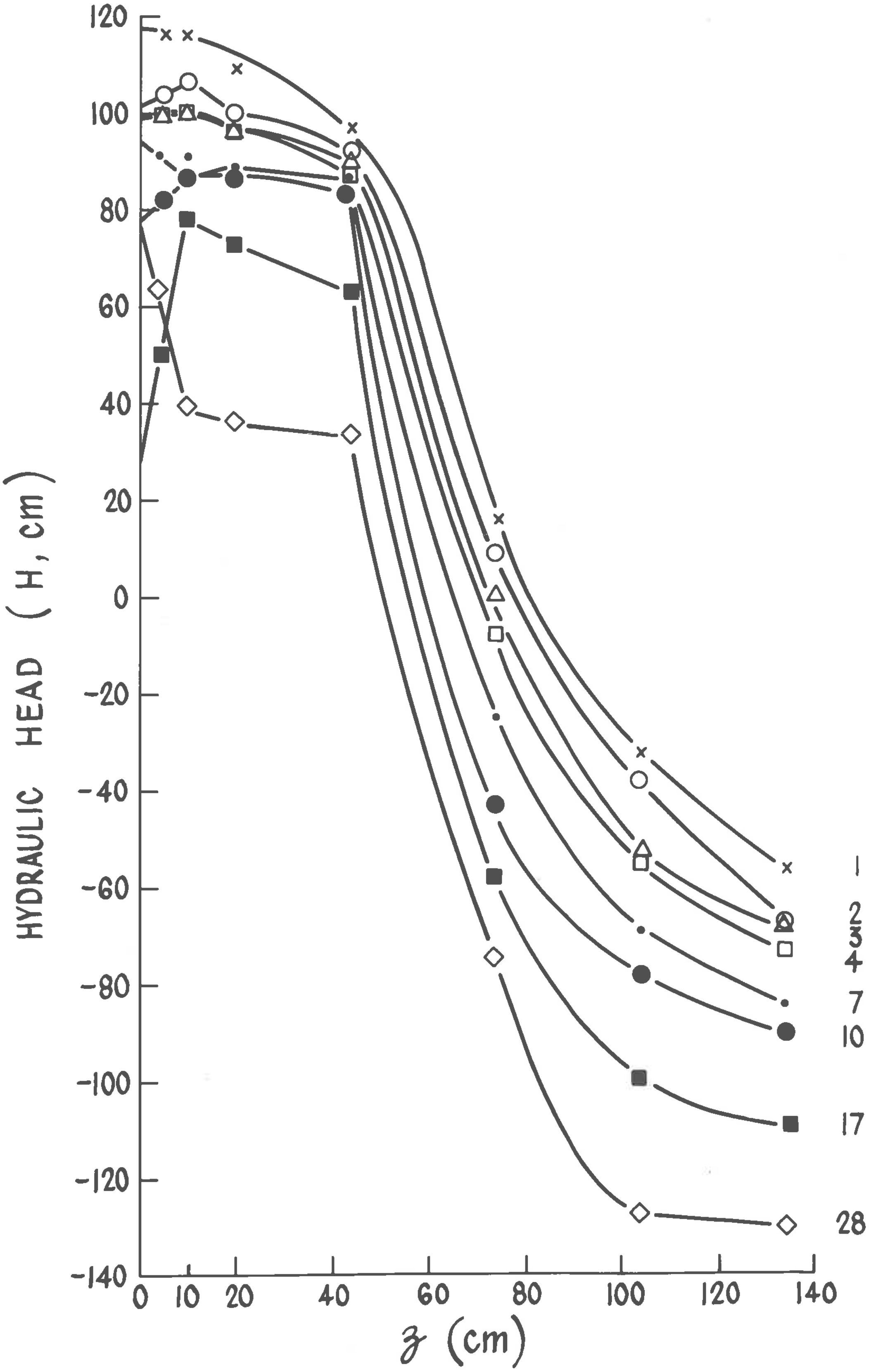

(a)
h (cm)
100
80
60
40
20
0
6
10
14
18
22
2
6
TIME (hr)
104
134
74
5
10
20
(b)
TEMPERATURE (°C)
60
40
20
0
6
10
14
18
22
2
6
TIME (hr)

Fig. 7. z, H relation at Parafield 1972. The numbers on the curves indicate the number of days after cessation of infiltration.


HYDRAULIC HEAD (H, cm)
120
100
80
60
40
20
0
-20
-40
-60
-80
-100
-120
-140
0
10
20
40
60
80
100
120
140
z (cm)
1
2
3
4
7
10
17
28

within each layer at each location over the time interval, and $\overline{\frac{\Delta H}{\Delta z}} = \frac{1}{2}(\frac{\Delta H}{\Delta z,t=1} + \frac{\Delta H}{\Delta z,t=2})$ is the mean hydraulic gradient obtained from the readings of the tensiometers at 74 and 104 cm depth at each location over the time interval. This assumes that the hydraulic head varied directly with depth.

The results are shown in Fig. 8 on semi-log paper and are given in detail in Appendix Table 1. A log-normal distribution of $K(\theta)$ was assumed (Nielsen *et al.* 1973). Linear regression (log transformation) was used to analyse the data at each position. The slopes of the lines were not significantly different, so the data from the four positions were pooled to obtain a mean hydraulic conductivity function for the site. Bouwer (1969) has shown that the mean $K(\theta)$ is most closely approximated by the geometric mean of a sample set of values of $K(\theta)$. The use of a regression equation fitting the logarithmic transformation of $K(\theta)$ is consistent with the use of a geometric mean. The regression of $\log_e K$ on θ was:

$$\log_e K = 68.3\ (\pm\ 11.3)\ \theta - 20.8$$

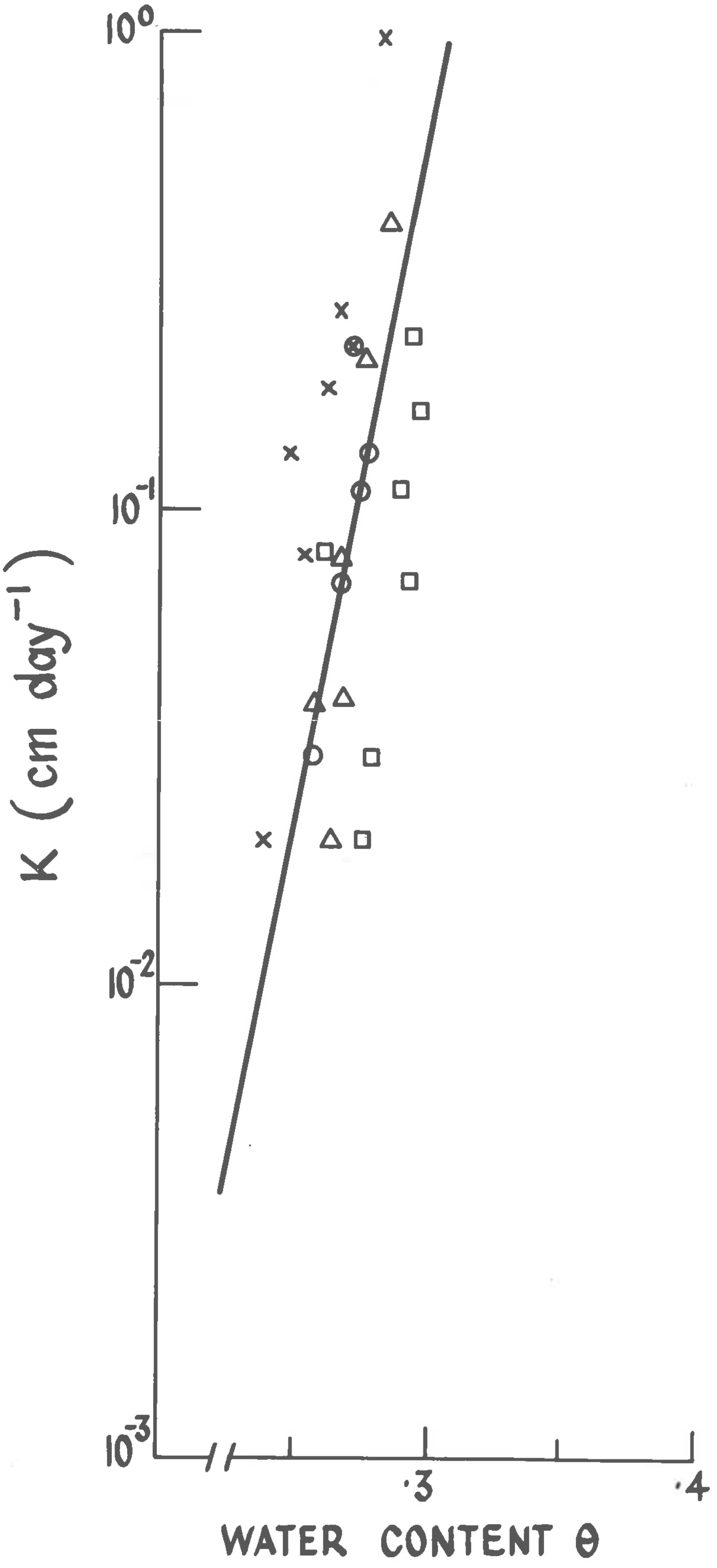
Because of the small number of samples, the range was used to estimate the standard deviation as described by Snedecor and Cochran (1971). This gave a value of 1.308 for the standard deviation of $\log_e K$ at a particular value of θ. This corresponds to an anti-$\log_e$ standard deviation value of 3.70, and implies that 68 percent of the values of K will fall within the limits $3.70\overline{K}$ to $\overline{K}/3.70$; this range represents an order of magnitude difference in the value of K at a particular water content. The value of 3.70 is considerably higher than the value of

2 suggested by Rogowski (1972) as a criterion of uniformity of K for a soil (see Section 2.1.3). The standard deviation of θ for the four sites at each reading by the NMM at 80-110 cm depth did not exceed ± 0.01. The error arising in estimating the hydraulic conductivity due to this error in θ would be a factor of 2 in K (see Fig. 8) or a deviation of 0.693 in $\log_e$ K. This is approximately one half of 1.308, the value found for the standard deviation of $\log_e$ K; consequently in this experiment variance in θ accounts for 30 percent of the variance in $\log_e$ K. At 74 and 104 cm depth error in $\frac{dH}{dz}$ arising from the diurnal fluctuation in temperature was shown to be negligible. Thus, the variation in K(θ) was derived from intrinsic variation in K(θ) and from error in the measurement of θ.

For the soil at Parafield using the field values of K(θ) to calculate U may lead to error of one order of magnitude. The anti-$\log_e$ standard error of the mean of four measured values of K(θ) is 1.92; this implies a standard error of $\overline{K}(\theta)$ of almost 100 percent (1.92 $\overline{K}$ to $\overline{K}/1.92$). Water balance studies generally require a precision of 30 percent in $\overline{K}(\theta)$. To obtain this degree of precision for this soil 25 measurements of K(θ) must be made at random locations at the selected depth ($1.308/\sqrt{25} = 0.262$; anti-$\log_e$ $0.262 = 1.30$). Sixty eight percent of the values of $\overline{K}$ will fall between $1.30\overline{K}$ and $\overline{K}/1.30$, or approximately ± 30 percent.

According to Rogowski's criterion for uniformity of K(θ) - an anti-$\log_e$ standard deviation≈2 - the red brown earth at Parafield cannot be considered uniform. The sampling requirement to obtain reasonable

Fig. 8. $K(\overline{\theta})$ function at 74 to 104 cm depth at Parafield. x, o, Δ and □ , sites I, II, III and IV respectively.


10⁰
10⁻¹
10⁻²
10⁻³
K (cm day⁻¹)
·3
·4
WATER CONTENT θ

accuracy is unacceptably high. Water balance investigations on non-uniform soils are probably not feasible using the deterministic procedure outlined above. For a uniform soil Rogowski's criterion represents - for the positive value of the standard deviation - an error of 100 percent. When nine randomly located samples are measured this error falls to 26 percent.

2.3.4 Laboratory measurements

2.3.4.1 The moisture characteristic

For the field moisture characteristic, values of θ at 80 and 100 cm depth were measured with the NMM. From Fig. 5 values at 80 cm were in error due to the radius of influence of the NMM encompassing layers of different θ. On January 21 and February 14, 4 and 28 days after cessation of infiltration respectively, θ measured by the NMM was less than the value of θ measured gravimetrically by a constant amount 0.01. For this reason values of θ at 80 cm depth, obtained over the duration of the experiment with the NMM, were corrected by adding 0.01. Equilibrium suction measurements for the corrected water contents were taken from the tensiometer readings. The θ, h function obtained from field data is plotted in Fig. 9. The moisture characteristic has been fitted by eye as a dashed line.

Laboratory measurements of the moisture characteristic made on 7.6 cm cores are also given in Fig. 9. The upper solid line represents the drying curve starting from an initial suction of zero. The lower solid line on the left hand side represents the drying curve starting from 30 cm suction, that is, the lowest suction head attained in the 74 to 104 cm layer during irrigation and drainage. The horizontal bars represent the standard deviation of θ values obtained for 12 cores in the laboratory at specified suctions. No overburden effect was apparent in this soil because, as shown in Fig. 9, the field moisture characteristic was similar to the drainage scanning curve obtained in the laboratory from soil wetted initially at 30 cm suction head.

The difference in water content for this soil due to hysteresis is 0.06 at a suction head of 30 cm. This represents a 40-fold difference in $K(\theta)$. Hysteresis should be kept in mind when planning studies involving the comparison of hydraulic properties of soil in the field and in the laboratory, and especially when attempting to characterize the θ, h relation of field soils by means of water retention measurements on intact samples in the laboratory.

The above results were used to check the performance of the empirical model of Rogowski (1971), Eq. (18), in describing the moisture characteristic for this soil. The water content at air entry was taken as 0.367, the air entry value h_e as 0. In place of h_{15} and θ_{15} the suction head and water content at 0.2 bar suction were used for the dry end of the range. From Fig. 9 $\theta_{0.2} = 0.24$. It follows from Eq. (18) that

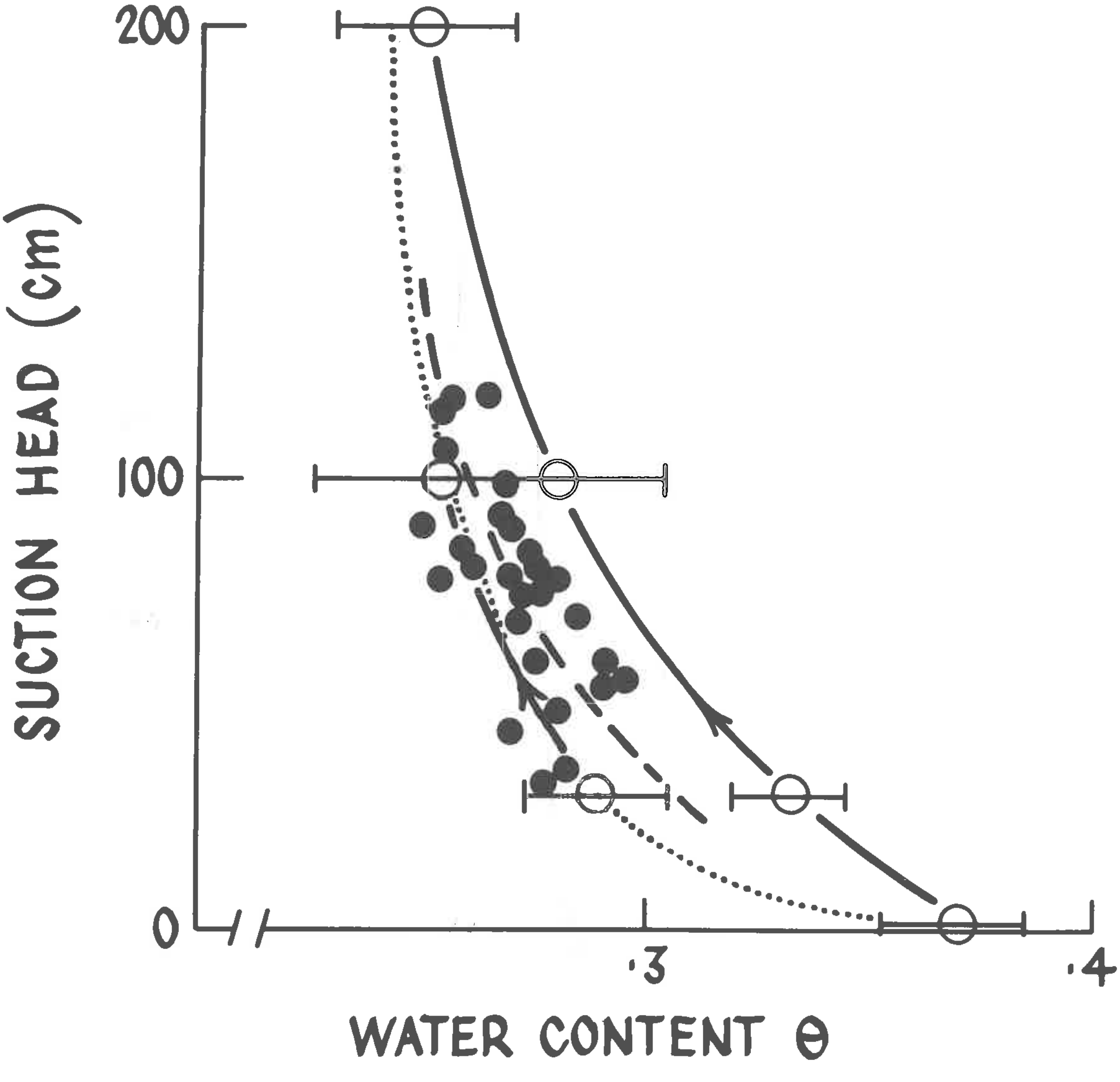
$$\begin{aligned} \alpha &= (.24 - .367)/\log_e(200 - 0 + 1) \\ &= -0.024, \end{aligned}$$

and

$$\theta = 0.367 - 0.024 \log_e(h + 1).$$

Fig. 9. Moisture characteristic.

———	Laboratory (main desorption curve, initial $h=0$, and desorption curve, initial $h=30$)
– – – –	Moisture characteristic (fitted by eye to field data)
●	Field data
·······	Estimated desorption curve from Rogowski's model


SUCTION HEAD (cm)
200
100
0
·3
·4
WATER CONTENT θ

From this expression θ was calculated as a function of h to give a moisture characteristic based on Rogowski's equation. The function is plotted in Fig. 9, and corresponds reasonably well with the field moisture characteristic.

2.3.4.2 K_0 values

K_0 was determined on the 12 undisturbed soil cores taken from the field. The results are shown in Table 1. The values vary by an order of magnitude. The mean is taken as the geometric mean of the hydraulic conductivity as suggested by Bouwer (1969). The mean volumetric water content of the saturated cores was 0.355 ± 0.019. This was not significantly different from the water content of the saturated cores that were used for the moisture characteristic. The geometric mean of K_0 was 24.3 cm day^{-1} with a standard deviation (s $\log_e$) of 1.152. That is, 68 percent of the values of K_0 are likely to fall within the limit 3.16 X 24.3 to 24.3/3.16 cm day^{-1}. The variability of K_0 determined on the 7.6 X 7.6 cm cores is close to that obtained from the field method, even though the volume of soil used in the two techniques differs greatly. This suggests that the variation in hydraulic conductivity of this soil occurs chiefly on a macro-scale (location to location on the plot). The anti-log standard deviation of 3.16 is considerably in excess of the value of 2.0, the criterion proposed by Rogowski (1972) as an upper limit of variation describing a uniform soil. The geometric mean hydraulic conductivity at mean θ_0 is close to the value of K derived from the θ, $K(\theta)$ relation obtained in the field.

Table 1. Saturated hydraulic conductivity (cm day^{-1}) of undisturbed samples taken from the lower boundary layer (74 to 104 cm) of a red brown earth at Parafield.

Sample No.	θ_o	K_o (cm day^{-1})
1	.376	91.5
2	.356	135.0
3	.350	49.0
4	.376	18.3
5	.385	50.0
6	.329	3.0
7	.354	7.2
8	.353	9.7
9	.363	12.6
10	.330	28.8
11	.349	40.5
12	.336	24.2

2.3.5 Comparison of $K(\theta)$ function derived from field data with $K(\theta)$ derived from Marshall's equation

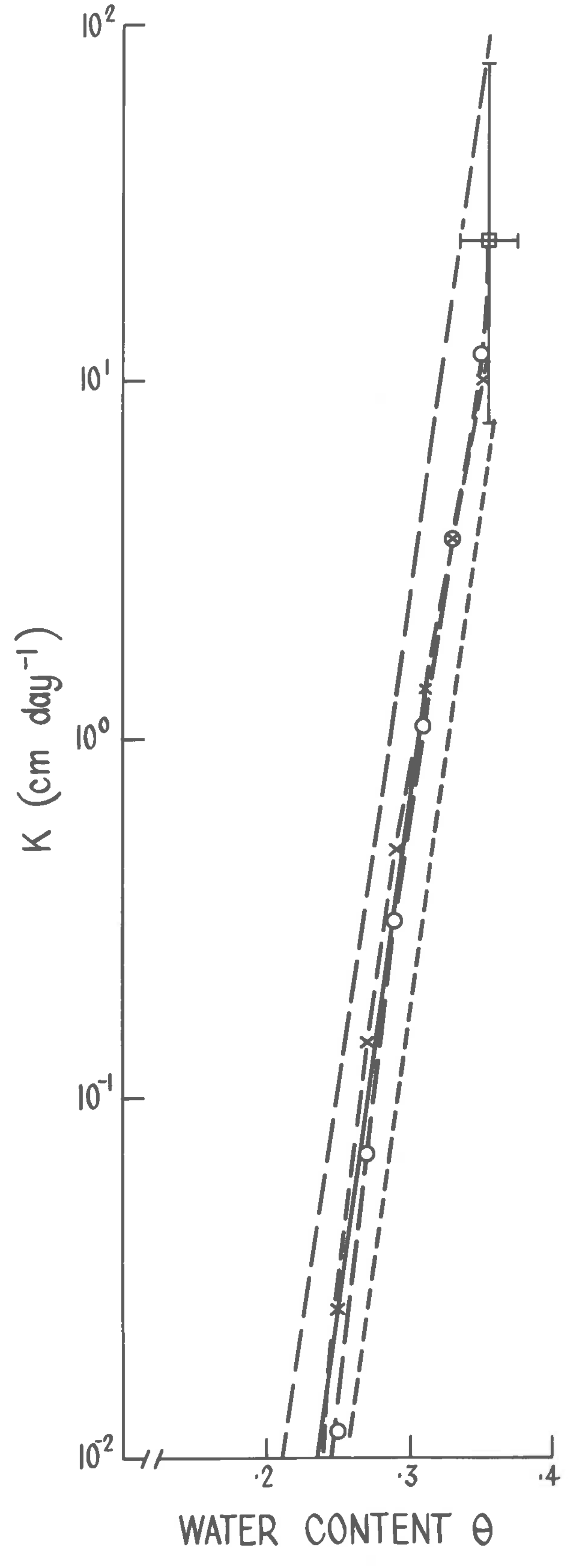
Eq. (11) based on Marshall (1959) was used to compute the $K(\theta)$ relation. The geometric mean of K_o determined in the laboratory at mean θ_o was used to obtain the matching factor. Using Eq. (11) $K(\theta)$ was calculated from the main desorption curve shown in Fig. 9. The results, plotted as (X), are given in Fig. 10. The derived values of $K(\theta)$ agree with the field values of $K(\theta)$, even though hysteresis is a source of error. At $\theta = 0.3$, corresponding to a value of $h = 30$ cm, the suction head in the transmission zone, the value of $K(\theta)$ obtained from Eq. (11) deviated from the $K(\overline{\theta})$ found in the field by a factor less than 1.5. For this soil Eq. (11), used with a matching factor, gives sufficient accuracy for the description of the $K(\theta)$ function.

As shown in Section 2.3.4.1 the water characteristic obtained from the field, that obtained in the laboratory on cores with the same wetting history, and the moisture characteristic from Rogowski's model agree well with one another. $K(\theta)$ may also be calculated using the moisture characteristic obtained from Rogowski's equation (Eq. (18)). The results are shown as (O) in Fig. 10. Using only 3 data values θ_o, $\theta_{0.2}$ and K_o, and Rogowski's equation to give a moisture characteristic, and Eq. (11) to give $K(\theta)$, $K(\theta)$ may be predicted with an accuracy well within the error associated with field measurements.

The use of measured K_o to obtain a matching factor for the drainage investigation does not agree with the principle of selecting an experimental conductivity for matching at a water content close to the range encountered in the process under investigation (Roulier *et al.* 1972). In practice, field or laboratory methods for determining K(θ) over the range of 30 to 150 cm suction head are difficult to employ, the main problem being the number of measurements needed to assess variability.

Fig. 10. Comparison of hydraulic conductivity measured in the field and that calculated from laboratory data.

————————	Field K(θ)
— — X — —	M equation, using laboratory moisture characteristic
— — o — —	M equation, using field moisture characteristic
□	$\bar{K}_o$ from laboratory measurements
├────────┤	Standard deviation of laboratory measurements of K_o
– – – – – – – – – –	Standard deviation of field measurement of K(θ)


10^2
10^1
10^0
10^-1
10^-2
K (cm day^-1)
·2
·3
·4
WATER CONTENT θ

PART II. WATER UPTAKE

3.0 INTRODUCTION

The effects of a shortage of water on plant growth and metabolism have been examined in reviews by Stocker (1960), Vaadia, Raney, and Hagan (1961) and by Hsiao (1973). These authors have demonstrated the importance of the ability of plants to meet the evaporative demand for water. Given an unlimited supply of water by rain or irrigation and mild or moderate evaporating conditions, mesophytes can generally match atmospheric demand; but under adverse conditions with relatively dry soil and with high evaporative demand E_t falls below E_o (Denmead and Shaw 1962). To extract water from the soil at a rate sufficient to match E_o the plant has to overcome resistance to flow located in the soil and in the plant itself. Soil physicists have often claimed that soil resistance is the major factor that causes E_t to fall below E_o when the matric suction in soil exceeds 2 bar. However Newman (1969a) argued that, under well established crops, the root resistance exceeded soil resistance when suction head was less than 15 bar. Newman agreed that soil resistance may be dominant when the roots were widely spaced in the deeper layers of the soil. Passioura (1972a) suggested that in temperate cereals resistance to upward flow of water in the xylem of the root might become important when water is being elevated from the lower layers of the root zone.

In seeding rate experiments, Kirby (1970), and Walter and

Barley (1974) found that crops growing either at low or at high plant densities had difficulty in withdrawing water from depths greater than 60 to 75 cm. Kirby (1970) hypothesized that the difficulty could be due to low root density at depth; Walter and Barley (1974) suggested that, at low plant density, axial resistance was large in the deeper layers due to a small number of root axes per unit ground area. They showed that at an intermediate plant density the roots penetrated more deeply than at low or at high plant densities. However, axial root resistance was not measured either by Kirby or by Walter and Barley.

The present study is designed to assess axial resistance to the flow of water in the root. A few measurements have also been made to indicate the likely order of magnitude of root resistance in the radial direction.

The first section of Part II reviews relevant literature dealing with withdrawal of water from the soil by roots and with root geometry and its relation to the hydraulic conductance of roots. The second section deals with experimental work on the determination of hydraulic conductance of segments of wheat and pea roots in the laboratory. The third section is concerned with a study of root* networks of wheat grown in the field at different seeding rates. From these data conclusions are reached about the probable importance of

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* The term 'root' will be taken to mean a main axis together with its first and higher order laterals.

axial and radial root resistances in relation to the rate of withdrawal of water from the subsoil by wheat.

3.1 LITERATURE REVIEW

The review deals chiefly with the withdrawal of water from the soil by plant roots with particular reference to root resistance.

3.1.1 General description of withdrawal of water from the soil by roots

Richards (1928) pointed out that the concept of the availability of water involves both the ability of the root to withdraw water from the soil, and the rate at which water may be withdrawn to replace that evaporated from the plant. Richards and Wadleigh (1952) observed that not much progress had been made over a period of twenty years or more in separating these two aspects of water availability, chiefly because of the difficulty of determining water content gradients in the immediate vicinity of roots. At first progress was limited by lack of information about the water transmitting properties of soil at low water contents. Later, Gardner (1956) and others introduced improved methods designed to measure the hydraulic conductivity of unsaturated soil $K(\theta)$. The theory of withdrawal of soil water by sets of roots as contrasted with a single root was first outlined by Philip (1957).

Withdrawal of water from the soil by a long stationary zone of a single root member has been investigated in some detail. The emphasis has usually been placed on the suction gradient likely to be found around the root at given rates of water uptake (Philip 1957;

Gardner 1960).

Following the work of Philip (1957) the rate of withdrawal of water from the soil by a set of roots has been studied theoretically by Gardner (1960, 1964), Cowan (1965), and Cowan and Milthorpe (1968a). Gardner (1960, 1964, 1965) assumed that the rate of flow from the soil to a set of roots was proportional to the difference between the hydraulic head of water within the xylem of the root and that in the surrounding soil. He postulated the following relation to describe the rate of withdrawal under steady state conditions:

$$\frac{d\nu}{dt} = \frac{h_x - h_s}{R + \Lambda_s} \tag{25}$$

where ν is the reduction in volumetric water content due to withdrawal of water from a prescribed volume element of soil by the set of roots crossing the boundaries of the volume element considered; h_x (cm) is the suction head of water in the xylem; h_s (cm) is the suction head of water within the bulk of soil in the volume element considered; R (cm sec) is the resistance opposed to the flow of water into and within the xylem of the set of roots concerned; and Λ_s (cm sec) is the resistance to flow of water within the soil pores. Gardner (1964) postulated further that the resistance Λ_s is related inversely to $K(\theta)$ and to L_v and can be expressed as:-

$$\Lambda_s = \frac{1}{BK(\theta)L_v} \tag{26}$$

when B is a matching factor for a given volume element of soil; and L_v is the total length of root members per unit volume of soil (cm^{-2}). Eq. (26) assumes that resistance across the boundary between the soil and root is negligible or, if not negligible, includes any such resistance within Λ_s. The assumption that resistance at the boundary is negligible seems questionable. Under high water stress, the root may shrink away from the soil (Cole and Alston 1974). This could greatly increase the resistance at the boundary as vapour diffusion is a relatively slow process compared with liquid flow. Jenny and Grossenbacker (1963) studied the region between the epidermis of the root and soil particles using an electron microscope. They found that the space between the epidermal wall of the root and the soil grains was filled with mucilage. Perhaps the mucilage maintains liquid continuity between the water in the epidermis and the water in the soil.

Combining Eqs. (25') and (26)

$$\frac{d\nu}{dt} = \frac{(h_x - h_s)}{\dfrac{1}{BK(\theta)L_v} + R} \qquad (27)$$

Gardner and Ehlig (1962a) concluded from a pot experiment that R was relatively small in relation to Λ_s, even when the soil water suction was as small as 0.1 bar. Consequently they reduced Eq. (27) to:-

$$\frac{d\nu}{dt} = (h_x - h_s)\, BK(\theta)L_v \qquad (28)$$

Gardner used Eq. (28) to predict soil water distribution on day 2 and day 8 of a drying period, after calculating the product BL_v from data obtained on the fourth and the sixth days. In this comparison water was extracted from soil in a 120 cm deep pot by sorghum (*Sorghum vulgare*, cv. Double dwarf). However, Gardner was unable to predict the distribution of rooting density at depths below 40 cm in the pot. The model predicted values less than the actual rooting density. Gardner himself suggested that the discrepancy between the estimated and observed values of L_v was probably due to root resistance at depth.

Molz and Remson (1970) modified Gardner's model by including the vertical flow of water through the soil. They derived the continuous distribution of effective rooting density using a matching factor similar to that of Gardner (1964), and substituting data of Gardner and Ehlig (1962a). The latter authors had grown birdsfoot trefoil (*Lotus corniculatus*, var. *tennuifolius*) in a deep pot of Pachappa fine sandy loam, with a water table maintained at 110 cm depth. Molz and Remson then estimated the distribution of water content using Gardner's (1964) data for sorghum growing in soil columns. However Molz and Remson were unable to predict the measured distribution of soil water content better than had Gardner. Molz and Remson (1970) considered that, even though they had calculated the effective rooting density with a matching factor derived from another experiment and with a different crop, that their model predicted the water content profile reasonably well. They pointed out, nevertheless, that the withdrawal of water by a set of roots could not be explained adequately without an understanding of factors determining effective rooting density as contrasted with observed rooting density.

Gardner's (1964) conclusions concerning the relative values of R and Λ_s have been questioned by Newman (1969a). Newman argued that since the rooting density exceeded 5 cm^{-2} in the top soil under well established pastures and crops, soil resistance was too small to exert much influence on the rate of water uptake until the soil had been dried nearly to the wilting point. However it seems unlikely that the whole of the observed root length participates in water uptake. A well suberized endodermis is usually present except in the early stages of root development, and the outer files of cortical cells, together with the epidermis and its root hairs, are often lost from older basal zones.

An alternative method of describing the rate of depletion of soil water content at given depths due to withdrawal of water by the root network, λ (day^{-1}) was introduced by Ritjema (1965) and Rose and Stern (1967). Those workers proposed the use of the instantaneous water balance equation:-

$$\int_{t_1}^{t_2}(I'-G'-U-E_s)dt - \int_{o}^{Z}\int_{t_1}^{t_2}\lambda dzdt - \int_{o}^{Z}\int_{t_1}^{t_2}\frac{d\theta}{dt}dzdt = 0 \qquad (29)$$

where I' is the rate of precipitation and/or irrigation (cm sec^{-1}); G' is the rate of surface runoff (cm sec^{-1}); U is the vertical drainage flux (positive downwards) of water in the soil at depth Z (cm $\sec^{-1}$), where Z is the depth of the rooting zone; E_s is the rate of evaporation (cm $\sec^{-1}$) from the soil surface; λ is the rate of decrease of volumetric water content at depth z due to withdrawal by plant roots ($\sec^{-1}$), and θ is the volumetric water content of soil at depth z (cm). Depth is taken as positive in the downwards direction, and measured from the soil surface.

The measurement of U has been described in Part I of this thesis. E_s can be determined in the field using either the energy balance method as outlined by Denmead (1973), or the soil water flux method as outlined by Rose and Stern (1967). When the soil surface is dry E_s can be ignored compared with the transpiration from agricultural crops having L.A.I. >> 2 (Rose and Stern 1967; Denmead 1973). Given values of the other variables Eq. (29) can be solved to find λ as a function of z and t. Using Eq. (29) Rose and Stern (1967) found that under irrigated cotton crops (*Gossypium* spp.), λ decreased with depth. They postulated that this could be because an increase in soil resistance with depth reduced local flow to the roots. Unfortunately, they obtained no data on rooting density.

Similar studies of water withdrawal from soil by root systems have been carried out by van Bavel *et al.* (1968a, b), Feddes and Ritjema (1972), and Walter and Barley (1974). van Bavel *et al.* found that the calculated values of $\int_0^Z \lambda dz$, where Z is the maximum depth of rooting, differed by 30 percent compared with an independent measurement of E_p

obtained with a weighing lysimeter. The discrepancy could arise from an error in estimating U due to spatial variability of K(θ). van Bavel *et al.* measured K(θ) from four sites near their weighing lysimeters. They obtained K(θ) by fitting a line by eye to a plot of K as a function of θ. Then they assumed that values of K(θ) obtained from the fitted line gave K(θ) for the soil in the lysimeters. Further discrepancies could have arisen from the low frequency of measurement of the hydraulic gradient (one per day), leading to error in the estimation of U.

Even though Eq. (29) enables the rate of withdrawal by roots to be calculated at given depths and times, it does not by itself explain the factors governing the rate of withdrawal of water by roots. The instantaneous water balance equation may in appropriate conditions be used in the simplified or reduced form:-

$$\int_{t_1}^{t_2} (U_{z_1}-U_{z_2})dt - \int_{z_1}^{z_2}\int_{t_1}^{t_2} \lambda dzdt - \int_{z_1}^{z_2}\int_{t_1}^{t_2} (d\theta/dt)\, dz.dt \quad = \quad 0 \qquad (30)$$

for intervals bounded by time $t_1 < t_2$ and depth $z_1 < z_2$.

Recently Walter and Barley (1974) used Eq. (30) to study the rate of withdrawal of water by wheat roots (λ) from a field soil. The smallest depth at which λ and U were calculated was 5 cm. They measured the vertical distribution of L_v under a crop sown at low, intermediate and high rates of seeding. They found that at a high rate of seeding the major resistance to the extraction of the deeper water at anthesis was located in the soil. At the lowest rate of seeding the major resistance appeared to have been located within the roots.

Information on the hydraulic conductance of single root members immersed in solution has been obtained by Rosene (1937, 1941), Hayward *et al.* (1942), Slatyer (1960), Brouwer (1965), Hansen (1974a), and Graham *et al.* (1974). Graham *et al.* found that the rate of water uptake by zones of the seminal root axis of barley (*Hordeum vulgare*, cv. Midas) and marrow (*Cucurbita pepo*, cv. Greenbush) was inversely proportional to the degree of suberization of the endodermis. Where the endodermis had become fully suberized, the rate of water absorption fell sharply to a low value, which remained relatively constant in more basal zones of the axis. They also found that the pattern of uptake of water along first order laterals of barley differed from that along a seminal axis. The decline in the rate of water uptake at the base of the first order laterals, where suberized lamellae were probably present, was not very pronounced. They considered that, when barley plants were grown in solution culture, the laterals would be responsible for two-thirds of the total water uptake by the plant. Furthermore, one-half of the total amount of water absorbed by the main root axis would be absorbed by the zones having a partly suberized endodermis and located more than 7 cm from the tip.

There is little information on the uptake of water by single root members *in situ* in soil. Recently Walter and Barley (1974) suggested that that part of the root length bearing intact root hairs might be a more relevant attribute than the total root length in regard to the uptake of water from soil, as the older, proximal zones are often highly suberized or lose the outer files of cortical cells. They calculated the apparent rate of water uptake, $q = \left(\int_{z_1}^{z_2} \lambda dz \Big/ \int_{z_1}^{z_2} L_H dz\right)$ (cm^2 day^{-1}) at various stages of growth, where L_H is the length of hair-bearing root per cm^3 of soil. The maximum value of $q(1 \cdot 10^{-2}$ cm^2 $day^{-1})$ occurred for the 50 to 75 cm depth interval at 13 weeks for the roots of wheat growing in a sandy red brown earth.

3.1.2 Root geometry

Geometry here denotes the anatomy, morphology and distribution of the roots. A detailed description of the root geometry of wheat is given by Hector (1936), Troughton (1962), and Walter (1971). The root geometry of field peas is described by Hayward (1938), and Bond (1948). In this section emphasis will be given to anatomical features of roots likely to influence the uptake and conduction of water. Literature on the distribution of roots in the soil is also reviewed; and attention is given to those factors affecting anatomy and distribution which are particularly relevant to the experimental work reported in the thesis.

3.1.2.1 Anatomy of wheat roots

Seminal roots arising from the embryo, and the nodal or adventitious arising from the basal nodes of the stem, need to be considered separately as their anatomy differs.

i) Seminal axes

The seminal root axis shows the following distinct tissues:

Piliferous layer - A continuous layer consisting of thin elongated cells, many of which develop root hairs.

Cortical tissue - The thickness of cortical tissue is approximately 200 µm and the cortex usually consists of 6 to 8 layers of parenchymatous cells (Percival 1921; Hector 1936) with small intercellular spaces (Dunn 1921; Jackson 1922). The individual cells of the cortex are between 20 and 40 µm wide and 170 to 350 µm long (Percival 1921). The innermost layer of the cortex is differentiated as the endodermis, a single unbroken layer of closely fitting cells initially with thin outer walls, but, in older zones, with strongly thickened and cutinized inner tangential and radial walls exhibiting lines of stratification (Percival 1921; Jackson 1922; Hector 1936). In the sub-apical zone, the cell walls of the endodermal cells opposite the xylem poles are not thickened (Jackson 1922; Avery 1930). Tanton and Crowdy (1972), and Clarkson *et al.* (1973) showed that the walls of these passage cells are the last to thicken.

Vascular cylinder. The vascular cylinder is polyarch. A single layer of cells at the periphery of the cylinder constitutes the pericycle. Its cells are at first thin-walled and nearly equal in size, except at the point opposite the protoxylem poles, where the cells are smaller (Percival 1921; Hector 1936). Jackson (1922) found similar differences in cell size within the pericycle in barley.

At the centre of the stele in the main seminal axes of wheat roots, there are 1 or 2 metaxylem vessels 45 to 60 µm in diameter (Percival 1921; Avery 1930; Hector 1936; Svensson 1971; and Russel 1970). Jackson (1922) described the central vessel in the main axes of seminal roots of barley as a duct; but it is in fact a single vessel (Troughton 1962). In wheat, the metaxylem vessel or vessels are surrounded by 7 to 10 protoxylem strands each containing a vessel approximately 10 µm in diameter (Hector 1936).

The phloem bundles are arranged alternately with the xylem strands, and, in the seminal axes of wheat, each generally has three sieve tubes (Percival 1921; Avery 1930).

Root anatomy differs greatly at each stage of development. In the seminal roots of wheat the piliferous layer often disappears as the root ages, the cortical layer immediately below becoming suberized, forming an exodermis. Later the bulk of the cortex may shrivel and die. The cells of the exodermis then become markedly thickened and suberized, the inner walls exhibiting distinct stratification. The cell walls of the pericycle also thicken and become lignified. The ground tissue of the stele becomes sclerotic.

ii) Nodal axes

The anatomy of the axes of nodal roots differs distinctly from that of the seminal axes within the stele. The nodal axes have from 1 to 7 metaxylem vessels approximately 50 µm in diameter. The diameter of these vessels decreases towards the apex of long axes, and the number of metaxylem vessels may also decrease (Jackson 1922; Kokkonen 1931). The endodermis in the nodal axes is more prominent than that in the axes of the seminal roots. Where an exodermis develops, two or three layers of cortical cells below the exodermis become sclerotic.

The roots appearing just above the level of divergence of the coleoptile are called coleoptile roots. Their number varies from 1 to 3 (McCall 1934). The axes of coleoptile roots are similar in their anatomy to the axes of seminal roots (Jackson 1922; Hector 1936).

iii) Laterals

Laterals originate in the pericycle, arising directly opposite the phloem groups and between two adjacent protoxylem strands. The pericycle becomes multi-layered by successive periclinal divisions, a conical mass of meristematic cells is formed, and the histogens develop which give rise to tissue as described for the seminal root (Hayward 1938). Clarkson *et al.* (1973) found that the endodermis in first order laterals of barley roots became completely suberized at 6 cm from the tip. Usually, laterals of the first, second, and third orders are found in wheat roots.

3.1.2.2 Anatomy of pea roots

The root of peas comprises a main axis or tap root and laterals of first, second and third order. The anatomy of laterals of the first order is similar to that of the main axis (Hayward 1938; Bond 1948). The roots show distinct tissues homologous with those of the wheat root, namely an epidermis with root hairs, cortical tissue, and stele. The cortex is relatively wide compared with the stele. It consists of parenchymatous cells with intercellular spaces at their corners (Hayward 1938). There are 6 to 10 layers of cells in the wider roots and 4 to 5 layers in higher order laterals (Bond 1948). The innermost layer of the cortex is differentiated at an endodermis, with well defined Casparian thickenings (Hayward 1938; Bond 1948). The thickenings are at first less prominent adjacent to the protoxylem poles (Bond 1948).

Where the protoxylem elements abut the pericycle, the latter may occasionally be two or three cells in width. In zones showing only primary growth the stele is clearly triarch. The centripetal differentiation of the metaxylem results in the formation of primary xylem strands. The primary metaxylem elements consist of scalariform and pitted vessels. Early in the ontogeny of the primary phloem three groups of fibres are differentiated adjacent to the single-layered pericycle. A broad zone of interstitial parenchyma remains between the phloem and the metaxylem. The phloem consists of sieve tubes and companion cells, fibres, and parenchyma (Bond 1948).

Older zones of the axes of the main root and lower order laterals in pea differ greatly in anatomy from the axes of wheat roots since the former undergo secondary growth. After completion of primary growth, the wider axes develop secondary tissue through the activity of the vascular cambium; the xylem produced by this meristem is called the secondary xylem.

3.1.2.3 Xylem vessels in wheat and peas

A xylem vessel comprises a series of vessel members of finite length joined end to end. The members of the series are connected to each other initially by imperforated walls in the same manner as tracheids.

Esau (1953) explains the formation of a xylem vessel as originating from a longitudinal series of meristematic cells. The primordial vessel members may or may not elongate before they develop secondary walls, but they usually enlarge laterally before secondary thickening of the wall occurs. After primary wall growth is completed, a secondary wall layer is deposited. The portions of the primary wall that are later transformed into perforations are not covered by secondary wall material (Esau and Hewitt 1940). Nevertheless, they commonly become thickened mainly by swelling of the intercellular substance. After the secondary walls, where they occur, have been fully formed and lignified, the swollen parts of the primary wall break down. Finally, the protoplasts disappear.

Vessel members have evolved from tracheids and occur in the following groups:

(a) The highest gymosperms, the Gnetales.

(b) The dicotyledons, except representatives of lower taxonomic groups (Bailey 1944a).

(c) The monocotyledons (Cheadle 1942, 1944).

(d) The fern Pteridium (Bliss 1939).

(e) The genus Selaginella of the Lycopodiaceae (Duerden 1934).

In the dicotyledons the evolution of tracheids into vessel members occurred first in the secondary xylem, and later in the primary xylem (Bailey 1944b). During evolution of the monocotyledons, vessels appeared first in the root and later extended into the stem, inflorescence axes, and leaves (Cheadle 1942, 1944).

3.1.2.4 Factors affecting root anatomy

At lower temperatures, roots tend to be more white in colour, more succulent, and relatively large in diameter with relatively few scattered laterals. The cortex generally persists, even at the older or proximal end. At relatively high temperatures, the zones of the root mature rapidly, and show earlier loss of the cortex, less succulence, more complete suberization, and more frequent branching. Roots grown at higher temperatures are generally light brown, relatively small in diameter, and have extremely fine laterals. Nightingale (1935), and Proebsting (1943) described the effects of temperature on the roots of apple (*Malus pumila* Mill.) (Stayman var.), peach (*Prunus persica* (L.) Batsch) (Elberta var.), and apricot (*Prunus armeniaca* L.), and Stuckey (1942) described an effect on grass roots. The volume of intercellular space in the cortex of roots appears to be independent of temperature (Dunn 1921).

Soper and Mitchell (1956) grew perennial rye grass in the glasshouse at different temperatures and light intensities. They found that the number of metaxylem and protoxylem elements and the width of the cortical tissue decreased at lower light intensities; transferring the plants from full daylight at 14°C to 20 percent daylight at 24°C resulted in a reduction in root diameter, and a browning of existing nodal roots.

Kramer (1950) suggested that suberization proceeded more rapidly in dry soil. Hayward and Spurr (1944) showed that in ~~corn~~ flax growing in nutrient solution having a high osmotic pressure, the cambium of the stem was less active, the secondary xylem cells were smaller, and the phloem fibres fewer and smaller in diameter. Kmock *et al.* (1967) found that when wheat was grown in the field, with a limited supply of soil water, the roots were finer with more numerous and longer branches than when grown with an unlimited supply of water.

In general, roots growing in relatively well aerated media elongate rapidly, are lighter in colour, and better supplied with root hairs than roots growing in poorly aerated media; inversely, with a poor supply of oxygen they generally become thickened, shorter, darker, and have less than the normal number of root hairs (Sifton 1945). Beal (1918) and Andrew and Beal (1919) found that the cortical cells of non-aerated roots of *Zea mays* L. contained large air cavities separated by narrow strands of tissue. Bryant (1934) found that secondary differentiation started nearer the tip in non-aerated compared with aerated roots. However, the cell walls of aerated roots thickened more rapidly than those of non-aerated roots. Reducing aeration sometimes decreased root diameter. The width of the xylem vessels is also reduced in non-aerated culture solution (Bryant 1934; Shtrausberg 1973).

The anatomy of pea roots is affected locally by the development of *Rhizobium* nodules, most of which arise initially at sites occupied by root hairs (Hector 1938; and Bond 1948). The development of nodules grossly affects the cortical tissue, the endodermis, pericycle and the degree of secondary growth. Where nodules develop the cambium does not produce secondary growth, and this in turn reduces the number of xylem vessels (Hayward 1938).

Barley (1965) found that mechanical compression of the developing apex of pea radicles results in a marked reduction of cortical cell length and an increase in cortical cell diameter. In the field the growing apex of the root is compressed by the reaction of the soil as the root tip pushes its way through the soil.

In general there is rather little in the literature on the effect of environmental factors on radius and number of xylem vessels. Further research is needed on this topic.

3.1.2.5 Distribution of roots in the soil

The number of seminal roots initiated per plant in wheat may range from 1 to 6 (Percival 1921; McCall 1934). The radicle grows vertically. The other seminal axes grow at an angle of about 60 degrees to the vertical until they are 5 to 10 cm long, when they turn downwards and become vertical (Weaver 1926; Simmonds and Sallans 1933). The nodal roots begin to appear during the second or third week after seedling emergence, and their number increases with tiller number (Weaver 1926; Pinthus 1969). Pinthus (1969) found that the number of nodal roots per tiller tended to be inversely proportional to the number of tillers. The number per tiller tended to decrease from 16 to 5 as tiller number increased from 6 to 17. The growth and survival of seminal roots are both reduced in the following circumstances: deep planting (Percival 1921; Taylor and McCall 1936), when germination occurs on the soil surface (Pavlychenko 1942), with intense competition in communities of one or more species (Pavlychenko 1937; Kaufmann 1958), at low soil water content (Weaver and Crist 1922; Pavlychenko and Harrington 1934), at low soil temperature (Seimens 1929; Taylor and McCall 1936), in dense soil - $\rho_b > 1.70$ g cm^{-3} - (Portas 1973), and when seeds are undersized (Taylor and McCall 1936; Vágneravá and Ehrenbergerová 1970; Pope 1945). The seminal roots generally continue to grow until maturity, but their rate of growth is reduced after ear emergence (Derera *et al.* 1969).

The main nodal roots grow most rapidly during the period from spikelet initiation to ear emergence (Pinthus 1969; Black 1970); but they may continue to grow at a lower rate until maturity (Pinthus 1969). According to Pinthus, initiation of main nodal roots is reduced during the period immediately preceding ear emergence but it is renewed thereafter. The renewed growth of older axes, together with initiation of further nodal roots by the young tillers, continues until maturity. The number of nodal roots produced per tiller and the number of tillers is affected mainly by plant density (Weaver 1926; Pinthus 1969). Widely spaced plants in the field may have 100 or more nodal roots per plant but at usual plant densities - 150 plants per m^2 - from 5 to 30 nodal roots are produced per plant (Simmonds and Sallans 1933; Pavlychenko 1937). Pinthus and Eshel (1962), and Pinthus (1969) found significant varietal differences in the production and growth of nodal axes in wheat. At ear emergence the later cultivars had produced 90 per cent of their final number of main nodal roots, but the early cultivars had produced only 60 percent.

In well developed plants, main seminal and nodal axes of temperate cereals contribute only about 4 percent of the total length of root. The first order laterals contribute 76 percent, and higher order laterals comprise the remainder (Pavlychenko 1937; Dittmer 1937; May *et al.* 1965, 1967; Hackett 1968a, b; Lungley 1973).

May *et al.* (1965, 1967) studied the root development of barley (*Hordeum vulgare* L., cv. Piroline). They found that the rate of elongation of root members differed for the various kinds of root member; the higher the order of the lateral, the smaller was its mean rate of elongation. The mean spacing between laterals on the main axis was 0.22 cm, the mean spacing on first order laterals was 0.17 cm. Pavlychenko (1937) found that the number of first order laterals decreased with increasing plant density. The most obvious reason is the decreased length of axes. Hackett (1963) and Hackett and Bartlett (1971) showed that the number of first order laterals per unit length of subtending axis decreased by from 10 to 30 percent with increasing degrees of deficiency of P and K. Deficiency of P or K also decreased the mean length of the first order laterals. The percentage reduction varied with the cultivar. Lungley (1974) found that the density of branching along wheat root axes was higher at a higher concentration of nitrogen in flowing nutrient solution. Hackett (1972b) and Drew *et al.* (1973) found that the localized application of nitrogen fertilizer increased both the branching density and the elongation growth of first order laterals of seminal roots in the local zone where nitrogen was supplied.

Weaver (1926) showed the orientation of first order laterals of wheat diagrammatically. The first order laterals of wheat were perpendicular to the main axes in spring wheat, but they grew at an angle to the vertical - the 'liminal' angle - in winter wheat. Rufelt (1969) found that the angle at which first order laterals arose from the main seminal axes in wheat varied between cultivars. The extreme values were 12 to 15^{o} and 70 to 80^{o}. Rufelt's results were drawn from observations on 200 wheat cultivars.

The rate at which the total length of root members increases with time can be predicted given the rate of elongation and frequency of branching of root members of each class. Hackett and Rose (1972a) derived an analytical solution giving the rate of increase of total length of all members for a single root.

Hackett and Rose assumed that rate of extension and density of branching of each class of root member (axes, first order and second order laterals) were uniform throughout the root system and constant in time, and that branching extended to the tip. Their solution gives the length of main axes, first order laterals, second order laterals and the total root length for a single seminal root. Their equation successfully predicted L for one single seminal root grown in nutrient solution for times as large as 23 days (Hackett and Rose 1972a).

Lungley (1973) described a numerical model of root growth designed to predict L_V as a function of t and z. Lungley included axes, first order laterals, and second order laterals, and he showed that the model could easily be elaborated to include laterals of higher order. He included both seminal and nodal roots; and allowed for a sub-apical zone without laterals on the main axes and on the first order laterals. Lungley's model is two-dimensional and the liminal angles of the axes and first order laterals are included. Lungley (1973) suggested that his model could be used to predict the effects of fertilizer placement on root distribution, given local growth responses expressed in terms of rates of root elongation and branching. He used his model to predict the vertical distribution of L_V under wheat in the field. The estimated value of L_V was lower at 0-10 cm and higher at 10-40 cm than values measured in the field. The discrepancy could have been due to error in his assumptions concerning the orientation of the first order laterals, as little information was available. Alternatively, the distribution in the field could have been affected by vertical heterogeneity in soil properties. Generally the topsoil is better supplied with nutrients than the subsoil.

The equation of Hackett and Rose (1972a) can be used to estimate the length of a single root growing in homogeneous media for periods of a few weeks. The use of this equation is limited by the requirements of constant rates of elongation and branching. It cannot be used to estimate L_V. Lungley's numerical model is more flexible and useful, as the rates of elongation and branching can be varied in time and space. Furthermore it enables the prediction of L_V as well as L.

The extreme depth of penetration of wheat roots found by Kmock *et al.* (1957) in deep light soil in Nebraska was as great as 4 m; but wheat roots do not usually penetrate so deeply. Pavlychenko (1937) found that at a high plant density - 400 m^{-2} - the roots of wild oats (*Avena fatua* L.), wheat, cv. Marquis, spring rye (*Secale cereale* L., cv. Prolific) penetrated less deeply than at low plant density, 0.11 m^{-2}. Walter and Barley (1974) found that at anthesis the roots of wheat penetrated deeper at a plant density of 90 m^{-2} than at plant densities of either 20 m^{-2} or 470 m^{-2}. The roots had penetrated to a depth of 110 cm at 20 and 470 m^{-2}, and to a depth of 130 cm at 90 m^{-2}.

The depth of root penetration varies with soil texture and structure (Weaver 1926), with initial water content of the soil (Weaver

1926; Kmock *et al.* 1957), and with soil water regime during the season (Bennett and Doss 1960). The latter workers found that depth of rooting increased with decreasing soil water content until the soil became so dry that plant growth was seriously restricted. Weaver (1926) showed that irrigation decreased rooting depth; however, Kmock *et al.* (1957) were unable to confirm this, possible because Kmock *et al.* irrigated only before commencing their observations, whereas Weaver irrigated throughout the growing period.

Bosemark (1954) and Lungley (1974) found that in nutrient solution the main axes of wheat elongated more slowly and produced branches at closer intervals in high-N than in low-N solution. Crist and Weaver (1924), Weaver (1926) and Walter (1971) found similar effects in the soil. Working in the field in New South Wales, Lees (1924) observed that the addition of superphosphate tended to increase the rooting depth of wheat. Rooting depth is also strongly influenced by genotype (Lees 1924; Bennett and Doss 1960), by depth of water table (Goedewaagen and Schurrman 1956), aeration (Bryant 1934; Michael and Bergmann 1954), and by mechanical resistance offered by the soil (Barley 1962; Taylor and Ratliff 1969).

Under dry conditions, nodal roots tend to be confined to the upper layers of the soil, say above 40 cm (Weaver 1926; Simmonds and Sallans 1933; Balazs 1954; Grammatikati 1955; Gliemoroth 1957; Jonker 1959).

The number of root axes per plant or per unit ground area at various depths has been measured mainly for widely spaced plants and with little replication (Weaver 1926). The number of root axes penetrating to various depths at various crop densities has not been reported.

Pavlychenko (1937) found that the length of roots of wheat per unit ground area L_A was greater at a high plant density than when the plants were widely spaced. At maturity, at plant densities of 0.11 and 400 m^{-2}, L_A was 80 and 3600 cm^{-1}. Extreme plant densities had similar effects in wild oat and spring rye. Welbank and Taylor (1970) found that at maturity the average values of L_A for four dwarf winter wheats was 200 cm^{-1} at a plant density of 400 m^{-2}. Working on a sandy red brown earth at Roseworthy, South Australia, Walter and Barley (1974) measured L_v (cm^{-2}) at various depths and at different plant densities at several stages of growth. They found that in the early part of the season, higher plant densities (470 m^{-2}) resulted in higher values of L_v in the top soil, and during the middle and later parts of the season in the layers below 50 cm also. At maturity L_A was close to 400 cm^{-1} at low, intermediate and high plant densities (20, 90 and 470 m^{-2}). Schultz (1974) found that phosphorus fertilizer increased L_v from 0 to 90 cm depth. In contrast nitrogen fertilizer decreased L_v at all depths examined compared with the control. Schultz also found that sowing in July in one year (1968) tended to increase

L_v at 0 to 90 cm depth, compared with sowing in June. Sowing in August gave the lowest values of L_v. Schultz could not detect any significant difference in L_v from 0 to 90 cm depth between three varieties (Insignia, Raven and Mexico 120).

3.1.3 Process of water uptake

For present purposes the flow of water in the radial path from the surface of a root member to the xylem vessels in that member can be expressed as

$$J = K_H \Delta h + K_\Pi \Delta h_\Pi \tag{31}$$

where J is the inflow to the xylem per unit length of absorbing root member ($cm^2 \ sec^{-1}$); Δh and Δh_Π are the differences in suction and osmotic heads (xylem - ambient solution) (cm); and K_H and K_Π are the radial hydraulic conductance and radial osmotic conductance of a segment of a root member ($cm \ sec^{-1}$).

The first term on the right hand side of Eq. (31) represents the flow due to the difference in hydrostatic pressure between the root surface and the xylem. This pressure difference develops when water evaporates from the cell walls of the leaf mesophyll. The pressure drop across the water menisci in the cell walls of the leaf mesophyll causes water to move into the walls from the xylem of the leaf veins. The pressure drop is transmitted to the xylem, and through the continuous water columns of the xylem elements to the xylem in the root. Reduction of hydrostatic pressure in the root xylem produces a gradient across the root, and when sufficiently large this causes water to flow from the soil at the root surface across the root and into the xylem. The second term on the right hand side of Eq. (31) represents the flow of water driven by any difference in osmotic pressure of the soil solution at the root surface and that of the xylem sap. The difference in osmotic pressure arises because cells of the stele of the root secrete salts and sugar into the xylem sap. This process causes water to flow into the xylem vessels. It is debatable whether the flows $K_H \Delta H$, $K_{\Pi} \Delta H_{\Pi}$ are additive as claimed by Mees and Weatherley (1957a, b), as shown in Eq. (31). In certain conditions, the flow caused by one of the head differences is predominant. Then the flow may sometimes be described by one of the following reduced forms of Eq. (31):

$$J = K_{\Pi} \Delta h_{\Pi} \tag{32}$$

$$J = K_{\beta} \Delta h \tag{33}$$

Eq. (32) applies only when the hydrostatic pressure is uniform as in the dark or in a detopped plant, or less certainly, when transpiration is slow and the plant is growing in a warm medium of high water content. The secretion of sugar or salts into the xylem sometimes results in guttation (Burgerstein 1920; Büsgen and Müunch 1926; Head 1964), and the development of a positive 'root pressure' in the xylem sap. The applicability of Eq. (32) has been questioned by Dainty (1963, 1965) and Briggs (1967). They pointed out that Eq. (32) can be used only when the membrane is perfectly impermeable to the solutes. They postulated that the driving force associated with differences in osmotic pressure contains both hydrostatic and osmotic terms. Even when no difference in hydraulic head develops as a result of transpiration, hydraulic head differences can exist within the osmotic unit. This difference in hydraulic head is induced within the pores of the semi-permeable membrane by solute diffusion at pore apertures.

As the rate of transpiration rises, solutes are swept out of the xylem, until their concentration becomes so low that osmotic flow of water is negligible (Lopushinsky 1964; O'Leary 1965). Eq. (33) then applies. Generally Eq. (33) describes water uptake sufficiently well when dealing with plants in the field during periods of bright sunlight and while the stomata are open (Slayter 1967; Kramer 1969).

Kramer (1940) found that at a given pressure difference, the osmotically induced flow was less than that produced by hydrostatic pressure. Brouwer (1965) showed that at a given difference in either hydrostatic or osmotic pressure between the solution in the xylem and the external solution, the rate of uptake of water by maize roots was greatest when excess hydrostatic pressure existed in the external solution, intermediate when a suction was induced in the xylem by transpiration and least when the flow was induced by excess osmotic pressure in the xylem.

3.1.4 Resistance offered by roots to water uptake

Root resistance to water flow is located in two distinct pathways: root resistance in the axial direction R_α and root resistance in the radial direction (epidermis to xylem) R_β.

3.1.4.1 Axial resistance R_α

The axial resistance to the flow of water in a root member R_α (cm^{-3} sec) is defined here as $R_\alpha \equiv 1/K_\alpha$, where K_α (cm^3 sec^{-1}) is defined by

$$K_\alpha = J\frac{\Delta L}{\Delta h} \qquad (34)$$

where J (cm^3 sec^{-1}) is the constant rate of flow along the segment, and $\frac{\Delta h}{\Delta L}$ is the gradient in suction head in the direction of flow. Most of the axial flow occurs in the xylem (Slatyer 1967; Kramer 1969).

Slatyer (1967), Cowan and Milthorpe (1968a), and Kramer (1969) subscribe to the view that the axial resistance within the xylem is small compared with the radial resistance. Wind (1955) and Passioura (1972a) argued that the resistance in the xylem vessels of grasses and temperate cereals (wheat, oats and barley) may be important when flow occurs through roots of considerable length.

Wind (1955) measured the vertical distribution of the weight of roots per unit volume of soil in the soil profile under rye grass pastures. He assumed that the fresh weight of root was equal to its volume and that all roots had a radius of 0.02 cm, a value appropriate for a main axis. He then calculated the number of axes in each soil horizon. Wind defined an equivalent radius $r_e = \sqrt[4]{\sum_i^n r_i^4}$. This is the radius of a tube equivalent to the set of n vessels in a root member. After measuring meta-xylem radii and calculating r_e, Wind obtained a relation between root radius and r_e;

when the radius of the roots was 0.02 cm, $r_e = 16.3\ \mu m$. He assumed further that all the calculated number of roots were in a vertical position, and that all roots participated in the transport of water. The estimated resistance to flow of the metaxylem vessels was twice that calculated from Poiseuille's equation and the measured radius. Wind calculated the pressure drop needed to elevate the water from depths ranging from 0 to 50 cm. He found that below 20 cm depth root resistance exceeded soil resistance when the water table was at a depth of 50 cm. The calculations of Wind may have underestimated the resistance of xylem vessels because he assumed that all roots contributed to vertical flow.

Passioura (1972a) calculated the resistance to water flow of the xylem of temperate cereals (wheat, barley and oats). Passioura drew his description of root geometry from the literature, and calculated the pressure drop required to elevate water from various depths, when the plant derived water solely from the deeper layers of the soil. Unfortunately, data on root geometry in the literature were scarce, most data referring to plants growing at wide spacing. Passioura assumed that, under dry conditions, the nodal roots plus the later seminals would be restricted to the top 40 cm of the soil, and that only the first three seminal roots would grow vertically to a depth of 1 m or more. Following Wind (1955) he assumed that the resistance in a xylem vessel was twice that calculated from Poiseuille's equation. He then calculated the pressure drop required to elevate water from depths below 40 cm at a given E_p and at a plant density of 150 plants per m^2. He found that when transpiration was rapid, a large pressure drop would be required to elevate water from depths greater than 40 cm. He suggested that the plants could not sustain this drop, and that their stomates would close.

The assumption that Wind (1955), and later Passioura (1972a), had made that root xylem resistance was twice that obtained from Poiseuille's equation was derived from a few measurements made on grass roots at low suctions by Emerson (1954).

Poiseuille's law may be written as:-

$$Q = \frac{\pi r^4 \Delta P}{8\eta \Delta L} \qquad (35)$$

where Q is the (constant) rate of flow of water ($cm^3\ sec^{-1}$); r is the radius of a tube of uniform circular cross-section (cm); ΔP is the pressure drop along length ΔL in the direction of flow ($dyne\ cm^{-2}$); η is the viscosity (poise). The length L is taken as positive in the direction of flow (cm).

Poiseuille's law applies to tube-flow subject to the following conditions:

(i) The walls of the tube are smooth on the internal surface and stationary.

(ii) Flow is laminar. For this to be so the ratio $R_e = V\rho r/\eta$ (Reynold's number where V is the apparent velocity, must be less than 1,000. At higher values the flow may become turbulent (Reynolds 1900). The velocity of water flow in a xylem vessel is generally less than 15 cm sec^{-1} (Passioura 1972a) and R_e is much less than 1,000.

(iii) The tube must have a constant radius and a uniformly circular shape in cross-section.

(iv) $\Delta L/r$ must be bigger than 67 (Ewart 1908).

Water flow within the xylem vessels may not proceed under conditions that satisfy all the above conditions. Firstly, the walls of the xylem vessels are not smooth because perforated transverse septa occur at intervals along their length. However these septa are widely spaced, and the central pore is generally only a little narrower than the rest of the vessel. Secondly, the radius of the xylem vessel is not uniform over an extended long length, although it is usually constant or nearly so over lengths of 2 to 3 cm. Thirdly, at a low suction the radius of the xylem vessel is independent of the suction, but this may not be so at high suctions. Fourthly, the shape of the xylem vessel is not always circular but may, for example, be elliptical. The conductance of a tube with an elliptical cross section can be obtained analytically in a similar manner to Poiseuille's law. Preston (1938) showed that for an elliptical tube having major and minor axes of length l_1 and l_2 the true conductance could be approximated by substituting a value of $r = (l_1 l_2)^{\frac{1}{2}}/2$ in Poiseuille's equation (Eq. (35)). If ratio $l_1/l_2 < 1.3$, the error introduced by this approximation is less than three percent. We conclude that Poiseuille's equation can be used to estimate hydraulic conductance of the root at low suctions and over relatively short lengths; its applicability at high suctions and over considerable lengths is less certain.

Emerson (1954) measured K_α for seminal axes of perennial rye grass (*Lolium perenne* L.), timothy (*Phleum pratense* L.) and cocksfoot (*Dactylis glomerata* L.) by using a syphon technique at a small head difference (3 cm of water). Roots were dug from 4 year-old grass plots in the field, and were washed free from soil. The root axes were cut under water into segments and kept in water before measuring K_α. Emerson deaerated the root by evacuation under water, after which he measured K_α. The tube radii calculated from Emerson's data on outflow using Poiseuille's equation (Eq. (35)) were compared with a mean radius obtained from measured radii of metaxylem vessels. Results are shown in Table 2. Values of r_e were obtained from the data for both the basal and subapical sections of each root segment. For a whole segment, since these two sections are in series, the appropriate mean r_H is the harmonic mean (Section 4(a)). This is given in column 4 of Table 2. The ratio $(\frac{8\eta\rho g}{\pi r_H^4})/R_\alpha$, where $R_\alpha = \frac{1}{K_\alpha}$ and K_α is as defined by Eq. (34) is given in column 6. These values show that the actual resistance is approximately twice that calculated from Poiseuille's law using r_H, as calculated previously from Emerson's data by Wind (1955) and Passioura (1972a). Emerson's data are doubtful because evacuation of the roots before the measurement of flow would have flooded the intercellular spaces.

Table 2. Calculated and measured radii of individual metaxylem vessels.

Root number	Measured radii		r_H	Calculated radii	$\frac{8\eta\rho g}{\pi r_H^4} / R_\alpha$
	Basal	Sub-apical			
		(a) *Lolium perenne*			
1	28	17	22.2	18	2.3
2	26	24	25.0	22	1.7
3	25	22	23.5	19	2.3
		(b) *Phleum pratense*			
1	21,19,14,12,15	24,21,15	26.7	25	1.3
2	20,19,14,12,15	24,21,15	26.3	30,26	0.59,1.0
		(c) *Dactylis glomerata*			
1	12,10,10,8,7, 7,6,6,6,6	11,9,8,7,6, 6,6,6,6,5	14.5	11	3.0

Kozinka and Luxova (1971) concluded that one quarter of the total flow in the axial direction could move through cortical tissue of nodal axes of maize (*Zea mays* L.). However this could be an overestimate because water was caused to flow under positive pressure, and water would have been forced into spaces normally occupied by air. The pathway for water flow at positive pressure is known to differ from that at pressures below atmospheric (Ewart 1908).

Cox (1966) tried to evaluate axial conductance k_α and radial conductance k_β of a set of roots, using 17 day-old wheat plants. He expressed the flow equations as:-

$$Q_\alpha = k_\alpha \frac{dH_x}{dz} \tag{36}$$

$$\frac{dQ_\alpha}{dz} = -k_\beta(H_e - H_x) \tag{37}$$

where Q_α is the rate of axial flow in the xylem of a set of roots ($cm^3\ sec^{-1}$), k_α is the axial conductance of a set of roots ($cm^3\ sec^{-1}$), H is the hydraulic head (cm), z is the depth from the base of the roots (cm), k_β is the radial conductance of a set of roots ($cm^2\ sec^{-1}$), e and x are subscripts defining the location at the root surface and in the xylem vessels respectively. Eq. (37) assumes that, under the conditions of the test, osmotically induced inflow is negligible.

Combining Eq. (36) and Eq. (37) and setting $H_e = 0$ Cox obtained:

$$\frac{d(k_\alpha \frac{dH_x}{dz})}{dz} = k_\beta H_x \tag{38}$$

This is a linear and homogeneous second-order differential equation in H. He solved Eq. (38), obtaining:-

$$k_\alpha = \frac{k_\beta(Q_{open} - Q_{plug})^2}{\frac{dQ_{open}}{dz} \cdot \frac{dQ_{plug}}{dz}} \qquad (39)$$

where Q_{plug} is the positive upwards rate of outflow (cm^3 sec^{-1}) from the base of a set of roots of depth z, when inflow at the apical end is prevented by means of plugging; Q_{open} is the rate of outflow (cm^3 sec^{-1}) from the same set of roots when direct inflow of water into the xylem is enabled by cutting the roots at depth z. Further when $Q_{open} >> Q_{plug}$

$$k_\beta = \frac{\Delta Q_{plug}}{\Delta z H_x} \qquad (40)$$

Cox assumed that for plugged roots H_x was uniform throughout the xylem and equivalent to the suction applied to the xylem after severing the stem near its base. Also,

$$\bar{k}_\beta \equiv k_\beta/L \qquad (41)$$

where L is the total length of roots remaining above depth z (cm). Cox conducted an experiment using wheat growing in sand in a room having controlled temperature and light. After washing the soil away from the root, he cut the stem above the base of the root and sealed the cut end into a capillary tube. He immersed the root system in deaerated, distilled water, the roots being spread out horizontally within a flat dish. A suction head of 540 cm of water was applied at the open end of the capillary tube. Cox measured the length of the main root axes only. He measured the rate of outflow of water as follows:-

(i) He cut the roots near the ends at a depth of 2 or 3 cm from their apices and measured the flow rate Q_{open}.

(ii) He plugged the cut ends, then he again measured the flow rate, Q_{plug}.

(iii) Steps (i) and (ii) were repeated until the cut ends of the roots were 7.5 cm from the base of the root.

Because of failure of the seals with the capillary tube, Cox (1966) gave results for two root systems only. The calculations were made using Eq. (40) for k_β, Eq. (39) for k_α, and Eq. (41) for $\overline{k}_\beta$.

Cox's results are difficult to interpret because:

(i) He ignored water flowing within the laterals and thus his values of $\overline{k}_\beta$ probably exceed the true values.

(ii) The roots may have been damaged when soil was washed away.

(iii) Two root systems were insufficient to permit generalization.

(iv) Measurements were made when plants were at one stage of growth only.

Axial root resistance needs to be evaluated carefully, as there are uncertainties in previous measurements.

3.1.4.2 Radial resistance R_β

Radial root resistance is the root resistance from the outermost edge of the epidermis to the lumen of the xylem vessel. The nature of this water flow pathway has been described by Weatherley (1963, 1970), Slatyer (1967), Ginsburg and Ginzberg (1970) and Tanton and Crowdy (1972). Various pathways for water flow in the cortex have been described.

(i) The free space of the cellulose cell wall from the epidermis to the endodermis.

(ii) The cytoplasm from plasmodesmata of the epidermis to and through the plasmodesmata of cortical cells. Water may also flow in series-parallel paths through the cytoplasm and cell vacuoles.

(iii) The combination of (i) and (ii).

Although there is uncertainty about the relative importance of the various pathways for water transfer across the root (Ginsburg and Ginzberg 1970), the most widely held theory is that most of the water flow proceeds within the free space of the cell walls, except at the endodermis when it has to cross the protoplast and its boundary membranes.

The location of the main resistance in the radial path within the root depends on the developmental zone considered. The overall root resistance is relatively low in the region where the xylem is well differentiated, but suberization has not progressed far (Hayward and Spurr 1943). This region is generally 1.5 to 10 cm from the tip in long main roots of corn, onions (*Allium cepa* L.), wheat and broad beans (*Vicia faba* L.), and marrow (Rosene 1937; Gregory and Woodford 1939; Hayward *et al.* 1942; Hansen 1974a; Graham *et al.* 1974). In the more proximal zone, increasing suberization tends to increase R_β (Graham *et al.* 1974).

Rosene (1941, 1943) showed that root hairs were more permeable to water than hairless cells in the zone of elongation and cells in the meristem. Barley and Rovira (1970) demonstrated that root hairs increased the rate of ion uptake from soil but not in a stirred nutrient solution. The velocity of water intake per unit area of root hair varies from species to species. Also the velocity of uptake of water by a root hair varies with age, length of hair and extent of the immersed area as well as with temperature. In unsaturated soil root hairs may be important for water and nutrient uptake by maintaining liquid continuity between water in the cell wall and pore water in the soil (Barley 1970).

Newman (1973) measured the osmotic permeability of root systems of broad bean (*Vicia faba* L.), dwarf bean (*Phaseolus vulgaris* L.), corn, sunflower (*Helianthus annuus* L.), and tomato (*Lycopersicon esculentum* Mill.). He used a bleeding technique similar to that described by Arisz *et al.* (1951). Exudation was measured through the cut stem just above the junction with the root after changing the external osmotic pressure. Newman suggested that the main resistance lay in the endodermis. Graham *et al.* (1974) showed that water flow into seminal roots and first order laterals of barley (*Hordeum vulgare*, cv. Midas) and marrow (*Cucurbita pepo*, cv. Greenbush) varied inversely with the frequency of suberized cells in the endodermal ring.

Brouwer (1965) measured a radial conductance $K_B = J/\Delta(h + h_\Pi)$ where, as before, Δ refers to xylem sap - ambient solution for the apical 10 cm zone of radicles of broad bean (*Vicia faba* L.). Brouwer varied and measured E_p together with $(h + h_\pi)$ in the xylem. The values of K_B ranged from 9.10^{-10} cm sec^{-1} when the difference in the water potential between water in the xylem and in the ambient solution was 2.5 bar to 1.10^{-10} cm sec^{-1} when the potential difference was 1.3 bar. Cox (1966) found $\bar{K}_B$ values of 1.5 to 6.5 . 10^{-10} cm sec^{-1} when a suction of 0.54 bar was applied to the base of the stem of 16 to 17 day-old wheat plants at 20°C. Hansen (1974a) measured a radial conductance $K_H = \frac{J}{(\psi/\rho g)}$, where ψ is the leaf water potential (bar), for short (1 cm) zones of seminal axes of wheat cv. Gabo. The value of K_H was 5 . 10^{-10} cm sec^{-1} at 22°C. Hansen assumed that the water potential in the xylem of the root was equal to that in the leaf.

3.1.5 Factors affecting root resistance to the flow of water

3.1.5.1 Axial resistance

The axial root resistance R_α differs from the radial root resistance R_β in that R_α is not affected by respiratory inhibitors. The resistance to flow of water needs to be considered both for individual root members and for sets of root members (root systems).

(i) Individual root members

Any factor that alters r, when r is the radius of a metaxylem vessel has a proportionately large effect on R_α, since $R_\alpha \propto \frac{1}{r^4}$. Gausman and Fuelleman (1952) and Gibson and Schultz (1953) found that in white clover (*Trifolium repens* L.), the cultivar Ladino has fewer xylem vessels in the petioles than did the cultivar Intermediate White. Gibson and Schultz further showed that the petioles of Ladino and Intermediate White growing in a cool moist field had more xylem vessels than when grown in a greenhouse, and that the plants grown in the greenhouse had more xylem vessels in their petioles than plants grown in a hot, dry field. Adela (1924), quoted by Gausman and Fuelleman (1952), found that different cultivars of white clover had different arrangements of xylem vessels in the root. Meyer (pers. comm.) grew 25 wheat cultivars in nutrient solution at different temperatures using seed of different sizes for each cultivar. He found that the radius of the metaxylem vessel in the seminal root differed between cultivars. Increasing the temperature from 18° to 28°C decreased the vessel radius in the seminal root axes in all cultivars. The larger the seed size the greater was the value of vessel radius r. Soper and Mitchell (1956) found that the number of metaxylem vessels per nodal root decreased when plants were grown with an inadequate supply of light.

Greacen (pers. comm.) found that R_α increased when the ambient pressure around young seminal axes of wheat exceeded the pressure in the water within the xylem. When the difference was 2 bar R_α increased by 30 percent.

A factor that greatly affects R_α is infection of the root by *Fusarium*. *Fusarium* spp. are well known pathogens of wheat and certain other species (Simmonds *et al.* 1935). Waggoner and Dimond (1954) first suggested that *Fusarium* increased R_α. Later Duniway (1971) demonstrated that tomato plants infected by *Fusarium* had extremely high R_α values. *Fusarium* hyphae penetrated and clogged the xylem vessels.

In woody dicotyledons much of the xylem in the stem or trunk is occupied by air, tyroses, and by masses of gum. This must increase R_α (Ewart 1908; Dixon 1914). Air bubbles in the xylem vessel may arise from the release of air dissolved in water when the hydrostatic pressure of the xylem sap is reduced to values below atmospheric pressure, or following rupture of water columns, by the flow of air from outside the trunk to the xylem vessels (Lundegärdh 1954).

In legumes *Rhizobium* may increase R_α as it locally reduces the number of secondary xylem vessels where nodules are formed (Hector 1936; Hayward 1938; Bond 1948).

(ii) Sets of roots

Any factors that alter R_α for individual members of the set, or the number of root members penetrating to any given depth influences the axial resistance of the set of roots at that depth. In the topsoil the number of axes depends mainly on the initiation of both nodal and seminal roots. Root initiation has been discussed in

Section 3.1.2.5. In this section emphasis will be given to the factors that affect the number of roots penetrating to the deeper layers of the soil. Weaver (1926) found that in a drought year the number of root axes penetrating to lower depths decreased in certain temperate cereals. Nitrogen or phosphorus fertilizers (Chist and Weaver 1924; Lees 1924; Weaver 1926; Walter 1971) affect root distribution and hence root resistance in deeper soil layers. Nitrogen fertilizer tends to decrease the depth of root penetration, while phosphorus tends to increase the depth of penetration.

Gair (1964) reviewed the effects of nematodes on the growth of wheat roots, and on their distribution in the soil. He concluded that the nematodes (*Heterodera avena*, Woll.; *Pratylenchus minyus*, Sher and Allan) penetrated the root just behind the tip of the main axis and first order laterals. The roots became slightly thickened in the region where infected, and many laterals arose rapidly in or near this zone. As the tips of the laterals became infested, they branched producing further laterals, so that the infested root became a cluster of short, thickened, much branched laterals. Where nematodes infect wheat, they reduce the depth to which the roots penetrate, and so reduce the ability of the crop to withdraw water from the deeper layers of the soil.

3.1.5.2 Radial and total root resistance

Respiration inhibitors and uncouplers such as azide (Rosene 1947; Lopushinsky 1964), cyanide (van Overbeak 1942; Brouwer 1954;

Ordin and Kramer 1956; Mees and Weatherley 1957), carboxyl cyanide m-chlorophynyl hydrazone (Brouwer 1954; Bledsoe *et al.* 1969), 2,4-dinitrophenol (Ordin and Kramer 1956; Wooley 1965), fluoride (van Andel 1953; Woolley 1965), iodoacetate (van Andel 1953; Woolley 1965), arsenate (van Andel 1953), all affect R_β. In order to maintain a high radial conductivity the root requires a minimum supply of oxygen (Crafts and Broyer 1938; Kramer 1940; Rosene 1950), and of metabolic energy (Stuart 1973).

When the concentration of CO_2 in solution is increased by bubbling it through nutrient solution, or under water-logged conditions, R firstly increases and then decreases (Hoagland and Broyer 1942; Kramer and Jackson 1954). Aeration affects the young zones more profoundly than the older root zones (Brouwer 1954).

Suberization decreases the permeability of the endodermal wall, and this, in turn, increases R_β (Brouwer 1965). The degree of suberization varies with the stage of development of the zone considered. The effect of suberization on R_β is more pronounced when the hydraulic head difference developed by transpiration is small (Brouwer 1965). Heat killed roots have a lower total resistance R than the living root at low E_t (Renner 1929; Kramer 1933, 1940; Ordin and Kramer 1956). However, at a high E_t, R of heat killed roots is approximately equal to that of living roots (Stocker 1968, quoted by Weatherley 1970).

The hydraulic head developed during transpiration may change R. As the hydraulic head gradient across the root is increased in certain species, R decreases (Brewig 1936; Brouwer 1953, 1954; Mees and Weatherley 1957a, b; Kuiper 1963). This decrease of R was due to the decrease of R_β in the older or suberized zone (Brouwer 1965). One explanation given is that the mean pore size in the suberized zone will increase as h in the wall increases (Hylmö 1955; Brouwer 1965). Increasing h_Π in the solution around the root, decreased R_β in proximal zones and increased R_β in younger sub-apical zones of broad bean (Brouwer 1965). In the whole root system the total resistance increased where osmotic pressure of the ambient solution was increased (Eaton 1941; Drew 1967).

Increasing the rate of transpiration sometimes alters R_β (Tinklin and Weatherley 1966; Janes 1970; Stocker and Weatherley 1971; Barrs 1973). The effect of transpiration rate varies with plant species (Hailey *et al.* 1973).

Skidmore and Stone (1964), Barrs and Klepper (1968) demonstrated that R exhibits a diurnal fluctuation with a minimum near morning and a maximum near midnight. The diurnal effect depends on the shoot-root ratio - the bigger the ratio the less the fluctuation. Although out of phase, this diurnal fluctuation in root resistance is probably associated with diurnal change in the water potential in the root (Brouwer 1965).

Kramer (1955, 1969) showed that the temperature affected R_β, the nature and magnitude of the effect depending on the species. Temperature may affect the viscosity of water and permeability of cell membranes. Furthermore, temperature affects R_β indirectly through its influence on root growth. Bialoglowski (1936), Clements and Martin (1934), Kramer (1942), Kuiper (1964) and Brouwer (1965) show that temperatures $< 10^oC$ and $> 30^oC$ reduce the rate of water absorption by roots.

3.2 THE MEASUREMENT OF AXIAL (K_α) AND RADIAL (K_β) CONDUCTANCES OF SEGMENTS OF WHEAT AND PEA ROOTS IN THE LABORATORY

3.2.1 Plant culture

Wheat (cv. Halberd) and field peas (*Pisum sativum* L., cv. White Brunswick) plants were cultured in nutrient solution in the glasshouse. The composition of the nutrient solutions used for wheat and peas is described in Appendix Table 2.

For the first harvest at 18 days plants were grown in pots (30 cm I.D. X 38 cm high). The pots were kept in a stirred water bath at 15°C. Nutrient solution was changed weekly and the pH was adjusted to 5.4 daily by adding 0.1N KOH. The solution in the pots was stirred and aerated by bubbling air.

For the later harvests the plants were grown in deep tanks (30 X 2.5 X 120 cm). The bulk of the nutrient solution was contained in a large fibreglass reservoir (260 l. capacity). This reservoir was kept at 15°C, by immersing in a stirred, thermostatically controlled water bath. Solution from the large fibreglass reservoir was pumped to an elevated constant head reservoir. Solution flowed under gravity from the constant head reservoir to the tanks and back to the fibreglass reservoir. The solution in the fibreglass reservoir was stirred continuously with a pump. The solution in each tank was aerated by bubbling air through the tanks. The rate of inflow of nutrient solution into each tank was 75 $cm^3 min^{-1}$, corresponding to a vertical flow velocity of 0.017 cm sec^{-1}, and to replacement of solution in the tank every 2 hours. The solution in the reservoir was changed weekly, and the pH was adjusted to 5.4 daily by adding 0.1N KOH. The equipment has been described in detail by Lungley (1974).

Seeds were soaked overnight in aerated nutrient solution, then put onto a blotting-paper tension-table kept one centimetre above the nutrient solution used to wet the paper. The seeds were germinated in light at a temperature of 15 ± 2°C. When the radicles were approximately 3 cm long, seedlings having radicles of uniform length were chosen. Four seedlings were transferred to each pot and one to each tank. Four pots and eight tanks were planted for each species.

Wheat seedlings from the pots were harvested 18 days after transplanting, when the first nodal root from the first node of the stem had just appeared and the seminal roots were approximately 30 cm long. At later harvests plants were obtained from the tanks. Only the first three tillers were allowed to grow on each seedling, later tillers being excised soon after they appeared. After 18 days the plants were shaded with a hessian screen, the light intensity being reduced by approximately one-third.

The second and third harvests were made when the wheat was at the flowering and dough stages. The plants removed at each harvest were chosen using tables of random numbers.

Peas were harvested at three times. The first harvest was made four weeks after transplanting when the tap root was approximately 22 cm long. The second and third harvests were made when the peas were flowering and when the grain in the earliest pods was ripe, 8 and 11 weeks from transplanting respectively. The plants removed at each harvest were chosen at random.

3.2.2 Preparation of root segments for measurement of K_α

Harvested plants were transferred from the glasshouse to the controlled temperature room (15 ± 2°C) in nutrient solution, and kept in aerated nutrient solution for 30 minutes before sectioning.

i) First harvest

Three 3 cm long segments of the axis were obtained from the radicle and first pair of seminal roots of the wheat seedlings by cutting at 5 and 8 cm from the base of each axis, from the middle of the axis, and at 5 and 8 cm from the apical extremity as shown in Fig. 11. The root was supported in moistened pith and cut with a 'Gem' razor blade. The cuts were made under nutrient solution to prevent air bubbles entering the cut ends of the vessels. Nine segments were obtained from each of six plants.

For peas, the tap root was cut into segments in the same manner as for the wheat roots. In addition, each fifth first order lateral, counting from the most basal lateral, was sampled until the length of the laterals was less than 10 cm. Two 3 cm long segments were obtained from first order laterals longer than 15 cm by cutting at 5 and 8 cm from the base and from the apex. A single 3 cm long segment was cut from the middle of laterals of length > 10 < 15 cm. From three to nine first order laterals were sampled per plant. Three pea plants were harvested at the first harvest.

ii) Second and third harvest

For wheat the radicle and first pair of seminal roots were cut into segments in the same manner as at the first harvest. Segments were also excised from the axes of roots arising from nodes at the base of the stem. Three 3 cm long segments were obtained from nodal axes > 20 cm long by cutting at the same positions used for seminal axes. Nodal axes of length > 15 < 20 cm were cut at 5 and 8 cm from the base and from the apex to obtain two segments. A single 3 cm long segment was cut from the middle of nodal axes of length > 10 < 15 cm.

Two plants were sampled at the second harvest (flowering stage) and eight at the third harvest (dough stage).

In addition to the seminal roots of wheat grown in nutrient solution, seminal roots were sampled from the field at flowering and dough stages. These roots were taken from a crop of wheat cv. Halberd grown on a sandy red brown earth at Roseworthy Agricultural College (Section 3.3.4.2). Soil was washed away from pin boards and 3 cm long segments were obtained by cutting at 5 and 8 cm, 30 and 33 cm and 60 and 63 cm from the basal end.

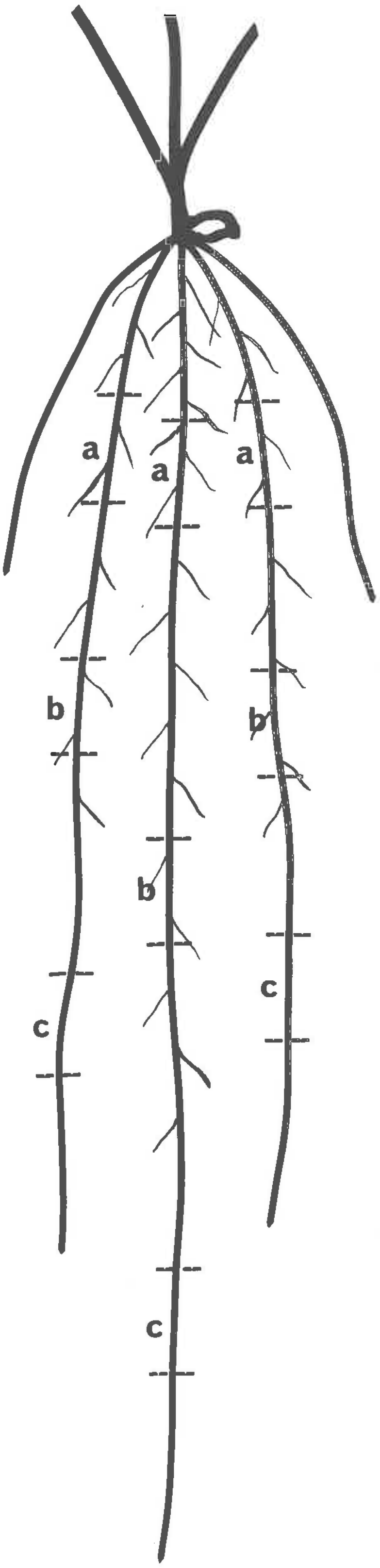
For peas, the tap root and first order laterals were cut in the

Fig. 11. Location of cuts used to obtain segments from the axis of seminal roots of wheat for measurement of K_α.

a) 5 to 8 cm from base

b) 3 cm long segment in middle of axis

c) 5 to 8 cm from apex


a
a
a
b
b
b
c
c
c

same manner as at the first harvest. However, only each tenth first order lateral was sampled.

3.2.3 Measurement of K_α

A 5 mm long zone at the basal end of each segment was wiped with a tissue soaked in 95 percent ethyl alcohol and again with a dry tissue. The basal end was then sealed into the flared end of a capillary tube of bore 0.3 or 0.6 mm. The basal end of the segment and the capillary were joined with a mixture of molten wax-lanolin five percent and paraffin 95 percent - (MP 47°C). The mixture was applied to the joint with an electrically heated hypodermic needle. The needle resembled that described by Evan and Vaughan (1966). It was made by grinding the tip flat, coating with 'Araldite', and wrapping with 40 turns of B & S number 26 Nichrome wire. Finally the coil was coated with 'Araldite'. The resistance of the coil was 3.5 ohm. The molten wax was kept in a water bath at 50°C, and the current through the coil was adjusted with a voltage regulator, to keep the wax just above melting point during delivery. Sealing took one minute. The root segment attached to the capillary was next held in a vertical position for 10 minutes with two-thirds of its length in aerated nutrient solution to allow the wax to set and harden. Then the distal end of the segment was excised with a razor blade 0.5 cm from its extremity while immersed in nutrient solution. The segment and capillary were next rapidly transferred to a suction manifold with a drop of solution adhering to the distal end of the segment (Fig. 12). The free end of the capillary was connected to the suction hose. The distal end of the 3 cm long root segment was curved gently downwards until it dipped into nutrient solution in the manifold-reservoir. This solution had been deaerated by bubbling with nitrogen gas, and mixed with a drop of 0.1 percent methyl red in water, so that the meniscus in the capillary could be seen distinctly. The surface of the nutrient solution was kept 0.5 cm below the capillary. The capillary tube was positioned horizontally. The temperature of the room and nutrient solution were maintained at 15°C, measured with mercury thermometers.

Suction was applied to the proximal end of the root segment, the suction heads being held constant using a water tower (Peck 1966) at either 100 or 300 cm of water depending on K_α. After the meniscus had travelled 2 cm along the capillary tube, the displacement of the meniscus was recorded at 5 minute intervals.

The hydraulic conductance in the axial direction K_α was calculated from Eq. (34), $K_\alpha = J\frac{\Delta L}{\Delta h}$, where K_α is the axial conductance of the root segment ($cm^3\ sec^{-1}$); J is now the rate of outflow from the basal end of the segment ($cm^3\ sec^{-1}$); Δh is the difference in suction head between the proximal and distal ends of the segment (proximal - distal) (cm); ΔL is the length of the segment (cm). The difference in height between the surface of the solution in the reservoir and the capillary - 0.5 cm - was not taken into account in

Fig. 12. Suction-manifold used to measure K_α.

a) reservoir

b) root segment

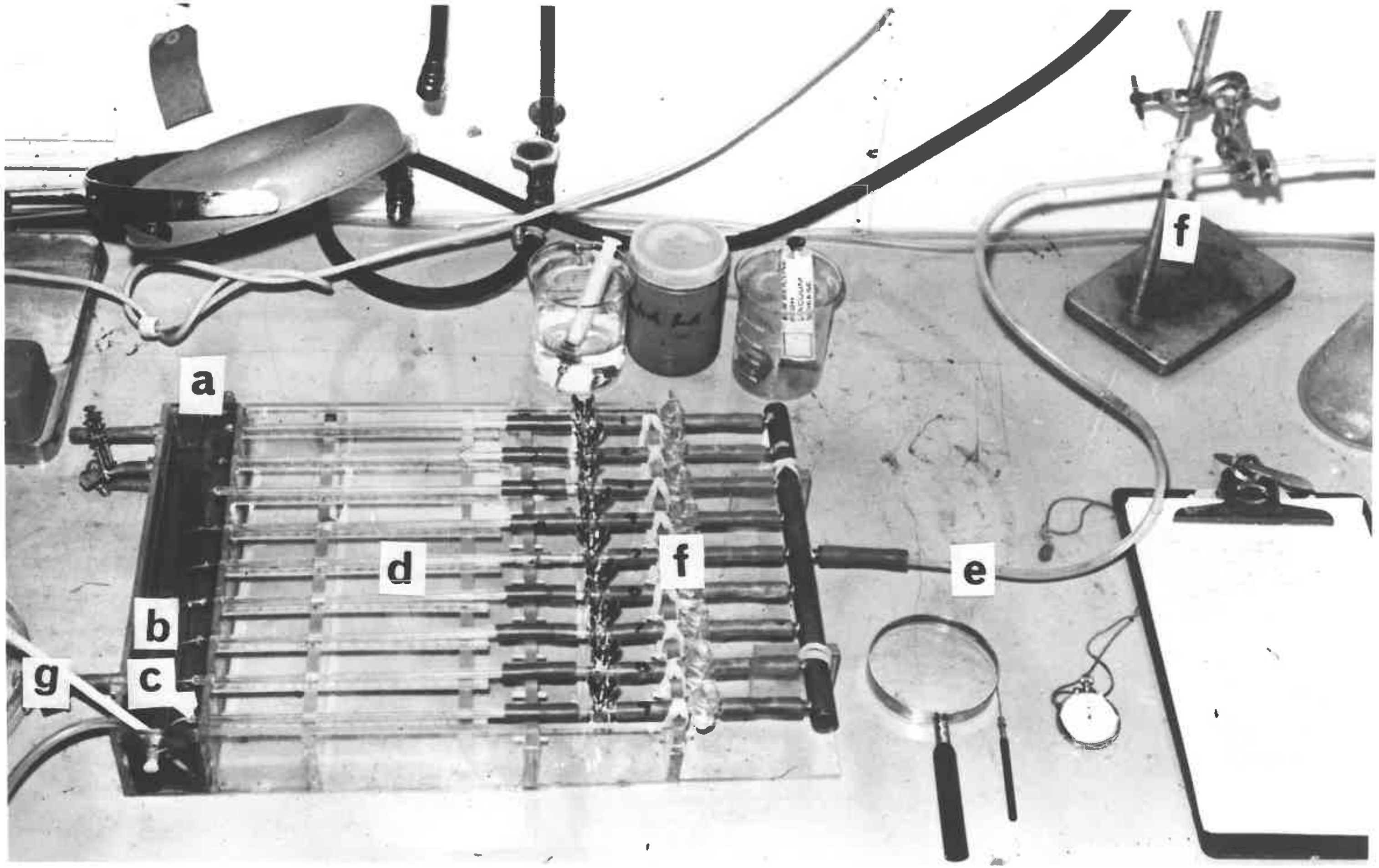
c) wax seal

d) capillary

e) suction hose

f) tap

g) thermometer


a
f
d
f
e
b
g
c

the calculation, because it was small compared with Δh.

3.2.4 Measurement of the radius of the xylem vessel

One centimetre long zones of the root members of both wheat and peas were excised immediately above and below each segment used for measurement of K_α. These zones were preserved in formaldehyde-acetic acid - F.A.A. - fixative (Sass 1958). The composition of the particular F.A.A. was:

Formaldehyde (37-40%)	10 cc
Glacial acetic acid	6 cc
Ethyl alcohol	50 cc
Deionized water	34 cc

The fixative was prepared just before fixing the root zones. Tests were conducted to determine whether fixative altered the diameter of the metaxylem vessel. The diameter of the metaxylem vessel in each of a set of wheat root members was measured before and after fixing. Measurements were made 5 cm from the basal and 5 cm from the apical end of the radicle and on the first pair of seminal roots when the plants were 18 days old. The root zones were preserved in the F.A.A. for three weeks before being sectioned by hand. The zones were sectioned in the transverse direction with a moistened 'Gem' razor-blade, using moistened pith as a support. Three to five transverse sections were cut per zone, before and after fixing, and the diameter of the metaxylem vessel measured. Arithmetic means of diameters found in three transverse sections from individual zones before and after fixing are given in Table 3. The diameters of the metaxylem vessel before and after fixing were compared using a paired t-test. The difference between the mean diameters was not significantly different from zero.

As fixative did not alter vessel diameter, all root segments used for routine measurement of vessel diameter were stored in F.A.A. for periods of three to six weeks before measurement. Three centimetre long zones from above and below the segment used to determine K_α were preserved in fixative. These zones were hand-sectioned as described above. Six transverse sections were cut from each zone.

All sections used in the preliminary test and subsequently were mounted in glycerine on a slide and vessel diameter was measured with an eyepiece scale at x105. The eyepiece scale had been calibrated using a stage-scale. The arithmetic mean of the radius of the xylem vessel was then calculated from values for the six sections from the 3 cm long zone. The difference between individual values for a particular zone was generally less than 5 μm.

3.2.5 Measurement of K_β

Plants of wheat and peas were harvested 18 days after transplanting. The presence of suberized tissue along the main root axis was determined using the H_2SO_4 - I_2 - KI procedure (Scott 1950). No suberized tissue was detected within 12 cm from the apex in either species. At this distance from the apex the first order laterals had

Table 3. Comparison of metaxylem vessel diameter in seminal roots of 18 day old wheat plants before and after fixation with F.A.A.

Plant No.	Fresh (μm)	Fixed (μm)
1	62.20	65.64
	75.42	75.42
	59.78	59.78
	59.22	57.82
2	67.32	66.48
	67.04	66.20
	63.97	62.57
	67.32	69.83
	61.73	59.56
	63.13	63.41
3	68.16	67.04
	75.42	75.42
	59.03	57.55*
4	67.04	67.60
	67.04	67.04
	67.04	67.32
	58.66	62.01
	64.11	72.15*
	57.26	57.87
5	70.95	67.04
	75.42	75.42
	60.89	61.45
	58.66	58.66
	46.93	49.44
6	62.85	62.01
	74.86	69.83
	69.04	59.82*
	61.45	65.64
	67.04	67.60
	67.85	66.48
7	67.04	67.04
	83.80	81.84
	58.38	55.67
	53.35	69.28
	67.04	67.04
8	48.49	49.72
	50.28	53.07
	64.53	64.25
	58.66	59.50
	65.64	59.22
	66.20	61.45
9	65.64	66.76
	67.04	65.64
	58.66	58.66
10	67.04	67.04
	58.66	58.66
	53.81	60.47*
	59.50	58.66
11	65.35	58.74
	59.78	58.67
	64.25	66.20
	67.04	67.04
	67.04	67.04
	67.04	67.04
12	67.04	67.04
	58.66	58.66
	61.45	61.45
	58.66	58.66
$\bar{x}$	63.82	63.04
C.V. %	15.86	16.25

* Equivalent radius, r_e, for two metaxylem vessels.

There are sometimes less than six values per plant because not all plants produced the three seminal axes required, or some axes were shorter than 15 cm and these were not sectioned.

either started to emerge or had begun to elongate. The main axes were firstly severed 10 to 12 cm from the tip. These lengths were cut into three smaller segments, each 3.5 cm long by cutting at 3.5 cm from the first 1st order lateral, in the middle of the apical unbranched zone, and 3.5 cm behind the apex, as shown in Fig. 13. The above procedure was followed for both wheat and pea axes. The proximal end of the segment including the root tip was sealed into a capillary in the manner described previously in Section 3.2.3. The root tip was then coated with molten wax (Section 3.2.3). Then the whole segment was immersed in deaerated nutrient solution. The second and the third segments were treated in a similar manner; but the distal end was firstly crushed with forceps, then dipped briefly into the molten wax at 50^{o}C. After 10 minutes when the wax had set, a suction head of 300 cm of water was applied to the base of the segment. The displacement of the meniscus was measured at successive times. Each measurement took less than one hour.

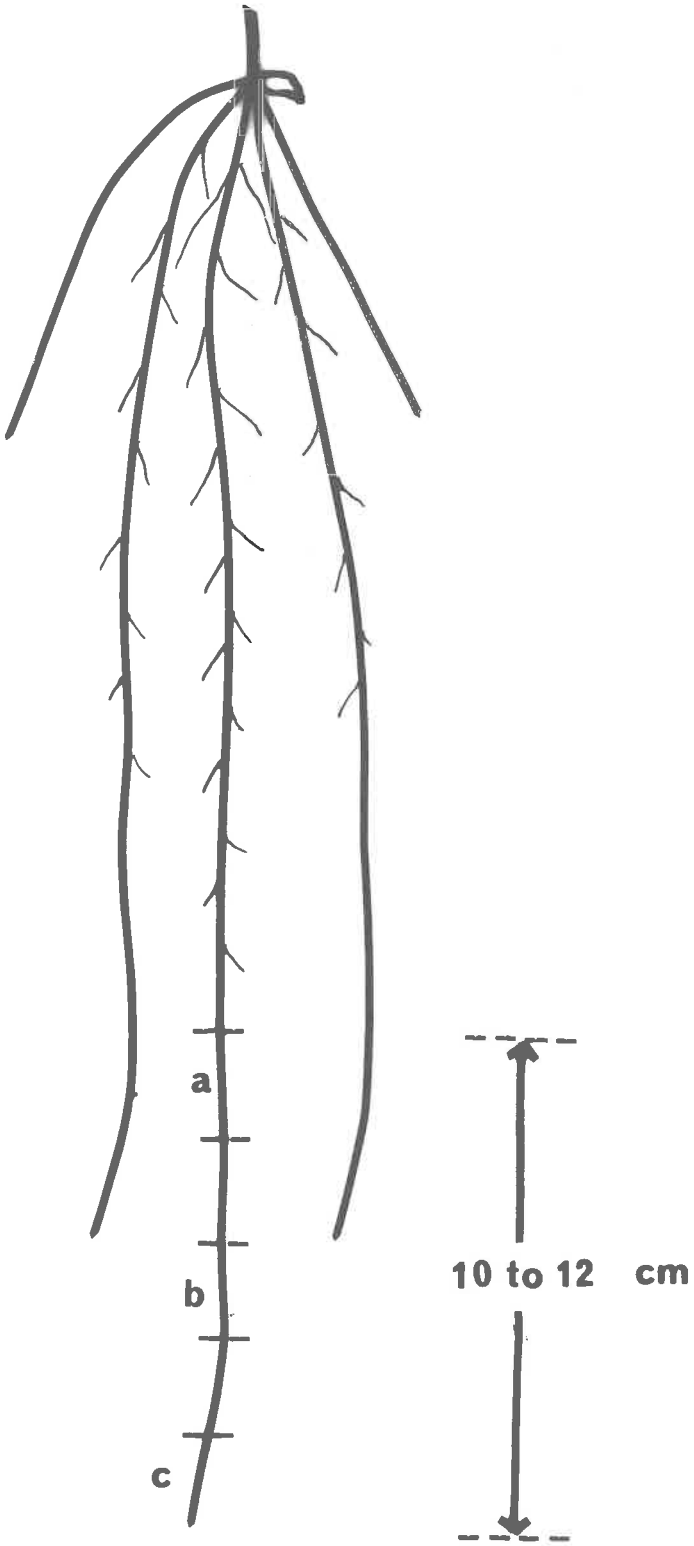
The radial conductance K_β was calculated from Eq. (33) $K_\beta = J/\Delta h$, where K_β is the radial conductance of the segment (cm sec^{-1}); J is now the rate of outflow from the basal end of the segment per unit length of unwaxed zone (cm^2 sec^{-1}); and h is now the suction head applied to the base of the segment (cm). It was assumed that, for the 2.5 cm long segments employed, and for the suction head applied,

Fig. 13. Location of cuts used to obtain root segments for K_β measurement.

a) basal 3.5 cm of apical unbranched zone

b) middle 3.5 cm

c) apical 3.5 cm



a
b
c
10 to 12 cm

the head drop along the segment was negligible compared with the head drop across the segment. Also Eq. (33) assumes that Δh_{Π} is small compared with Δh at the rates of inflow observed.

3.2.6 Results

3.2.6.1 Anatomy of seminal roots of wheat cv. Halberd

Each seminal axis usually has a single metaxylem vessel but occasionally has two vessels. The metaxylem vessel or vessels are located centrally in the stele, and 6 to 14 smaller xylem vessels are distributed amongst the xylem strands. In the cultivar Halberd the internal diameter of the smaller vessels ranges from 10 to 15 μm, while the internal diameter of the metaxylem vessel ranges from 40 to 110 μm, 60 to 80 μm being common. The diameters of the metaxylem vessel in seminal axes that were grown in nutrient solution and axes grown in the field were similar. When there was only one metaxylem vessel, the vessel was nearly circular in transverse section. In contrast, where there were two vessels the shape of each vessel was closer to a semi-circle (Figs. 14A and 14B). The diameter of the metaxylem vessel in the seminal axes usually increased with distance from the base of the axis until a certain distance and then decreased markedly towards the tip. Longitudinal sections of metaxylem vessels showed that, where differentiation had just been completed, transverse septa occurred at intervals of 110 to 150 μm. However, in more proximal zones the septa were perforated (Fig. 15) and only a

<u>Fig. 14</u>. Transverse section of seminal root.

A) Single metaxylem vessel (x 490)

B) Double metaxylem vessel (x 490)

m = metaxylem vessel

en = endodermis

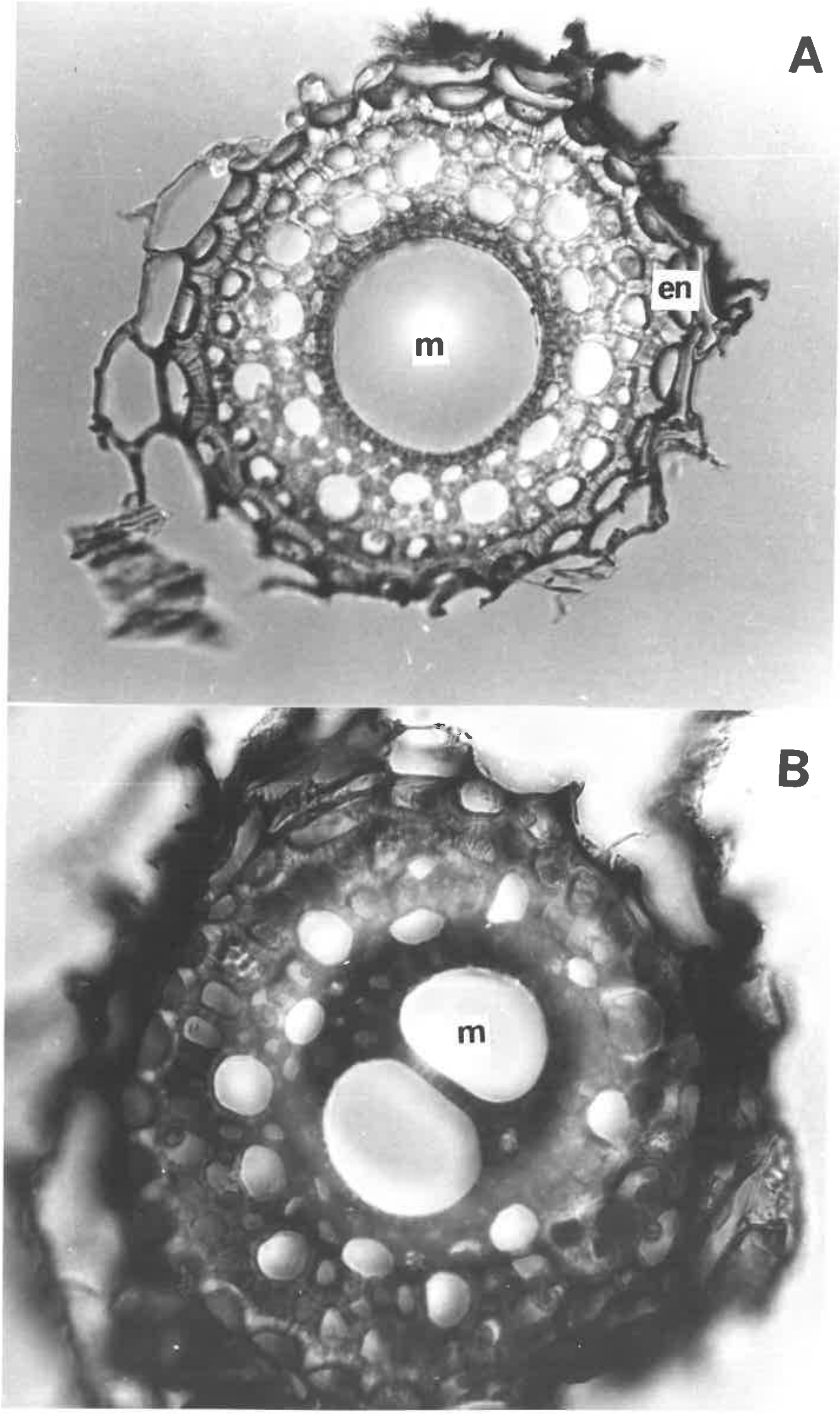
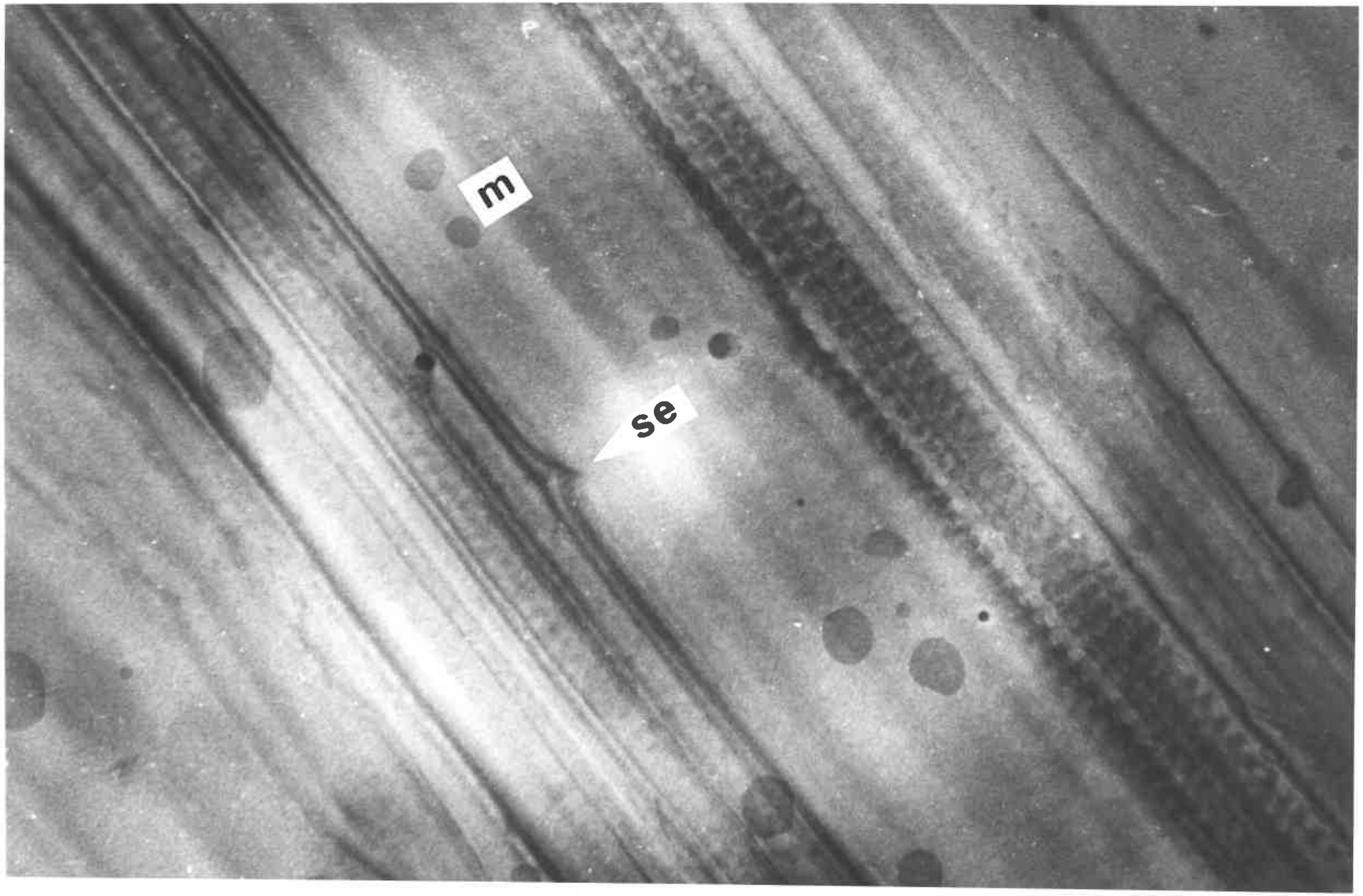

A
en
m
B
m

Fig. 15. Longitudinal section of seminal root (x 420) showing the perforated transverse septa.

m = metaxylem vessel

se = perforated transverse septa



m
se

small band remained. The band projected 2 to 3 μm into the lumen of the vessel, and was 1 μm thick.

The cortical tissue disintegrated towards the base of the seminal axes, the degree of breakdown being greater for field roots than for roots grown in nutrient solution.

The first order laterals of the seminal roots had a single central metaxylem vessel having a diameter of 15 to 25 μm. The endodermis was less thickened than in the main axes.

3.2.6.2 K_α, seminal axes of wheat roots

Figs. 16 and 17 show the natural logarithms of K_α values as a function of the natural logarithm of arithmetic means of metaxylem vessel radius for individual segments of seminal axes. When there were two metaxylem vessels in a root segment, the equivalent radius r_e was calculated from

$$r_e = \sqrt[4]{\sum_{i=1}^{n} r_i^4} \qquad (42)$$

Smaller xylem vessels were ignored as their radius was approximately one-fifth of r_e for the metaxylem, and, as calculated using Poiseuille's equation (Eq. (35)), they collectively contributed less than one percent of the total water flow through the axes. The first harvest in the field and the second harvest for plants grown in solution were made at the flowering stage.

The conductance calculated from Poiseuille's equation, Eq. (35), K_p is defined as the rate of flow through a tube of circular cross-section and uniform radius under unit head gradient. At 15°C when r (μm) is the tube radius,

$$K_p \ (\mathrm{cm}^3\ \mathrm{sec}^{-1}) \quad = \quad 3.85 \times 10^{-12} \times r^4$$

and

$$\log_e K_p \quad = \quad -26.28 \times 4 \log_e r \qquad (43)$$

The line given by Eq. (43) is shown in Fig. 16 and is called the theoretical line.

The homogeneity of the conductances at the first, second and the third harvests was assessed using the specific axial conductivity κ (cm sec^{-1}), where κ is defined by

$$\kappa \quad = \quad \frac{K_\alpha}{\pi r^2} \qquad (44)$$

Values of $\bar{\kappa} = \sum_{i=1}^{n} \kappa/N$ for a set of N segments were compared for different harvests and for segments obtained from roots grown in solution culture and in the field. $\bar{\kappa}$ values were not significantly different for roots grown in solution and in the field. $\bar{\kappa}$ values were not significantly different for the first and second harvests, but $\bar{\kappa}$ for the pooled data of the first and second harvests differed significantly from $\bar{\kappa}$ for the third harvest (P, 0.05). Linear regression analysis was therefore performed for the regression of $\log_e K_\alpha$ on $\log_e r_e$, by pooling data for all roots for the first and second harvest; and on data for all roots for the third harvest. The results are shown in Table 4, and the linear regression lines are plotted in Fig. 16 for the first and second harvest , and in Fig. 17 for the third harvest.

Table 4. Correlation coefficient (R), intercept (a) and slope (b) of linear regression of $\log_e K_\alpha$ on $\log_e r_e$ (± s.e.)

Harvest	N	R	a	b
1st and 2nd	52	0.75**	-24.01 ± 1.39	3.23 ± 0.40
3rd	24	0.64**	-21.38 ± 2.23	2.64 ± 0.64

** Significantly different from zero at P, 0.01.

The slope b at the first and second harvest did not differ significantly from the theoretical value of 4.0; but at the third harvest b was significantly lower (P, 0.05) than the theoretical value. The intercepts a at the first and second and at the third harvest were highly significantly greater than the theoretical value (P, 0.001).

For the first and second harvest, at $r_e = \overline{r}_e = 34.00$ µm, where $\overline{r}_e$ is the geometric mean of r_e, $K_\alpha = K_P/1.25$. At $r_e = r_{e\ min} = 20.48$ µm $K_\alpha \approx K_P$ and at $r_e = r_{e\ max} = 47.48$ µm $K = K_P/2.06$. For the third harvest at $r_e = \overline{r}_e = 31.70$ µm, $K_\alpha = 1.25\ K_P$. At $r_e = r_{e\ min} = 24.50$ µm $K_\alpha = 1.78\ K_P$, and at $r_e = r_{e\ max} = 54.60$ µm, $K_\alpha = K_P/1.65$. At any given value of r_e, K_α at the first and second harvest was lower than K_α at the third harvest.

3.2.6.3 Anatomy of nodal axes of wheat

The axes of the nodal roots were wider than the axes of the seminal roots at given distances from the base. The diameter of the nodal root, and of the stele decreases with increasing distance from the base of the root. From 1 to 7 metaxylem vessels were present when maturation was complete (Fig. 18A, B). The number varied with the age of the zone, decreasing from base to apex. Perforated transverse septa were found in metaxylem vessels at intervals of 0.1 cm. The equivalent radius of the set of metaxylem vessels in each root was calculated from Eq. (42).

3.2.6.4 K_α, segments of nodal axes of wheat

$\overline{\kappa}$ values were not significantly different for roots grown in solution culture and in the field (P, 0.05). $\overline{\kappa}$ at the dough stage was significantly greater than $\overline{\kappa}$ at flowering. No nodal axes were present at the seedling stage.

Owing to the small number of segments obtained, N = 11, and to the narrow range of values of r_e, 32.24 to 54.96 µm, linear regression

Fig. 16. $\mathrm{Log}_e K_\alpha$ ($\mathrm{cm}^3\ \mathrm{sec}^{-1}$) as a function of $\log_e r_e$ (μm) for segments of seminal axes of wheat cv. Halberd at the seedling stage and at flowering.

o 18 days after transplanting) nutrient
Δ flowering stage) solution

▲ flowering stage) field

—— Poiseuille's equation (Eq. (43))

-·-·- Regression line for first and second harvests

····· Confidence limits (P, 0.05)

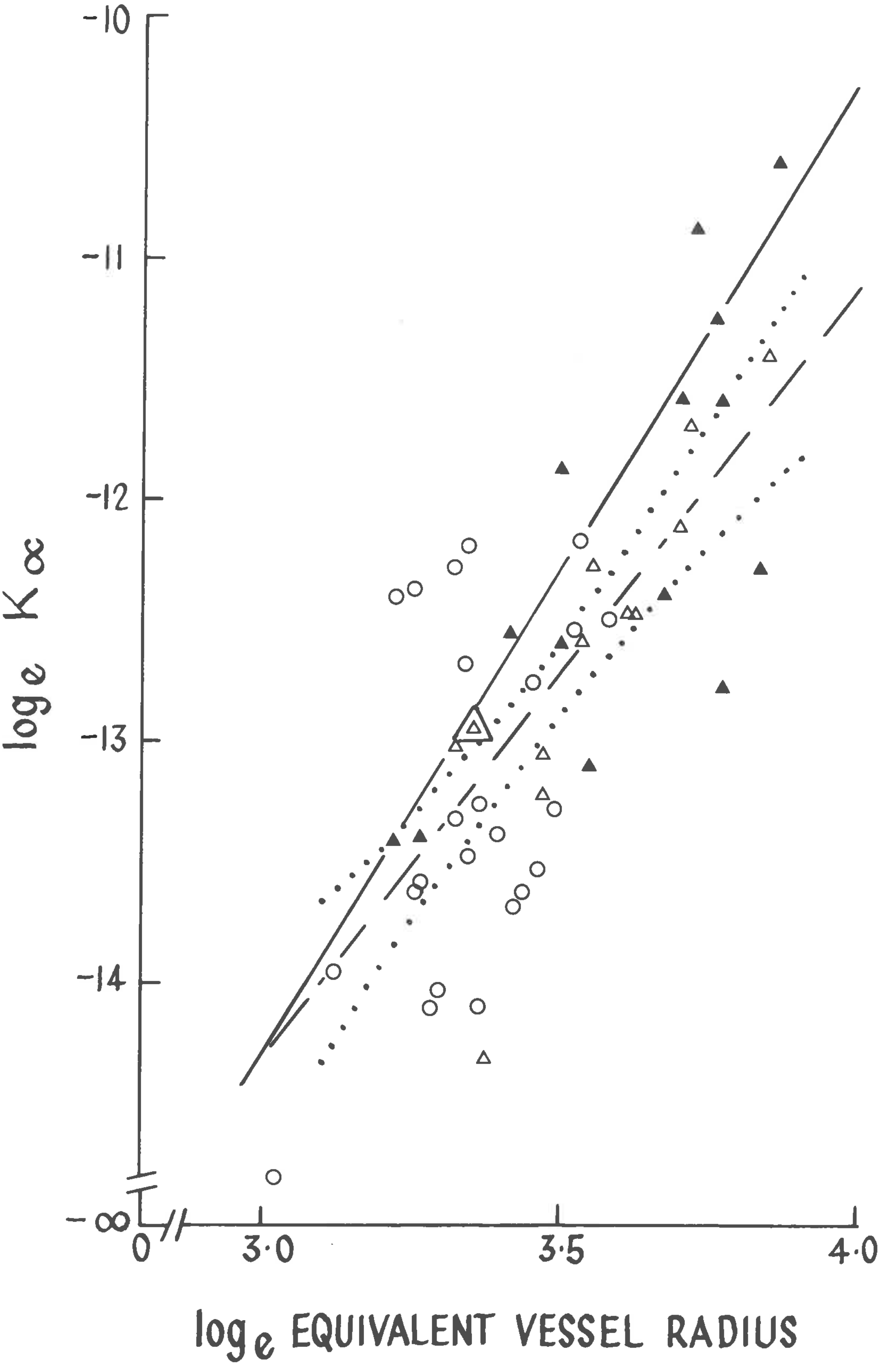
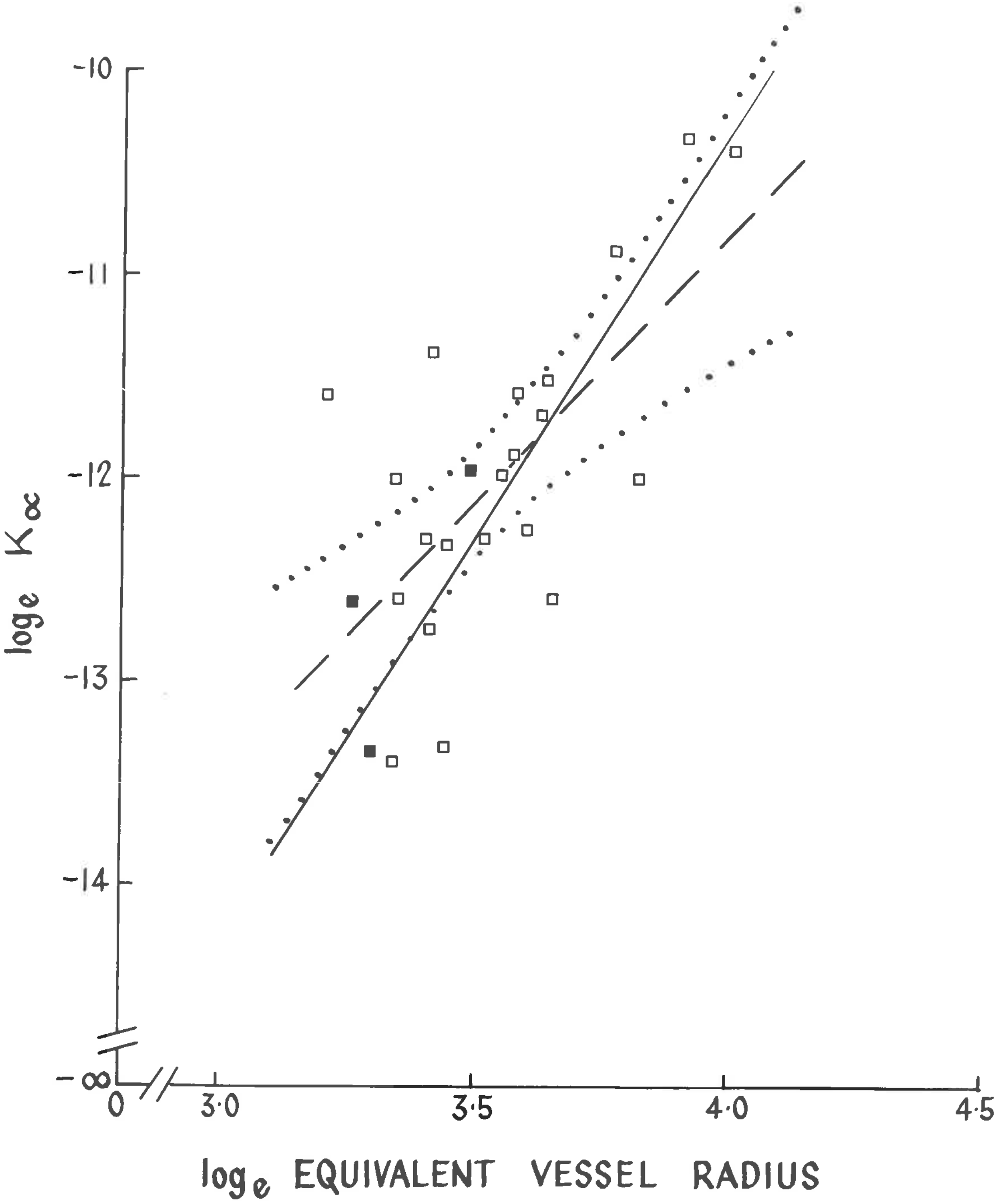

-10
-11
-12
-13
-14
- ∞
log$_e$ K∞
0
3·0
3·5
4·0
log$_e$ EQUIVALENT VESSEL RADIUS

Fig. 17. $\text{Log}_e\ K_\alpha$ ($cm^3\ sec^{-1}$) as a function of $\log_e r_e$ for segments of seminal axes of wheat cv. Halberd at the dough stage.

□	nutrient solution
■	field
——	Poiseuille's equation (Eq. (43))
– – –	Regression line
·····	Confidence limits (P, 0.05)


-10
-11
-12
-13
-14
-∞
0
3·0
3·5
4·0
4·5
loge Kα
loge EQUIVALENT VESSEL RADIUS

analysis was not attempted on data from the second harvest. At this harvest, $\bar{\kappa} = 5.28 \cdot 10^{-6}$ cm^3 sec^{-1}, variance $s^2 = 5.44 \cdot 10^{-6}$. For the third harvest, R = 0.47**, a = -22.94 ± 0.20 and b = 2.91 ± 1.04. The regression line is shown in Fig. 19, together with the theoretical line. The slope b of the regression line did not differ significantly from the theoretical value. However, as shown in Fig. 19, the variability was high. The intercepts differed significantly (P, 0.01). At the third harvest at $r_e = \bar{r}_e = 45.10$ µm, $K_\alpha = K_P/2.28$. At $r_e = r_{e\ min} = 32.00$ µm, $K_\alpha = K_P/1.61$; at $r_e = r_{e\ max} = 65.19$ µm, $K_\alpha = K_P/3.39$.

3.2.6.5 Anatomy of segments of roots of pea cv. White Brunswick

The root of pea comprised a main axis (tap root), first order, second order and third order laterals. The stele in the main axis was triarch. The endodermis showed well defined Casperian thickenings. The main axes and first order laterals were similar in anatomy until conspicuous secondary growth occurred in the former. The number of metaxylem vessels in the main axis decreased from the base of the root towards the tip. The number of xylem vessels (primary and secondary) varied from one in the sub-apical zone to more than 60 in basal zones. A transverse section of the stele, 53 cm from the base of the main axis at the flowering stage is shown in Fig. 20. The equivalent vessel radius r_e was calculated using Eq. (42). Small xylem vessels ($r \leqslant 20$ µm) were omitted from this calculation, as their collective contribution to the total conductance,

Fig. 18. **B)** Transverse section of basal zone of nodal root (x 105).

A) Transverse section of stele in basal zone of nodal root (x 420).

m = metaxylem

en = endodermis

cr = cortical cell

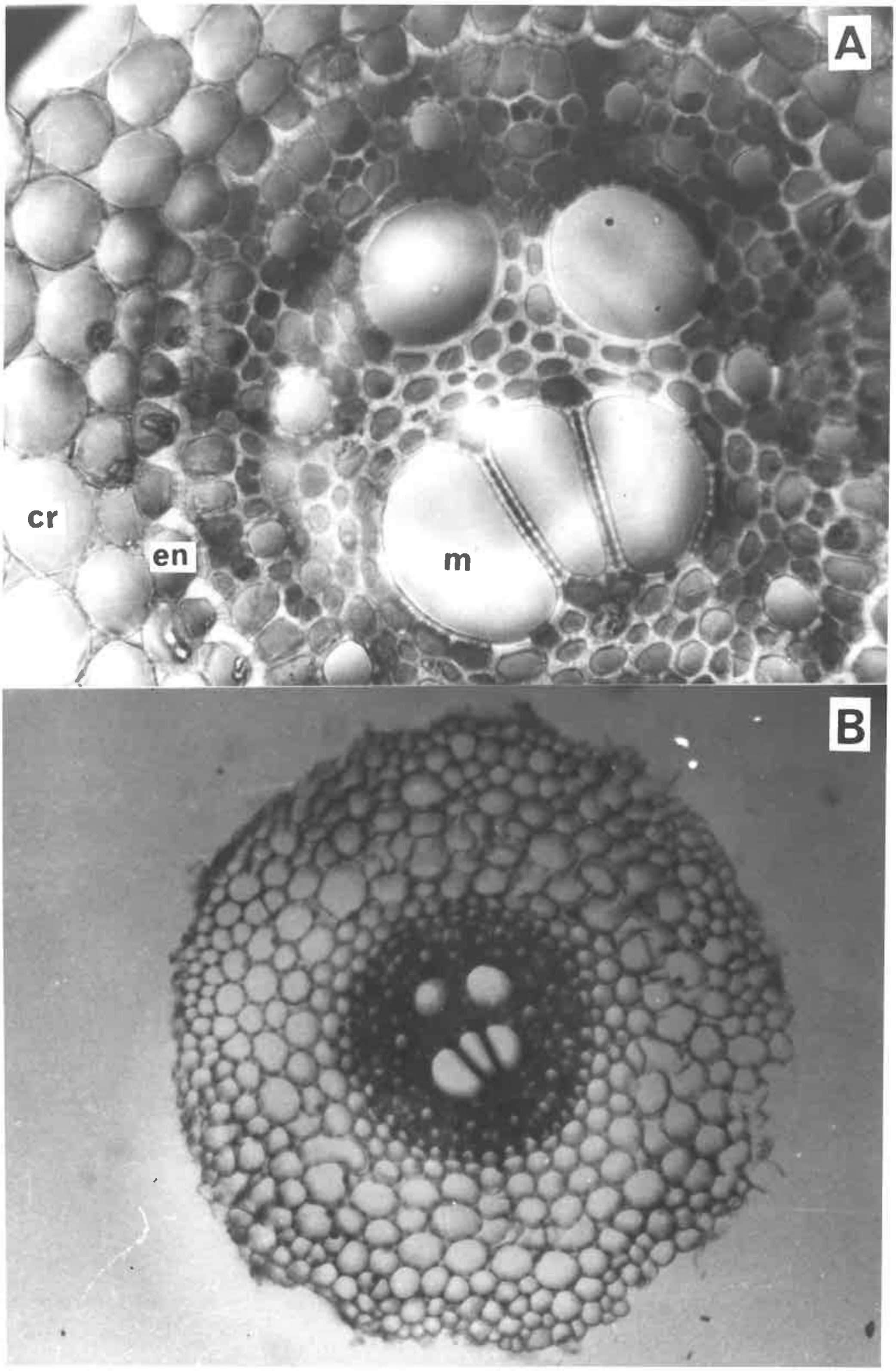

A
cr
en
m
B

Fig. 19. $\text{Log}_e K_\alpha$ ($\text{cm}^3\ \text{sec}^{-1}$) as a function of $\log_e r_e$ for segments of nodal axes of wheat cv. Halberd. Data obtained at dough stage for segments of roots grown in nutrient solution.

□ nutrient solution

▨ field

——— Poiseuille's equation (Eq. (43))

– – – – – regression line

········· confidence limits (P, 0.05)

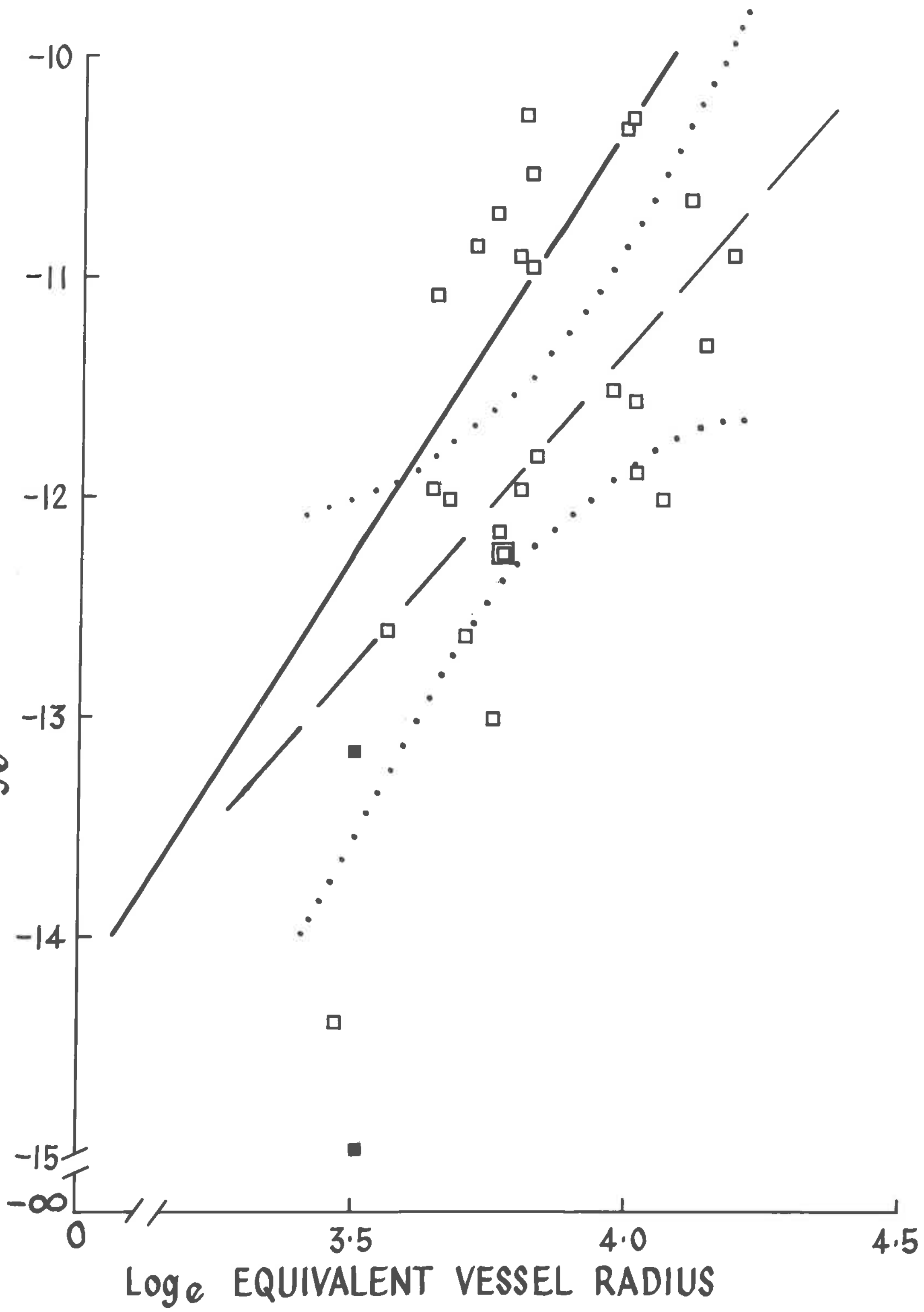
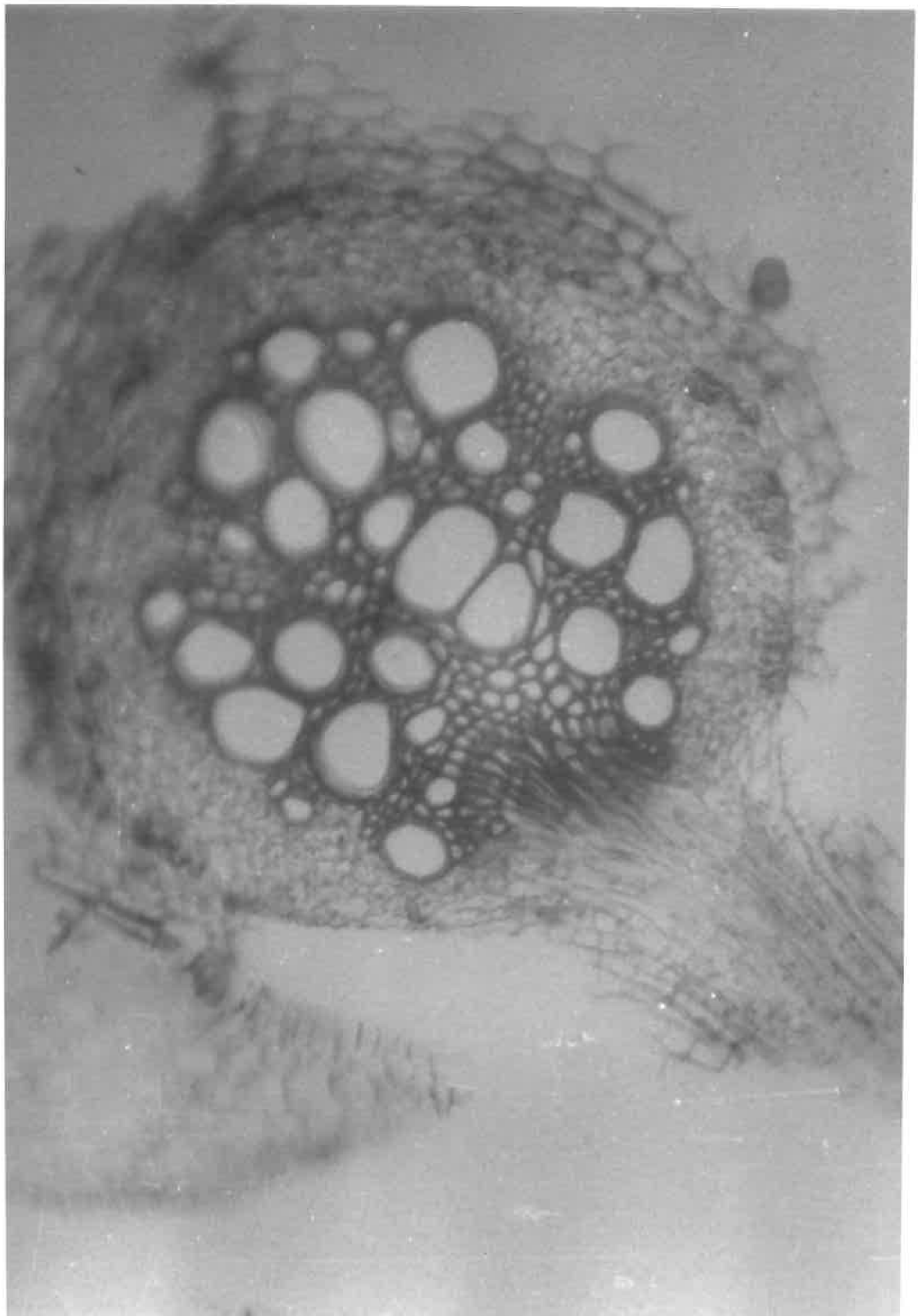

-10
-11
-12
-13
-14
-15
-∞
0
3·5
4·0
4·5
Log$_e$ Kα
Log$_e$ EQUIVALENT VESSEL RADIUS

Fig. 20. Transverse section of main axis of pea root, 53 cm from base, at flowering stage.



calculated using Eqs. (42) and (35) was less than one percent.

3.2.6.6 K_α, main axis and first order laterals of pea roots

As $\overline{\kappa}$ did not significantly differ between the main axis and first order laterals or between harvests, data were pooled for all segments. Fig. 21 shows $\log_e K_\alpha$ as a function of $\log_e r_e$.

For the segments of pea roots, R = 0.84**, a = -25.82 ± 0.85 and b = 3.71 ± 0.25. The slope b of the regression line was not significantly different from the theoretical value. The intercept a was highly significantly different (P, 0.01) from the theoretical value. At $r_e = \overline{r}_e = 30.30$ μm, $K_\alpha = K_P/1.73$. At $r_e = r_{e\ min} = 5.13$ μm, $K_\alpha \simeq K_P$, and at $r_e = r_{e\ max} = 68.52$ μm, $K_\alpha = K_P/1.82$.

3.2.6.7 K_β, unsuberized zones of wheat and pea root axes

K_β was determined for segments located within the unsuberized zone of the main axis of seminal roots of wheat and the main axis of pea roots. Segments were cut 0 to 3.5 cm, 4.75 to 8.25 cm and 8.50 to 12.0 cm from the apex. The age of the segments varied from 1 to 6 days. The results are shown in Table 5. The distances from the apex, shown in Table 5, represent the unwaxed length. Because of failure of the seals, only seven values were obtained for each species.

The arithmetic mean $\overline{x}$ and standard deviation s of K_β for the segments of seminal axes of wheat were $\overline{x} = 5.54 \cdot 10^{-9}$, $s = 7.88 \cdot 10^{-9}$ cm $\sec^{-1}$. For the main axis of the pea root $\overline{x} = 1.4 \cdot 10^{-9}$, $s = 2.06 \cdot 10^{-9}$ cm $\sec^{-1}$.

Fig. 21. $\log_e K_\alpha$ (cm^3 sec^{-1}) as a function of $\log_e r_e$ for segments of roots of pea cv. White Brunswick.

o	tap roots	) 18 day old plants
●	First order laterals	)
□	tap roots	) flowering stage
■	First order laterals	)
△	tap roots	) maturity
▲	First order laterals	)
——	Poiseuille's equation (Eq. (43))	
----	Regression line	
....	Confidence limits (P, 0.05)	

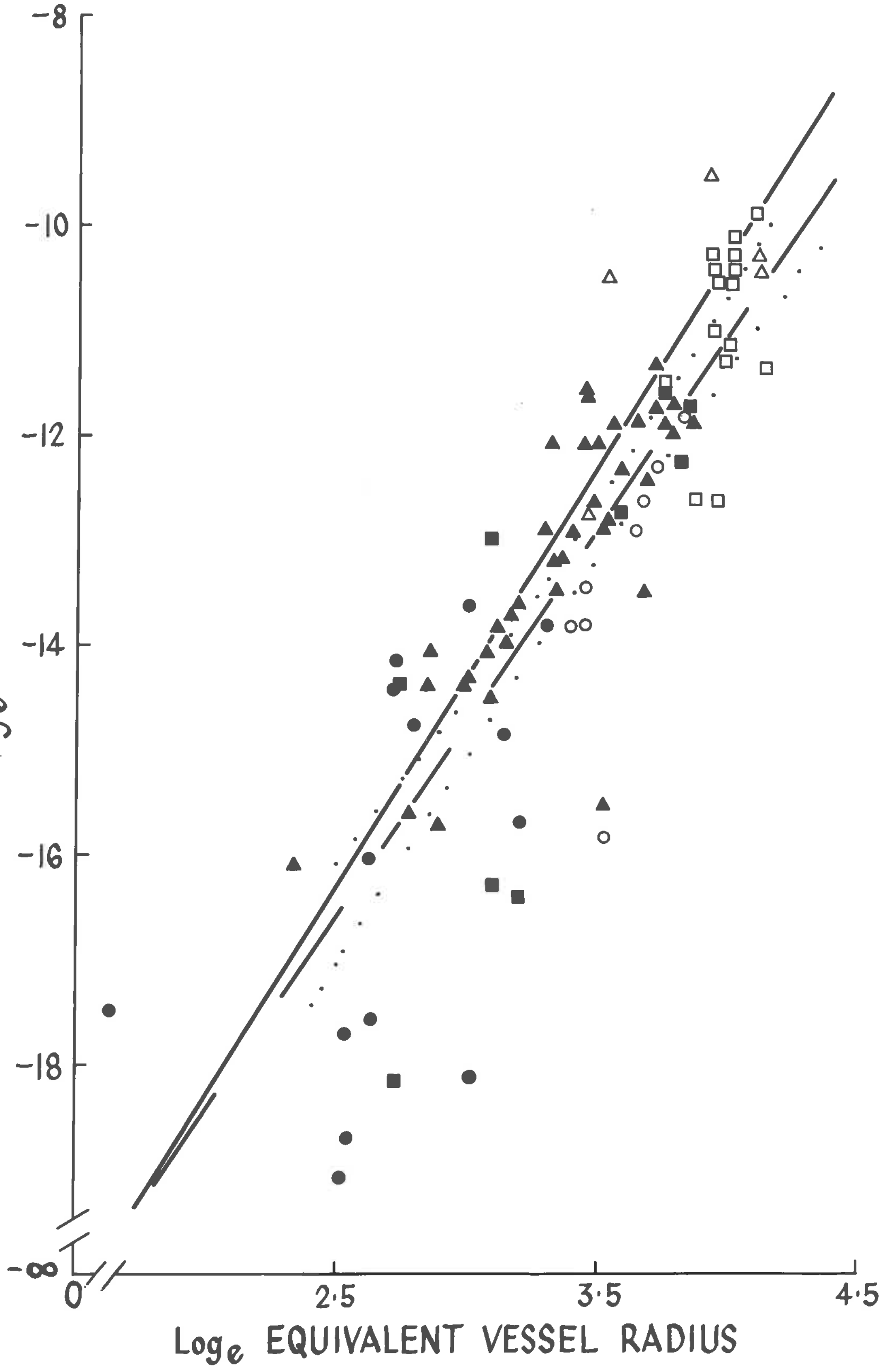

-8
-10
-12
-14
-16
-18
-∞
Log$_e$ Kα
0
2·5
3·5
4·5
Log$_e$ EQUIVALENT VESSEL RADIUS

Table 5. Radial resistance K_β of the unsuberized zone of segments of the main axis of seminal roots of wheat and the main axis of pea roots.

Species	Root No.	Distance from apex (cm)	K_β (cm sec^{-1})
Wheat	1	1.0 to 3.0	$3.8 \cdot 10^{-10}$
	2	1.0 to 3.0	$2.0 \cdot 10^{-9}$
	2	5.5 to 7.5	$1.6 \cdot 10^{-8}$
	3	5.5 to 7.5	$1.8 \cdot 10^{-8}$
	4	1.0 to 3.0	$1.9 \cdot 10^{-9}$
	4	5.5 to 7.5	$3.1 \cdot 10^{-10}$
	5	1.0 to 3.0	$2.2 \cdot 10^{-10}$
Peas	1	1.0 to 3.0	$3.8 \cdot 10^{-10}$
	2	1.0 to 3.0	$1.2 \cdot 10^{-10}$
	3	1.0 to 3.0	$2.1 \cdot 10^{-10}$
	4	1.0 to 3.0	$1.7 \cdot 10^{-10}$
	4	5.5 to 7.5	$2.9 \cdot 10^{-9}$
	5	1.0 to 3.0	$4.2 \cdot 10^{-10}$
	6	3.5 to 6.0	$5.4 \cdot 10^{-9}$

3.2.7 Discussion

The anatomy of the mature zones of the wheat and pea roots agreed with the descriptions of Percival (1921), Avery (1930), Hector (1936) and Troughton (1962) for wheat, and of Hayward (1938), and Bond (1948) for peas. In wheat the transverse septa in the metaxylem vessel of the root axes were perforated. This contrasts with an observation of Jackson (1922) that the septa in the metaxylem vessels of seminal and nodal roots of barley remained unperforated even in mature zones. The transverse septa in the metaxylem in nodal axes were more widely spaced than those in seminal axes. No attempt was made to study the septa in peas.

We deal firstly with the conductance of the segments of the seminal axes of wheat roots at the first and second harvests. The values of K_α were usually but not invariably lower than the values of K_P derived from the values of r_e determined for each segment. Fifty two data points for the first and second harvests are shown in Fig. 16. Forty three of them lay below the theoretical line. The negative bias in K_α could have been due partly to irregularities in the shape of the vessels. The following irregularities were noted:

i) constriction of the lumen when perforated septa occurred;

ii) departures from circularity in cross-section. The ratio of the length of the major axis l_1 to the length of the minor axis l_2 did not exceed 1.3. As the non-circular shapes were too irregular to be idealized as ellipses, the mean radius $l_1 + l_2/4$ was substituted. If the vessels had been elliptical in cross-section and the ratio $l_1/l_2 = 1.3$, then if r had been set equal to $(l_1 l_2)^{\frac{1}{2}}/2$ the deviation in K_α would have been -3 percent (Preston 1938).

iii) the internal radius varied with distance from the base of the vessel. Usually the internal radius of the vessel within segments used for the determination of K_α decreased in the direction of flow. This would have caused only a small additional loss of pressure (Prandtl 1952, p. 170).

Error in K_p could have arisen from the following errors inherent in the measurement of vessel radius:

i) parallax in measuring vessel radius when the image of the vessel was not in the same plane as the image of the scale.

ii) when the cross-section was close to circular the axis lying in the direction of the scale was measured.

iii) the vessels may have been distorted when mounting the cross-section of the root on the slide, and when covering the section with a coverslip.

Kozinka and Luxová (1971) showed that, in addition to flow within the xylem, water could flow in the axial direction through the cortical tissue of axes of nodal roots of maize. Under a positive pressure, gradient 0.80 bar cm^{-1}, the flow in the cortex was 30 percent of the total flow. That is, the total flow was 1.4 times that in the xylem vessels. In the present series of measurements, which were made under suction, there is less likelihood of water having entered intercellular spaces normally occupied by air. Furthermore, even when measurements were made on basal zones of older axes that had little or no cortical tissue, K_α sometimes exceeded K_P at a given r_e. For such segments occasional positive deviations of K_α from K_P were probably due to random errors associated with measurements.

At the third harvest, the intercept a of the regression line was significantly greater than that at the first and second harvests combined. That is, at any given value of r_e, the conductance K_α tended to be greater at the third than at the earlier harvests. Moreover, 15 of 24 data points lay above the theoretical line as shown in Fig. 17. The reasons why K_α increased at the third harvest are not known with certainty. However, by staining with Sudan III it was shown that the walls of the metaxylem vessel in older zones of seminal axes became impregnated with lipid (Barley, pers. comm.). It is possible that, instead of wetting the walls, the water in older zones behaved as a non-wetting liquid. If so, the water may tend to slip in the boundary region adjacent to the walls, and less head would be dissipated in overcoming resistance due to viscosity. This implies that for a given head gradient, the rate of flow would be increased. Alternatively, although the F.A.A. fixative did not affect the radius of young vessels (Section 3.2.4.), it may have reduced the radius of old, suberized vessels. This possibility remains to be examined.

As shown in Fig. 19, at the third harvest, most values of K_α for nodal axes of wheat roots lay below the theoretical line. Negative deviation could have again been due to irregularities in shape of the vessels: the following irregularities were noted in the nodal axes:

i) departures from circularity in cross-section;

ii) unlike r_e in the seminal axes, r_e decreased continuously with distance from the basal end of the vessel, that is r_e increased continuously in the direction of flow. As noted by Prandtl (1952, p. 170), gradual widening of a tube leads to a larger loss of pressure than does gradual narrowing, as the fluid tends to become separated from the walls. Typically, the equivalent radius r_e of the metaxylem vessels in the 2.5 cm long segments of the nodal axes increased from 50 to 55 μm at the distal end to 60 to 65 μm at the basal end;

iii) the lumen was constricted where perforated septa occurred.

In addition to irregularities in shape of the vessels, the number of vessels usually increased towards the base of the nodal axes. This occurred in about seven out of ten roots. It is not known whether some vessels terminated closer to the base, or whether the vessels were joined.

As noted for seminal roots, errors were introduced in measuring the radius of the vessels due to parallax, etc. Occasional positive deviations of K_α from the corresponding K_p values would be expected as a result of random error associated with measurements. For nodal roots at the second harvest $\overline{r}_e$ = 42.8 μm and $\overline{K}_\alpha = 3.3 \,.\, 10^{-6}$ $cm^3\ sec^{-1}$. At the third harvest, for nodal axes, at r_e = 42.8 μm $K_\alpha = 6.2 \,.\, 10^{-6}$ $cm^3\ sec^{-1}$. Again the increase in K_α may have been due to the deposition of fatty substances on the walls of the older xylem vessels between the second and third harvests. The degree of staining with Sudan III was greater than that found for the walls of older vessels in the seminal axes (Barley pers. comm.).

For the pea roots, as shown in Fig. 21, 54 out of 73 data points lay below the theoretical line. The negative bias in K_α probably arose for reasons similar to those outlined above for the young seminal axes and the nodal axes of wheat.

Emerson (1954) measured K_α of segments of seminal axes of perennial ryegrass, timothy and cocksfoot. He obtained results for a total of only six segments. Five out of six of Emerson's values of K_α are less than the corresponding value of K_p calculated from Emerson's data on vessel radius.

In the present experiment values of K_α were measured at a small suction head ($\leqslant$ 300 cm). At high suctions. K_α may not be as large. Cole and Alston (1974) showed that the diameter of seminal roots of wheat decreased by 60 percent when the root water potential decreased from zero to -10 bar, most of the decrease occurring within the range -5 to -10 bar. The xylem vessels may also shrink to some extent with a consequent decrease in K_α. Greacen (pers. comm.) found that, when the gas pressure outside the seminal axes of 10 days old wheat roots exceeded the pressure within the water filled xylem by 2 bar, K_α decreased by 30 percent.

The measured values of radial conductance for the unsuberized zone of the main axes of wheat and pea roots were commensurate with:

i) values found by Brouwer (1965) for main axes of broad bean;

ii) values found by Cox (1966) for seminal axes of an unspecified cultivar of wheat;

iii) values found by Hansen (1974a) for seminal axes of wheat cv. Gabo.

All these measurements were made on roots immersed in water. The unsuberized zone of main axes of barley and marrow roots absorbs water four to five times more rapidly than the older suberized zone when immersed in water (Graham *et al.* 1974). When in unsaturated soil older cutinized and suberized zones may be even less effective in water uptake than when immersed. This is because the cutin and suberin are lipids and they may make the surface of the root water-repellent. Whether or not they become cutinized and suberized, the older zones of the root often lose their epidermis together with the outer files of cortical cells, so that an air gap may be present between the surface of the root and an unsaturated soil. Also roots may tend to shrink away from the soil, either when the soil becomes drier (Hansen 1974a) or when the roots lose water faster than they absorb it, in periods of high evaporative demand (Huck *et al.* 1970). Clearly, K_β needs to be measured *in situ* in unsaturated soil as well as on roots immersed in water.

3.3 GEOMETRY OF THE ROOT SYSTEM OF WHEAT IN RELATION TO THE WITHDRAWAL OF WATER FROM FIELD SOIL

3.3.1 Location of experiments

The experiments were carried out at the Roseworthy Agricultural College, South Australia, latitude 34.5°S, longitude 138°E.

3.3.2 Climate

The locality has cool, wet winters, and hot, dry summers. The mean annual rainfall (1931 to 1971) is 430 mm. The mean monthly rainfall and pan evaporation are shown in Fig. 22a, and values for 1972 and 1973 are shown in Fig. 22b and 22c. The mean maximum and minimum temperature for each month for the period 1931 to 1971 and in 1972 and 1973 are given in Table 6. The mean duration of the growing season is five months (Prescott and Thomas 1949).

3.3.3 Description of the soil

The soil was a sandy red brown earth, classified as Dr.2.2.3 in the Australian Factual Key (Northcote 1965). Red brown earths comprise a large proportion of the soils in the wheat belt of southern and south eastern Australia.

The A horizon varied from grey, loamy sands, to light brown sand. The B_1 horizon consisted of a red brown medium clay with a well developed coarse prismatic structure. The clay was friable when moist

Fig. 22. Monthly rainfall and pan evaporation (Australian standard tank).

a) Mean (1931 to 1971)

b) 1972

c) 1973

Source: Roseworthy Agricultural College records

o—o pan evaporation

..... rainfall

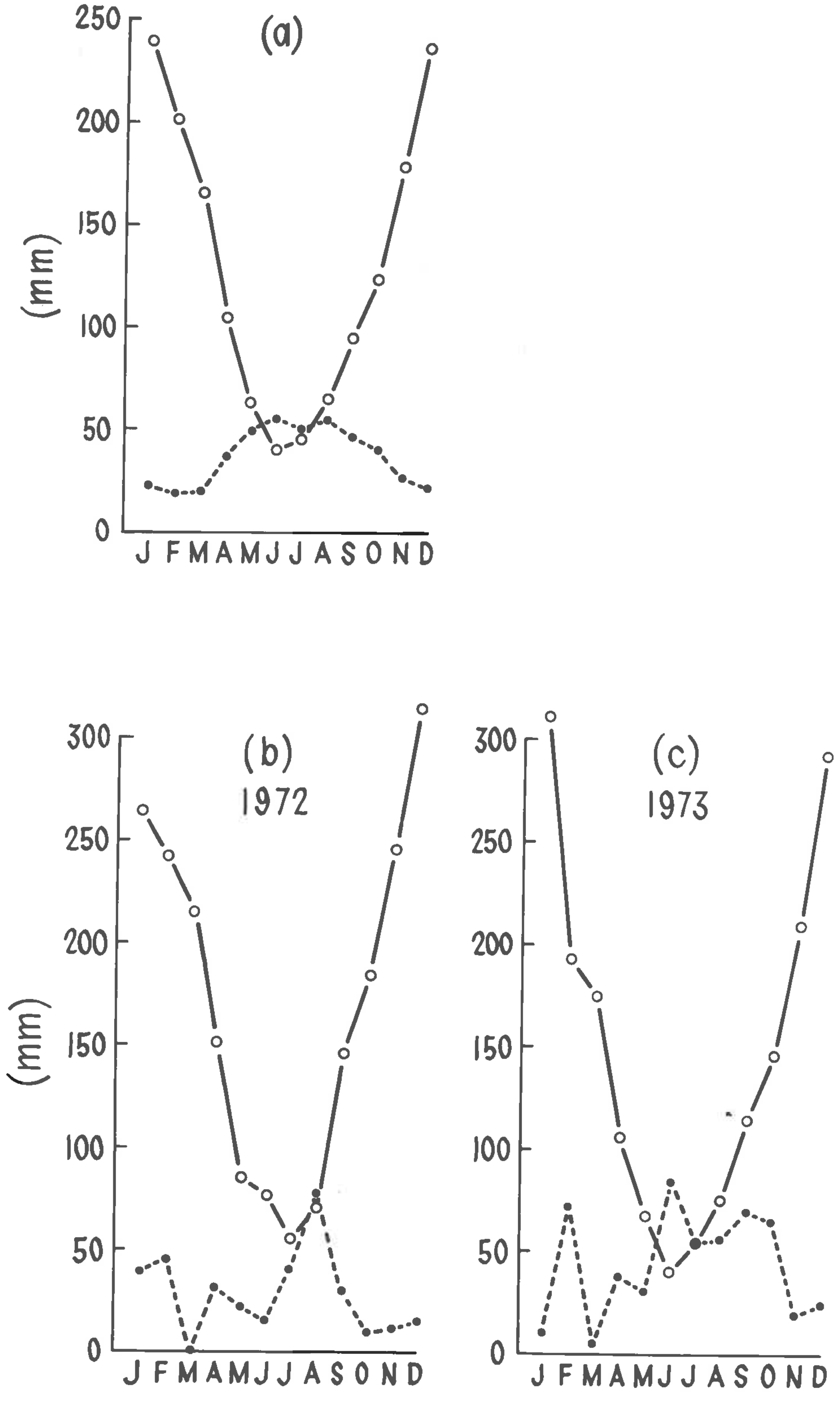

(a)
250
200
150
100
50
0
(mm)
J F M A M J J A S O N D
(b)
1972
300
250
200
150
100
50
0
(mm)
J F M A M J J A S O N D
(c)
1973
300
250
200
150
100
50
0
J F M A M J J A S O N D

Table 6. Mean monthly maximum and minimum air temperature (^{o}C) 1931-1971 and 1972 and 1973.

Source: Roseworthy Agricultural College records.

Month	1931-1971		1972		1973	
	Maximum	Minimum	Maximum	Minimum	Maximum	Minimum
January	28.3	14.3	28.2	15.0	31.8	18.7
February	28.2	14.2	29.6	16.3	28.9	16.2
March	26.2	12.6	25.9	12.1	26.1	14.4
April	21.8	10.6	24.3	11.9	23.4	12.2
May	19.5	8.5	20.4	8.8	19.8	9.6
June	15.1	6.5	17.9	5.4	13.3	6.8
July	14.2	5.8	14.4	7.6	15.8	6.8
August	15.4	6.0	16.1	7.5	16.1	7.3
September	18.1	6.9	19.8	7.8	18.8	8.8
October	25.2	8.6	22.5	9.2	21.9	10.6
November	24.4	11.2	25.2	11.0	24.7	11.6
December	26.7	13.7	28.8	14.0	28.2	15.7

and hard when dry. The red brown B_1 horizon overlay a B_2 consisting of a light brown, calcareous loam grading into a light brown, calcareous clay loam. In trench I and II the B_2 horizon contained concretions of calcium carbonate. The concretions occurred in clusters of discrete nodules, the abundance of nodules increasing with depth within the range 15 to 25 cm. The calcareous horizon overlay a red brown to yellow clay C horizon having a coarse blocky structure, the peds showing well developed skins.

3.3.4 Preliminary observations on root distribution of wheat in the field, 1972

3.3.4.1 Objective

The aim was to measure the spatial distribution of different kinds of root axes.

3.3.4.2 Methods

Wheat, cv. Halberd, was sown 5 cm deep in rows 18 cm apart at 55 kg per ha on July 17, 1972 in fields N_5 and W_5. The location of these fields, the area of which was 80 ha each, is shown in Fig. 24. "Buctril M.A." was applied as a pre-emergence weedicide at a rate of 1.4 l. per ha. Superphosphate was applied with the seed at sowing at the rate of 125 kg per ha.

The distribution of root axes across and along the row was measured with a pin-board technique (Blaser 1937). Three trenches, each 110 X 120 X 120 cm deep were dug on the day before sampling, at the time of flowering on October 13, 1972, and at the dough stage on

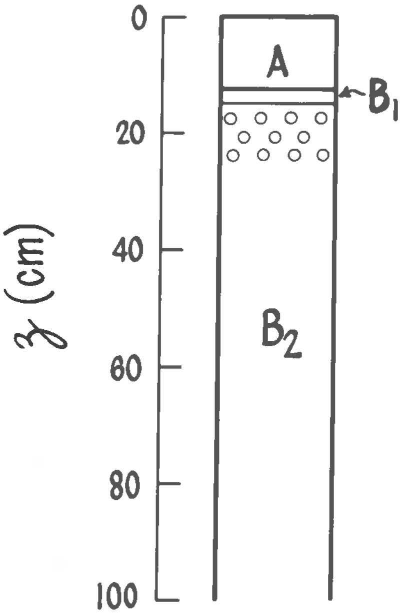
November 3, 1972. On October 13, 1972 two pin-board samples were taken per trench from trenches I, II and III, and on November 3, 1972 two were taken per trench from trenches II, III and IV (Fig. 24). At the second sampling, the pin-board samples were taken from trench IV in place of trench I, because the tractor and back-hoe used to dig the trenches had damaged the crop around trench I. The pin-boards, each 60 cm wide X 110 cm, were lined with black polyethylene sheeting. The pins were 8 cm long and 0.3 cm in diameter. They were spaced 5 cm apart on a square grid. The pin-boards were jacked into the walls of the trenches. At each trench one board was oriented in the direction normal to the plant row, and one was placed along the row. After the pins had been forced into the soil, a crowbar was used to lever off a prism of soil approximately 17 cm thick at 0 to 30 cm depth and approximately 10 cm thick from 30 to 100 cm depth. The soil prisms were brought on the pin-boards to the Waite Agricultural Research Institute, where they were stored at 1 to 2°C. Later the prisms were soaked overnight, before washing the soil away with an adjustable fine spray of water delivered from a "rose". Finally the polyethylene backing sheet together with the set of roots was lifted from the pin-board.

The following data were collected: Number of tillers per plant, number of nodal axes per plant, number of nodal axes reaching a depth of $\geqslant$ 5 cm, the maximum spread and maximum depth of the main axes of nodal roots, number of main axes of seminal roots per plant, number of main axes of seminal roots reaching a depth $\geqslant$ 12 cm, and the maximum depth of seminal roots. The soil profiles exposed in the trenches

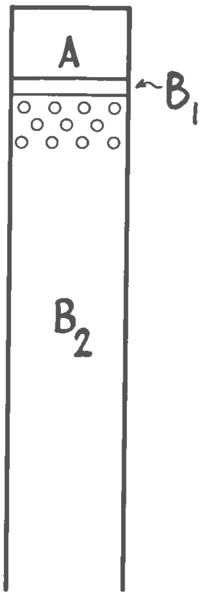
Fig. 23. Depth (cm) of soil horizons exposed in trenches I, II, III and IV.

ooo nodules of carbonate

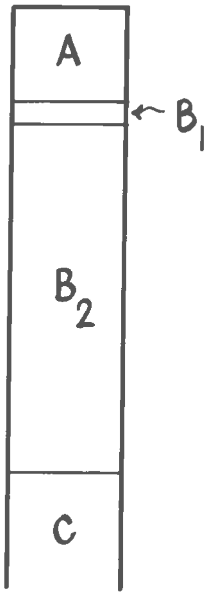
I


0
20
40
60
80
100
z (cm)
A
B1
B2

II


A
B1
B2

III


A
B1
B2
C

IV

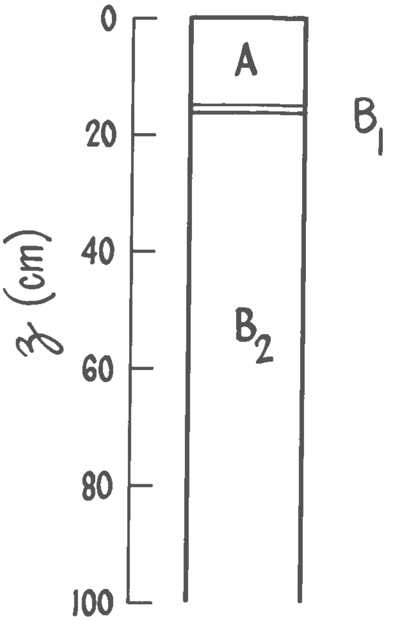
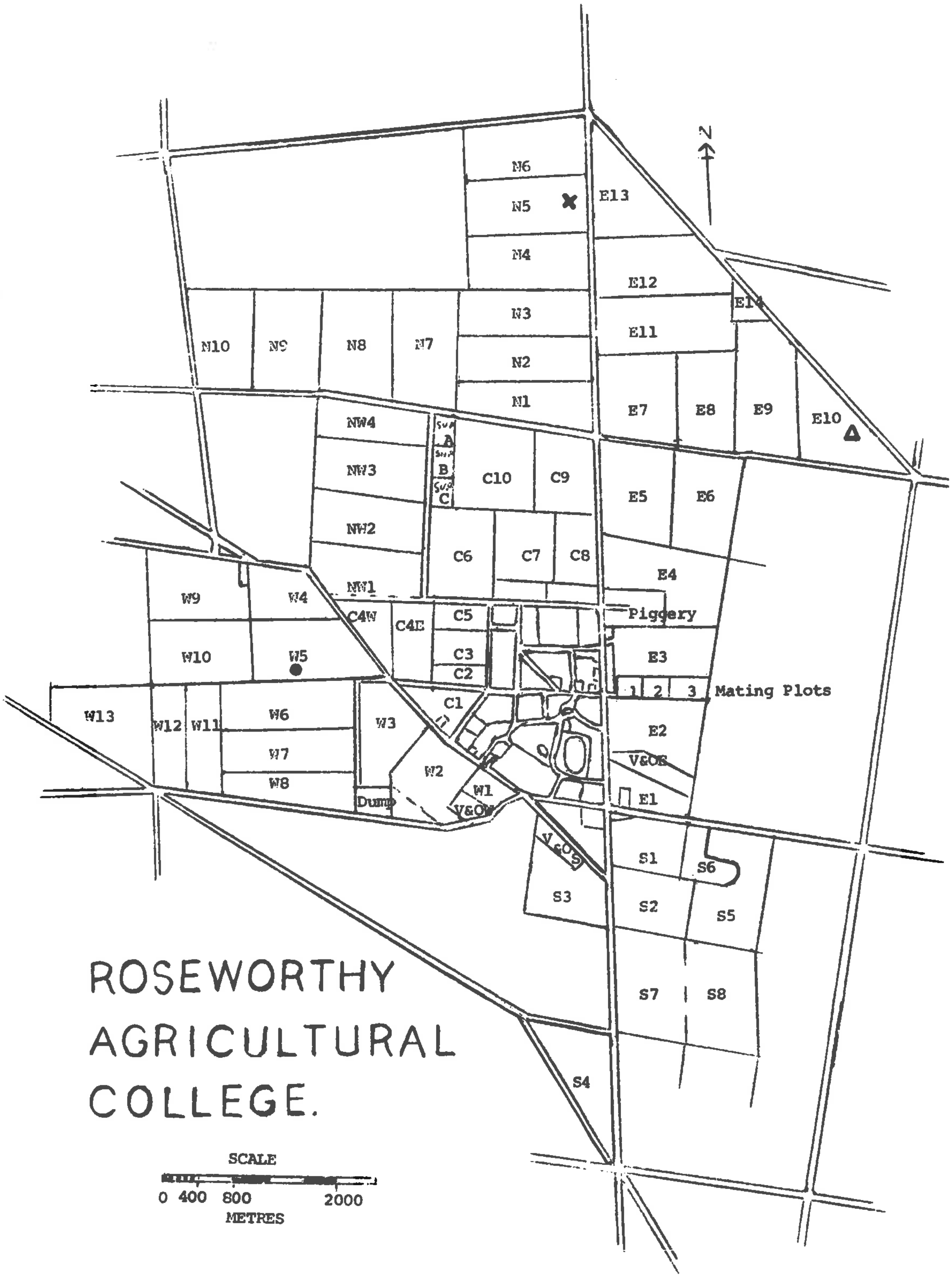

0
20
40
60
80
100
z (cm)
A
B1
B2

Fig. 24. Map showing the location of trenches (x).

x I, II and III (N_5)

● IV (W_5)

Δ Main experiment (E_{10})



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are described in Fig. 23.

3.3.4.3 Results

At flowering a total of 17 plants were present on the six soil prisms. The results are shown in Table 7. The number of tillers per plant ranged from 3 to 5. This is similar to the number recorded by Waltèr (1971) for Heron, cv. at his intermediate seeding rate (55 kg per ha) and at the same stage of growth. The number of nodal roots per plant varied from 13 to 14. This is less than the number reported by McKey (1973) for wheat plants grown in granular media in columns in a glasshouse at Uppsala, Sweden, and also less than the number reported by Pinthus (1969) for wheat grown in the field at a density of 21 to 42 plants per m^2. The maximum spread of nodal roots was 18 cm. No significant difference in spread was detected between the two principal directions - along and across the row. The spread was less than the value of 40 cm found across the rows by Walter in 1971 at flowering. Nodal roots penetrated less than 40 cm deep. This agreed with results obtained by Derera *et al.* (1969) for wheat grown in packed soil columns and exposed to dry conditions. This depth is similar also to that reported by Weaver (1926), Simmonds and Sallans (1933), and Pavlychenko and Harrington (1934) for wheat varieties growing in dry conditions.

The number of seminal roots per plant varied from 4 to 6. Only one or two of these seminal roots grew deeply, namely the radicle and one or two of the first pair of seminal roots.

Table 7. Root geometry of wheat cv. Halberd at Roseworthy Agricultural College in 1972.

a) At flowering

	Mean ± Standard deviation
Number of tillers per plant	4.1 ± 1.6
Total number of nodal roots per plant	13.8 ± 4.8
Number of nodal roots (depth ⩾ 5 cm) per plant	5.2 ± 2.8
Lateral spread of nodal roots (cm)	11.4 ± 5.4
Depth of nodal roots (cm)	18.0 ± 6.6
Total number of seminal roots per plant	5.4 ± 0.6
Number of seminal roots (⩾ 12 cm deep)	2.4 ± 0.8
Maximum depth of seminal roots (cm)	> 75 < 100
Number of plants examined	17

b) At dough stage

Number of tillers per plant	3.3 ± 0.8
Total number of nodal roots per plant	15.1 ± 3.6
Number of nodal roots (depth ⩾ 5 cm) per plant	5.7 ± 3.7
Lateral spread of nodal roots (cm)	14.0 ± 4.3
Depth of nodal roots (cm)	11.8 ± 5.6
Total number of seminal roots per plant	5.2 ± 0.5
Number of seminal roots (⩾ 12 cm deep)	2.8 ± 0.5
Maximum depth of seminal roots (cm)	> 100
Number of plants examined	26

Further samples were examined at the dough stage when 26 plants were present on the six prisms sampled on this occasion. The results are given in Table 7. The total number of nodal roots had increased slightly, as had the maximum lateral spread of the nodal roots. The maximum depth reached by the seminal roots had increased.

3.3.5 Main experiment - Effects of seeding rate and water supply on root distribution in the field

3.3.5.1 Objectives

This experiment was performed to study the influence of seeding rate and water supply on the root distribution of wheat in the field. When combined with the data on conductance of root segments, information on root system geometry may enable us to estimate the resistance offered by the root network to the upwards flow of water.

3.3.5.2 Description of the soil

As in the preliminary experiment, the soil was a sandy red brown earth, classified as Dr. 2.2.3 (Northcote 1965). The depth of the soil horizons in each replicate is shown diagrammatically in Fig. 25, and the morphology of the horizons is shown in Fig. 26. The nature of each horizon was similar to that described in the preliminary experiment, and the sequence of soil horizons was uniform in the three replicates of the experiment - replicates I, II and III. In replicate I, the C horizon lay nearer the surface than in replicate II, where in turn the C horizon lay nearer the surface than in replicate III. In

Fig. 25. Mean depth of soil horizons (cm). The vertical bars represent the standard deviation (cm).

ooo ooo nodules of carbonate

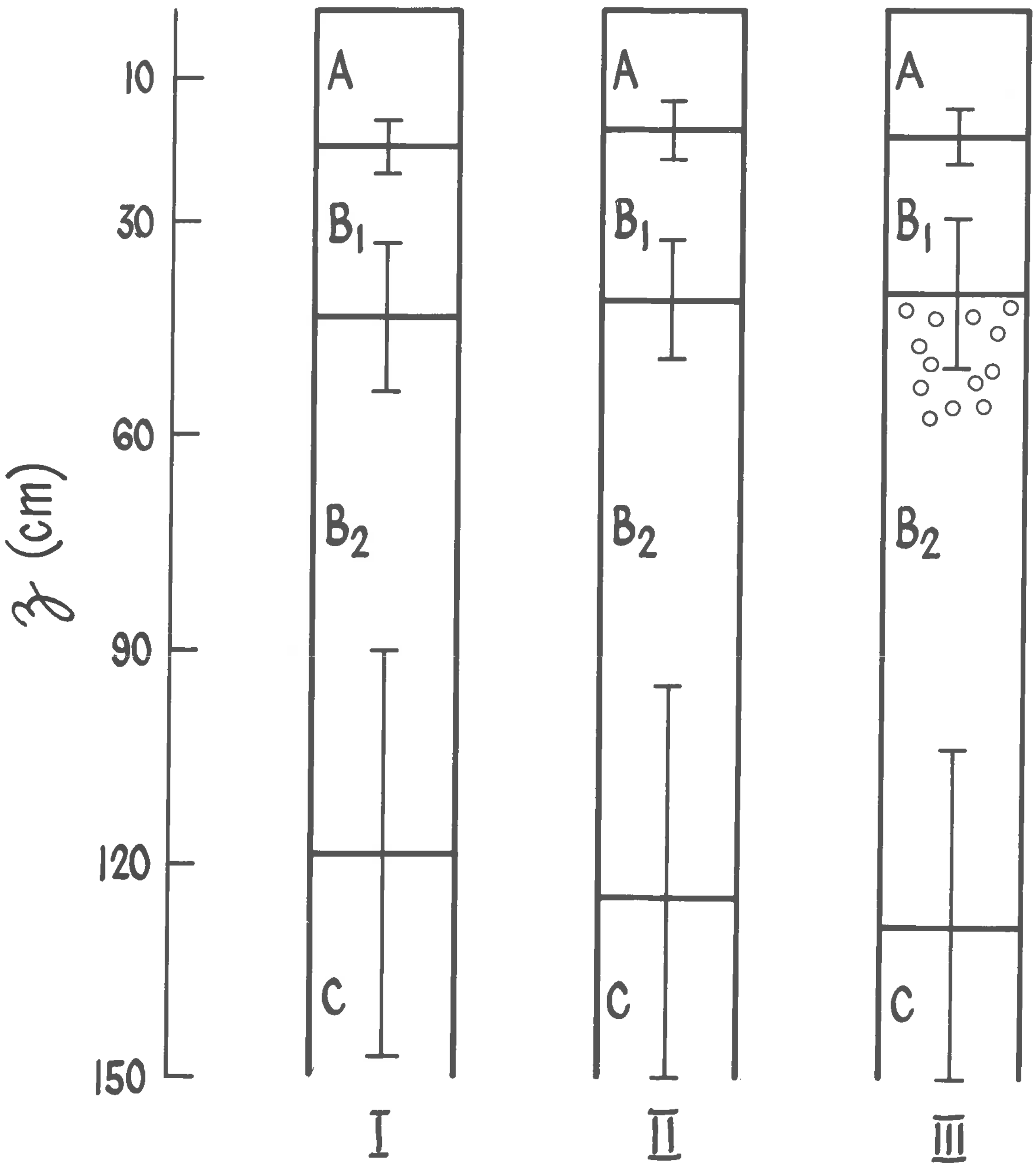
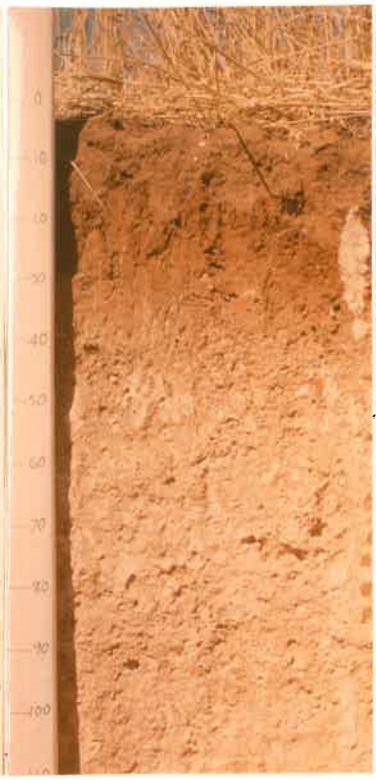
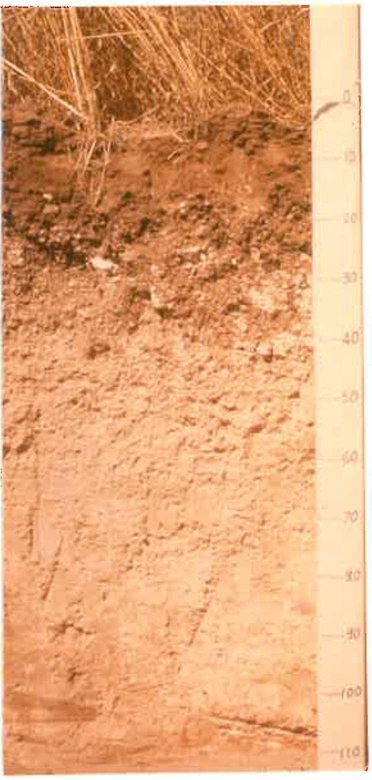

10
30
60
90
120
150
z (cm)
A
B1
B2
C
A
B1
B2
C
A
B1
B2
C
I
II
III

Fig. 26. Photographs showing the morphology of the soil profile in replicates I, II and III.

I



II



III

replicate III patches of nodular carbonate concretions occurred within the B_2 at 30 to 60 cm depth. The mean depth and standard deviation of the depth of each soil horizon were calculated from data obtained on 36 core samples. These cores were located along the lines indicated at a, b and c in Fig. 28, six cores being taken per sub-plot.

3.3.5.3 Climatic data

A class A pan evaporimeter, 120 cm diameter, and a rain gauge, 20 cm diameter, were installed adjacent to the experimental site as shown in Fig. 27. The potential evaporation and rainfall were measured weekly before irrigation began and more frequently thereafter. The weekly totals were closely similar to weekly totals for the Roseworthy Agricultural meteorological station located 5 km from the experimental site. The total rainfall during the months in which growth occurred (July to November) was 288 mm. This was higher than the mean July to November rainfall for the previous 42 years (211 mm), and considerably higher than the July to November rainfall in 1972 (170 mm). Monthly rainfall and pan evaporation during 1973 are shown in Fig. 22. The mean maximum and minimum air temperature for each month in 1973 are given in Table 6.

3.3.5.4 Methods

i) Experimental design

The experiment had a factorial 3 X 2 split plot, randomized block design. The blocks were replicated 3 times, with irrigated and non-irrigated treatments as main plots and seeding rates as sub-plots. The layout of the plots is shown in Fig. 27 and the location of the experiment is shown in Fig. 24. Adjacent fields were also sown with cereals. The three seeding rates were 10, 55 and 280 kg per ha, and these are denoted subsequently as S_1, S_2 and S_3. Seed of the cultivar Halberd was planted on July 13, 1973. The seed was sown 5 cm deep in rows spaced at 18 cm intervals. The row directions were north-south. The non-irrigated and irrigated treatments are denoted I_0 and I_1. Three centimetre of water was applied whenever the net evaporation $\Sigma(E_0 - I) = 3.0$ cm, where E_0 (cm) is the daily pan evaporation, and I (cm) is the daily precipitation. Four sprinklers were located 180 cm above ground at the corners of the irrigated main plots. The Monsoon jets deliver water uniformly over each plot when water is pumped at 2.3 bar pressure, provided wind velocity is less than 14 km per hour (Culver and Sinker 1966). The I_1 plots were watered four times after tillering on October 5 to 6, 15 to 17, 30 to 31, 1973 and on November 1, 9 to 11, 1973, the rate of application being 0.25 cm per hour.

All plots received 250 kg per ha of superphosphate containing 20 kg of P. The superphosphate was harrowed into the top 5 cm before sowing. Nitrogen was also applied uniformly over the experiment. The nitrogen was broadcast as urea in the period before stem extension on August 17, 1973 and on September 7, 1973 at the rate of 10 kg of N per ha on each occasion. A solution of a nematicide "Nemacur P" emulsifiable concentrate containing 43.6 percent W/V (ethyl 4-(methylthio)-

m-tolyl isopropyl-phosphoramidate)(1) was sprayed on the surface of the soil on May 4, 1973 at a rate of 0.77 l. per ha, to control the nematodes *Heterodera avenae* Woll. and *Pratylenchus minyus* Sher and Allan, which were known to be present in the area. As stem rust *Puccinia graminis* Pers. f.sp. *tritici* Eriks & Henn. attacked the wheat at the dough stage, "Plantvax" (Oxycarboxin) was supplied as a spray at a rate of 0.05 l. per m^2 (Hagborg 1972) on November 2, 1973.

ii) Measurements of crop growth

a) Establishment

A one metre wide border was left at each side and at the ends of each plot(2). The number of established plants was counted on rows chosen using random numbers of each sub-plot. A length of row was counted along each of four rows, the lengths being 2.5, 1.0 and 0.20 m at S_1, S_2 and S_3 respectively. The counted length was randomly located along each randomly chosen row within the sampling area.

b) Number of tillers per plant, number of seminal roots per plant, and number of nodal roots per plant

Except on S_1, where there were only one or two plants per prism, and where all plants were examined at each sampling, the number

---

(1) Made by Bayer Australia Ltd.

(2) Establishment counts were made on the 20 X 6.67 m sub-plots shown in Fig. 27, before the nitrogen treatments were applied in the experiment conducted by K.V. Parameswaran.

Fig. 27. Layout of the experiment.

θ	sprinkler
▨	sampling area for this experiment
▯	sampling area for independent[1] experiment
x	rain gauge
Δ	class A pan evaporimeter

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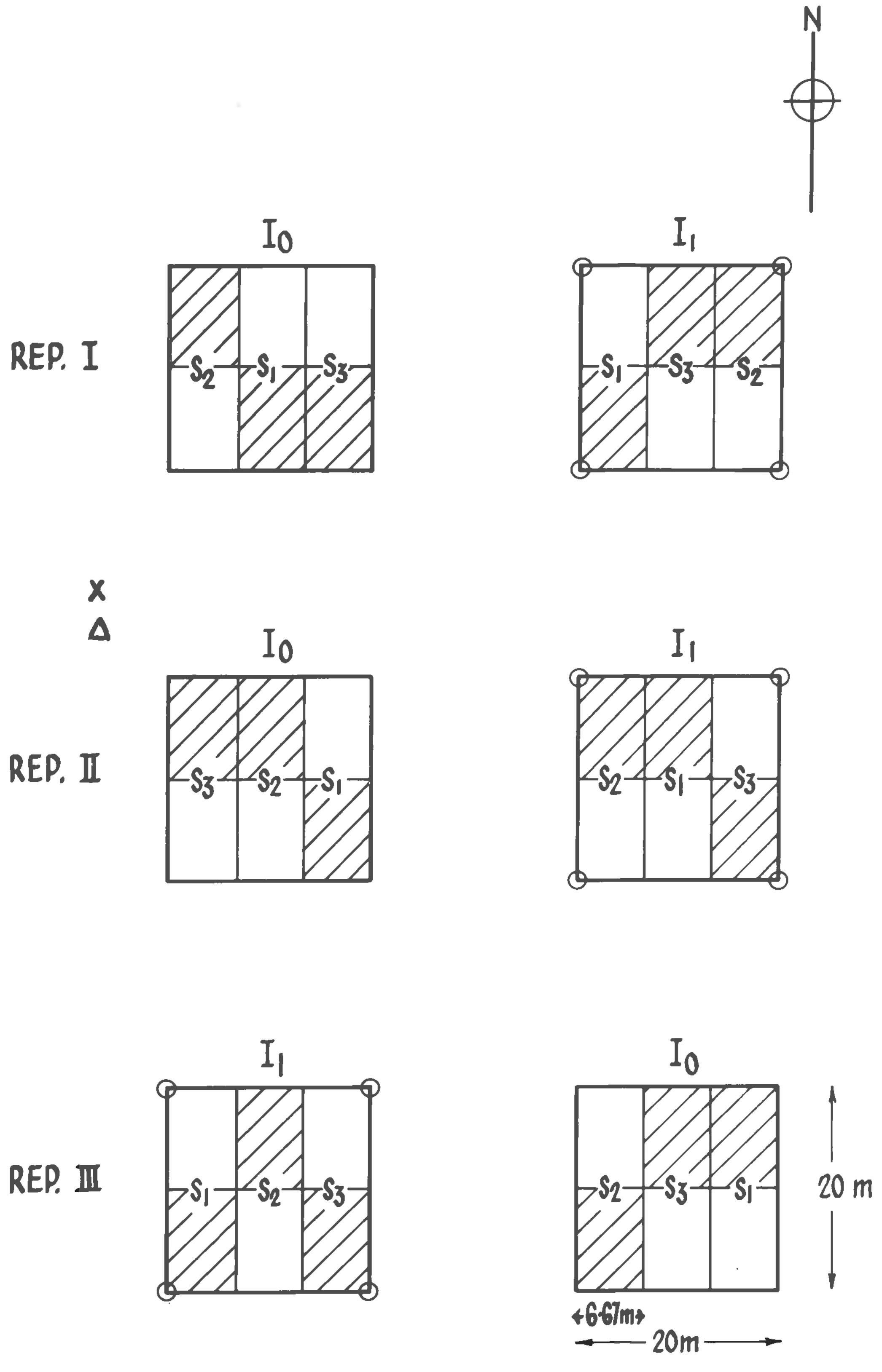
(1) The layout was shared with an independent experiment on time of application of N conducted by K.V. Parameswaran.

N
I0
I1
REP. I
S2
S1
S3
S1
S3
S2
X
Δ
I0
I1
REP. II
S3
S2
S1
S2
S1
S3
I1
I0
REP. III
S1
S2
S3
S2
S3
S1
20 m
6·67m
20m

of tillers per plant, the number of seminal roots per plant and the number of nodal roots per plant were counted on three plants from the set present on each soil prism. These plants were chosen at random. At least 18 plants were examined per sampling for each sub-treatment. There were two times of sampling, one at anthesis 15 weeks after sowing - October 22, 1973 - and one at the dough stage 19 weeks after sowing - November 19 to 23, 1973. The seminal roots counted included the radicle, 1st pair, and, where present, the 2nd pair, and the 6th seminal root. The nodal roots counted included any roots arising from the coleoptile node as well as those arising from the nodes of the stem. The roots were counted at their points of origin.

c) Yield of tops

The dry weight of tops was determined after cutting 3 X 1 m rows within the half of each 10 X 6.7 m sub-plot remaining after excavation of the soil prisms. Rows to be harvested were chosen using random number tables. A 1.5 m border was left on each side and at the end of each sub-plot as shown in Fig. 28. The dry weight of tops was determined after drying at 85°C for 24 hours. Two harvests were made, the first at the dough stage on November 18, 1973, and the second at maturity on December 11, 1973. At maturity the total dry weight of grain, the mean weight per grain, and the number of seeds per square metre were also determined.

Fig. 28. Sampling areas within sub-plot,

——— a, b and c sampling lines for soil cores.

□ trench

▯ pin-boards[1]

▤ sampling area for measurement of yield of tops

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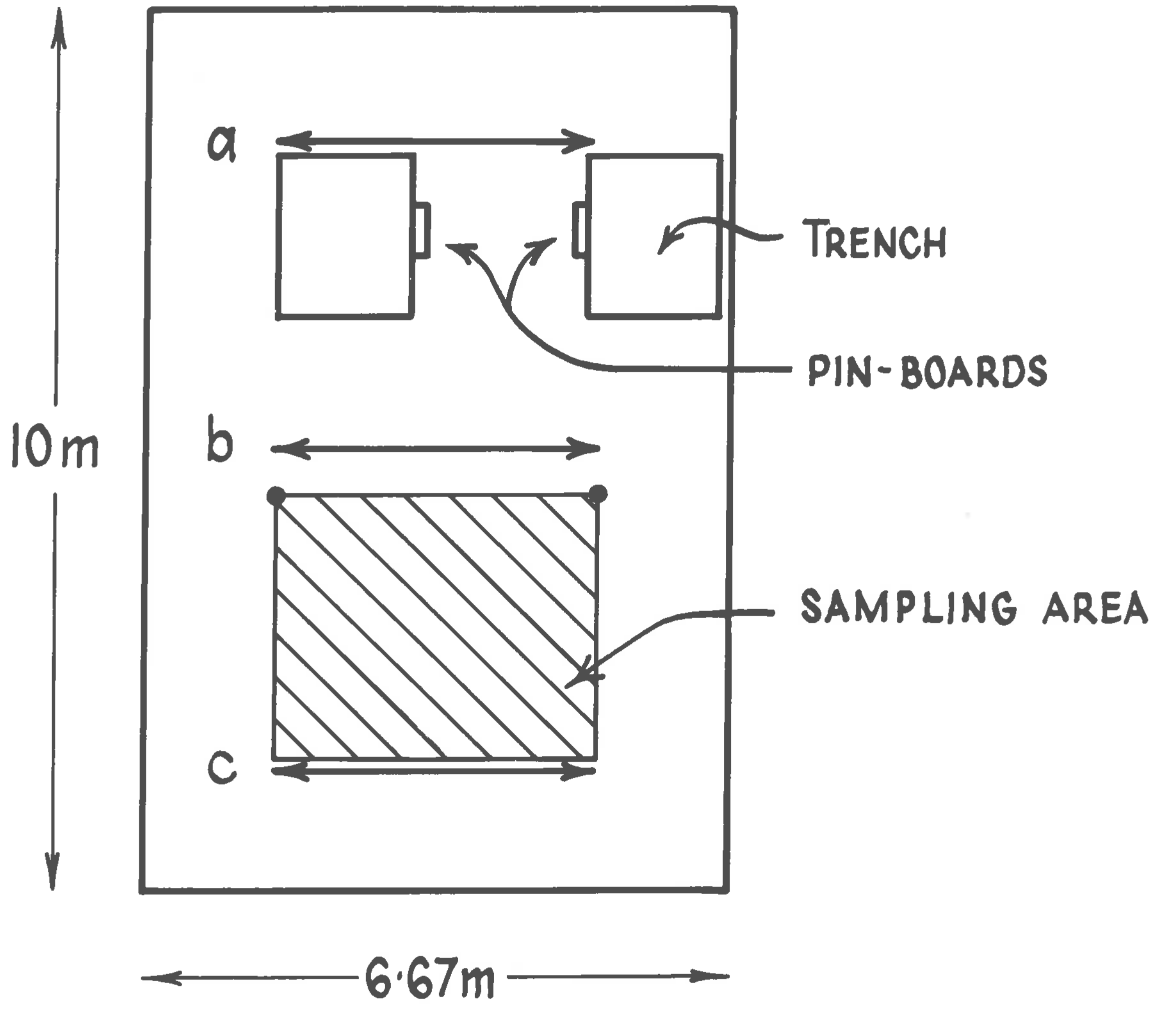
(1) S_2 and S_3 were sampled as shown in Fig. 28, but on S_1 two pin-boards were located side by side in the middle of the trench face.


a
TRENCH
PIN-BOARDS
b
10m
SAMPLING AREA
c
6·67m

iii) Measurement of root geometry

a) Number of root axes at various depths

A back hoe powered by a tractor was used to excavate the trenches needed for the pin-boards. One trench was excavated on each sub-plot at flowering, and one at the dough stage. One trench was dug towards the edge of the sub-plot and one was located more centrally (see Fig. 28) the position used at flowering being chosen randomly. Both trenches were located 1.5 m from the north or south end of each sub-plot, the end being chosen using random numbers. The trenches were 1.5 m wide by 2 m long by 1.5 m deep. The trenches were dug on the day before inserting the pin-boards and extracting the soil prisms. After the pin-boards and soil prisms had been extracted on each occasion, all faces of the trenches were covered with black polyethylene sheet to prevent evaporation.

Pin-boards were used to extract soil prisms at flowering 15 weeks after sowing on October 22 to 29, 1973, and at the dough stage 19 weeks after sowing on November 19 to 23, 1973. A single prism was extracted per sub-plot except at S_1, where two soil prisms were taken on each occasion. The prisms were always oriented parallel to the plant rows. The procedure was similar to that described in Section 3.3.4.2, and is illustrated in Fig. 29A, B.

Before washing, each prism was levelled from side to side and the width of the prism was measured at 30, 60 and 90 cm depth. After the soil had been washed away, the polyethylene backing sheet and roots were lifted from the pin-board. Fig. 30 shows a set of roots

Fig. 29. Extraction of a soil prism.

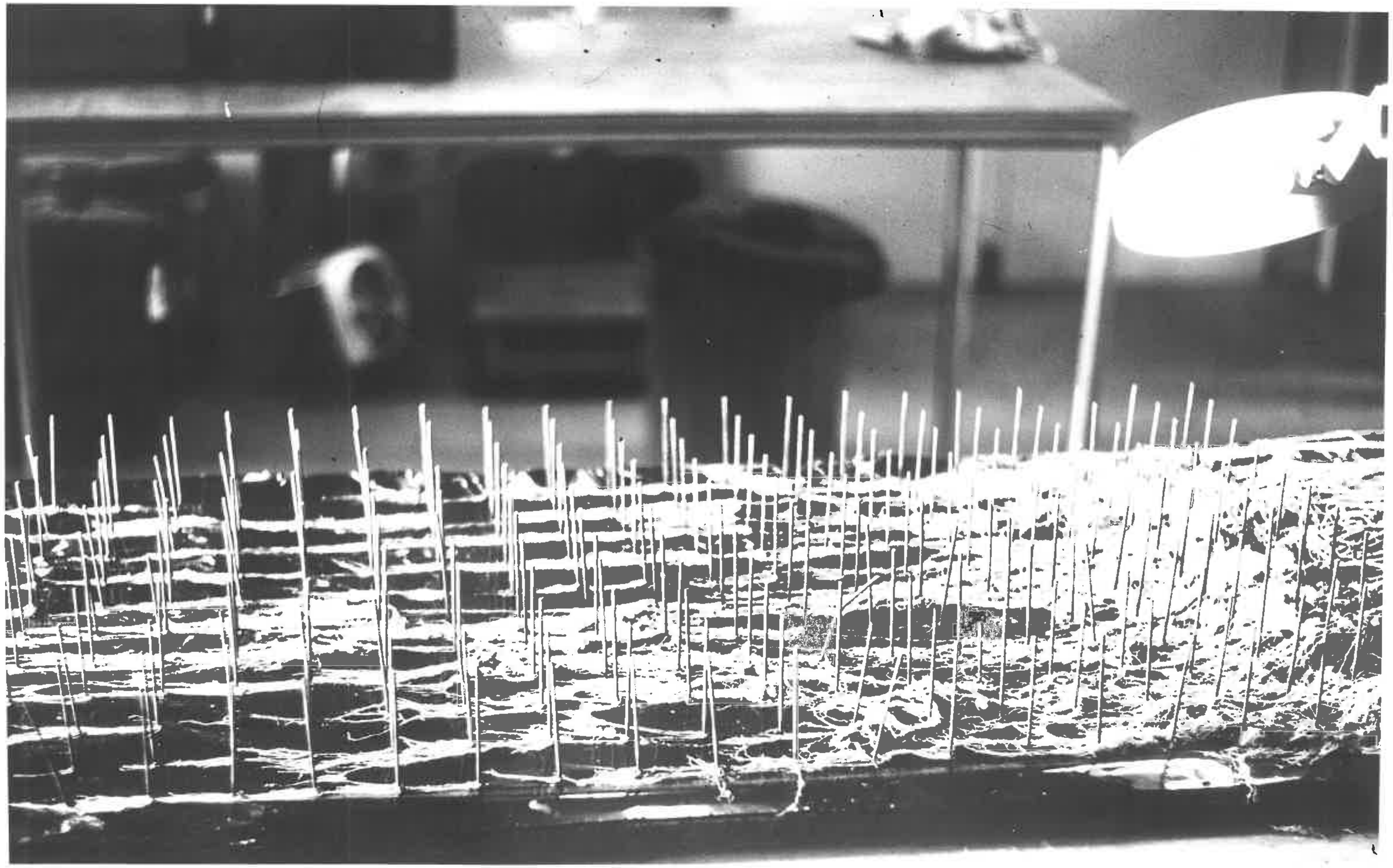
A) Jacking the pin-board into the trench face

B) Cutting and levering the soil prism away from the trench face


A


B

Fig. 30. Set of roots on a pin-board (x $\frac{1}{10}$); treatment I_0, S_2.



as displayed on a pin-board. Counts were made of the total number of axes at 30, 60 and 90 cm depth, and of the number of 1st order laterals having a large (> 10 cm) vertical component centred on the depths 30, 60 or 90 cm. The total counts of axes were converted to number per square metre N using the equation

$$N = \frac{n \times 10^4}{w_1 \times w_2} \qquad (45)$$

where at any given depth N is the number of axes per square metre, n is the number of axes counted per prism, w_1 is the thickness (cm) and w_2 (cm) is the width of the prism.

The number of axes of each class was also counted on each plant at the points of origin of the axes as described in Section 3.3.5.4 (II, b).

b) <u>Radius of metaxylem vessels at various depths</u>

After counting, 2.0 cm long segments were cut from each axis. Segments were cut at 30 to 32, 60 to 62 and 90 to 92 cm depth. The segments were immediately transferred to F.A.A. fixative, prepared as described in Section 3.2.4. Three sections were cut per segment.

Where the metaxylem vessel was not circular in cross-section, the maximum and minimum radii, r_1 and r_2, were measured. The arithmetic mean $r_1 + r_2/2$ was calculated and used to represent the radius. This procedure was applied to approximately one in seven seminal vessels, and to one in five nodal vessels. It would have been better to determine the cross-sectional area A of these non-circular vessels and to obtain an equivalent radius $r = \sqrt{A/\pi}$. However, this was not thought to be necessary, in view of other uncertainties in the data. Arithmetic means of the vessel radii measured on the three sections of each segment were then calculated. Where more than one metaxylem vessel was present, the equivalent radius r_e was calculated from Eq. (42). Segments from ten roots were generally measured per soil prism at each depth. These 10 root members were chosen at random from the set of vertical root members at each depth except at 90 cm depth, where, when a prism yielded less than 10 roots, all segments were counted.

c) Occurrence of nodal roots at various depths

Nodal roots, excluding those arising from the coleoptile node, were identified upon examination of the transverse sections used in measuring vessel radii. The anatomy of nodal roots differs from that of the seminal roots, as described previously in Sections 3.2.6.1 and 3.2.6.3 and as shown in Figs. 14 and 18. Sections were available at the flowering and at the dough stages. On each occasion root segments were obtained for sectioning from a total of 22 soil prisms at S_1 and 11 prisms at S_2 and S_3. As noted above 10 segments were generally sectioned at each depth.

d) Rooting density L_v, and percentage of root length bearing root hairs

Measurements were made only at anthesis 15 weeks after sowing on October 23, 1973. Three core samples were taken from each sub-plot at 0 to 5, 5 to 10, 10 to 15, 15 to 25, 25 to 50, 50 to 75 and 75 to 100 cm depths. The procedure used to take the samples is described in Section 3.3.5.4 (iv, c). The samples were bulked for each sub-plot and depth. Later the soil was air-dried and crushed in a Cristy and Norris mill, and sub-samples were taken for measurement of L_v. The weight of the sub-sample varied from 20 to 200 g depending on the rooting density. The mill cut the roots into short - < 2 cm - lengths.

Macro-organic matter was separated from fragmented soil by a stirring and decantation method similar to that described by Barley (1955). After the soil had been soaked in 500 cc of "Calgon" solution (200 g per l.), it was stirred rapidly with a Bouyoucos high speed stirrer for 30 sec. The suspension was allowed to stand for 1 minute, after which the material remaining in suspension was decanted onto a 0.25 mm aperture sieve. Further water was added to the sediment, and the procedure was repeated three times. Macro-organic matter was washed from the sieve onto a 5 cm X 5 cm flat dish that had been marked with a square grid. Then the macro-organic matter was spread out evenly.

The length of root in each sub-sample was determined using the intercept counting method of Newman (1966). At each of 100 positions on the grid, the number of intercepts made by a hair line in the eyepiece of a microscope with the longitudinal axes of root segments was recorded. A binocular microscope was used at a magnification of X 20. The total length of root L in the separate is given by:

$$L = \pi NA/2nl \qquad (47)$$

where N is the number of intercepts between the hair line and the axes of the root segments; A (cm^2) is the plan area of the dish (5.0 cm X 5.0 cm); n is the number of transects (100); and l is the length of the transect (0.10 cm).

The rooting density - L_v - root length per unit volume of soil is given by:

$$L_v = L \, . \, \rho_b/W_s \ (cm^{-2}) \qquad (48)$$

where W_s is the dry weight (g) of soil per determination, and ρ_b is the bulk density. Determinations were made in duplicate.

The percentage of hair bearing root was determined using a composite sample of soil prepared by bulking the milled samples from the three replicates for each depth. The same procedure as that described above was used to separate macro-organic matter. A total of 64 transects were counted located in the central part of the flat dish, root intercepts without root hairs and with hairs being counted separately. The percentage of the total length of root bearing hairs is $\frac{n_h}{n_t}$ X 100 where n_h is the number of intercepts made with the longitudinal axes of root segments bearing root hairs, n_t is the total number of intercepts between the transects and the axes of root segments, both with hairs and without hairs. Finally, L_H, the hair bearing root length per unit volume of soil (cm^{-2}) was calculated from the relation $L_H = L_v \times \frac{n_h}{n_t}$.

iv) Measurement of soil water content at various depths

a) First sampling

On the first occasion on May 16, 1973, the soil was sampled using a tube described by Stace and Palm (1962). The tube had an I.D. of 4.3 cm. Cores were taken from 0 to 5 cm, 5 to 10 cm, 10 to 15 cm, 15 to 25 cm, 25 to 50 cm, 50 to 75 cm, and 75 to 100 cm depth. To characterise the site twelve cores were taken in the areas between the blocks. The samples were taken from these areas to prevent compaction of the soil on the plots by the truck carrying the core-drilling and extracting apparatus. On this occasion the sampler was driven in and extracted hydraulically. Gravimetric water content was determined as described in Section 2.2.1.2. Values of ρ_b for successive depths were found from the dry weight and core dimensions. The volumetric water content θ was calculated using Eq. (20), substituting values of W and ρ_b for each depth interval.

b) Second sampling

Samples were taken within the experimental area between September 11 and 19, 1973 before the crop was at the stage of stem extension. The same tubes were used as at the first sampling, but on this occasion they were driven in with an electrical jack-hammer. Three cores were taken per sub-plot, one core at a point along line a, one at b, and one along line c where shown in Fig. 28. Each core was again taken to 100 cm depth, but in an attempt to reduce variability at the second sampling, each core was divided into A_1, B_1, B_2 and C horizons. As this procedure did not significantly reduce the variability, the simpler method of sampling by fixed depths was again used in later samplings. When the depth of any horizon exceeded 25 cm, the horizon was divided into two equal lengths. The depth of each core sample was recorded, and W was determined as in Section 2.2.1.2. The arithmetic mean of ρ_b was found for each soil horizon from the dry weight and core dimensions. θ was calculated using Eq. (20).

c) Third sampling

This sampling was conducted at flowering, on October 23, 1973. As at the first sampling, an hydraulic jack was used to drive and to extract the Stace and Palm tube. To avoid driving the prime mover onto the plots, the cores were taken only along line a (Fig. 28), three cores being taken per sub-plot. Samples were taken at the same depths as at the first sampling, and in addition at 100 to 125 and 125 to 150 cm depth. W and ρ_b for each depth interval were measured. θ was calculated using Eq. (20). In addition to θ, values of L_V and L_H were determined on sub-samples.

d) Fourth sampling

Cores were taken at maturity on December 4 to 5, 1973. The cores were located along lines b and c (Fig. 28), three cores being taken per sub-plot. Two cores were taken along line b and one core along line c. Cores were not taken along line a, because the back hoe had previously damaged the crop in the vicinity of line a. The cores were taken with an hydraulic jack as on the first and third occasions.

3.3.5.5 Results

i) General attributes of crop growth

a) Establishment

Germination was rapid and fairly even. Establishment counts made four weeks after sowing on August 13, 1973 are shown in Table 8. The number of plants per square metre was directly related to the rate of seeding.

Table 8. Plant establishment on August 13, 1973, 4 weeks after sowing.

Seeding rate	No. of plants per square metre
S_1	26.9
S_2	136.8
S_3	594.9
L.S.D. (P, 0.05)	107.7

b) Number of tillers and roots per plant

Results are shown in Table 9. The number of tillers per plant at flowering was affected by seeding rate: $S_1 > S_2 > S_3$ (P, 0.05). Row counts were not made at flowering.

The number of seminal roots per plant did not differ significantly between the three seeding rates; however, the number of nodal roots per plant differed significantly: $S_1 > S_2 > S_3$ (P, 0.05). The sequence was reversed when the numbers of nodal roots per tiller were compared (Table 9). Irrigation had no effect on the above attributes at flowering; and there was no significant interaction of seeding rate and irrigation treatments.

Table 9. Numbers of tillers and roots at flowering on October 22 to 29, 1973.

Treatment	No. of tillers per plant	No. of seminal roots per plant	No. of nodal roots per plant	No. of nodal roots per tiller
S_1	8.1	4.8	53.6	7.2
S_2	3.4	4.6	30.6	9.0
S_3	1.1	4.6	14.5	14.0
L.S.D.(P,0.05)	1.4	N.S.	10.5	1.4

c) Number of tillers and roots, and yield of tops at dough stage

Numbers of tiller and roots are shown in Table 10 and the total dry weight of tops is given in Table 11.

Table 10. Number of tillers per plant, number of seminal roots per plant, number of nodal roots per plant and number of nodal roots per tiller at dough stage on November 19 to 23, 1973.

Treatment	No. of tillers per plant	No.of seminal roots per plant	No. of nodal roots per plant	No. of nodal roots per tiller
S_1	7.9	4.7	61.5	8.3
S_2	3.2	5.0	25.3	8.1
S_3	1.0	4.8	10.8	10.9
L.S.D. (P, 0.05)	1.8	N.S.	11.2	1.3
I_0	4.5	4.6	33.0	8.6
I_1	3.5	5.1	32.1	9.6
L.S.D. (P, 0.05)	N.S.	0.1	N.S.	N.S.

Generally, seeding rate had similar effects on the number of tillers and roots as at the flowering stage. However, the number of nodal roots per tiller ranged as follows: $S_3 > S_2 \approx S_1$ (P, 0.05). Irrigation had one statistically significant effect at the dough stage. This was to slightly increase the number of seminal roots found per plant.

The dry weight of tops ranged as follows: $S_3 > S_2 > S_1$ (P, 0.05) - Table 11. The total dry weight of tops was not affected by irrigation. There was no significant interaction between seeding rate and irrigation treatments.

Table 11. Total dry weight of tops of wheat cv. Halberd at soft dough stage on November 15, 1973.

Treatment	Total dry weight ($g . m^{-2}$)
S_1	472.8
S_2	642.2
S_3	800.1
L.S.D. (P, 0.05)	77.1
I_0	607.3
I_1	669.4
L.S.D. (P, 0.05)	N.S.

d) Yield of tops and grain at maturity

The plants ripened at different times on different seeding rate and irrigation treatments. S_3 ripened 7 days before S_2 and 10 days before S_1. At S_3 the grain was completely ripe both on I_0 and I_1 by December 4, 1973, ripening being only one or two days later on I_1 than on I_0. At S_1 and S_2 the grain on the irrigated plots ripened 5 to 6 days later than the grain on the non-irrigated plots, and not all ears had ripened completely at S_1 and S_2 on the irrigated plots at the final harvest on December 11, 1973.

The yield of tops and grain at maturity is shown in Table 12. At S_3, but not at S_1 or S_2, the total dry weight of tops decreased between the dough stage and maturity due to loss of leaf (see Tables 11 and 12). Grain yield increased with seeding rate due both to an increase in the number of grains per square metre: $S_3 = S_2 > S_1$ (P, 0.05), and to an increase in mean weight per grain: $S_3 > S_2 = S_1$ (P, 0.05). Irrigation increased the mean weight per grain and the yield of grain. There was no interaction between seeding rate and irrigation treatments.

Stem rust was first seen on November 1, 1973. Even though the crop was sprayed with "Plantvax", the degree of infestation continued to increase until harvest, rusting being greater on the later maturing plots.

ii) Root distribution and metaxylem vessel radii

a) Number of root axes and long 1st order laterals per unit ground area at various depths at flowering and dough stages

At flowering axes were counted on two replicates only. The main axes were generally vertical at depths greater than 30 cm. The first order laterals were generally short, or had only short vertical components in their path below 30 cm depth. The number of first order laterals having vertical paths ⩾ 10 cm centred on the depths examined ranged from 15 to 27 per square metre at 30 cm depth and from 45 to 51

Table 12. Dry weight of straw and flag. number of grains, mean weight per grain, grain yield, and dry weight of total tops at maturity.

Treatment	Weight straw and flag (g.m^{-2})	No. of grains (m^{-2})	Mean weight per grain (mg)	Weight of grain (g.m^{-2})	Total weight of tops (g.m^{-2})
S_1	381	7,213	12.5	90	472
S_2	488	10,030	13.7	137	625
S_3	500	9.780	16.5	160	660
L.S.D.(P,0.05)	N.S.	763	1.8	19	60
I_0	455	9,130	12.7	118	573
I_1	458	8,890	15.7	140	598
L.S.D.(P,0.05)	N.S.	N.S.	1.5	16	N.S.

at 90 cm depth. Number of axes per unit ground area at the various depths are shown in Table 13. The counts at 30 cm depth may have been underestimated due to the difficulty in separating the roots from the concretionary carbonate occurring at this depth. There was no significant difference between either seeding rate or irrigation treatments.

Table 13. Number of root axes per square metre at various depths at the flowering stage.

Depth (cm)	Seeding Rate			L.S.D. (P,0.05)	Mean	L.S.D. (P,0.05)
	S_1	S_2	S_3			
30	433	433	489	N.S.	407	134
60	369	396	557	N.S.	441	
90	133	303	231	N.S.	223	

The number of axes at 30 and 60 cm depths were significantly greater than at 90 cm depth (P, 0.05).

Mean numbers at 30, 60 and 90 cm depths are compared in Table 13.

At the dough stage axes and long first order laterals were counted on all three replicates. Results are shown in Table 14. Again seeding rates and irrigation had no significant effect at any depth. However, at 30 cm depth, the number of axes per square metre at S_3 tended to be greater than at S_2 or S_1 (P, 0.1). As at flowering, there were few laterals with vertical displacements $\geq$ 10 cm compared with the number of axes.

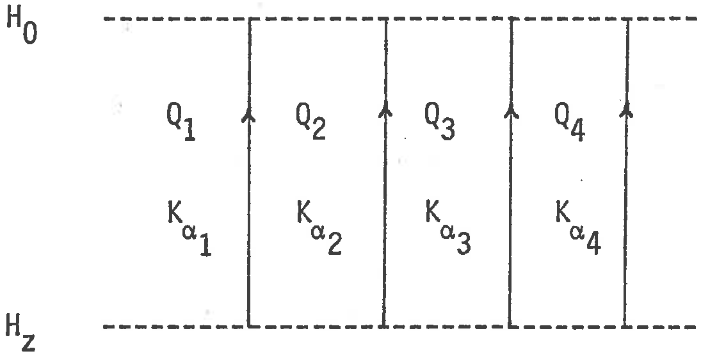
Table 14. Number of root axes per square metre at various depths at dough stage.

Depth (cm)	Seeding Rate S_1	S_2	S_3	L.S.D. (P, 0.05)	Mean	L.S.D. (P, 0.05)
30	614	634	910	N.S.	719	91
60	521	596	696	N.S.	604	
90	157	200	232	N.S.	196	

The mean numbers of axes at 30, 60 and 90 cm are compared in Table 14. By the dough stage the mean number of axes per square metre had increased at 30 and 60 cm depth, the ranking now being 30 cm > 60 cm > 90 cm (P, 0.05).

b) Mean radius r_A of metaxylem vessels at various depths

In describing the radii of the vessels it is convenient to define an appropriate mean radius. We consider flow in a set of parallel, vertical vessels. As shown in the diagram below, we assume that flow occurs between depths at which the hydraulic head is H_0 and H_z, where $H_0 < H_z$.



For a steady state (no losses or gains of water within the region bounded by H_0 and H_z)

$$Q = Q_1 + Q_2 + Q_3 + \ldots + Q_n$$

since $Q_i = K_{\alpha_i}$, per unit head gradient

$$Q = K_{\alpha_1} + K_{\alpha_2} + K_{\alpha_3} + \ldots + K_{\alpha_n}, \text{ per unit head gradient}$$

Assuming Poiseuille flow

$$K_{\alpha_i} = kr_i^4$$

where

$$k = \frac{\pi\rho g}{8\eta}$$

Therefore

$$Q = k(r_1^4 + r_2^4 + r_3^4 + \ldots + r_n^4) \tag{49}$$

also

$$Q = k(nr_A^4) \tag{50}$$

where r_A is the mean radius of a metaxylem vessel. Combining Eqs. (49) and (50)

$$nr_A^4 = r_1^4 + r_2^4 + r_3^4 + \ldots + r_n^4$$

$$= \sum_{i=1}^{n} r_i^4$$

Therefore

$$r_A = \sqrt[4]{\sum_{i=1}^{n} r_i^4/n} \tag{51}$$

Segments were obtained only from replicates I and II at the flowering stage. Neither seeding rate nor irrigation affected r_A significantly at flowering (Appendix Table 7). However, the mean value of r_A for the various treatments was less at 90 cm depth than at 30 and 60 cm depth (P, 0.05) - Table 15.

Segments were obtained from each replicate at the dough stage, when r_A was significantly smaller at 30 cm depth at S_3 than at S_1 or S_2 (P, 0.05). Data are given in Table 16. Irrigation had no effect on r_A at 30 and 90 cm depth but at 60 cm depth r_A was significantly greater on irrigated than on the non-irrigated plots (P, 0.05). As at the flowering stage r_A decreased with depth. Mean values of r_A decreased between the flowering and dough stages particularly at 30 and 60 cm depths, where the radius decreased by from 3 to 5 μm.

Table 15. Mean radius of metaxylem vessels r_A (μm) at each depth at flowering.

Depth (cm)	r_A (μm)
30	42.8
60	39.9
90	32.0
L.S.D. (P, 0.05)	5.6

Table 16. Mean radius of metaxylem vessels r_A (μm) at each depth at the dough stage.

Depth (cm)	Seeding Rate S_1	S_2	S_3	L.S.D.	I_0	I_1	L.S.D	Mean	L.S.D.
30	42.3	40.2	36.4	3.0	38.7	40.5	N.S.	39.6	
60	34.9	34.8	33.4	N.S.	32.7	36.1	1.9	34.4	2.5
90	33.1	33.2	29.3	N.S.	31.8	31.9	N.S.	30.0	

Detailed data on the radii of the vessels are shown in Appendix Table 6.

c) The occurrence of roots of each class at various depths

The occurrence of nodal roots at 30, 60 and 90 cm was inferred from the anatomy of the stele as described previously (Fig. 18). Roots arising from the coleoptile node were not included in the nodal category, because their stele had an anatomy similar to that of the stele in the seminal axes. At the nominal zero depth nodal roots were identified by their points of origin not by their anatomy, and the nodal category at zero depth here included any roots arising from the coleoptile node. The percentage of the total number of soil prisms having one or more nodal axes present at each depth is shown in Table 17.

A few nodal roots penetrated more than 90 cm deep at all seeding rates. The data were analysed using Friedman's two-way analysis of variance by ranks as described by Siegel (1956, p. 166). The analysis showed that the occurrence of nodal roots decreased significantly with depth.

Table 17. Percentage of total number(1) of soil prisms having one or more nodal roots at given depths.

Depth (cm)	Seeding Rate S_1	S_2	S_3
0(2)	100	100	100
30	59.1	45.5	27.3
60	22.7	27.3	18.2
90	13.6	9.1	9.1

(1) 22 prisms were examined at S_1 and 11 at S_2 and S_3.

(2) Counted at the base of roots.

After examining the anatomy of the stele of the segments of the axes from each depth, the number of nodal segments was calculated as a percentage of the total number of segments examined. Irrigation appeared to have no effect on the percentage of nodal roots. However the percentage of nodal roots appeared to be higher at S_1 than at S_2 or S_3. Data are given in Table 18.

Table 18. Total number of segments of axes examined, number of nodal segments, and nodal segments percent of total number at the three seeding rates.

Depth (cm)	S_1			S_2			S_3		
	Total	Nodal	% Nodal	Total	Nodal	% Nodal	Total	Nodal	% Nodal
30	219	28	13	110	4	4	110	2	2
60	219	10	5	110	2	2	110	1	1
90	129	3	2	93	1	1	99	1	1

d) Vertical distribution of L_v at flowering

The root length per unit volume of soil L_v (cm^{-2}) was determined from 0 to 100 cm depth at the flowering stage. The results are shown in Fig. 31 and in Appendix Table 8.

The values of L_v differed significantly between seeding rates at 0 to 15 cm depth: $S_3 = S_2 > S_1$ (P, 0.05). No significant differences between seeding rates were found between 15 and 75 cm depth, but, at 75 to 100 cm there was a significant interaction of seeding rate and irrigation treatments. The interaction is described in Table 19.

Table 19. Root length per unit volume of soil L_V (cm^{-2}) at 75 to 100 cm depth.

	I_0	I_1
S_1	0.4	0.8
S_2	1.5	0.6
S_3	1.2	1.0

L.S.D. (P, 0.05) = 1.0 for comparison between means of irrigation treatments at the same or different seeding rates.

L.S.D. (P, 0.05) = 0.6 for comparison of seeding rates within an irrigation treatment.

L_V decreased with depth at each seeding rate. It decreased rapidly from 0 to 15 cm, then more gradually with increasing depth.

Irrigation significantly increased L_V at 50 to 75 cm depth, the means of I_0 and I_1 being 1.96 and 2.17 cm^{-2}, L.S.D. (P, 0.05) = 0.03 cm^{-2}.

Root length per unit ground area L_A (cm^{-1}) was significantly greater at S_2 and S_3 than at S_1 (P, 0.01), but there was no significant difference between irrigation treatments. The means of L_A at S_1, S_2 and S_3 were 241.9, 341.2 and 347.6 cm^{-1}, L.S.D. (P, 0.01) = 52.2 cm^{-1}.

The percentage of the total root length bearing root hairs was also determined. Percentages are shown in Table 20. The length of hair-bearing root per unit volume of soil L_H is shown in Fig. 31. The percentage length of hair-bearing root increased with depth, increasing from 4 to 11 percent at 0 to 5 cm depth to 41 to 75 percent at 75 to 100 cm depth. Changes in L_H with depth were relatively gradual compared with the changes in L_V.

Table 20. Percentage of total length of root bearing root hairs for wheat cv. Halberd at flowering at various depths in 1973.

Depth (cm)	I_0			I_1		
	S_1	S_2	S_3	S_1	S_2	S_3
0-5	11	10	8	10	7	4
5-10	10	5	9	6	5	10
10-15	19	10	13	17	9	8
15-25	27	13	23	28	16	16
25-50	43	29	33	37	20	18
50-75	72	40	46	27	45	33
75-100	45	44	75	61	41	41

iii) Vertical distribution of soil water content θ and depletion of soil water

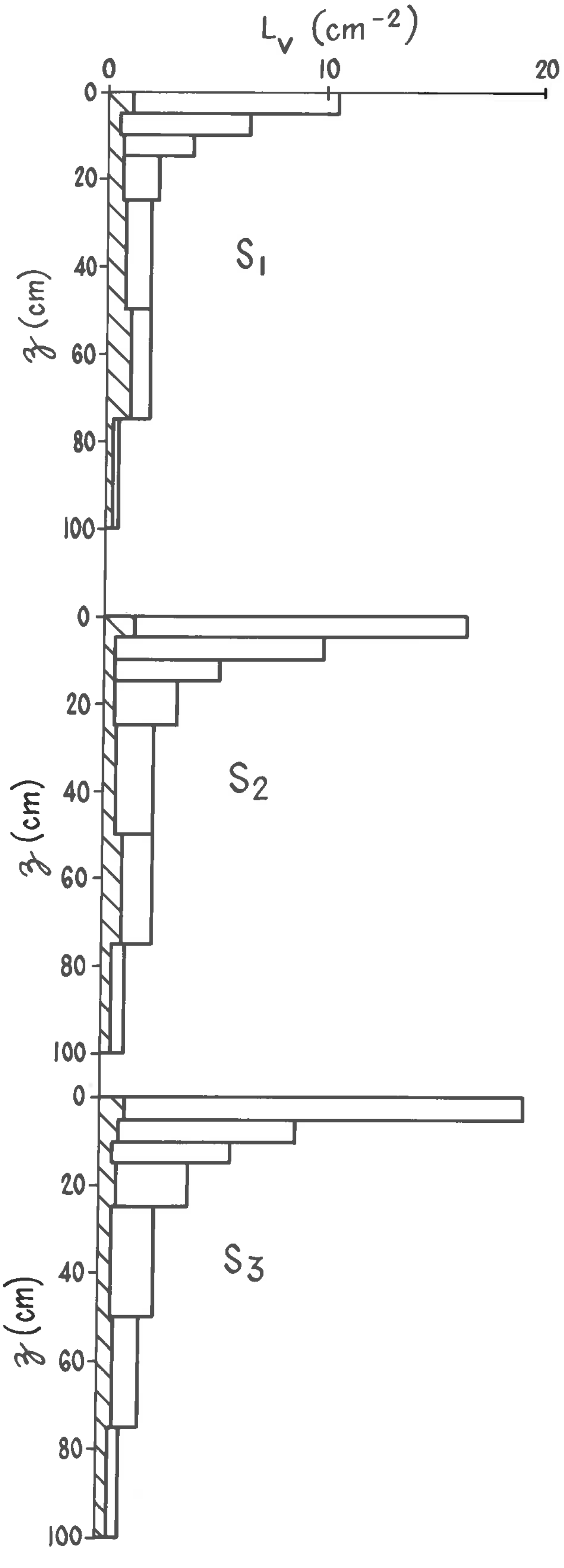
The vertical distribution of water content measured 2 months before planting on May 16, 1973 is shown in Fig. 32(1). At this time rainfall had wetted the profile to field capacity to a depth of 25 cm.

---

(1) The distribution of θ was measured in May before sowing the crop for the first time. The seedlings from the first sowing were damaged by a weedicide used as a post-emergence spray on the experimental area. The area was cultivated, and the crop was resown on July 13, 1973.

<u>Fig. 31</u>. Rooting density L_V (cm^{-2}) and density of hair-bearing roots L_H (cm^{-2}) at various depths at flowering for each seeding rate. The bars on the right hand side show the L.S.D. (P, 0.05) for L_V.

▨ L_H (cm^{-2})


L$_v$ (cm^{-2})
0
10
20
0
20
40
60
80
100
z (cm)
S$_1$
0
20
40
60
80
100
z (cm)
S$_2$
0
20
40
60
80
100
z (cm)
S$_3$

In the period between May 16, 1973 and resowing on July 13, 1973, the rainfall exceeded E_0 by 45 mm as shown in Fig. 22c. At sowing time the soil would probably have been wetted to 80 cm depth. Fig. 3~~5~~3 shows the distribution of water content on September 11 to 20, 1973 at stem extension. At this time, θ did not differ significantly between treatments at any depth. The soil was at field capacity between 20 and 100 cm depth.

From the first week of October onwards E_0 exceeded rainfall; and irrigation commenced on October 5 and 6, 1973. At flowering, 14 weeks after sowing, on October 23, 1973, the distribution of θ was again determined. At this time θ showed no significant difference between seeding rates when compared at 20, 50, 80 and 100 cm depth. At 80 cm depth, S_1 tended to be wetter than S_2 and S_3 (P, 0.10). The top metre of soil in the irrigated plots tended to be wetter than the non-irrigated at 0 to 100 cm depth (P, 0.10).

At maturity on December 4 to 5, 1973, 20 weeks after sowing, the soil tended to be wetter at 20 cm depth at S_1 than at S_2 or S_3 (P, 0.10). No differences between seeding rates were found at other depths. The crop tended to dry the soil more deeply at S_2 than at S_1 or S_3. The soil appeared to have been dried to 15 bar suction to depths of 70, 100 and 80 cm at S_1, S_2 and S_3. The irrigated plots tended to be wetter than the non-irrigated from 0 to 90 cm depth (P, 0.10).

The amount of depletion of water between stem extension and flowering tended to differ between treatments in the depth

Fig. 32. Vertical distribution of θ at the first sampling.

- - - - - - - - - - - - May 16, 1973

———————— θ at suction of 15 bar

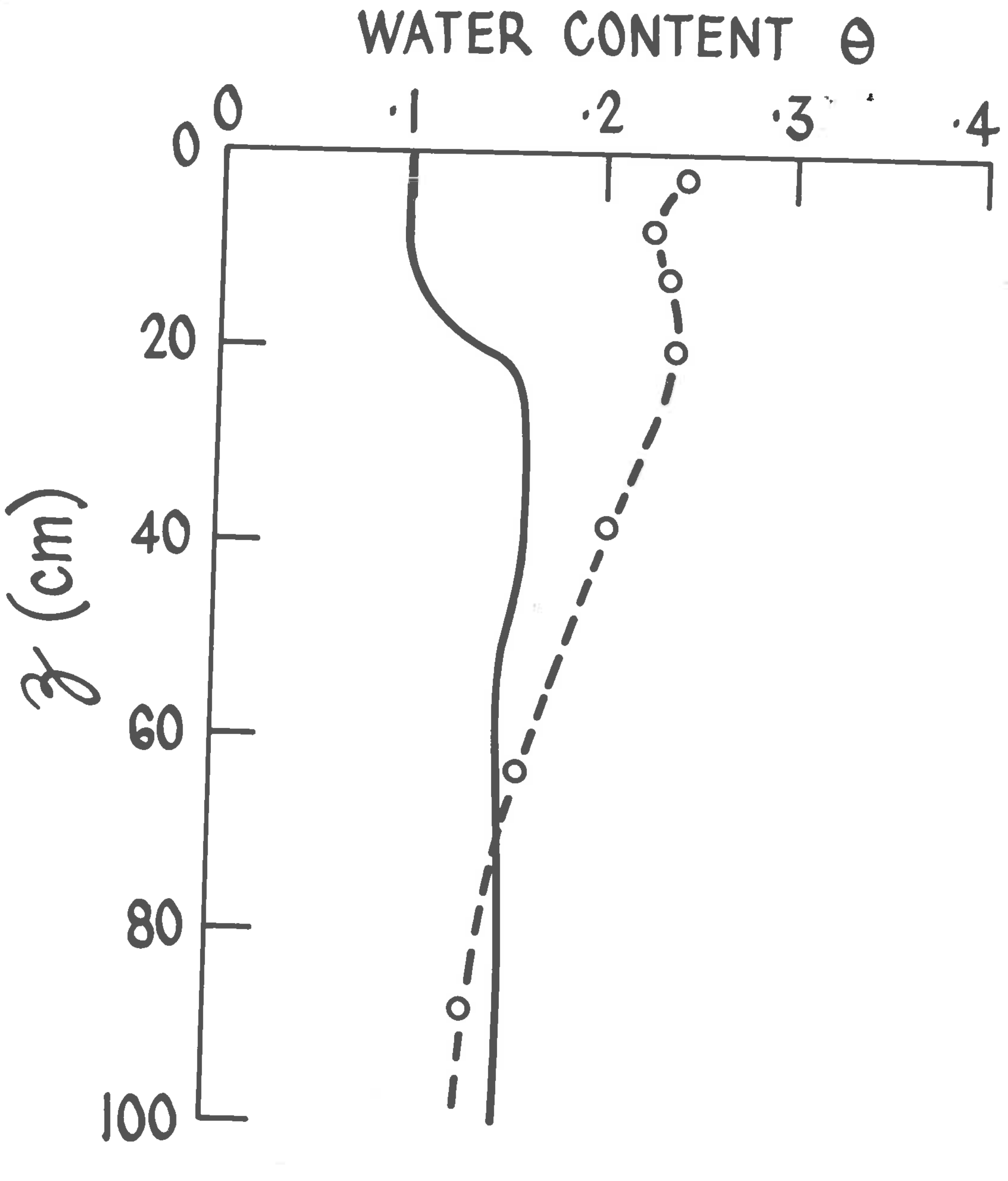
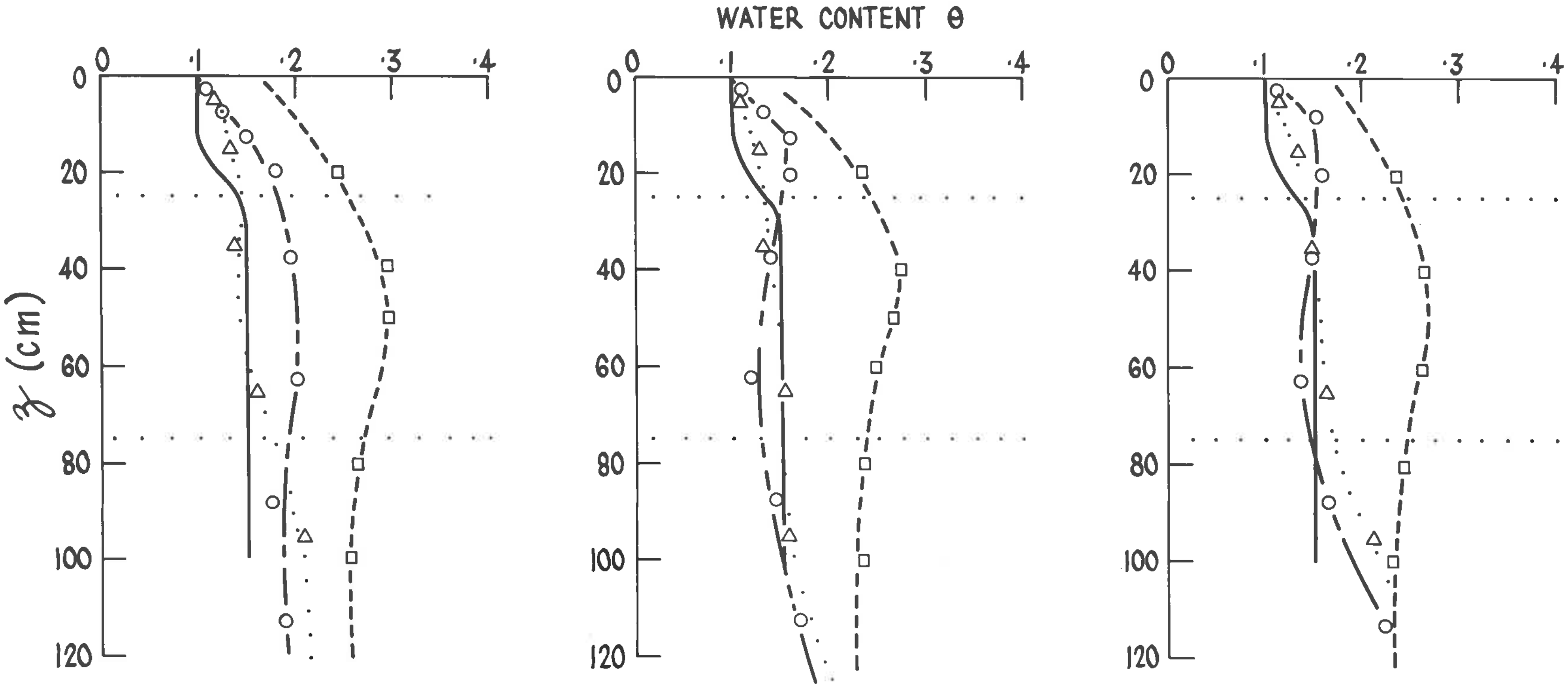
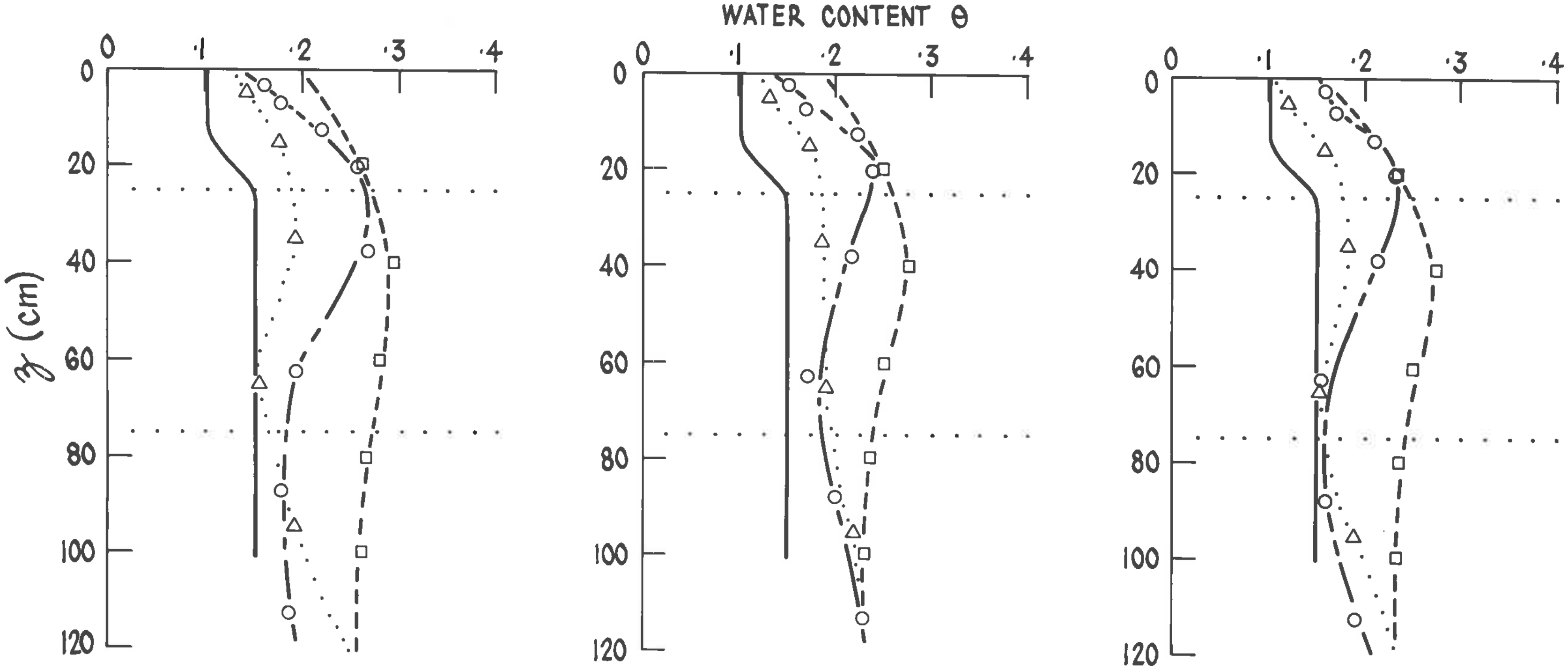

WATER CONTENT θ
0
·1
·2
·3
·4
0
20
40
60
80
100
z (cm)

Fig. 33. Vertical distribution of θ for each treatment.

□ ---------	at stem extension (September 11 to 19, 1973)
○ — — —	at flowering (October 23, 1973)
△	at maturity (December 4 to 5, 1973)
————	θ,15 bar suction
....	Indicates the depth limits for integration of water content in calculating depletion



Io, S_1 Io, S_2 Io, S_3



I_1, S_1 I_1, S_2 I_1, S_3

interval from 25 to 75 cm. Results are given in Table 21. The depletion ($-\int_{25}^{75} \Delta\theta dz$) tended to be greater at S_2 and S_3 than at S_1 (P, 0.10), and greater on I_0 than I_1.

Table 21. Depletion of soil water (cm) ($-\int_{25}^{75} \Delta\theta dz$) from stem extension to flowering.

Treatment	Depletion (cm)
S_1	3.5
S_2	4.7
S_3	4.5
L.S.D. (P, 0.10)	1.1
I_0	5.0
I_1	3.5
L.S.D. (P, 0.10)	0.9

3.3.5.6 Discussion

The influence of seeding rate on the number of tillers per plant at the flowering and dough stages was consistent with the results of studies conducted previously in South Australia (Wassermann 1964; Puckridge and Donald 1967; Walter and Barley 1974). The number of tillers per plant decreased significantly as seeding rate increased. This may have been due chiefly to competition for light

(Puckridge and Donald 1967). Donald (1963) noted that, when there was an adequate supply of water and nutrients from the soil, the supply of light became the main factor influencing the number of tillers per plant. During the period when most of the tillers were produced in the main experiment $E_0 << I'$. The only nutrients likely to be deficient in the soil concerned - P and N - were supplied in liberal amounts. No symptoms of nutrient deficiency were noticed during this period. Irrigation had no effect on the number of tillers per plant. This confirms the view that the supply of water from rainfall was adequate during tillering in 1973. The number of tillers per plant at the seeding rate common to both experiments (S_2) was similar at both harvests in the preliminary and in the main experiment.

At the dough stage, the total dry weight of tops increased with seeding rate. This may be expected, as leaf production is dependent on tiller production. The effect of seeding rate on the dry weight of tops agreed with previous studies in South Australia by Wassermann (1964), Puckridge and Donald (1967), and Walter (1971). Between the dough stage and maturity, the dry weights of tops decreased at S_3, owing to rapid senescence and greater loss of leaf in the denser canopies. This has been demonstrated previously (Kamel 1959; Stern 1960; Wassermann 1964; Puckridge and Donald 1967). Wassermann (1964) showed that the increased senescence and death of leaves with increase in plant density was due to increased competition for water and nutrients as well as for light. The principal factors affecting senescence and loss of leaf material in dense canopies in the 1973 experiment are uncertain. As mentioned in Section 3.3.5.5, irrigation had little effect on the growth of either roots or tops, although it delayed maturity at S_2 and S_1 more than at S_3.

Wassermann (1964), Puckridge and Donald (1967), Kirby (1967, 1969), and Walter and Barley (1974) found that the highest yield of grain was obtained at an intermediate seeding rate. Different results were obtained in this experiment, because of the effects of a heavy infestation of rust. The mean seed weight per grain for all treatments (14 mg) was only 40 percent of that found by Wassermann (1964) for cv. Gabo, Puckridge and Donald (1967) for cv. Insignia 49, and Walter and Barley (1974) for cv. Heron. This difference is too large to be attributed simply to differences between the cultivars. The treatments that matured later were more affected by rust. The general effect of rust was to decrease grain size. The plants matured their grain first at S_3, then at S_2 and lastly at S_1. Grain size was ranked: $S_3 > S_2 \approx S_1$ (P, 0.05). The number of seeds per square metre was greatest at S_2 and S_3. This result was similar to that found by Puckridge and Donald (1967) and Walter (1971). Irrigation had no effect on the number of grains per square metre. However, irrigation increased grain size and grain yield. Parameswaran (pers. comm.) showed that after anthesis the leaf water potential was less for I_0 than I_1. For example, on November 7, 1973 between 1200 to 1400 hr the values were -30 bar on I_0 and -21 bar on I_1. This shows that irrigation reduced the incidence of water stress after anthesis.

Translocation of dry matter to the grain is known to be impaired by water stress (Hsiao 1973). Moreover, a greater area of leaf remained green on the irrigated plots after flowering, and this would presumably have increased photosynthesis during the period of grain filling.

During the pre-tillering period there was an adequate supply of water both in 1972 and in 1973, and the number of seminal root axes produced per plant was not affected by seeding rate. In the absence of water stress the main factors determining seminal root number are genotype and the supply of stored metabolites within the seed (Taylor and McCall 1936; Derera *et al.* 1969). Apparently only one seminal axis per plant reached 30 cm depth at S_3(1). This

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(1) There appeared to be little if any plant mortality during the growing season even at the highest rate of seeding. When counted at the dough stage on a treatment that received no fertilizer nitrogen during the season, the number of tillers found by K.V. Parameswaran at S_3 in the independent experiment exceeded 700 m^{-2}. Table 10 shows that the number of tillers per plant in the main experiment was 1.0 at S_3 at the dough stage. So the plant density at S_3 at the dough stage is not likely to have been less than that measured when establishment counts were made on August 13, 1973, the mean number of plants recorded at S_3 then being 595.

was unexpected. There was no evidence of root rot and no root knots due to nematodes or other causes were found on September 28, 1973 when samples from the top 15 cm of the soil were inspected. It seems unlikely that competition for light would have been responsible, as the seminal roots would probably have penetrated to 30 cm depth within two or three weeks. Further examination is needed to check this result.

The number of nodal root axes per plant is highly dependent upon the number of tillers per plant (Weaver 1926; Manner 1957; Pinthus 1969; Black 1970). In the main experiment the number of nodal roots arising per tiller at flowering was ranked: $S_3 > S_2 > S_1$ and at maturity $S_3 > S_2 \approx S_1$ (P, 0.05). The difference was due to the fact that S_1 had a relatively high proportion of young tillers without nodal roots, as at S_1 the plants continued to tiller until late in the season. In the main experiment the number of nodal axes per plant followed the usual ranking ($S_1 > S_2 > S_3$, P, 0.05). The number of nodal axes per square metre arising from the base of the plant - number per plant X plant density - depended on seeding rate. If we assume that there was no plant mortality during the growing season (see footnote (1), p. 185), the ranking would have been $S_3 > S_2 > S_1$. These results agreed generally with those of Pinthus (1969). The number of nodal roots per plant was less in 1972 than in 1973 at the common seeding rate (S_2) both at flowering and at the dough stages. Pinthus found that nodal roots were produced rapidly by wheat during the period from spike initiation to spike emergence. During this period in 1972 $I' \ll E_o$ and the plants probably experienced water stress. This may have reduced nodal root production in 1972.

In 1973 some nodal axes penetrated as deeply as 90 cm at all seeding rates (Table 17). This contrasted with 1972, when no nodal axes penetrated more deeply than 40 cm. Weaver (1926), Simmonds and Sallans (1933), Balazs (1954), Grammatikati (1955), Gliemoroth (1957) and Jonker (1959) found that, under dry conditions, nodal roots tended to be confined to the uppermost layers of the soil. Presumably, the greater depth of penetration of nodal roots in 1973 was associated with the higher rainfall in 1973. The abundance of nodal roots decreased with depth. It also tended to decrease with increasing seeding rate at any given depth (Tables 13 and 18). This effect of seeding rate could result from plant competition for either light, water or nutrients. The supply of water in 1973 was probably adequate until late in the season, as irrigation had no effect on the growth of tops until grain filling, or on root length (L_A) measured at flowering.

The only nutrients likely to be deficient in the red brown earth were nitrogen and phosphorus, which, as noted previously, were supplied in generous amounts. Competition for light is likely to have become intense at the high seeding rate during the period of nodal root production. Burn (1972) found that low light intensity decreased the length of main roots of Bermuda grass (*Cynodon* spp., var. FB-137) in a greenhouse experiment. In the present experiments earliest nodal roots were initiated two to three weeks after emergence. Competition for light is likely to have begun shortly after this time at S_3 (Puckridge and Donald 1967), and this may have soon led to a shortage of assimilates for root growth. After 10 weeks competition for light is intense (Puckridge and Donald 1967), and it may by then be reducing the supply of assimilates for root growth at S_2 also.

It was most surprising to find that, even though the number of plants per square metre was increased 22 times in going from S_1 to S_3, the total number of root axes per square metre at depths below 30 cm was not significantly different between seeding rates. Presumably competition for some environmental factor reduced the number of deeply penetrating axes at higher plant densities. If we assume that there was no plant mortality during the growing season, the total number of root axes per square metre arising from the base of the plants at flowering may be obtained from the data in Tables 8 and 9: S_1 = 1,650, S_2 = 4,830, S_3 = 10,950. In contrast the maximum number of axes found per square metre at 30 cm depth was 489. Thus, the number of axes per square metre decreased markedly from 0 to 30 cm depth at all seeding rates, the decrease being greater at higher seeding rates. The number of root axes per square metre at 30 and 60 cm depth increased after flowering at all seeding rates, showing that root growth was still proceeding at these depths. This agreed with an earlier observation of Pinthus (1969).

At the dough stage r_A at 30 cm depth was significantly less at S_3 than at S_1 and S_2. Also, at the dough stage, r_A at 60 cm depth was significantly less on the non-irrigated than on the irrigated plots. These differences persisted where r_A was calculated for seminal root axes alone (Appendix Table 10). The greater abundance of nodal roots at S_1 at 30 cm depth may explain the high value of r_A at S_1, as the vessel radius (r_e) for nodal roots exceeds that of seminal roots (Appendix Table 6). The other factors affecting r_A were probably competition for water and possibly for light. At S_3 the plants depleted the water stored in the topsoil more rapidly than at S_1 and S_2. Paramesawaran (pers. comm.) showed that at the dough stage the leaf water potential was higher under irrigation. For example, on November 6, 1973 at 1200 to 1400 hr, $\psi_{I_0} = -29.5$, $\psi_{I_1} = -21.2$ bar, L.S.D. (P, 0.05) = 4.6 bar. The mean values of r_A tended to be greater on the irrigated plots at all depths (+ 2 μm), although the difference was statistically significant only at 60 cm depth. It was at this depth that the water content of the soil differed most between the irrigation treatments. At 30 cm depth the soil water content was more strongly influenced by rain; and the irrigation water may not have penetrated to 90 cm depth as the soil water content at 90 cm did not differ significantly between the irrigation treatments. Changes in r_A may have occurred when the prisms were soaked in water or during washing. Also the F.A.A. fixative may have affected r_A in old root zones even though it had no effect on r_A in young zones (Table 3). These matters require further examination.

L_A at flowering ranged from 242 to 348 cm^{-1}. This agrees with earlier measurements on wheat made by Welbank and Taylor (1970), Walter and Barley (1974) and Schultz (1974). The L_A values are considerably less than those found by Pavlychenko (1937) and Pavlychenko and Harrington (1934, 1935) at Saskatchewan, Canada. The values of L_A measured at Saskatchewan under wheat ranged from 1,000 to 4,000 cm^{-1}. The reason for this large difference is not clear. Day length would have been relatively long in Saskatchewan (latitude 50° to 60°N) than near Adelaide (latitude 35°S) where the experiments of Walter and Barley and of Schultz were conducted, but not greater than that at Rothamsted (latitude 51° to 52°N) where Welbank and Taylor worked. If radiation levels were high in Saskatchewan, net daily photosynthesis may have provided a large surplus of assimilate for translocation to the roots. This may have led to the appearance of laterals of a higher order of branching, and to a considerable increase in root length. Only five plants were measured by Pavlychenko (1937), and the number of plants measured by Pavlychenko and Harrington (1934, 1935) was not recorded. The soil block technique used by Pavlychenko and by Pavlychenko and Harrington may have led to errors of estimation. Using this technique it is difficult to separate roots from the soil and to separate the root system of one plant from that of its neighbours. The method is so laborious that replication is usually inadequate.

At all seeding rates L_v and the number of root axes per square metre decreased similarly with depth. However, L_v values at 0 to 15 cm depth were ranked differently: $S_1 < S_2 \simeq S_3$ (P, 0.05) from the likely ranking of number of root axes per square metre at zero depth: $S_1 < S_2 < S_3$. At S_3 there were many short nodal axes but the roots were less branched. At 75 to 100 cm depth L_v values at S_2 and S_3 were again greater than at S_1. These differences between seeding rates were similar to those reported by Walter (1971), except that Walter also detected differences ($S_3 = S_2 > S_1$) at 50 to 75 cm depth. The vertical paths described by the first and higher order laterals at 30, 60 and 90 cm depths were short. Hence the laterals cannot contribute much to the upwards flow of water at these depths. Furthermore, the diameter of the metaxylem vessel in first order laterals was only 15 to 25 μm. According to the Poiseuille equation, when the vessel radius in the first order laterals is half that in main axes the flow through 16 first order laterals would be equivalent to the flow through a single main axis. Using a similar argument Cowan and Milthorpe (1968b) concluded that the flow of water from higher order laterals into the first order laterals of cereals and grasses may be small compared with that moving across the cortex of first order laterals.

The percentage of the total root length with root hairs increased with depth. The trend was probably associated with the downwards growth of the rooting front, and with the high proportion of young roots in depth. Also, the soil remained relatively moist in the deeper part of the root zone. This result agreed generally with that obtained by Walter (1971). However the percentage of the total root length having root hairs in this experiment was considerably higher in the deeper layers than that found by Walter for the cultivar Heron. Such differences are to be expected between cultivars and seasons. Unlike the distribution of L_V, the distribution of L_H at flowering was nearly uniform with depth within the top metre.

Walter and Barley (1974) found that the maximum depths of root penetration at anthesis were S_2 = 130 cm, S_1 = S_3 = 110 cm depth. Pavlychenko (1937) found that at high plant density - 400 m^{-2} - the roots of wheat penetrated to 117 cm, while for widely spaced plants - density 0.11 m^{-2} - roots penetrated to only 71 cm. The maximum depth of penetration in this experiment was not measured systematically, but observations made during root washing showed that some roots had penetrated $\geqslant$ 110 cm at all seeding rates. This was close to the maximum depth of penetration.

When the supply of water is plentiful, and after the top few centimetres of the soil have become dry, the rate of evapotranspiration from the crop canopy depends chiefly upon the LAI until the LAI $\geqslant$ 2 (Cowan and Milthorpe 1968a). At stem extension the values of LAI were: S_1 = 0.3, S_2 = 0.9 and S_3 = 2.2; L.S.D. (P, 0.05) = 0.8 (Parameswaran pers. comm.). Soil water was probably extracted more rapidly at the higher seeding rates, but this did not lead to detectable differences in soil water content, since rainfall exceeded E_0 from sowing until stem extension at 8 weeks. Indeed at this stage, the top metre of the soil was at field capacity, and drainage into the deeper subsoil was probably still occurring. At the flowering stage, LAI values were as follows: $S_1 = 1.0$, $S_2 = 2.0$ and $S_3 = 2.8$; L.S.D. (P, 0.05) = 0.2 (Parameswaran pers. comm.). Between stem extension and flowering in the region from 25 to 75 cm depth the soil water was depleted more at S_2 and S_3 than at S_1 (P, 0.10). Kirby (1970) found that, from stem extension to flowering, barley sown at an intermediate seeding rate extracted more water from the deeper subsoil than barley sown at either low or high seeding rates. Kirby hypothesised that more roots may have been present in the subsoil at the intermediate seeding rates, however, he did not measure root growth. Walter and Barley (1974) measured the vertical distribution of the instantaneous rate of withdrawal of water by roots λ (day^{-1}) and related this to the distribution of L_v. They found that during the drying period the soil water content decreased significantly to a greater depth at an intermediate than at low or high rates of seeding. L_v values in the subsoil were greater at the intermediate and high seeding rates than at the low seeding rate, and the subsoil still contained water at low to moderate suctions at maturity at the low seeding rate. Walter and Barley proposed that the amount of water extracted from the soil at different plant densities depended on differences in root resistance between densities as well as on differences in the diffusive resistance of the crop canopy.

In the main experiment on the unirrigated plots mean suctions for all seeding rates at flowering on October 23, 1973 were 1, 11, 11, and 6 bar at 20, 50, 80 and 110 cm depth. At maturity on December 4 to 5, 1973 the corresponding suctions were 1, $\leqslant$ 15, 11, and 1 bar. The suction head at 20 cm was only 1 bar at both times of sampling, as the samples were taken after rainfall on each occasion. Thus the crop failed to extract water efficiently from below one metre depth. This finding agrees with results of Pelton (1969), Kirby (1970), and Walter and Barley (1974). The failure of the crop to extract water efficiently below one metre from the red brown earth at Roseworthy Agricultural College was not due to the osmotic effect of salts, as subsoil water in this soil has a negligible osmotic potential (Greacen pers. comm.).

The failure of crops to extract water from the deepest part of the root zone needs to be explained in terms of the effects of resistances to the withdrawal of water offered by the root themselves and by the soil. These resistances will be assessed in Section 4.0.

By maturity, the soil water suction was approximately 15 bar in the region from 25 to 75 cm depth. In this region $L_v \geqslant 2$ cm^{-2}. This corresponds with a theoretical estimate of the value of L_v needed to dry soils to wilting point (Philip 1957), and with earlier field results of Walter and Barley (1974).

GENERAL DISCUSSION

4.0 GENERAL DISCUSSION

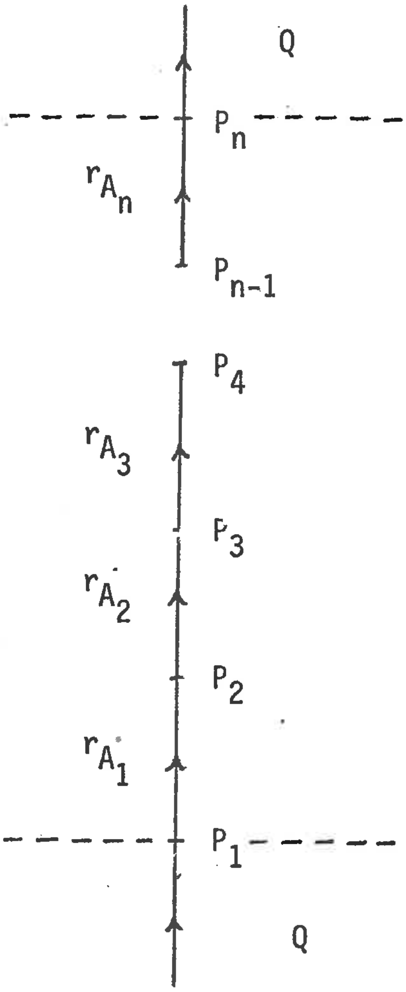
In Section 3.3.5.5 (iii) we noted that the crop appeared not to extract water efficiently below 70, 100 and 80 cm depth at S_1, S_2 and S_3 respectively, even though the roots penetrated to 110 cm depth or more. The poor extraction of water towards the bottom of the root zone needs to be explained. The resistances of the roots at the specified depths have been estimated both in the axial and radial directions. Soil resistance has also been assessed.

The axial and radial resistances of root segments R_α and R_β cannot be compared directly because their units differ. However, the drop in pressure along and across a set of roots can be calculated for a specified flow rate given values of R_α and R_β and sufficient information on the root geometry. The pressure drops can then be compared directly.

a) Pressure drop within the roots in the vertical direction

Within the root network water was elevated from the deeper layers of the soil almost exclusively within the main axes. When water is being absorbed by the roots at a constant rate from a deep, moist layer, provided there are no gains or losses of water from or to the overlying soil, the flow rate within each axis supplied with water will be constant at all depths within the dry layer. In the field it was not practicable to measure the conductance of each root axis at each depth. However it was possible to measure the axial conductances of a number of segments of axes representing a sample of the population of axes at each depth, and to measure the total number of root axes at each depth. From these data the axial conductance of the set of axes at each depth can be estimated, and hence we can estimate the pressure drop for a given upwards flow.

The following diagram represents the upflow of water within successive segments of an imaginary axis representative of the axes found at each depth, and with the radius r_A differing between the successive segments.



Assuming Poiseuille flow and neglecting gravity, the pressure drop ΔP (dyne cm^{-2}) along a given segment of length Δl is given by

$$\Delta P = \frac{Q 8 \eta \Delta l}{\pi r_A^4} \qquad (52)$$

where Q is the (constant) flow rate ($cm^3\ sec^{-1}$).

At a steady state the total pressure drop along a series of n vertical segments, each of length Δl, is

$$P_1 - P_n = \frac{Q 8 \eta \Delta l}{\pi} \left(\frac{1}{r_{A_1}^4} + \frac{1}{r_{A_2}^4} + \frac{1}{r_{A_3}^4} + \ldots + \frac{1}{r_{A_n}^4} \right) \qquad (53)$$

Let

$$\sum_{i=1}^{n} \left(\frac{1}{r_{A_i}^4} \right) = n \left(\frac{1}{r_H^4} \right)$$

so that

$$r_H = \sqrt[4]{\frac{n}{\sum_{i=1}^{n} \frac{1}{r_{A_i}^4}}} \qquad (54)$$

then

$$P_1 - P_n = \frac{Q 8 \eta \Delta l}{\pi} \left(\frac{n}{r_H^4} \right) \qquad (55)$$

The pressure drop (dyne cm^{-2}) required for a given flow $Q = E_p/N$, where E_p is the transpiration rate (cm sec^{-1}) and N is the number of axes per unit ground area (cm^{-2}), in the axial direction within a vertical interval ΔL (cm) $= n\Delta l$ is

$$\Delta P = \frac{E_p 8\eta\Delta L}{N\pi r_H^4} \qquad (56)$$

In Section 3.2.6 it was shown that K_α varied between the two classes of axes - seminal and nodal - and with stage of growth. We need to allow for the apparent discrepancies from Poiseuille flow.

For the seminal axes, the mean flow per axis $\overline{Q}_s$ ($cm^3\ sec^{-1}$) is given by

$$\overline{Q}_s = \frac{\pi f_s\ r_{H_s}^4\ \Delta P_s}{8\eta\Delta L} \qquad (57)$$

where $f_s \equiv K_{\alpha_s}/K_{P_s}$ at $r_e = R_{H_s}$, other variables are as previously defined and the subscript s identifies values for the class of seminal axes alone.

Similarly, for the nodal or adventitious axes

$$\overline{Q}_A = \frac{\pi f_A\ r_{H_A}^4\ \Delta P_A}{8\eta\Delta L} \qquad (58)$$

Now,

$$E_p = N_s\overline{Q}_s + N_A\overline{Q}_A \qquad (59)$$

Assuming that the hydrostatic pressure of the water in the plant is equalized at the basal node of the stem, $\Delta P_s = \Delta P_A \equiv \Delta P$. Then

$$E_p = \frac{\pi\Delta P}{8\eta\Delta L}(f_s N_s r_{H_s}^4 + f_A N_A r_{H_A}^4) \qquad (60)$$

Therefore,

$$\Delta P = \frac{E_p 8\eta\Delta L}{\pi}\left[\frac{1}{(f_s N_s r_{H_s}^4 + f_A N_A r_{H_A}^4)}\right] \qquad (61)$$

In calculating ΔP the following assumptions were made:

(1) Soil water was elevated entirely from below the lower boundary of the depth interval specified;

(2) There were no sources or sinks within the depth interval specified;

(3) Values of numbers of axes and radii r_A measured at 30 cm depth apply to the region from 0 to 30 cm, at 60 cm depth to the region from 30 to 60 cm, and at 90 cm to the region from 60 to 90 cm;

(4) The temperature of the water was 15^oC - $\eta = 0.01$ poise.

Making the above assumptions Eqs. (56) and (61) were used to calculate the pressure drop required for water to be elevated at a rate corresponding to $E_p = 1$ cm day^{-1} from 30, 60 and 90 cm depth. Data on r_A and numbers of root axes of each class per cm^2 at various depths were obtained from the main 1973 experiment. Results are given in Tables 22 and 23 for the flowering and dough stages respectively. At flowering arithmetic means of r_A and of numbers of axes for non-irrigated and irrigated treatments were used, as irrigation had no significant effect on these values at any depth. As there were few nodal axes at depths greater than 30 cm their inclusion in the computation had little effect on the estimated pressure drop from 0 to 60 cm and from 0 to 90 cm depth.

At flowering, assuming Poiseuille flow, the mean pressure drop along the root axes for all seeding rates was 1, 2 and 9 bar, when water was elevated from 30, 60 and 90 cm depth. When allowance was made for discrepancies from Poiseuille flow using Eq. (61), the corresponding pressure drops were 1, 3 and 12 bar. As shown in Table 22, the pressure drop between 0 and 90 cm depth was greater at S_1 than at the other seeding rates.

At the dough stage, the pressure drop calculated assuming Poiseuille flow showed only minor differences between the irrigation treatments (Appendix Table 11). Accordingly, pressure drops were again calculated from the arithmetic means of r_A and of number of axes at each depth for non-irrigated and irrigated treatments. In contrast to the flowering stage, when allowance was made for deviations from Poiseuille flow, the estimated pressure drop was less than when Poiseuille flow was assumed. This arose because at this stage $f_s = K_{\alpha_s}/K_{P_s} > 1$. The corrected pressure drop required to elevate water from 60 cm depth generally decreased between the flowering and dough stages. This was because of an increase in the mean number of root axes present at and above 60 cm depth. The corrected pressure drop required to elevate water from 90 cm also decreased between the flowering and dough stages at S_1, due partly to an increase in the number of axes and partly to an increase in the radius r_A for both seminal and nodal axes.

An estimate of the pressure drop required at the seeding rate (S_2) common to both experiments was also attempted for the 1972 season. Only seminal axes penetrated below 40 cm in 1972, and frequently only one seminal axis per plant reached 90 cm (Section 3.3.4.3). This may have been due to the relatively low rainfall during the growing period in 1972. The radius r_H was obtained from Eq. (54), substituting r_A values calculated for seminal axes only, and obtained from the 1973 experiment, as data on r_A were not obtained in 1972. At flowering for $E_p = 1$

cm day^{-1}, the pressure drop between 60 and 0 cm depth ranged from 2 to 3 bar and between 90 and 0 depth from 5 to 9 bar (Table 24). In contrast to 1973, the pressure drop required increased from the flowering to the dough stages at each depth. This happened because, while the number of axes per cm^2 passing through 60 and 90 cm depths remained unchanged between the flowering and dough stages in 1972, the values of r_H taken from the 1973 data decreased. In 1973, on the other hand, the number of axes penetrating into the deeper subsoil increased between the flowering and dough stages, and the increase in number of axes more than offset any decrease in r_H. The estimated pressure drop between 90 and 0 cm depth was considerably higher in 1972 than in 1973 at the dough stage. This difference arose because fewer axes penetrated to 90 cm depth in 1972 than in 1973. Moreover, the estimate for 1972 is conservative, as the topsoil became dry earlier in 1972 than in 1973. As shown in Section 3.3.5.4 the vessel radius tends to decrease when the soil dries, hence the true values of r_A at given depths in 1972 may have been less than the 1973 values that were used in the calculation.

Only limited use can be made of the data on axial conductance for peas, as the geometry of the root system in the field was not examined. The main axes of the pea radicle is known to have a basal unbranched zone, generally extending to 5 cm below the base of the root (Barley pers. comm.). The pressure gradient $\frac{\Delta P}{\Delta T}$ along the basal unbranched zone of the pea radicles was found from $\frac{\Delta P}{\Delta T} = \frac{E_p \quad 8\eta}{N\pi f \; r_A^4}$, where f is a discrepancy factor defined by $f \equiv \frac{K_\alpha}{K_p}$ at $r_e = r_A$. N, the number of axes per cm^2 was assumed to be equal to the usual plant density of field peas = 75 plants m^{-2}. The radius r_A was found using Eq. (51) from values of r_e measured at 5 cm below the base of main axes. The calculated pressure gradient in the unbranched basal zone for E_p = 1.0 cm day^{-1} at four weeks from sowing, at flowering and at maturity was 0.2, 0.1 and 0.04 bar per cm of root. The gradient decreased after flowering because of an increase in the number of secondary metaxylem elements in the basal zone of the main axis. The pressure gradients were similar to those estimated to exist in the main axes of wheat roots. Pressure gradients cannot be calculated at lower depths for peas until information is available on the geometry of the root network. It is known that in contrast to wheat, first order laterals in peas have large vertical components in their paths (Barley pers. comm.); and presumably these laterals conduct water upwards in addition to the flow within the main axis.

Table 22. Estimated pressure drop (bar)* between the depth specified and zero depth in the axial direction within the main axes of roots of wheat, cv. Halberd at flowering in 1973; E_p = 1 cm day^{-1}.

Depth (cm)	S_1	S_2	S_3	Mean
30	1(1)	1(1)	1(1)	1(1)
60	3(2)	3(2)	2(2)	3(2)
90	21(14)	7(6)	9(6)	12(9)

* Values without brackets corrected for deviations from Poiseuille flow (Eq. (61)).

Bracketed values derived assuming Poiseuille flow (Eq. (56)).

Table 23. Estimated pressure drop (bar)* between the depth specified and zero depth in the axial direction within the main axes of roots of wheat, cv. Halberd at dough stage in 1973; E_p = 1 cm day^{-1}.

Depth (cm)	S_1	S_2	S_3	Mean
30	1(1)	1(1)	1(1)	1(1)
60	2(2)	1(2)	2(2)	2(2)
90	10(14)	8(11)	9(16)	9(14)

* Values without brackets corrected for deviations from Poiseuille flow (Eq. (61)).

Bracketed values derived assuming Poiseuille flow (Eq. (56)).

Table 24. Estimated pressure drop (bar)* between the depth specified and zero depth in the axial direction within the main axes of roots of wheat, cv. Halberd at flowering and dough stages in 1972; E_p = 1 cm day^{-1}, seeding rate = S_2.

Depth (cm)	Stage of growth Flowering	 Dough
60	2-3**	3-5
90	5-9	11-25

* Calculated from Eq. (61).

** The range of values refers to the minimum and maximum values found for individual prisms.

b) Pressure drop across roots at a given flow rate

The pressure drop between the root surface and the lumen of the metaxylem was estimated for a prescribed constant rate of transpiration

$E_p = 1.0$ cm day^{-1}. It was assumed that water was extracted solely by the hair-bearing length of root; and that, for this zone, $K_\beta = 6.10^{-4}$ cm day^{-1}. Furthermore, it was assumed that the depth interval specified was the only source of water, and that there were no sources or sinks elsewhere. The pressure difference (ambient solution - xylem) was calculated from

$$\Delta P = \frac{\rho g}{K_\beta} \left(\int_{z_1}^{z_2} 10^{-5} \lambda dz \; / \int_{z_1}^{z_2} L_H dz \right) \qquad (62)$$

where K_β is the constant radial conductance of the hair-bearing roots within the interval $z_1 < z_2$ (cm); and λ and L_H are as previously defined.

Data on L_H were available for the flowering stage only. Calculations were made of the radial pressure difference required to extract water at the given rate from the region bounded by the depths 90 to 100, 60 to 100, 30 to 100 and 0 to 100 cm. Results are given in Table 25. The estimated pressure differences were < 1 bar for all depth intervals and treatments.

Graham *et al.* (1974) showed, using potometers, that in main axes of barley and marrow the conductance of the zone having a well suberized endodermis was only one fifth that of the unsuberized zone. The endodermis would not have been suberized in the distal part of the hair-bearing zone, but may have been suberized to some extent in the more proximal part of the zone. Also the radial conductance of roots *in situ* in unsaturated soil may be less than the conductance observed when the roots are immersed in solution, as water will tend to infiltrate into intercellular spaces normally occupied by air. To allow for such effects the calculations of pressure difference across the root were repeated substituting $K_\beta/5$, results then being five times the values shown in Table 25. The radial pressure difference required to extract water at the given rate remained less than 1 bar except for the depth interval 90 to 100 cm, where the estimated ΔP was as great as 4 bar. As a few roots penetrated deeper than 100 cm, the length of hair-bearing root involved in water uptake in the field would have been somewhat greater than the values used in the above calculations. This error leads to a positive bias in the estimated value of ΔP, and the error may become important when considering uptake from the 90 to 100 cm depth interval. As noted in Section 3.2.5 the use of Eq. (33) assumes that Δh_Π is small compared with Δh during the measurement of K_β. This may not be so. If Δh_Π had been appreciable, K_β would have been over-estimated, and, consequently, ΔP would have been under-estimated. This matter needs further examination.

In general, even when it is assumed that water is extracted only by hair-bearing roots, as in the present calculations, ΔP in the radial direction was much less than that in the axial direction, the resistance in the axial direction always being the major resistance when the roots withdrew water exclusively from below 30 cm depth.

c) The theoretical maximum rate of flow of water to roots in the deeper layers of the soil

Where the roots are widely spaced, q_{max} may be obtained, following Lang and Gardner (1970), by solving the radial flow equation subject to $h = \infty$, $r = r_1$, $h = h_s$, $r_2 >> r_1$ where h is the suction head (cm), r_1 is the radius of the root, and r_2 is the radial distance from the root axes. The required solution is:

$$q_{max} = \frac{2\pi a}{\log_e (\frac{r_2}{r_1})(n-1)h_s{}^{(n-1)}} \qquad (63)$$

where a and n are empirical coefficients (constants) for a particular soil; r_2 is the half distance between roots (cm) defined by $r_2 \equiv \frac{1}{(\pi L_H)^{\frac{1}{2}}}$, and h_s is the suction head in the bulk of the soil where $r >> r_1$. To derive a and n, it was assumed that the capillary conductivity, K (cm day^{-1}) varied with the suction head, h_s, as

$$K = \frac{a}{(h_s)^n} \qquad (64)$$

In order to find a and n, $K(h_s)$ has to be measured at at least two suctions. Values of K at two suctions, 0.2 and 1.5 bar were available for a sandy red brown earth similar to the soil used in this experiment (Walter 1971). Walter's values for the B_2 horizon were used to derive a and n in Eq. (64). The B_2 horizon occupied the 90 to 100 cm depth in the main experiment. Following Bouwer (1969), geometric means of $K(h_s)$ were calculated from values given for four cores by Walter. The geometric means of $K(h_s)$ were $2.0 \,.\, 10^{-3}$ and $4.4 \,.\, 10^{-5}$ cm day^{-1} at arithmetic mean suctions of 0.2 and 1.5 bar respectively.

It is worth noting that the above geometric means of K agree to an order of magnitude with values obtained for the subsoil of the

Table 25. Estimated pressure difference ΔP (bar) across the roots at the flowering stage for wheat, cv. Halberd, when water is extracted by the hair-bearing length of roots only from within the depth interval specified. $E_p = 1$ cm day^{-1}; $K_\beta = 6.10^{-4}$ cm day^{-1}.

Depth Interval (cm)	I_0			Mean	I_1			Mean
	S_1	S_2	S_3		S_1	S_2	S_3	
0 - 100	0.03	0.03	0.02	0.03	0.04	0.03	0.04	0.04
30 - 100	0.04	0.04	0.03	0.04	0.05	0.05	0.06	0.05
60 - 100	0.08	0.10	0.05	0.08	0.09	0.09	0.10	0.09
90 - 100	0.70	0.80	0.80	0.77	0.43	0.90	0.49	0.61

red brown earth at Parafield by extrapolation of the observed $\overline{K}(\theta)$ relation (Fig. 10). By substituting pairs of values of K and h_s in Eq. (64), and solving for a and n, a = 56.1, n = 1.9. This value of n is just outside the range of values for field soils reported by Lang and Gardner (1970).

In considering the main experiment Eq. (63) was applicable only for S_1 below 90 cm depth, where the roots were relatively widely spaced. From Fig. 29 the estimated mean value of L_H at S_1, I_0 for the depth interval 90 to 100 cm between stem extension and flowering was 0.15 cm^{-2}. This corresponds to $r_2 = 1.46$ cm. At flowering on treatment I_0, S_1 the roots had depleted the soil water content within the layer from 90 to 100 cm depth to a value corresponding to a suction of 3 bar. Estimated values of q_{max} were obtained by substituting appropriate values of a, n, r_2 and r_1 in Eq. (63). The value of r_1 employed was 0.01 cm ($r_2/r_1 = 146$), this being the radius of the axial part of the predominant class of root members, namely the first order laterals. The derived value of q_{max} was $4.9 . 10^{-2}$ cm^2 day^{-1} at h_s = 3 bar. In the period from stem extension to flowering at 90 to 100 cm depth, $\overline{q} = (-\int_{90}^{100} \Delta\Theta dz/(\int_{90}^{100} L_H dz))/\Delta t = 2.10^{-3}$ cm^2 day^{-1}. As shown in Section 2.3.3 for the subsoil of the red brown earth at Parafield, the likely range of values of K at a particular suction is $\frac{\overline{K}}{3.7}$ to 3.7 $\overline{K}$. The sub-soil at Parafield resembled the B_2 horizon in the main experiment. The estimated values of q_{max} still exceeded the observed value of $\overline{q}$, even when the conductivity was reduced to $\overline{K}/3.7$, when at h_s = 3 bar, $q_{max} = 6.4 . 10^{-3}$ cm^2 day^{-1}. We conclude that, if soil resistance were the only resistance to water flow, the roots in the 90 to 100 cm layer could have been expected to extract water more rapidly than was observed, at least when the suction at the root surface was large. The suction at the root surface would not have had to be unduly large to induce near maximum rates of flow, as these are obtained when $h_{r=r_1}/h_s > 1.5$ (Lang and Gardner 1970).

d) <u>Apparent uptake of water per unit length of root</u>

From stem extension on September 17, 1973 to flowering on October 23, 1973, I' = 0.19 cm day^{-1} and E_0 = 0.45 cm day^{-1}. The top soil appeared to be dry for most of this time. However, rain occurred five days before sampling at flowering, and, following this rain, water infiltrated to approximately 25 cm depth. Between 75 to 85 cm at flowering, no vertical gradient in total head was observed at any seeding rate. The water uptake per unit length of root q ($cm^2\ day^{-1}$) was calculated for the region from 25 to 75 cm depth for each seeding rate on the non-irrigated treatment, assuming that vertical flow through the soil pores was negligible across the upper and lower boundaries of this region. The mean apparent rate of uptake $\bar{q}$ was calculated from

$$\bar{q} = \left(-\int_{25}^{75} \Delta\theta dz / \left(\int_{25}^{75} \bar{L}_v dz\right)\right)/\Delta t \qquad (65)$$

where $\bar{L}_v$ (cm^{-2}) is the arithmetic mean of L_v at each depth at the stem extension and flowering stages; $\Delta t = 38$ days was the number of days from stem extension on September 17, 1973 to flowering on October 23, 1973. L_v was not measured at stem extension in 1973. For wheat cv. Heron grown in the field at Roseworthy, Walter (1971) showed that, between the growth stages mentioned above, in 1968 the values of $\int_{25}^{75} L_v dz$ increased by the following percentages: S_1 : 43, S_2 : 46, S_3 : 45 percent. The values of $\int_{25}^{75} L_v dz$ at flowering in the main 1973 experiment at S_1, S_2 and S_3 were 110, 105 and 103 cm^{-1} respectively. Assuming that the root length increased in the same proportion between these growth stages in the present experiment as in Walter's 1968 experiment, the values of $\int_{25}^{75} L_v dz$ at stem extension in 1973 would have been S_1 : 63, S_2 : 57 and S_3 : 57 cm^{-1}. Using these values the estimated values of $\int_{25}^{75} \bar{L}_v dz$ for S_1, S_2 and S_3 in 1973 were 87, 81 and 80 cm^{-1}. The values of the integral $-\int_{25}^{75} \Delta\theta dz/\Delta t$ at S_1, S_2 and S_3 were 0.11, 0.14 and 0.14 cm day^{-1}. Finally, $\bar{q}$ is calculated from Eq. (65), the values being S_1 : 1.3 . 10^{-3}; S_2 : 1.7 . 10^{-3} and S_3 : 1.8 . 10^{-3} cm^2 day^{-1}.

The local apparent rate of uptake of water $q_{,z} = \lambda / L_{v,z}$ (cm^2 day^{-1}) between the stem extension and flowering stages reached maximum values at 45 cm depth for S_1 and S_2, where q = 3.0 . 10^{-3} cm^2 day^{-1} at S_1 and 3.7 . 10^{-3} cm^2 day^{-1} at S_2, and at 55 cm depth for S_3, where q = 4.8 . 10^{-3}. Values of $\bar{q}$ were four times higher than the values reported by Walter and Barley (1974) at the heading stage, but the ranking of $\bar{q}$ followed the same trend with seeding rates. Values of both $\bar{q}$ and local maximum values of q were smaller than those postulated by Gardner (1964) and Cowan (1965). Gardner and Cowan postulated q = 0.1 cm^2 day^{-1} and q = 0.16 cm^2 day^{-1} respectively in their theoretical studies.

The values of $\bar{q}$ and q given above are probably conservative estimates of actual rates, as some parts of the root are known to absorb water more readily than others. If uptake of water had been confined to that part of the root length with root hairs, as suggested by Walter and Barley (1974), the values of $\bar{q}$ at S_1, S_2 and S_3 would have been 6.8 . 10^{-3}, 1.2 . 10^{-2} and 1.1 . 10^{-2} cm^2 day^{-1}. These values are 3 to 4 times greater than those based on total root length. These magnitudes are similar to those calculated for the hair-bearing length of root by Walter and Barley (1974). Shearer (1968) found in a short term pot experiment conducted in a controlled environment chamber that seminal roots of 18 day old plants of wheat, cv. Gabo, absorbed water from sands at rates ranging from $\overline{q} = 3 \, . \, 10^{-3}$ to $6 \, . \, 10^{-3}$ $cm^2 \, day^{-1}$. Shearer calculated $\overline{q}$ using the entire root length. As the plants were young, hairs probably occupied most of the root length.

In Part I of the thesis it was shown that 68 percent of the values of hydraulic conductivity at 80 to 110 cm depth in a red brown earth fell within $\overline{K}/3.7$ to $3.7 \, \overline{K}$. This variation shows the difficulty that confronts us in trying to use Darcy's law to calculate precisely either the water flow to plant roots or the drainage term in a water balance. A profitable approach appears to be to derive K from the moisture characteristic, using a matching factor obtained after measuring K at a suction within the range of interest. In water balance work it is recommended that a uniform soil be selected, and that a sufficient number of core samples be taken with minimum disturbance of the soil: these should be used in the laboratory to obtain a measure of the moisture characteristic and a reliable estimate of the matching factor. Hysteresis should be kept in mind when attempting to characterize the suction-water content relation in the field from measurements made on core samples in the laboratory.

In Part II of the thesis, the results suggest that, irrespective of seeding rate, at $E_p = 1$ cm day^{-1}, the resistance within the roots in the axial direction is much greater than the resistance within the roots in the radial direction, when the roots withdraw water exclusively from below 30 cm depth. The radial resistance within the root is substantial only when water is being withdrawn from the lower extremities of the root zone, and when the seeding rate is low.

Comparison of the observed rates of withdrawal of water by the roots and the theoretical maximum rates of withdrawal suggested that the resistance offered by the soil was not the only resistance operating in the soil-plant system. Large values of E_p cannot be sustained when there is a large suction drop within either the soil or within the plant, as the stomates will then tend to close.

Understanding of water uptake by plant roots in the field will be furthered by more realistic and reasonably precise measurements of the radial and axial conductances of the sets of roots at various depths. In particular the influence of the components of water potential within the root on these resistances, and the effect of suctions within the xylem on metaxylem vessel radius need to be examined. The possibility of resistance to water flow at the root-soil boundary due to separation of the root from the soil also needs to be examined by *in situ* measurements of flow at known potential differences.

The attributes of the plant that affect resistance to upwards flow of water in the root - number of vertical root axes and metaxylem vessel radius - may be of interest to plant breeders, when selecting and breeding genotypes for environments in which water supply is limiting.

APPENDICES

Appendix Table 1. Field hydraulic conductivity (K, cm day^{-1}) at 80-110 cm depth of Parafield red brown earth soil for the individual sites.

Site							
I		II		III		IV	
θ	10K	θ	10K	θ	10K	θ	10K
.283	9.6	.277	1.3	.286	4.0	.297	1.6
.271	2.2	.275	1.1	.276	2.1	.293	2.3
.267	2.6	.271	2.2	.269	0.4	.289	1.1
.261	1.8	.269	0.7	.266	0.8	.283	0.7
.254	0.8	.263	0.3	.264	0.2	.279	0.3
.247	1.3	.257	0.7	.259	0.4	.276	0.2
.239	0.2	-	-	-	-	.261	0.8

Appendix Table 2. Nutrient solution for wheat and peas.

Compound	Concentration (mM)
KCl	0.15
KNO_3	0.10
NH_4NO_3	0.10
$Ca(NO_3)_2$	0.25
$MgSO_4.7H_2O$	0.10
*KH_2PO_4	1.0×10^{-2}
**Fe.EDTA	5.0×10^{-3}
$CuSO_4.5H_2O$	1.0×10^{-4}
H_3BO_3	3.0×10^{-3}
$MnSO_4.4H_2O$	1.0×10^{-3}
$ZnSO_4.7H_2O$	5.0×10^{-4}
$CoSO_4.7H_2O$	4.0×10^{-5}
$Na_2MoO_4.2H_2O$	2.0×10^{-5}

* For peas 25.0 mM KH_2PO_4 was used.

** Dissolve 50.0 g of $FeSO_4.7H_2O$ and 67.0 g of Na-EDTA in 2.0 l. of distilled water, bubbling air through overnight and store in refrigerator.

Appendix Table 3. Axial hydraulic conductance K_α. of segments of axes of seminal roots of wheat cv. Halberd.

Age of plant (days)	Stage of growth	Method of culture	Equivalent metaxylem vessel radius, r_e (μm)	K_α (10^{-6} cm^3 sec^{-1})
18	One shoot	Nutrient solution	28.17	5.10
			28.06	3.10
			34.80	5.10
			27.70	4.60
			24.94	4.20
			33.72	3.50
			25.74	4.20
			26.10	1.20
			26.46	0.74
			30.74	1.20
			31.54	2.80
			35.89	3.70
			20.48	0.37
			22.84	0.86
			29.00	0.74
			27.55	1.60
			29.55	1.50
			26.83	0.79
			28.28	1.40
			31.90	1.30
			26.10	1.30
			28.78	1.70
			26.10	1.30
			30.45	1.10
			32.63	1.70
54	Flowering	Nutrient solution	28.98	0.61
			46.40	11.00
			28.64	2.40
			27.69	2.20
			31.98	2.10
			31.99	1.80
			36.98	3.90
			34.81	4.70
			40.97	8.10
			37.70	3.90
			34.08	3.40
			40.57	5.40
			28.43	2.40
87	Flowering	Field	30.45	3.50
			34.78	2.00
			39.40	4.20
			26.01	1.50
			31.87	3.50
			42.44	9.30
			43.50	9.10
			46.06	4.60
			41.33	19.00
			47.48	9.00
			25.23	1.50
			43.50	2.80
			42.76	13.00
			34.06	6.90
91	Dough	Nutrient solution	28.28	7.80
			31.23	4.40
			38.42	8.10
			33.92	4.40
			36.62	4.70
			30.45	2.90
			38.41	3.40
			28.49	3.40
			35.61	6.70
			28.28	1.50
			31.17	1.60
			34.80	6.00
			30.45	4.50
			30.45	11.00
			24.65	9.50
			35.98	9.50
			54.38	30.00
			37.69	8.10
			43.50	19.00
			50.03	32.00
			45.68	6.00
109	Dough	Field	26.08	3.30
			27.06	1.60
			32.63	6.30

Appendix Table 4. Axial hydraulic conductance K_α of segments of axes of nodal roots of wheat, cv. Halberd.

Age of plant (day)	Stage of growth	Method of culture	Equivalent metaxylem vessel radius, r_e (μm)	K_α (10^{-6} cm^3 sec^{-1})
54	Flowering	Nutrient solution	49.49	1.10
			36.59	1.50
			46.89	11.00
			54.96	3.90
			38.88	6.60
87	Flowering	Field	39.74	0.68
			33.09	3.70
			39.24	2.80
			32.78	5.60
			39.00	2.20
			37.33	19.00
91	Dough	Nutrient solution	42.59	2.20
			43.05	5.20
			65.19	1.80
			55.21	6.80
			40.73	19.00
			43.46	4.70
			40.48	3.20
			45.00	17.00
			45.72	27.00
			39.24	6.10
			35.09	3.30
			32.00	0.56
			38.02	6.20
			54.38	9.40
			44.61	6.20
			38.26	15.00
			60.16	23.00
			62.29	12.00
			54.01	33.00
			57.97	5.90
			54.36	35.00
			45.18	35.00
			45.53	7.40
			43.58	4.70
			44.22	18.00
			52.20	10.00
			42.42	22.00
109	Dough	Field	33.43	1.90
			33.45	0.31

Appendix Table 5. Axial hydraulic conductance K_α of segments of main axes and first order lateral roots of peas (*Pisum sativum* L. cv. White Brunswick) grown in culture solution.

Age of plant (days)	Stage of growth	Type of root member	Equivalent metaxylem vessel radius, r_e (μm)	K_α (10^{-6} cm^3 sec^{-1})
28	Seedling	Main axes	45.65	7.00
			39.45	3.30
			29.76	0.95
			40.81	4.50
			31.35	2.30
			31.69	1.40
			31.98	1.00
			34.10	0.13
		First order lateral	24.44	0.15
			23.13	0.34
			5.13	0.03
			15.23	0.70
			21.22	1.20
			16.46	0.38
			21.03	0.013
			27.01	1.00
			14.49	0.023
			12.81	0.005
			13.14	0.0075
			13.78	0.11
			13.05	0.02
56	Flowering	Main axes	50.91	33.00
			52.93	28.00
			47.71	3.30
			50.92	29.00
			52.48	24.00
			42.71	10.00
			54.74	14.00
			60.07	50.00
			56.97	11.00
			52.86	12.00
			60.18	39.00
			58.51	27.00
			54.87	29.00
			54.87	32.00
			51.47	16.00
			51.82	3.20
		First order lateral	15.23	0.013
			22.01	2.30
			22.17	0.082
			24.35	0.077
			36.28	2.90
			45.80	4.70
			42.73	8.50
			46.80	7.80
			15.27	0.56
			15.22	0.56

(continued)

Appendix Table 5 (continued).

Age of plant (days)	Stage of growth	Type of root member	Equivalent metaxylem vessel radius, r_e (μm)	K_α (10^{-6} cm^3 sec^{-1})
80	Grain at dough stage	Main axes	68.52	75.00
			31.67	2.90
			61.10	33.00
			62.35	28.00
			33.97	28.00
		First order laterals	35.74	4.50
			47.65	6.80
			40.20	4.10
			31.46	5.60
			44.34	8.20
			20.05	0.61
			28.01	1.80
			24.51	1.20
			21.51	0.73
			32.91	5.80
			39.19	1.40
			18.16	0.14
			16.09	0.17
			26.83	2.50
			23.52	1.10
			28.72	1.90
			34.35	2.70
			22.86	0.83
			23.59	1.20
			35.54	4.30
			40.90	12.00
			37.62	6.70
			35.05	6.90
			31.71	8.90
			22.00	0.50
			22.43	0.98
			10.35	0.75
			17.40	0.78
			29.86	2.40
			41.26	7.80
			27.87	1.40
			32.36	3.20
			42.85	6.80
			31.85	8.70
			44.23	6.30
			27.68	5.60
			33.66	0.18
			33.93	2.70
			17.03	0.56
			19.45	0.58
			18.02	0.15

Appendix Table 6. Equivalent metaxylem vessel radius r_e (μm) for segments of sampled axes and the derived radius r_A (μm) at different stages of growth and at different depths.

Replicate	Depth	Irrigation	Seeding rate	r_e										r_A
				FLOWERING										
1	30	I_0	S_1	34.5	50.2	39.0*	52.7	35.5	46.8	46.8	52.5	55.5	25.1	
				33.8	52.0	46.7	58.0	44.5	29.8	41.2	29.8	36.0	54.7	45.4
			S_2	29.8	46.8	38.3	42.5	47.7	52.2	45.7	32.0	42.2	31.8	42.7
			S_3	46.8	42.5	36.2	46.2	51.0	43.0	51.0	34.8	39.7		44.5
		I_1	S_1	29.8	36.0	38.7	25.5	42.2	34.9	34.0	37.2	38.3	29.8	
				31.6	62.5	52.8	54.0	34.5	38.3	44.6	42.5	49.4	42.6	43.0
			S_2	21.6	34.0	43.6	43.3	38.3	36.3	48.3	43.8	21.3	46.8	40.4
			S_3	57.7	39.6	54.0	30.0	44.0	48.3	38.8	26.1	48.0	35.5	45.2
2	30	I_0	S_1	26.1	27.4	58.3	31.6	34.7	42.3	46.2	27.9	55.6	22.9	
				34.0	55.3	28.4	55.3	49.7	42.5	29.8	42.5	41.9	42.5	43.8
			S_2	36.5	27.9	40.0	52.5	30.5	29.8	53.2	29.8	41.7	29.8	40.5
			S_3	30.0	42.5	49.3	27.1	42.5	33.5	37.6	31.5	25.5	27.7	38.1
		I_1	S_1	49.2	61.2	35.5	55.0	51.6	56.2	25.5	49.0	48.3	42.5	
				42.5	42.0	45.5	45.7	49.2	50.5	27.2	40.0	38.3	41.3	47.1
			S_2	45.2	34.0	55.3	42.5	42.5	43.5	35.8	46.2	38.3	41.3	43.6
			S_3	29.8	46.8	42.5	36.3	40.3	38.5	39.3	42.5	41.0	34.1	39.9
1	60	I_0	S_1	39.5	42.2	48.3	21.6	24.9	19.1	33.9	23.0	34.3	33.0	
				30.2	34.5	36.5	27.1	29.1	44.0	31.3	28.0	34.2	26.0	34.5
			S_2	34.0	35.8	42.2	31.6	47.0	45.5	42.5	45.0	47.0	29.4	41.4
			S_3	44.5	38.3	38.7	34.0	36.9	32.2	27.0	38.7	40.9	45.2	38.6
		I_1	S_1	44.7	57.3	51.0	44.0	35.5	36.2	35.2	51.0	46.8	36.9	
				45.8	44.0	39.0	38.3	23.4	34.0	42.5	30.6	25.5	29.8	42.2
			S_2	36.9	55.3	22.0	38.3	33.1	38.5	31.9	41.9	44.5	42.0	40.9
			S_3	41.2	40.4	39.7	25.5	34.0	41.2	37.3	31.3	48.3	-	39.1
2	60	I_0	S_1	46.8	23.1	33.7	63.6	46.8	52.0	44.6	41.2	25.1	35.5	
				34.0	21.3	46.8	34.0	34.0	35.5	37.2	42.5	25.5	29.8	41.7
			S_2	36.9	55.3	22.0	35.3	23.1	37.5	31.9	41.9	44.5	42.0	40.9
			S_3	41.2	40.4	39.7	25.5	34.0	34.0	41.2	37.3	31.3	48.3	38.7
		I_1	S_1	30.8	25.5	29.8	46.8	38.3	55.2	46.8	42.6	29.8	25.5	
				50.8	34.0	48.5	41.2	25.5	21.9	42.5	34.0	21.3	-	40.2
			S_2	29.8	29.8	37.3	46.8	32.7	41.0	34.5	46.8	38.3	40.7	39.1
			S_3	32.7	34.0	41.2	34.2	47.3	51.0	38.9	34.0	42.5	46.2	41.6
1	90	I_0	S_1	44.7	43.6	55.3	41.8	46.8	33.3	38.3				44.8
			S_2	48.3	29.1	31.3	39.7	38.7	38.8					39.2
			S_3	25.5	36.9	30.1	29.1	26.0	37.7	29.8				31.7
		I_1	S_1	21.3	21.3	42.5	25.5							31.9
			S_2	36.2	33.3	34.0	46.8	35.2	45.5	44.0	35.5	42.5	30.1	39.5
			S_3	21.3	48.7	36.0	23.0	26.3						35.9
2	90	I_0	S_1	51.0	34.2	29.8	25.5	38.3	25.5	32.0	42.5	24.9	29.8	
				24.2	21.0	20.1	30.2	45.2	36.5					35.3
			S_2	34.3	25.5	34.0	25.5	25.5	21.3	25.0				28.5
			S_3	21.6	28.0	32.0	29.8	42.9	34.8	37.4	42.5			35.5
		I_1	S_1	30.1	25.5	18.3	24.9							25.7
			S_2	25.5	31.3	22.7	31.1	21.3	22.7	26.0	32.5			27.6
			S_3	35.5	33.8	42.9	34.0	42.5	46.2	34.0	42.5	29.8		39.0

(continued)

Appendix Table 6 (continued).

Replicate	Depth	Irrigation	Seeding rate	r_e										r_A
				DOUGH STAGE										
1	30	I_0	S_1	54.7	46.8	22.7	22.7	30.1	25.5	30.5	28.4	34.0	21.7	
				29.0	42.5	46.8	33.2	44.0	50.7	38.3	54.3	28.4		40.4
			S_2	39.0	35.6	43.2	34.2	39.0	41.2	30.5	45.0	31.2	41.2	38.8
			S_3	28.1	30.4	31.8	20.9	30.1	46.8	28.4	38.6	29.8	34.0	34.0
		I_1	S_1	49.2	43.9	53.2	48.5	28.3	43.2	22.2	34.3	30.5	34.0	
				50.0	58.2	32.6	52.2	61.0	29.8	45.7	17.7	29.8		44.4
			S_2	56.2	36.9	32.6	47.6	47.5	44.0	50.0	49.0			47.0
			S_3	38.3	32.7	38.9	35.5	36.9	38.3	49.7	40.3	29.8	31.3	38.4
2	30	I_0	S_1	43.7	39.1	23.0	18.9	30.2	49.0	44.0	38.3	39.7	36.1	
				57.3	34.0	44.2	45.4	64.9	20.5	49.0	33.5	34.0		43.7
			S_2	32.7	45.8	6.8	44.5	29.8	42.5	32.7	45.7	35.5	46.8	39.9
			S_3	43.1	28.4	44.7	44.5	35.5	36.2	41.7	25.5	32.7	32.7	38.1
		I_1	S_1	48.0	57.7	21.3	35.5	42.5	42.5	32.2	26.3	46.8	34.0	
				34.0	43.0	54.9	36.9	49.5	37.5	36.8	42.2	45.4		43.1
			S_2	35.5	37.5	45.7	38.3	37.5	28.4	42.5	32.7	33.8		37.8
			S_3	41.7	34.7	24.2	34.5	24.8	44.0	40.1	24.0	47.7		37.8
3	30	I_0	S_1	29.8	21.3	51.2	52.5	48.7	51.0	23.4	24.1	22.7	31.2	
				22.7	19.9	39.7	31.2	31.2	28.4	22.7	28.4			38.6
			S_2	44.7	29.8	18.4	46.8	45.0	28.4	45.4	32.7			39.7
			S_3	39.7	38.3	32.7	38.3	39.7	39.0	21.3	29.8	21.3	29.0	34.8
		I_1	S_1	49.5	22.5	39.7	41.2	25.5	42.3	38.3	25.5	38.3	61.4	
				44.0	52.5	32.7	27.0	34.7	45.4	46.8				42.9
			S_2	29.0	45.4	34.0	25.5	46.1	33.3	29.1	45.4	32.7		37.9
			S_3	24.8	40.4	38.3	26.2	29.8	30.5	42.5	20.0	42.5		35.3
1	60	I_0	S_1	38.3	18.5	29.8	40.0	26.1	35.0	35.5	21.3	30.1	19.1	
				23.1	23.4	35.6	44.0	29.8						32.6
			S_2	20.7	38.0	49.0	39.5	23.0	32.7	51.0	46.8	27.5	19.3	39.4
			S_3	26.5	23.4	38.6	28.8	23.5	24.4	20.5	28.4	25.5		28.1
		I_1	S_1	39.3	26.0	37.2	41.7	37.6	31.2	21.5	25.1	29.1	33.0	
				25.5	28.0	23.1	26.3							32.2
			S_2	44.7	48.7	24.2	30.2	27.6	22.7	52.5	38.3	42.5		40.7
			S_3	38.3	30.6	40.2	23.0	34.0	35.5	41.5	21.6	29.5		34.5
2	60	I_0	S_1	58.3	21.3	24.1	25.9	23.0	45.8	27.5	24.4	18.4	42.7	
				34.4	51.8	38.3	28.2	30.1	24.8	32.7	21.5	35.5		34.8
			S_2	34.7	48.2	35.5	31.9	31.2	31.2	20.5	24.1	42.5	32.7	35.7
			S_3	40.7	29.0	22.7	35.5	21.3	31.2	40.8	25.5	21.3	24.1	31.8
		I_1	S_1	29.8	44.0	21.3	26.8	27.0	32.7	34.0	37.2	26.5	38.3	
				40.7	37.5	46.8	25.9	24.0						36.8
			S_2	36.2	39.5	24.5	22.7	29.8	35.3	24.8	28.4	27.6	29.4	29.7
			S_3	41.2	37.5	45.6	45.4	37.5	44.0	40.7	41.7	24.1	38.3	40.7
3	60	I_0	S_1	34.1	17.0	27.0	17.0	46.8	21.3	34.0	42.5	47.0	36.2	
				29.8	46.8	27.6	27.0							35.2
			S_2	49.0	41.1	35.5	21.3	34.0	20.4	55.3	17.7	44.0		40.9
			S_3	21.3	28.4	24.1	36.9	34.0	34.0	21.3	24.1	30.5		29.9
		I_1	S_1	25.5	35.5	29.8	44.7	25.5	34.7	21.8	40.4	25.9	25.5	
				38.3	40.5	39.7	36.9	44.8	44.0	20.5	34.0			36.2
			S_2	29.8	31.2	44.7	24.4	45.8	45.4	34.0	36.9	39.7	25.5	38.0
			S_3	41.8	25.5	25.5	36.9	38.0	36.9					35.7

(continued)

Appendix Table 6 (continued).

Replicate	Depth	Irrigation	Seeding rate	r_e										r_A
1	90	I_0	S_1	23.4	38.3	34.0								33.5
			S_2	26.7	32.7	19.1	25.5	26.8						27.2
			S_3	29.6	21.3	26.0	29.8	34.0	16.6	25.5	35.3			29.0
		I_1	S_1	29.8	30.0	35.9	29.8	40.0						35.3
			S_2	35.5	17.6	23.9	22.3							27.4
			S_3	35.0	33.8	18.6								31.4
2	90	I_0	S_1	42.0	23.7	21.3	19.9	44.0	21.3	22.7	31.5	28.4	21.3	
				45.4	25.5	21.3	34.0	35.5						32.9
			S_2	28.5	25.6	35.5	25.5	28.1						29.4
			S_3	25.5	20.5	35.5	24.1	31.2						28.9
		I_1	S_1	46.2	32.2	16.3	40.1	51.0	39.4	25.5	23.7	34.0	41.2	
				29.9	27.5	36.9	48.2	21.3						28.0
			S_2	29.4										29.4
			S_3	40.4	47.5	32.6	44.0	37.5	47.5	42.5	38.3			42.1
3	90	I_0	S_1	$\underline{30.4}$	$\underline{17.5}$	44.0	38.3	$\underline{29.5}$	19.9	29.8				33.2
			S_2	25.5	21.3	30.5	29.8	24.1	29.0	29.0	27.0			27.5
			S_3	22.0	38.3	22.7	25.5	25.5	26.3	23.2	18.4			27.2
		I_1	S_1	34.0	29.8	30.5	25.5	29.8	22.7	37.5	26.3	26.0	29.4	
				17.0	27.9	28.5	25.5	29.8	51.0					32.3
			S_2	21.3	35.5	39.7	31.2	34.0	30.5					33.4
			S_3	21.3	19.5	27.4								23.5

* The underlined values are for nodal axes.

Appendix Table 7. Mean radius of metaxylem vessels r_A (μm) at each depth at flowering for each treatment.

Depth (cm)	Seeding Rate S_1	S_2	S_3	L.S.D. (P,0.05)	I_0	I_1	L.S.D. (P,0.05)
30	44.8	41.8	41.7	N.S.	42.5	43.1	N.S.
60	39.7	40.6	39.5	N.S.	39.3	40.5	N.S.
90	34.4	33.7	35.5	N.S.	35.8	33.2	N.S.

Appendix Table 8. Root length per unit volume of soil L_v (cm^{-2}) at flowering at different depths for each treatment.

Depth (cm)	Seeding Rate			L.S.D. (P,0.05)	I_0	I_1	L.S.D. (P,0.05)
	S_1	S_2	S_3				
0-5	10.55	16.62	19.26	3.53	17.02	14.06	N.S.
5-10	6.46	10.03	8.90	1.35	8.80	8.12	N.S.
10-15	3.89	5.43	6.02	0.98	5.23	5.00	N.S.
15-25	2.40	3.25	4.08	N.S.	2.99	3.50	N.S.
25-50	1.94	2.43	2.47	N.S.	2.27	2.29	N.S.
50-75	2.00	2.31	1.87	N.S.	1.96	2.17	0.03
75-100*							

* The values of this depth show interaction between irrigation and seeding rate treatments, and the interaction is shown in Table 19.

Appendix Table 9. The volumetric water content θ of the soil at different times and at different depths* for each treatment.

Depth (cm)	Seeding Rate S_1	S_2	S_3	L.S.D. (P,0.05)	I_0	I_1	L.S.D. (P,0.05)
				STEM EXTENSION			
20	.25	.24	.23	N.S.	.23	.25	.01
50	.29	.27	.26	N.S.	.26	.28	N.S.
80	.26	.24	.24	N.S.	.25	.24	N.S.
110	.26	.23	.23	N.S.	.24	.24	N.S.
				FLOWERING STAGE			
20	.21	.22	.20	N.S.	.18	.23	N.S.
50	.20	.17	.17	N.S.	.16	.20	N.S.
80	.18	.16	.16	N.S.	.15	.18	N.S.
110	.19	.19	.19	N.S.	.18	.19	N.S.
				MATURITY			
20	.16	.15	.15	N.S.	.14	.17	N.S.
50	.17	.16	.17	N.S.	.14	.19	N.S.
80	.17	.17	.16	N.S.	.16	.18	N.S.
110	.21	.21	.20	N.S.	.21	.20	N.S.

* Values at particular depths found by interpolation on smooth curves fitted to measured values plotted at mid-point of depth interval represented by each sample.

Appendix Table 10. Mean radius of metaxylem vessels r_A (μm) at each depth at the dough stage for each treatment.. Seminal axes only.

Depth (cm)	Seeding Rate S_1	S_2	S_3	L.S.D. (P,0.05)	I_0	I_1	L.S.D. (P,0.05)
30	40.5	40.2	36.4	3.1	38.1	40.0	N.S.
60	34.6	37.4	33.4	N.S.	34.3	36.1	0.7
90	34.7	29.0	30.3	N.S.	30.2	32.5	N.S.

Appendix Table 11. Pressure drop (ΔP bar) between the depth specified and zero depth in axial direction within the main axes of seminal roots of wheat, cv. Halberd, at dough stage, $E_p = 1$ cm day^{-1} and assuming Poiseuille flow.

Depth (cm)	I_0			I_1		
	S_1	S_2	S_3	S_1	S_2	S_3
30	<1	<1	<1	<1	<1	<1
60	2	3	2	2	2	2
90	20	12	13	11	16	16

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