WATER FLUX AND ION UPTAKE BY WHEAT SEEDLINGS

A Thesis submitted

by

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NOMENCLATURE

a - cross sectional area.

A - rate of water production per unit volume of soil (g/cc/sec)

A_B - constant as defined by Bouldin (1961).

b - dC_T/dC_1

B - ratio of number of ions in solution phase to number of ions adsorbed onto solid phase per unit volume of soil.

C - quantity of ions in solution per unit volume of soil.

C_1 - quantity of ions in solution per unit volume of solution.

C_{1_0} - initial quantity of ions in solution per unit volume of solution.

C_s - quantity of ions in solution on soil surface per unit volume of soil.

C_T - total quantity of ions per unit volume of soil.

D - diffusion coefficient (cm^2/sec)

D_B - diffusion coefficient as defined by Bouldin (1961).

D'_B - $D_B/(B+1)$

D_{BN} - diffusion coefficient as defined by Biggar and Nielsen (1964).

D_G - diffusion coefficient as defined by Gardner (1965).

D_N - diffusion coefficient as defined by Nye (1966).

D_o - diffusion coefficient for particular ion in water.

D_S - diffusion coefficient for ions moving along surface of soil particles.

E_o - evaporation from a free water surface (g/cm^2/sec)

f - heat flux density (cal/cm^2/sec).

F - ion flux density or flux per unit area of soil solution ($g/cm^2/sec$)

g - gravitational constant.

G - external gas pressure potential (erg/g).

h - pressure head.

H - relative humidity.

I - pressure potential (erg/g)

J - flux of ions in solution per unit cross section of soil ($g/cm^2/sec$).

J_1 - flux of ions in solution per unit cross section of solution.

J_s - ion flux along surface of soil particles per unit cross section of soil.

J_T - total ion flux per unit cross section of soil.

k - water conductivity function (cm/sec).

K - thermal conductivity ($cal/cm^2/sec/^{\circ}C$).

l - depth of bed.

L - quantity of ion produced or adsorbed per unit volume of soil.

La - leaf area.

m - matric potential (erg/cc)

M - matric potential (erg/g)

N - constant as defined by Bouldin (1961).

O - osmotic potential (erg/g)

P - vapour pressure of water in atmosphere under consideration (mm Hg)

P_o - vapour pressure at a free water surface (mm Hg).

q - water flux (cc/sec)

Q - quantity of ions transported per unit length of root per second.

Q' - quantity of ions transported per unit surface area of root per second.

r - radius variable.

R - gas constant

S - submergence potential (erg/g).

t - time variable.

T - temperature.

Tr - quantity of water transpired.

u - velocity of water (cm/sec).

v - volume flux density of water ($cc/cm^2/sec$).

v_T - total water flux density ($cc/cm^2/sec$).

v_v - water vapour flux density.

V - constant as defined by Bouldin (1961).

w - water flux per unit length of root (cc/cm/sec)

W - dry weight of plant material.

x - linear space variable.

Y - total plant yield.

z - vertical space variable.

Z - gravitational potential (erg/g).

α - constant relating Q and C_1.

β - index of dispersion.

γ - constant relating Tr to E_o.

δ - potential unit transpiration rate ($mg/cm^2/sec$)

ϕ - factor of dispersion.

Γ - specific water capacity.

θ - volumetric water content.

κ - thermometric conductivity (cm/g/sec)

ρ - density.

ψ - total water potential (erg/cc).

ψ' - total water potential (erg/g).

SUMMARY

Over recent years a number of models have been developed to describe the uptake of ions by plants. Although many models have been proposed, very little experimental work has been carried out to test the applicability of these models. There is sufficient indirect evidence from the available literature to suggest that certain limitations may be placed upon the use of these models. The present investigations were carried out into two aspects important to the use of ion uptake models. Firstly, the proposed equations have been solved by defining the internal ion flux boundary condition as a function of the ion concentration at the root surface. The investigations into chloride ion uptake by wheat seedlings revealed that under the conditions of the experiment, the ion uptake is a function not only of the bulk solution concentration but also of other environmental conditions. It was concluded that plant growth responses to the whole environment, necessitating the normalization of results, and the resultant plant-whole environment interaction affected ion flow to and through the plant. In general chloride ion flux into the roots increased with water flux into the roots over a wide range of solution concentrations. However cautions must be placed upon interpretation of such results as this may be due to an indirect effect and

not a direct effect of water flow. Sodium uptake on the other hand shows little direct response to water uptake but like chloride responds to indirect effects. Further, it was found that under the conditions of the experiment, the plant may offer greater resistance to the movement of water than the soil, and root length could limit unit transpiration rate. Linear relations between dry weight of plant material and the amount of water transpired were found and discussed in terms of NAR and UTR. The second part of the investigations was a study of the applicability of the steady state equation describing combined diffusion and convective transfer of ions. It was found in saturated soil with axisymmetric radial flow that the diffusion coefficient is not constant but depends upon the water flow velocity, including direction.

This thesis contains no material which 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.

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1. INTRODUCTION

A primary aim of agricultural research is to ensure the most efficient use of both water and nutrients in plant production. It has therefore become essential to understand the processes governing ion and water movement in soils and the uptake of these by the plant.

One approach to this problem has been to propose general theories or models "to provide a framework for discussion and experiment and to indicate the parameters that need to be measured for a complete quantitative description." (Nye 1966).

The first section of this thesis reviews the literature available on the various aspects of water and ion movement through soils and uptake by plants, and concludes with a description of the various models which have been proposed to describe ion uptake by plants from soils.

The basis of the models which have been proposed has been that the movement of ions in the soil occurs as a result of a concentration gradient, i.e. by diffusion, and an additive component due to the convection of ions along with the mass flow of water. Solutions of this system under various initial and boundary conditions imposed by the soil and the plant give the model. However two components of the above process have received little attention and deserve further study. Firstly there are effects of the environment, which gives rise to the different water uptake rates, upon the boundary conditions imposed by the plant. Secondly there is some question about the validity of the basic theory to describe ion movement through soils under the influence of a mass water movement. The present work was therefore undertaken to investigate these aspects.

The first section of the experimental work was designed to investigate the effects of the environment upon the plants' ability to take up water and ions. The second section was designed to develop a technique for investigating the applicability of the basic theory of ion movement in soils under the influence of mass water movement and varying concentration gradients, and to obtain some preliminary results on the above movement of ions in a saturated sand.

2. REVIEW OF LITERATURE ON WATER AND ION MOVEMENT THROUGH SOILS AND PLANTS

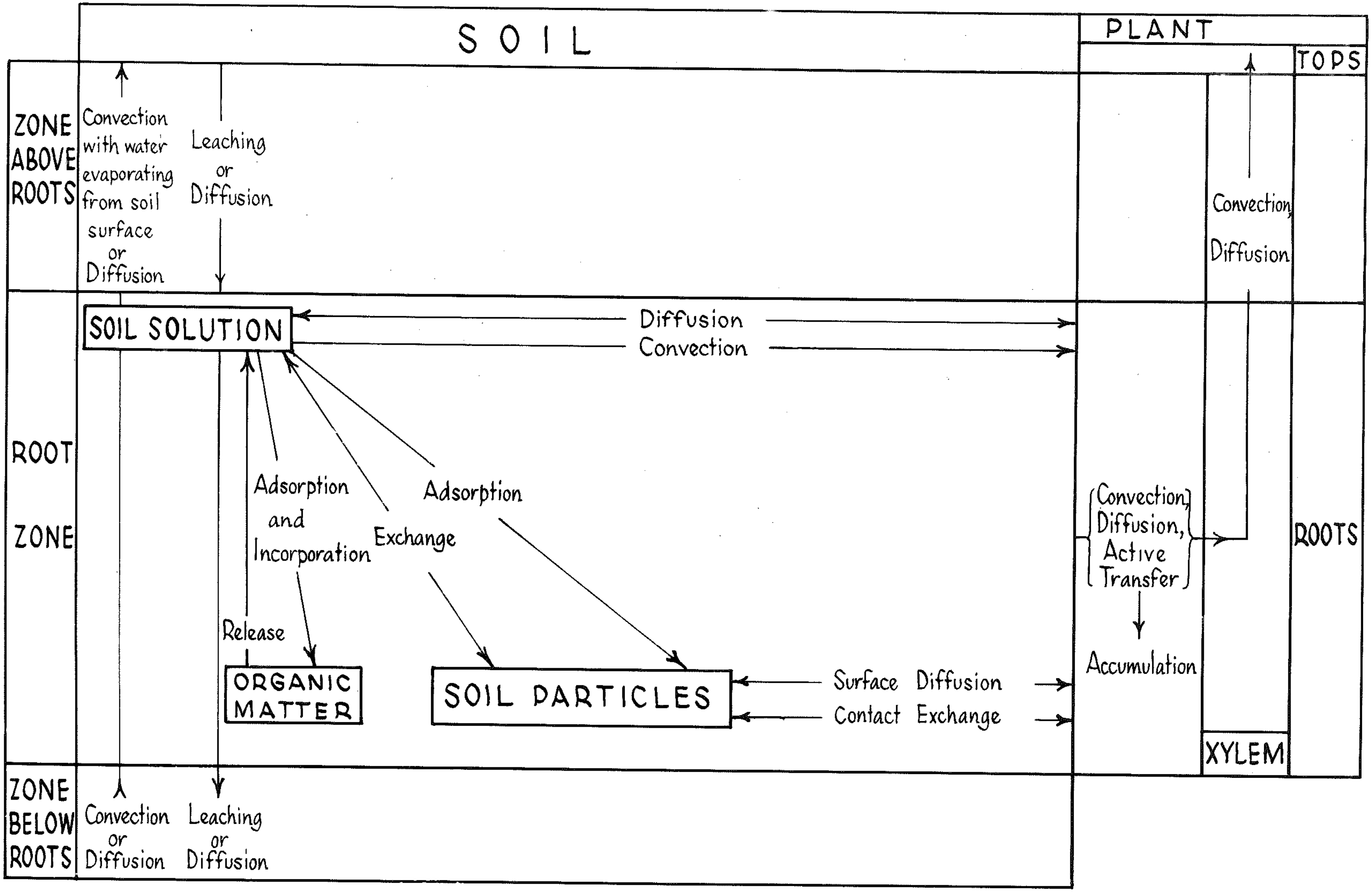
It is apparent from Kramer's review (1949) of the early history of plant nutrition, that before the twentieth century there was much speculation but little experimental work concerning the way in which plants obtained their "foods". During the present century there has been a large volume of experimental results pertaining to plant nutrition, but many conclusions still remain speculative.

The overall processes of ion movement from a point in the soil, distant to the root, up to the root surface and through the plant are summarized in Figure I (after Fried and Shapiro 1961). The transport mechanisms involved are considered in this review.

2.1 Water Movement into and through Plants

Two terms were proposed by Renner (1912, 1915) to describe the movement of water into and through plants. The water movement responsible for "root pressure" (Hales 1727) he called "active absorption", because it appeared to be dependent upon vital conditions maintained by living roots. Water which moved into and through the plant in response to transpirational loss he called "passive absorption" since the role of the root was passive.

Figure 1. <u>Diagrammatic Representation of Ion Transfer in Soils and Plants</u>.


SOIL
PLANT
TOPS
ZONE ABOVE ROOTS
Convection with water evaporating from soil surface or Diffusion
Leaching or Diffusion
Convection, Diffusion
ROOT ZONE
SOIL SOLUTION
Diffusion
Convection
Adsorption and Incorporation
Release
Exchange
Adsorption
ORGANIC MATTER
SOIL PARTICLES
Surface Diffusion
Contact Exchange
Convection, Diffusion, Active Transfer
Accumulation
ROOTS
XYLEM
ZONE BELOW ROOTS
Convection or Diffusion
Leaching or Diffusion

The above definitions have been used by some workers (Slatyer 1960) while others (Kramer 1955) have used a definition for active transport of water based upon the thermodynamic criterion used in ion transport. Thus a definition equivalent to that used by Kramer would be that active water movement is the transport of water against the water potential gradient (Oertli 1966). This water movement would therefore depend upon a supply of energy possibly from some metabolic process. The definition for active transport of water used by Oertli (1966) that "during an active transport or process, the water potential must increase and this gain must depend on the decrease in free energy in some metabolic process" and his assertion that water is actively transported when it moves as a result of an osmotic gradient resulting from an active transport of ions, seems to complicate the whole concept of active water transport.

It is preferable that the concept of active transport be used "in the sense of activation of the substance transported" (Levitt 1967) and to define passive transfer of water as that transfer resulting from water movement along the total water potential gradient. Thus, active water transfer may be defined as that transfer not accounted for by movement along a total water potential gradient and will depend upon a decrease in free energy in some metabolic process acting upon the water transported. These concepts are similar to those proposed by Levitt (1967).

2.1.1 Passive water movement

Knowledge of the mechanisms of passive water movement in plant tissue is by no means complete, but it is possible to approach the problem of the physical and mathematical description of water movement in plants in much the same way as the problem of water flow in soils, (see section 2.2). Thus the plant may be considered as a "porous medium" in which the volume flux density, v, i.e. volume of water passing through unit area of plant part per unit time, is proportional to the gradient of the total water potential, $\nabla\psi$, or

$$\underset{\sim}{v} = - k \nabla\psi \qquad \ldots\ldots (1)$$

where k is a constant of proportionality or a conductivity function.

The total water potential may be defined as the amount of work that must be done per unit quantity of pure water in order to transport reversibly and isothermally an infinitesimal quantity of water from a pool of pure water at a specific elevation at atmospheric pressure to the point under consideration, (International Society of Soil Science 1963). This potential, ψ , at any particular point in a system is equal to the sum of four component potentials, the osmotic potential (O), the gravitational potential (Z), the matric potential (M) and a potential due to external pressure (G) (I.S.S.S. 1963).

Rose (1966) adds M and G together to define the term pressure potential (I), i.e.

$$I = M + G.$$

This "sums the effect of all pressure changes on the potential of" the water "whatever the cause of these pressure changes may be" (Rose 1966).

Thus the total water potential at any particular point in the plant is equal to the sum of three component potentials, i.e.

$$\psi = O + Z + I$$

where all are expressed in erg/gm or erg/cc.

There is very little quantitative information available on the resistance (1/k) of component pathways of water movement in plants. Gradmann (1928), van den Honert (1948) and Edlefsen (1941) considered the path of water movement into and through plants as a thermodynamic continuum. The flow of water was therefore considered as movement through a number of "resistances" in series. For any given water flux, q, the decrease in the total potential across any component of the path was considered to be proportional to the resistance of that component. Brouwer (1961) and van den Honert (1948) concluded that most of the change in total water potential occurred at the site of evaporation of water from mesophyl cells of the leaves into the air spaces of the leaves and in the subsequent movement of water vapour out through the stomates, through the leaf boundary layer and into the air. This implied that the greatest resistance to water movement from the soil through the plant and out into the atmosphere was in the leaf-atmosphere region and that the energy required to take water from the evaporation cells was much greater than that required to take water from the soil and through the plant's vascular system in the "available moisture range". However Falk (1966) concluded that it was not always possible to apply the general idea of a simple catenary process to dynamic systems. He showed that the rate of transpirational water loss may increase even though the rate of water uptake was reduced. Most water flow in plants is also of a transient nature and is time dependent with both diurnal and seasonal fluctuations.

The flow of water must obey the general principle of conservation of matter, which is expressed in the equation of continuity including the presence of possible sources and sinks within the region of the flow, so that

$$\frac{\partial\theta}{\partial t} = -\nabla .\ \underset{\sim}{v} + A \qquad \ldots\ldots (2)$$

or substituting (1) into (2)

$$\frac{\partial\theta}{\partial t} = \nabla .(k\nabla\psi) + A \qquad \ldots\ldots (3)$$

where A is the rate of production of water per unit volume of soil per unit time, or is the sources minus the sinks, and θ is the plant water content on a volume basis. If circumstances are such that vapour movement can not be ignored, then another term must be introduced into equation (1), that is,

$$\underset{\sim}{v}_{tot} = \underset{\sim}{v}_{liq} + \underset{\sim}{v}_{vap}$$

where v_{tot} is the total flux density, v_{liq} the liquid flux density and v_{vap} the vapour flux density.

When circumstances are such that vapour movement can be ignored and the rate of production is negligible, then

$$\frac{\partial\theta}{\partial t} = \nabla .(k\nabla\psi) \qquad \ldots\ldots (4)$$

Equation (4) can also be expressed in terms of potential alone, because

$$\frac{\partial\theta}{\partial t} = \Gamma\frac{\partial I}{\partial t} = \nabla.(k\nabla\psi) \qquad ......\ (5)$$

and therefore

$$\frac{\partial I}{\partial t} = \frac{1}{\Gamma}\nabla.(k\ \nabla\psi) \qquad ......\ (6)$$

where Γ, the specific water capacity, is equal to $d\theta/dI$.

However for this approach to be useful it is necessary that there be a unique and known relation between θ and I and that the medium be homogeneous so that Γ and k are functions of θ (or I) only. It seems that a capacity function must be introduced to deal with transient flow of water in plants because of observed variations in turgidity. Consideration of transient flow is of primary importance since plant-environment systems seldom approach steady state conditions.

Many workers (Eaton 1943, O'Leary 1965) have concluded that, in detopped plants the transfer of water across the root and out of the stump was due to a water potential gradient determined primarily by the osmotic potential component. However the importance of osmotic potential gradients in whole transpiring plants is undetermined although it is considered to be of minor importance (Slatyer 1960).

Slatyer (1960), like Kramer (1956), considered that the most important process causing water to move into and through the plants was transpiration. This is substantiated by results obtained by careful ringing of plants in which phloem but not xylem tissue was severed. Water uptake rates were not affected but ion uptake rates and presumably osmotic potential gradients were impaired (Bowling 1965). Both Slatyer (1960) and Kramer (1956) agreed that even if water transfer was a passive process, it would nevertheless be affected by the permeability of the protoplasmic membranes and the concentration of solutes in the xylem. Both the latter can be dependent upon the release of energy from respiration. For example, Glinka and Reinhold (1964) found that the permeability of plant membranes to water varied markedly with changes in concentrations of carbon dioxide, chloroform and azide. All of these substances have been used to modify respiration rates of roots in order to demonstrate that water uptake is an active process. Further, ion transfer into the xylem can be dependent upon the release of energy within the plant (see section 2.3) so that metabolic activity may also affect the ion concentration within the xylem and hence the total water potential gradient via its osmotic component.

As water evaporates from the mesophyll cells of leaves it diffuses through intercellular spaces and thence into the air, via the substomatal cavities and stomates. This loss of water from the leaf cells is accompanied by a local decrease in the total water potential in the cells and water moves upwards through the xylem and across the root to the xylem. The difference in the total potential between the root cells and the soil causes water to move from the soil into the root. There is thus a potential gradient in the water continuum from the source in the soil to the atmospheric sink.

Movement of water in the above manner particularly at considerably reduced total potentials requires validity of the cohesion theory of sap ascent (Dixon and Joly 1895). This theory was fully discussed by Greenidge (1957). The results of Handley (1939) were not in agreement with such an hypothesis. He had found that there was no direct relationship between wilting and ice formation in the xylem. However Zimmermann (1964) repeated Handley's experiments, but with improved experimental techniques, and concluded that there was in fact a close relationship between wilting and ice formation in the xylem.

Different regions along the root have been found to offer varying resistance to radial water transfer. Brouwer (1954) found that at low water uptake rates a region just behind the root tip offered the least resistance to water transfer per unit length. As the demand of the plant for water increased and the rate of water uptake increased, the region just behind the root tip offered the same resistance to water movement as before. However the regions further from the root tip now offered less resistance than the region just behind the root tip. Thus different total water potential gradients across the root cause changes in the resistance of the water pathway to water movement.

Water can flow across the root to the endodermis through the cell walls and interstitial spaces (Mees and Weatherley 1957) or move through the cells (Brouwer 1954), or both (Woolley 1965). At the endodermis water must move through the cells, as the Casparian Strip is considered to be impermeable to water movement. Once inside the endodermis movement to the xylem can occur through the cell walls or through the cells themselves.

It is concluded then that water in the plant is in a state of dynamic balance, the turgor of the plant cells depending at any instant on the interplay of total water potential and osmotic potential at any given point in the plant. The total potential of the water in the tissue will therefore be determined by the resistances to flow offered by the components of the flow path and by the transpiration rate.

2.1.2 Active water movement

Van Overbeek (1942) and others (Rosene 1944, Arisz _et al_. 1951) proposed that active transport of water occurs across the root and into the xylem vessels. This active transport is achieved by way of some secretion process accomplished through various undefined mechanisms (Osterhout 1947, Franck and Mayer 1947).

Most data which have been used to demonstrate the occurrence of an active transport system have been obtained from exudation studies. However Raney and Vaadia (1965) in their study of exudation concluded that "the time required for longitudinal equilibration in the xylem during exudation precludes that the osmotic pressure of the sampled exudate will estimate correctly the osmotic pressure of the xylem sap at point of entry into the xylem." In view of this comment it is doubtful whether the conclusions reached by such workers as Arisz _et al_. (1951) are valid since it is clear that insufficient time was allowed for equilibrium to be reached. Therefore some doubt is placed upon the occurrence of active water uptake by plants.

2.2 Water Movement in Soils

2.2.1 A special case

The French engineer Henry Darcy (1856) being unable to find the required information on the downward flow of water through filter sands in the city of Dijon, resorted to experimental study of the problem (Hubbert 1957). He found that the volume, q, of water which passed through a saturated sand bed, in unit time, was directly proportional to the area of the bed, a, and the difference Δh between fluid heads at the inlet and outlet faces of the bed, and inversely proportional to the thickness l of the bed, i.e.

$$q = k\,a\,\frac{\Delta h}{l}$$

where k is a proportionality constant characteristic of the bed.

Since Darcy's proposal, the applicability of this equation has been examined (e.g., Philip 1957a, Lutz and Kemper 1959, Swartzendruber 1963, Olsen 1965) as well as the reasons for variation in the coefficient k (Childs and Collis-George 1950, Jackson *et al*. 1965). It is generally accepted that when the water velocity is small, or more specifically when Reynolds numbers are less than unity, Darcy's equation is applicable to water flow in porous beds (Childs and Collis-George 1950).

Studies of the proportionality constant k have shown that it varies markedly with moisture content (Gardner and Gardner 1950) being greatest in saturated soils and declining with decrease in moisture content. In fact, water flow can become negligibly small at small but finite soil water contents (Childs and Collis-George 1950). The texture of the soil has a considerable influence on the value of the coefficient k (Childs and Collis-George 1950). In sands its value is greater than that in soils of heavier texture at the same water content.

Many models have been proposed to permit calculation of k from more easily determined properties of the soil. The most successful model appears to be that of Millington and Quirk (1960) (see Jackson et al. 1965).

2.2.2 General approach

Buckingham (1907) initiated investigations into energy relationships of water absorption by porous media and later Schofield (1935) developed the concept of pF to express the energy with which water was held by the soil. The term capillary potential, introduced by Buckingham, is the same physical entity as the matric potential defined in section 2.1.1. The capillary potential varies from zero at saturation to very large negative values as the soil moisture content approaches zero and is markedly dependent on soil texture (Richards 1928) for a given water content.

Edlefsen and Andersen (1943) analysed soil-moisture phenomena by use of the thermodynamic function, free energy, which they took to be composed of osmotic, matric (capillary) and gravitational components. The magnitude of the free energy was relative to a free water datum, as specified in the definition of potential (I.S.S.S. 1963). In relation to water movement through the soil to plant roots, the gravitational component may often be ignored. When it is ignored the free energy of soil water is conceptually similar to the diffusion pressure deficit but with the algebraic sign reversed (Crafts et al. 1949, pp 76-77).

As was discussed in Section 2.1.1, the total water potential at any point in plants or soils is made up of three components, i.e.

$$\psi' = O + Z + I$$

where all are expressed in units of erg/gm. In the case of a point in a soil which lies below a water table, S, the submergence potential may be used instead of M (Rose 1966, pp 133-135), although Slatyer and Taylor (1960) treated S as part of G.

In general external gas pressure can be neglected in total soil water potential determinations, as absolute pressure changes are negligible and only in special cases is its use warranted. The total soil water potential is therefore equal to the sum of only three potentials, viz.

$O = C_1RT/\rho$ which is identical with classical osmotic pressure, (erg/gm.)

$Z = gz$ (erg/gm.)

$M = m/\rho$ (erg/gm.)

where C_1 = molar concentration of solute (mole/cc.),

R = gas constant (erg/degree absolute/mole),

T = temperature (degree absolute),

z = height above reference point (cm.),

g = gravitational constant (cm/sec.^{2}),

m = matric potential (erg/cc.),

and ρ = density of solution (gm./cc.),

therefore

$$\varphi' = C_1RT/\rho + gz + m/\rho$$

or $$\varphi = C_1RT + \rho gz + m \qquad \ldots\ldots (7)$$

where φ = total soil water potential in erg/cc.

The above nomenclature has been used as this is believed to be the most easily followed by soil and plant workers. Other nomenclature has been used (Babcock 1963, Noy-Meir and Ginzburg 1967) and is discussed by Bolt and Frissel (1960).

The rate of water movement is proportional to the total water potential gradient, thus

$$\underset{\sim}{v} = - k\nabla\varphi \qquad \text{......} \; (8)$$

where v is the volume flux density of water and k the hydraulic conductivity. This equation is formally the same as Darcy's Law for saturated flow. However in the above equation, k is not a constant but is a function of water content. Combining equation (8) with the principle of the conservation of matter gives

$$\frac{\partial\theta}{\partial t} = - \nabla.(-k\nabla\varphi) \qquad \text{......} \; (9)$$

where θ is the water content on a volume basis and t is time (sec.).

For horizontal flow of water and negligible solute effects, equation (7) reduces to

$$\varphi = m$$

and $$\frac{\partial\theta}{\partial t} = \frac{\partial}{\partial x}\left(k\frac{\partial m}{\partial x}\right) \qquad \text{......} \; (10)$$

For vertical flow

$$\frac{\partial\theta}{\partial t} = \frac{\partial}{\partial z}\left(\rho gk + k\frac{\partial m}{\partial z}\right) \qquad \text{......} \; (11)$$

Solutions of equations (10) and (11) have been obtained by expressing the matric potential, m, as a function of the water content, θ,

i.e. $$\frac{\partial m}{\partial z} = \frac{\partial\theta}{\partial z} \cdot \frac{dm}{d\theta}$$

and substituting $D = k\frac{dm}{d\theta}$ (Klute 1952b). Thus equation (10) would be

$$\frac{\partial\theta}{\partial t} = \frac{\partial}{\partial x}\left(D\frac{\partial\theta}{\partial x}\right) \qquad \text{......} \; (12)$$

which is formally the same as the well known diffusion equation. Diffusion theory can then be used to obtain particular solutions, (Gardner 1959b, 1962, Gardner and Mayhugh 1958, Gardner and Miklich 1962, Jackson 1964, Klute 1952a, Philip 1955, 1957b,c, 1960, Philip and Farrell 1964, Philip and de Vries 1957, Rijtema 1959). It must be noted that any hysteresis in m(θ) will complicate the use of equation (12). The variation of the diffusivity with hysteresis in m(θ) has been shown by Klute *et al*. (1964). The relationship between D and θ during wetting and drying of samples is best described as of "bowtie" form (Klute *et al*. 1964).

Jackson (1963) demonstrated that at least for one soil that he worked with, Pachappa loam, and under his experimental conditions diffusivity analysis did not "exactly" describe water movement through the soil, as also found by Nielsen et al. (1962), Bruce and Klute (1963) and Elrick (1963). However Peck (1964) concluded that as the diffusivities calculated from transient experiments agreed with those from steady state methods, the transient diffusivity equation does describe water flow. Philip and de Vries (1957) incorporated effects of a temperature gradient on water movement.

2.2.3 Water movement to plant roots

Gardner (1960) in his discussion entitled "Dynamic aspects of water availability to plants" developed the application of diffusion analysis to water transport through the soil to a root. He considered that the flow to the root was axisymmetrical and only in a radial direction and that the root acted as a line sink. The appropriate flow equation for such a system is

$$\frac{\partial \theta}{\partial t} = \frac{1}{r}\frac{\partial}{\partial r}\left(rD\frac{\partial \theta}{\partial r}\right), \qquad \ldots\ldots (13)$$

with initial and boundary conditions $\theta = \theta_o$, $m = m_o$,

$t = 0$, $r_a < r < \infty$ and $2\pi r_a k(\frac{dm}{dr}) = 2\pi r_a D(\frac{d\theta}{dr}) = w$, $r = r_a$, $t > 0$. Here r_a is the radius of the root and w is the rate of water uptake by the root (cc/cm root length/unit time). The solution given is, for sufficiently long times,

$$m - m_o = \Delta m = \frac{w}{4\pi k}(\ln \frac{4Dt}{r^2} - \gamma) \qquad ...... (14)$$

where $\gamma (= 0.57722..)$ is Eulers' constant, and m is the matric potential.

From the above solution when $r = r_a$ Gardner concluded that large variations in D would cause only very small changes in Δm and his assumption that D was constant was not serious. Similarly variations in root radius need cause only small changes in Δm, except at low suctions when the resistance to water entry into the root might be large compared with the resistance to water movement in the soil.

From equation (14) Gardner concluded that water moved to a plant root only from distances of a few centimeters; that the variation in k due to Δm was no larger than the uncertainties in the determination of k and that use of constant k was not unjustified for the infinite system and for not too large t.

Gardner (1960) also shows that the solution for the transient case above could be approximated by a series of steady-state solutions.

2.2.4 Water availability to plants

During the earlier part of this century the belief was held that the factor controlling the amount of water available to plants was the difference between the "suction" power of the plant and the soil (Buckingham 1907, Schofield 1935). Several workers (Lewis et al. 1935, Richard and Wadleigh 1952, Veihmeyer 1956, p.115) however pointed out that the ability of plants to obtain water was determined not only by the potential gradient but also by "the readiness or velocity with which the soil water moves in to replace that which has been used by the plant" (Richards and Wadleigh 1952, p.103). Gardner (1960) and his associates (Gardner and Ehlig 1962a,b, 1963) concluded that generally the amount of soil water available to plants was determined by the ability of the soil to transmit water to the plant root as rapidly as needed by the plant. That is, as a result of water uptake by the plant, a total water potential gradient is set up in the soil along which water moves from points distant from the root up to the root. Provided the soil can transmit sufficient water to the plant root to maintain the demand by the plant, there will be no deleterious water stress in the plant. However, should the demand exceed the quantity which can be transmitted through the soil, then plant water stress can occur.

Gardner (1960) concluded that the wilting point was that moisture content below which the conductivity of the soil was too low to permit water to move even short distances as rapidly as it was needed by the plant. The wilting point of a soil is therefore dependent upon the unsaturated permeability of the soil, the transpirational demand and some characteristics of the plant such as plant growth (Gardner and Nieman 1964) and root distribution (Gardner 1964).

The field capacity of a soil was defined by Gardner (1960) as the moisture content at which the capillary conductivity of the soil was so low that, under the total potential gradient operating, the redistribution of water in the soil profile was negligible.

2.3 Ion Movement in Plants

Two basic mechanisms, one active and the other passive, have been proposed to explain ion uptake and transfer processes.

As was done in Section 2.1, for water movement in plants, any ion transfer that cannot be accounted for by physical forces such as diffusion along activity gradients or resulting from viscous flow of solvent (both passive mechanisms) will be considered to result from an "active" mechanism (Ussing 1957). In the remainder of this thesis, the term "barrier" is used to describe any membrane across which the transport of ions is an "active" process.

Interpretation of experimental studies of ion accumulation and transfer in plants is made difficult by the variety of processes which can occur. Some ions or radicals containing the elements nitrogen, potassium, sulphur and phosphorus complex rapidly into organic forms within the root (Anderssen 1929, Tolbert and Wiebe 1955, Bollard 1957, 1960, Jackson and Hagen 1960), although the quantity so complexed may be only a small proportion of the total quantity taken up. Recently Siegel et al. (1966) found chloride in complexed organic form in plants. Because of complexing it is difficult to assess whether ions are moving with or against concentration or activity gradients. Rarely are experimental techniques used which measure only those ions which contribute to the establishment of chemical activity gradients (Lopushinsky 1964).

Not only must appropriate chemical activity gradients be determined but it is necessary also to ascertain that the component being measured is in fact part of the normal transport stream. The results of Raney and Vaadia (1965), have already demonstrated that the concentration of ions in xylem exudates need not reveal the true concentration at the point of entry of the ions into the xylem. Further, Morrison (1965) has shown that not all of the phosphorus in exuded root sap is part of the normal transport stream in whole plants, but is secreted by root cells in response to a wound stimulus.

Ion adsorption onto charged surfaces within the plant (Charles 1953, Hewitt and Gardner 1956, Barber and Russell 1961, Bell and Biddulph 1963) poses a similar problem. If the experimental techniques employed cannot differentiate between sorbed and non-sorbed ions estimates of chemical activity gradients again are misleading.

Measurements of electropotential gradients have been used by some workers (Etherton and Higinbotham 1960, Bowling *et al*. 1966) to identify electrochemical activity gradients. Dainty (1962) however has pointed out that any charged surfaces near to the points of measurement of such potentials modifies the currents obtained. Charged sites occur throughout the cell walls, cytoplasm and stele (Knight et al. 1961, Pitman 1965b, Bell and Biddulph 1963) and more caution must be exercised in interpreting electrochemical activity gradients obtained by present methods (Briggs et al. 1961, pp.106-116).

The conclusions which have been drawn from electrochemical gradients are that cations are passively transferred from the exterior solution into the cytoplasm (Etherton and Higinbotham 1960) and to the xylem (Bowling et al. 1966) as a result of an appropriate electropotential gradient set up by the active transfer of anions (Bowling et al. 1966).

Kinetic analysis has also been used to examine ion uptake mechanisms. It has been found (Epstein and Leggett 1954) that over a limited range of concentrations, the relation between the reciprocal of the steady rate of accumulation of ions in cells and the reciprocal of the external concentration is approximately linear. This result suggested that ion transfer systems behaved in a manner similar to that found in enzymatic reactions and has led to the application of enzyme kinetic theory to ion uptake (Noggle and Fried 1960, Epstein et al. 1963, Hodges and Vaadia 1964, Bange et al. 1965). In using kinetic analysis to interpret the effects of ion competition in ion transfer processes (Epstein 1956, 1962) it is necessary to assume that the change in concentration of the oppositely charged ion has no effect on the combination of the ion with the carrier or on the rate of movement of the carrier, and further that the ions compete only for combination with the carrier (Briggs et al. 1961, p.147). Although ion uptake behaviour of plants can be predicted from kinetic analyses, many observed results can also be interpreted in terms of the complexing or adsorption and exchange of ions within the cells (Leggett et al. 1965).

In exudation studies of ion transfer in plants with excised plant material the integrated dynamic processes of the whole plant system cannot always be adequately recognized. Phillis and Mason (1940) and Bowling (1965) have shown that the uptake of ions into plants can depend upon the transport of metabolites from tops to roots. Bange (1965) however has found that excision affected only the transfer of ions to the tops. Excision of roots however results in major changes within the root. Kylin and Hylmo (1957) found that the free space of intact roots was higher than that of similar but excised roots (27.5% as compared to 18.0%). This decline in free space following excision conflicts with the results of Jacobson et al. (1958) who found the reverse effect. Jacobson et al., using whole plants, found that no free space occurred in the stele of the roots, but in excised plants half of the measured free space was in the stele, as found by Pitman (1965b). Excision therefore causes changes in the behaviour of plant parts and caution is needed in applying results from excised plant parts to whole plants.

Interpretation of ion transfer processes in plants requires that the path by which ions move across the root to the xylem be identified. Brouwer (1954) attempted to define the regions of the root which were functional in ion uptake. He found at low water uptake rates that the uptake of chloride ions was greatest just behind the root tip, and that the uptake decreased with distance away from the root tip. Uptake could be detected at least 15 cm. from the root tip. Brouwer further showed that accumulation was at a maximum near the root tip and that transfer to the tops was at a minimum in that region. Further away from the root tip, total uptake per unit length was somewhat less, and the proportion accumulated was very small although the proportion transferred to the tops was large. At higher water flow rates, the uptake of ions just behind the root tip increased only slightly, while uptake in regions further from the root tip increased to a higher level. As water flow increased so did the proportion of ions transferred to the tops. The increase in transfer was greater in the region just behind the root tip compared to the region beyond the root hairs.

In view of the foregoing, it is difficult to assess the relative importance of active and passive uptake and transfer of anions and cations. Ions move into the apparent free space of roots (Hope and Stevens 1952, Briggs *et al*. 1961) by diffusion or by convection or both processes, and in this space their movement may be influenced by charged sites in the cell walls. Ions can also move into the root hairs or epidermal cells through the plasmalemma which is considered to be a barrier (Levitt 1957, Arisz 1964, Hendricks 1966). At low external concentrations the cations can move through the plasmalemma by exchange with H^+ ions (Hendricks 1966) or by "exchange diffusion" down charged pores (Tanada 1966). At higher external concentrations cations enter the cells by diffusion (Torii and Laties 1966b). The anions however are actively transported across the plasmalemma and released from their carrier by exchange with OH^- ions on the interior surface of the plasmalemma (Hendricks 1966). Under most conditions an excess of cations over anions is found in the root, accumulated in the vacuoles. Charge balance is required (Bear 1950, De Wit *et al*. 1963) and it is believed this is met by internal "titration" of organic acids such as malic acid (Torii and Laties 1966a).

The means by which plants distinguish between ions in the accumulation and transfer processes is not known but specific carriers (Bange 1962), exchange-diffusion down charged pores (Tanada 1966) and metabolic requirements of plants (Evans and Sorger 1966) have been proposed as possible explanations.

The anatomy of the plant root is such that parallel and series pathways exist between the xylem and the exterior. The exodermis, rarely absent in monocotyledons (Esau 1953), lies beneath the epidermis and is almost completely suberized after differentiation from the cortical cells. It may act as a barrier or at least be only partly permeable to ions via the passage cells which are unthickened.

Two pathways are possible for ion movement across the cortex; firstly via the free space and intercellular spaces and secondly through the symplasm. Movement along the symplasm is accepted as the major or dominant path today (Torii and Laties 1966b, Luttge and Laties 1967) and ion accumulation into the vacuoles is looked upon as a separate process. The accumulation processes are similar to those for transport across the plasmalemma (Torii and Laties 1966b).

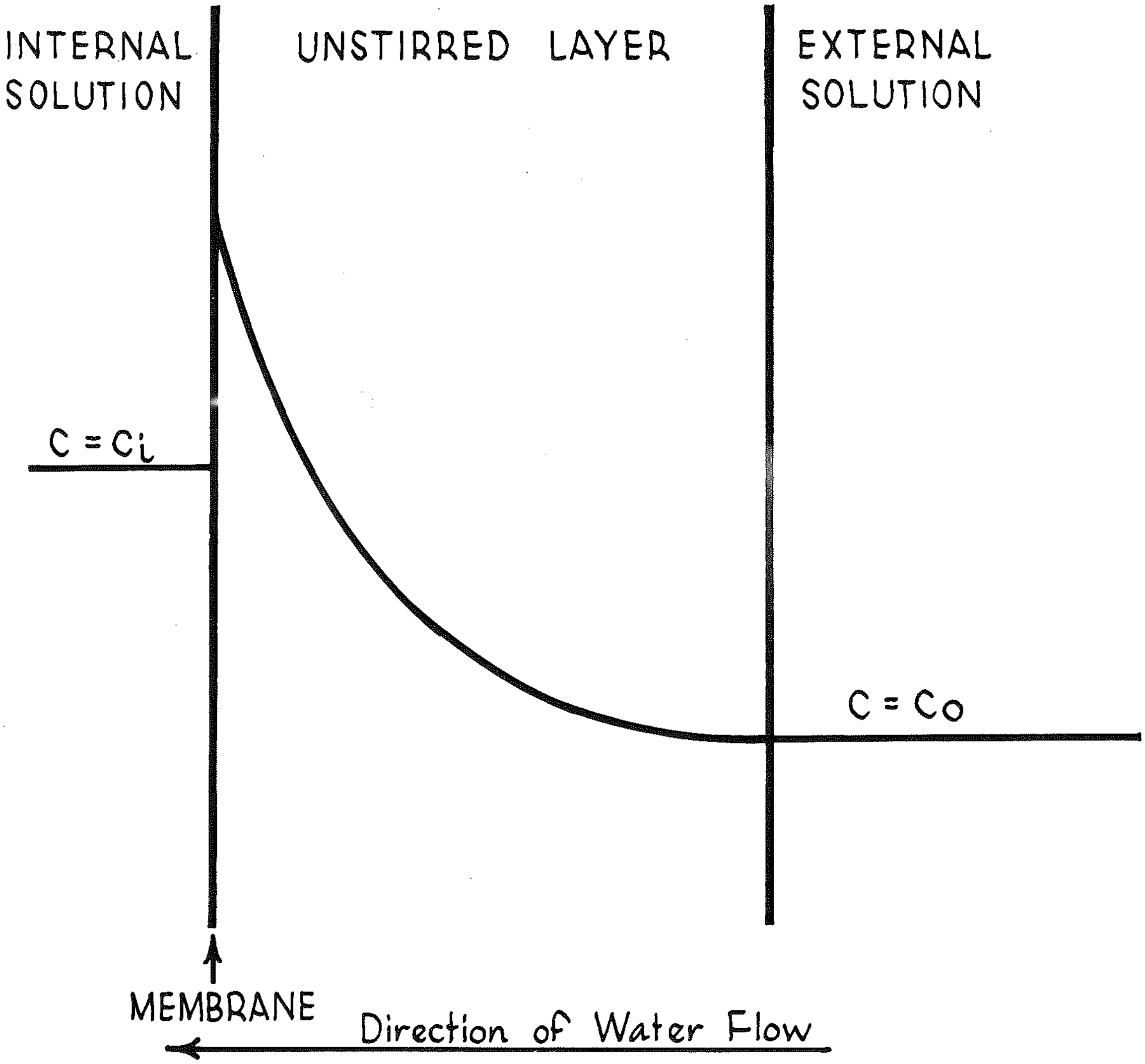
The structure of the endodermis is such that for ions in the free space to cross the endodermal cells they must first enter the cytoplasm of these cells and in so doing, pass through the plasmalemma. Once inside these cells the ions can move through the symplasm to the xylem cells by diffusion or by convective flow with water along the same path. However whether this barrier exists between cortex and stele is still debated (Bange 1965). Transfer up the xylem may be by convective flow, by diffusion coupled with ionic exchange or by surface diffusion.

Water flow has been shown to affect the total quantity of ions taken up and transferred by plants, especially at high external concentrations (Russell and Shorrocks 1959). At surfaces which are differentially permeable to ions and to water (Rapoport 1965) sufficiently rapid flow of solution results in more ions arriving at such surfaces than can be transported across them and ions will accumulate at these surfaces (Barber 1962). The concentration gradient across the surface can become sufficiently large that the need to invoke active transfer mechanisms is eliminated. This increase in concentration at the membrane surface could, if concentration determinations are made at some distance from the membrane surfaces, mislead one into believing that transport across the membrane has been against a concentration gradient (see Figure 2). With plants growing in culture solutions it has been found that even with vigorous stirring it is impossible to remove a stationary layer of solution around the root (Bowen pers.comm.). Thus if the epidermis or exodermis acts as a differentially permeable surface to water and ions, care must be taken in interpreting results whenever the gradient is obtained from the difference in concentration of external solution and that in the cortical cells.

Convection through charged membranes presents difficulties in interpretation. If, for example, the membrane is negatively charged, then with water flow, more cations than anions will be transferred through it and an electropotential, or "streaming potential" (Pidot and Diamond 1964) gradient will arise.

The importance of ion accumulation in vacuoles upon the total quantity of ions transferred to the tops is revealed in the results of Russell and Shorrocks (1959). They found that when the external concentration was low, more of the ions taken up were accumulated and water flow had little effect on ion transfer to the tops. At

Figure 2. The possible effects of Water Flow and an "Unstirred Layer" on Concentration Gradients Around a Membrane which is Differentially Permeable to Ions and Water.


INTERNAL SOLUTION
UNSTIRRED LAYER
EXTERNAL SOLUTION
$C = C_i$
$C = C_o$
MEMBRANE
Direction of Water Flow

intermediate external concentrations and with a sufficiently high rate of water flow, accumulation was relatively smaller and ion transfer to the tops appeared to be predominantly passive. At high external concentrations passive transport may occur at very low water flow rates.

Thus for whole plants growing in real environments it is not possible to predict what process is dominant in the transfer of ions from the soil to their site of use in the plant. The circular statement of Steward and Sutcliffe (1959) that "plants grow because they can absorb and accumulate salts; they also accumulate because they can grow" cannot yet be replaced by a more quantitative analysis of the phenomena.

2.4 Ion Movement in Soils

The availability of non-sorbed nutrients is principally governed by the movement of ions from points distant from roots up to the surfaces of roots (Jenny 1966). For ions which are strongly bound to soil particles, it may be necessary for the roots to approach very close to the ion source for contact exchange to occur. Jenny and Overstreet (1939) suggested that contact exchange between ions on the root surface and ions on the clay particles will occur when the root and clay particles are close together and their electric double layers intermingle. They proposed that hydrogen ions, associated with the pectin material on the root surface, were exchanged for cations of the soil colloids independently of the soil solution processes. Lewis and Quirk (1962) suggested "proximity exchange" would be a more appropriate term to use and is in keeping with the ideas of Low (1962a). Wallace (1962) suggested that for iron this process should be termed "contact chelation". Jenny and Grossenbacher (1963) after observing a mucigel layer between the roots and soil particles, proposed that this layer would allow much more intimate contact between roots and soil, which strengthened the notion of contact exchange.

Recently it has been proposed that root interception may be of some significance in the uptake of many ions (Al-Abbas and Barber 1964, Oliver and Barber 1966a,b).

Many soil properties affect ion movement in the soil and uptake by the plants and in this section consideration will be given to those properties which affect ion transfer through the soil.

Ions can move from a point in the soil up to the root surface by two processes:

(1) Diffusion; or mass transfer along a concentration gradient, from regions of high concentration to regions of lower concentration,

(2) Convection; where the ions are moved by the flow of water or solution.

2.4.1 Diffusion in soil solution

For ions to diffuse to a root surface the concentration of the ions at the surface must be lower than that in the soil. Barber (1962) using autoradiograph techniques showed that such concentration gradients do occur around roots and that ions can therefore diffuse to roots.

In bulk solution Fick's first law of diffusion may be written as

$$\underset{\sim}{J} = - D_o \text{ grad } C_l \qquad \ldots\ldots (16)$$

where J is flux density of ions, C_1 is the concentration of diffusing ion in solution, D_o is the proportionality constant or the diffusion coefficient of the ion in water.

In treating ion diffusion in soils the appropriate equation describing the flux density is

$$\underset{\sim}{J} = - D \text{ grad } C_1 \qquad \ldots\ldots (17)$$

where J is the mass of the ion transported per unit time across unit area of soil normal to the direction of flow, C_1 is the concentration of the ion in solution (mass per unit volume of solution) and D is the apparent diffusion coefficient for the ion in the soil. Many definitions have been used for diffusion coefficients (Bouldin 1961, Gardner 1965, Nye 1966b) leading to ambiguities and errors in interpretation. The definition above has been used to maintain uniformity with treatments of gaseous diffusion in soils, and as so defined includes all the effects of soil properties including water content, tortuosity etc. which contribute to reduction in D with respect to D_o.

The equation of continuity, or principle of conservation of matter, in the absence of sources or sinks can be written as

$$\frac{\partial C}{\partial t} = - \text{div}.\underset{\sim}{J}$$

where C is the quantity of ion in solution per unit volume of soil. Substituting equation (17) into this, gives in one dimension,

$$\frac{\partial C}{\partial t} = \frac{\partial}{\partial x}\left(D \frac{\partial C_1}{\partial x}\right) \qquad \ldots\ldots (18)$$

or

$$\frac{\partial C_1}{\partial t} = \frac{1}{\theta}\frac{\partial}{\partial x}\left(D \frac{\partial C_1}{\partial x}\right) \qquad \ldots\ldots (19)$$

as $C = C_1\theta$ (assuming θ to be constant with time and x).

The value of D in soils is always less than the value of D_o for that ion (Klute and Letey 1958, Porter _et al_. 1960, Patil _et al_. 1963) due to the smaller cross sectional area available, the increased path length arising from the tortuous nature of the pore space in soils, and possibly the higher viscosity of adsorbed water near particle surfaces (Low 1962b). As the moisture content is reduced so is the value of D (Romkens and Bruce 1964, Place and Barber 1964, Olsen _et al_. 1965). Particle size (Klute and Letey 1958, Romkens and Bruce 1964), cation exchange capacity of soil (van Schaik _et al_. 1966), clay content and fixation (Evans and Barber 1964) may also affect the diffusion of ions in soils.

In soils it has been found that D can vary slightly with ion concentration (Letey and Klute 1960, Place and Barber 1964), but this variation is generally ignored. The diffusion coefficient is also temperature dependent and in soils this may be of some importance (Graham-Bryce 1963).

In order to maintain electrical neutrality, the diffusion of any ion is accompanied by the diffusion of another ion of opposite charge. Counter diffusion of other ions can also occur in mixed electrolytes. In some literature, especially that associated with chemical engineering, it will be found that equation (17) is written in the form

$$J_1 = - D_{1,2} \frac{dC_1}{dx} \qquad \ldots\ldots (20)$$

where $D_{1,2}$ is the diffusion coefficient for ion 1 when diffusing against ion 2. This effect of the counter ion can be pronounced (Husted and Low 1954) as can be the effect of the accompanying ion (Nye 1966a), although effect of accompanying ion is considered to be small when ions are diffusing to plant roots (Nye 1966a). The methods of obtaining average coefficients are discussed by Low (1962a) and Nye (1966a), but since the determination of the diffusion coefficient in soils involves other errors, consideration of this point is deemed unnecessary (Gardner 1965).

In most soils there is some interaction between certain ions and soil particles which affects the quantity of ions transmitted to the root in a certain time (Olsen *et al.* 1965). When the ion under consideration is adsorbed or produced in the soil another term expressing the source or sink term must be included in equation (18) and by appropriate modification equation (18) becomes

$$\frac{\partial C}{\partial t} = \frac{\partial}{\partial x}\left(D\frac{\partial C_1}{\partial x}\right) + \frac{\partial L}{\partial t} \qquad \ldots\ldots \ (21)$$

where $\frac{\partial L}{\partial t}$ is the rate of production or adsorption of the ion. Equation (21) may be expressed in the form

$$\frac{\partial C}{\partial t} + \frac{\partial L}{\partial t} = \frac{\partial C_T}{\partial t} = \frac{\partial}{\partial x}\left(D\frac{\partial C_1}{\partial x}\right)$$

where C_T is concentration of ion per unit volume of soil, or

$$b\frac{\partial C_1}{\partial t} = \frac{\partial}{\partial x}\left(D\frac{\partial C_1}{\partial x}\right)$$

or

$$\frac{\partial C_1}{\partial t} = \frac{1}{b}\frac{\partial}{\partial x}\left(D\frac{\partial C_1}{\partial x}\right)$$

where $b = \frac{dC_T}{dC_1}$ (Nye 1966b).

For a linear adsorption isotherm and θ constant

$$C = C_1\theta \qquad \text{and} \qquad L = B\theta C_1 + \text{constant}$$

where B is the ratio of the number of ions in the adsorbed phase to the number of ions in the solution phase at equilibrium, per unit volume of soil,

then $$\frac{dC_T}{dC_1} = B\theta + \theta = \theta(B+1)$$

and $$\frac{\partial C_1}{\partial t} = \frac{1}{\theta(B+1)} \frac{\partial}{\partial x} \left(D \frac{\partial C_1}{\partial x}\right) \qquad \text{......} \; (22)$$

If D is independent of x then equation (22) can be written as

$$\frac{\partial C_1}{\partial t} = \frac{D}{\theta(B+1)} \frac{\partial^2 C_1}{\partial x^2} \qquad \text{......} \; (23)$$

which is analagous to that obtained by Gardner (1965) and Olsen _et al_. (1965).

To evaluate the quantity of ions which are diffusing across a particular plane at a particular time, it is necessary to solve the appropriate equation for the boundary conditions imposed upon the system. There is a formal analogy between the mathematics of diffusion and heat flow, and Carslaw and Jaeger (1959) provide many solutions to the heat flow equations. Care must be exercised in applying such solutions to problems of ion diffusion. With definitions used in this thesis, that is,

$$J = - D \frac{dC_1}{dx}$$

and $$\frac{\partial C_1}{\partial t} = \frac{D}{\theta}\frac{\partial^2 C_1}{\partial x^2}$$

Substitution of D for K and $\frac{D}{\theta}$ for $\mathcal{K}$ in heat flow equations will lead to solutions of diffusion equations in terms of C_1, where $\mathcal{K}$ and K are defined in heat flow by

$$f = - K \frac{dT}{dx}$$

and $$\frac{\partial T}{\partial t} = \mathcal{K}\frac{\partial^2 T}{\partial x^2}$$

where f is the flux density and T is the temperature. Other definitions of the diffusion coefficient have been used but the necessary substitutions must be completed by analogy as above to make use of the many solutions available to the heat flow equations.

2.4.2 Diffusion along solid surfaces

Another type of ion diffusion is possible, that is, movement along the surface of the soil particles. The importance of this surface diffusion in soils is not known. Lai and Mortland (1961), Graham-Bryce (1963) and van Schaik et al. (1966) concluded that surface diffusion may occur, but Husted and Low (1954) were unable to detect any surface transfer for Li, Na and K even after several weeks. Should surface diffusion occur as an ion "hopping" process from exchange site to exchange site (Lopez-Gonzalez and Jenny 1959, Lai and Mortland 1961) it would involve movement of cations in the opposite direction, but no accompanying movement of anions (van Schaik and Kemper 1966, van Schaik et al. 1966). The equation describing the flux density along surface could therefore be written as

$$\underset{\sim}{J}_s = - D_s \text{ grad } C_s \qquad \text{......} \; (24)$$

where J_s is surface flux (mole cm^{-2} sec^{-1}), C_s is the concentration of ions on the soil surface and D_s is a constant of proportionality between flux and concentration gradient along the particle surfaces.

2.4.3 Combined surface and liquid diffusion

Diffusion of ions both in solution and along the particle surfaces occurs, the appropriate equation for the total flux density, J_T, being

$$\underset{\sim}{J}_T = \underset{\sim}{J} + \underset{\sim}{J}_s \quad .$$

However the above equation assumes that transport by surface and liquid diffusion is in parallel. If diffusion also occurs in series, the non steady state equations become very complicated (Nye 1966a).

2.4.4 Diffusion plus convection

Water moves through the soil as a result of a total water potential gradient. Associated with the movement or mass flow of water there will be a movement of ions in solution (convection). The quantity of ions transported per unit area of soil in the x direction by convection, that is, flux density J, will be given by

$$J = v\ C_1 \qquad \ldots\ldots\ (25)$$

where v is the volume of water moved per unit area of soil in the x direction per unit time. The total flux J_T, will be the sum of the diffusive flux density and convective flux density, that is,

$$J_T = -\ D\,\frac{dC_1}{dx} + v\ C_1 \qquad \ldots\ldots\ (26)$$

(assuming surface diffusion is of no consequence) and combining this with the equation of continuity and assuming that there are no source or sink terms, and no moisture gradient

$$\frac{\partial C}{\partial t} = \frac{\partial}{\partial x}\left(D\,\frac{\partial C_1}{\partial x}\right) - \frac{\partial(v\ C_1)}{\partial x} \qquad \ldots\ldots\ (27)$$

Equation (27) over-simplifies the complex changes of concentration with time in a mixed diffusion and convection system due to the dependence of D on **v**.

Biggar and Nielsen (1964) proposed that for a linear system, where D and θ are not functions of x that

$$\frac{\partial C_1}{\partial t} = D_{BN} \frac{\partial^2 C_1}{\partial x^2} - u \frac{\partial C_1}{\partial x} \quad \ldots\ldots \ (28)$$

where u is the velocity of water flow in the x direction and D is the diffusion coefficient defined from $J_1 = - D_{BN} \frac{dC_1}{dx}$ where J_1 is the flux per unit area of solution. They found that whenever anNaCl solution displaced a solution of different concentration in a horizontal system of glass beads their results were not described by equation (28). Day and Forsythe (1957) used a constant or index of dispersion, β, in their analysis, where $\beta = 2\mathcal{D}/u$, $\mathcal{D}$ is Scheidegger's (1954) factor of dispersion and u is average velocity of fluid. This $\mathcal{D}$ is defined by equation

$$\frac{\partial C_1}{\partial t} = \mathcal{D} \frac{\partial^2 C_1}{\partial (x-ut)^2} \quad , \ (\text{Day } 1956).$$

Taylor (1953, 1954) found that, in a single tube, a slug of salt dispersed from the point of injection and that the dispersion was greater than that expected from a simple diffusion process. Radial variation in water velocity across the tube distorted salt concentration gradients and resulted in ion diffusion, across the tube.

At a constant outflow rate the narrower the tube, the greater would be the velocity gradients across the tube, and the greater is the lateral diffusive movement of ions. In porous media, with highly tortuous paths and a mixture of "tube" sizes, velocity gradients normal to the direction of flow, would vary considerably, leading to major departures from simple summation of convective and diffusive fluxes.

Equation (28) is not precise when water velocities are high since the dispersion effect or interaction term reflecting the dependence of D on u is not included.

Two main approaches have been used in recent attempts to describe dispersion due to molecular diffusion and macroscopic mixing in flow through porous media. Both methods employ statistical models, one considering the porous medium itself as a random network of capillaries (Saffman 1960) and the other describing the motion of the fluid as a random walk process with and without autocorrelation (Scheidegger 1958, Saffman 1959). However it would appear that the random walk models are unsuccessful in describing lateral dispersion (List and Brooks 1967). Saffman's model (1960) which is based upon a random network of capillaries appears to be useful but only if the flow remains laminar (List and Brooks 1967).

When the flow is completely turbulent the dispersion is adequately described by mixing cell models such as developed by Baron (1952) and Ranz (1952). Models describing flow can therefore be obtained only for situations where flow is laminar or turbulent. In the situation of mixed laminar and turbulent flow, that is, when both may occur in the medium, but not at the same point, there is no satisfactory model to describe the flow.

2.5 Models Describing Ion Uptake by Plants

The general approach used to describe ion uptake by plants, has been to solve appropriate equations for ion movement in soils under the boundary conditions imposed by the soil and plant.

The first model proposed to describe the above process was that of Bouldin (1961). He considered that the transfer of phosphorus to the root surface was an axisymmetrical diffusion problem, and that the root acted as a cylindrical sink in an infinite unstirred medium, at some initial concentration C_o, and the equation describing concentration change with time was

$$\frac{\partial C_1}{\partial t} = D_B \left(\frac{\partial^2 C_1}{\partial r^2} + \frac{1}{r} \frac{\partial C_1}{\partial r} \right) \quad .... \ (29)$$

where D_B is defined by equation $J = - D_B \frac{dC_1}{dr}$, and J is the flux density (cc/cm^2 solution/sec). By solving equation (29) under the initial and boundary conditions,

$$C_1 = C_{1_o}, \quad r_a < r < \infty, \quad t = 0$$

and

$$-J = D_B \frac{dC_1}{dr} = \alpha C_1, \ r = r_a$$

where r_a is the radius of the root, Bouldin (1961) obtained

$$Q' = \alpha C_1 \ I \ (\tfrac{1}{2}\pi N^{-\frac{1}{2}}, \ \tfrac{1}{2}\pi N^{\frac{1}{2}}; \ V) \quad .$$

Here $I(\frac{1}{2}\pi N^{-\frac{1}{2}}, \frac{1}{2}\pi N^{\frac{1}{2}}; V)$

$$= \int_0^{\infty} \frac{e^{-Vu^2}}{\left[\frac{1}{2}\pi N^{-\frac{1}{2}} u J_1(u) + \frac{1}{2}\pi N^{\frac{1}{2}} J_0(u)\right]^2 + \left[\frac{1}{2}\pi N^{-\frac{1}{2}} u Y_1(u) + \frac{1}{2}\pi N^{\frac{1}{2}} Y_0(u^2)\right]^2}$$

(Jaeger 1942)

and $N = \frac{r_a \alpha}{D_B}$ and $V = \frac{D_B t}{r_a^2}$.

He also considered the appropriate modifications of the solution given above when there is some reaction between ion and soil. This is of considerable importance in phosphate diffusion in soils (Lewis and Quirk 1967). The modification Bouldin gave is similar to that shown in equation (22), that is, D_B is replaced by D_B' where

$$D_B' = \frac{D_B}{B + 1},$$

$B = L/C_1$ and L is the amount of phosphorus adsorbed per unit volume soil.

The model proposed by Passioura (1963) includes the additional effects of root growth and convective flow of ions on the movement of ions to plants. Such a model should be applicable to long term studies of ion uptake by transpiring plants. Passioura assumed that the root length effective in ion uptake remained constant with time and that this length moves through the soil at a velocity u. Recent work (Ziegler et al. 1963) would indicate that in regions further from the root tip than the root hair zone, uptake is small and that Passioura's model is an apt one from this point of view.

Gardner (1965) has described the uptake of nitrogen by plants. His model included the boundary condition that the flux into the plant was directly proportional to the ion concentration in solution as used by Bouldin (1961). Gardner defined the total flux density of ions, J, in a soil under the influence of concentration gradients and convective transport as

$$J = - D_G \theta \frac{dC_1}{dx} + v\, C_1 \qquad \ldots\ldots (30)$$

where D_G is an apparent or effective diffusion coefficient. Thus

$$\frac{\partial C}{\partial t} = \frac{\partial}{\partial x} \left(D_G \theta \frac{\partial C_1}{\partial x}\right) - \frac{\partial (v\, C_1)}{\partial x} \qquad \ldots . (31)$$

Gardner (1965) transformed equation (31) to the axisymmetrical form and in so doing introduced w, the rate of water uptake per unit length of root, as

$$v = u\theta \text{ and } u = \frac{w}{2\pi r} .$$

Integrating axisymmetrical form of equation (31) in the steady state Gardner obtained

$$2\pi r\ D_G \frac{dC}{dr} + wC = Q \qquad \ldots\ldots (32)$$

where Q denotes the rate of uptake of nitrogen per unit length of root. The solution of equation (32) for the specified boundary conditions is

$$C_1 = (C_{1_o} - \frac{Q}{w})(\frac{r_d}{r})^{w/2\pi D_G} + \frac{Q}{w} \qquad \ldots\ldots (33)$$

where C_1 is the concentration at some distance r_d from the root. When the rate of uptake of ions by the plant is $Q = \alpha C_1$, with α constant, then Gardner obtained

$$Q = \frac{C_{1_o}\ w\alpha\ (\frac{r_b}{r_a})^{w/2\pi D_G}}{w + \alpha\left[(\frac{r_b}{r_a})^{w/2\pi D_G} - 1\right]} \qquad \ldots\ldots (34)$$

where r_a is the radius of the root.

Nye (1966b) has examined nutrient diffusion and mass flow in soils near planar absorbing surfaces. He defines his flux density in the medium as

$$J = -D_N \frac{dC_T}{dx} + v\ C_1$$

where D_N is used to distinguish his diffusion coefficient from that of Gardner (1965), D_G, and that D used by the author.

Thus,

$$\frac{\partial C_T}{\partial t} = D_N \frac{\partial^2 C_T}{\partial x^2} + v \frac{\partial C_1}{\partial x}$$

and by substituting $b = dC_T/dC_1$ he obtains

$$b \frac{\partial C_1}{\partial t} = b\ D_N \frac{\partial^2 C_1}{\partial x^2} + v \frac{\partial C_1}{\partial x} \qquad \text{......} \ (35)$$

He solves the above equation (35) under the initial and boundary conditions

$$t = 0, \quad x > 0, \quad C_1 = C_{1_o}$$

$$t > 0, \quad x = 0, \ \alpha\ C_1 = D \frac{\partial C}{\partial x} + v\ C_1.$$

His solution has the advantage of being applicable at all times rather than being a steady state solution as is Gardner's (1965).

Hale (1965) and Miles (1965) have extended the model approach to the situation where three dimensional flow to a moving sink is considered. These developments are not yet at a stage where the models are of any practical use to the biologist.

2.5.1 Discussion

There are difficulties in understanding the derivation of equations used by Bouldin (1961), for if the flux J, across unit area of soil is defined by

$$J = - D_B \frac{dC_1}{dr}$$

(this is formally the same as that used by Bouldin, see his equation (3)), the appropriate non steady state equation is

$$\frac{\partial C}{\partial t} = D_B \left[\frac{\partial^2 C_1}{\partial r^2} + \frac{1}{r}\frac{\partial C_1}{\partial r}\right] \quad \ldots\ldots (36)$$

His first solution assumes no interaction between soil particles and ions, and equation (36) may be written in the form,

$$\frac{\partial C_1}{\partial t} = \frac{D_B}{\theta}\left[\frac{\partial^2 C_1}{\partial r^2} + \frac{1}{r}\frac{\partial C_1}{\partial r}\right] \quad \ldots\ldots (37)$$

if θ is constant with r. The only possible way Bouldin could have obtained equation (29) from the definition of D obtained from his equation (3), that is

$$Q' = D_B \left[\frac{\partial C}{\partial r}\right]_{r = r_a}$$

was if Q' was the flux across a unit area of soil solution or if the treatment applies solely to uptake from unstirred nutrient solutions when D should be replaced with D_o. But from his definitions one can only assume that his equation (1) should be

$$\frac{\partial C_1}{\partial t} = \frac{D_B}{\theta}\left(\frac{\partial^2 C_1}{\partial r^2} + \frac{1}{r}\frac{\partial C_1}{\partial r}\right)$$

and the solution of this equation under the initial and boundary conditions given by Bouldin is

$$Q = \alpha C_1 I(\tfrac{1}{2}\pi N^{-\frac{1}{2}}, \tfrac{1}{2}\pi N^{+\frac{1}{2}}; V)$$

where $N = \frac{r_a \alpha}{D_B}$ and $V = \frac{D_B t}{r_a^2 \theta}$ (c.f. relationships on page 50) and $D_B = D$ as used by the author of this review.

There are difficulties also with the model of Passioura (1963). Passioura obtained his overall solution to ion uptake by plants, by combining two equations with different boundary conditions (Passioura 1965) thus invalidating his final solution.

Two errors have been drawn to the attention of Gardner (pers.comm.). Firstly $u = \frac{W}{2\pi r\theta}$ and not $\frac{W}{2\pi r}$ as published (Gardner 1965) and secondly integrating the steady state cylindrical form of equation (31) does not give Q, but $\frac{Q}{\theta}$ on R.H.S. of equation (32). Therefore throughout his equations, $\frac{W}{\theta}$ should replace w and $\frac{Q}{\theta}$ replace Q, and one obtains

$$C_1 = (C_{1_o} - \frac{Q}{W})(\frac{r_b}{r_a})^{w/2\pi D_G \theta} + \frac{Q}{W}$$

(c.f. equation (33)). Clearly solutions given by Gardner (1965) are appropriate to the solution of axisymmetrical form of equation (27), when

$$Q = \frac{C_{1_o}\, w\alpha \left(\frac{r_b}{r_a}\right)^{w/2\pi D}}{w + \alpha\left[\left(\frac{r_b}{r_a}\right)^{w/2\pi D} - 1\right]}$$

(c.f. equation (34)) and rearranging

$$\frac{Q}{C_{1_o} w} = \frac{\alpha\left(\frac{r_b}{r_a}\right)^{w/2\pi D}}{w + \alpha\left[\left(\frac{r_b}{r_a}\right)^{w/2\pi D} - 1\right]} \qquad \ldots\ldots (38)$$

The L.H.S. of equation (38) is the "transpiration stream concentration factor" (TSCF) of Russell and Shorrocks (1959) if Q is the uptake into the tops. Assuming therefore that D has some finite value, then for

(1) $w = \alpha$, TSCF = 1
(2) $w < \alpha$, TSCF > 1
(3) $w > \alpha$, TSCF < 1.

Values of TSCF > 1 are found when ion uptake is "active", but can also be found when ion uptake is "passive" but dominated by diffusion.

For TSCF < 1 the dominant process in ion uptake is convection. The importance of α is obvious in determining the water flow rate at which convective transport of ions becomes the dominant process.

If values of α, Q and w are calculated from Russell and

Shorrocks (1959), then TSCF > 1 when $w < a$, and TSCF < 1 when $w > a$.

Gardner's (1965) model does not include any uptake by root extension and his solution, when corrected, is applicable only to steady state conditions which rarely occur.

The applicability of Nye's (1966b) model is somewhat difficult to assess, as it relates to uptake of ions from an infinite planar surface. However several comments are pertinent to use of his equation (2), that is,

$$b \frac{\partial C_1}{\partial t} = v \frac{\partial C_1}{\partial x} + b \frac{D_N \partial^2 C_1}{\partial x^2} \qquad \text{.....} (39)$$

which was obtained from

$$J = - D_N \frac{dC_T}{dx} + v\, C_1.$$

Firstly equation (39) is applicable only if the adsorption isotherm is linear. When the adsorption isotherm is non-linear, D_N and b are both functions of C_T and x, and b must be written as equal to $\frac{\partial C_T}{\partial x} \frac{\partial x}{\partial C_1}$. The general form of equation (39) is then

$$b \frac{\partial C_1}{\partial t} = v \frac{\partial C_1}{\partial x} + \frac{\partial}{\partial x} \left[D_N\, b \frac{\partial C_1}{\partial x} \right] \qquad \text{.....} (40)$$

where $b = \frac{\partial C_T}{\partial x} \frac{\partial x}{\partial C_1}$.

If ions are considered to be non-sorbed, as in most of Nye's (1966b) discussion, then one can replace b with θ, and assuming θ and D to be constant with x, equation (40) reduces to

$$\frac{\partial C_1}{\partial t} = D_N \frac{\partial^2 C_1}{\partial x^2} + \frac{v}{\theta} \frac{\partial C_1}{\partial x} \quad .$$

The water content, θ, may be nearly constant with distance from an absorbing root, when water uptake rates are small and soil very permeable to water (this can be shown by calculation using equation (9)). However, in relatively dry soils, whose hydraulic conductivity is small and when the transpiration demand is large there can be large gradients in water content about absorbing roots. Thus b, D_N and θ may be functions of x.

Equation (35), as well as Gardner's, do not account fully for the complex changes of concentration with time in a mixed diffusion and convection system. As previously pointed out, Biggar and Nielsen (1964) found that for the linear systems they used, the displacement of a less concentrated by a more concentrated solution in the horizontal system was not capable of description by equations developed by Nye. It does not appear possible to incorporate the effect of dispersion into the definition of the diffusion coefficient unless D is considered a function of u or x (or r) since it will have a different value for each water velocity (Nielsen and Biggar 1963, Biggar and Nielsen 1964).

In the case of the radial movement of ions (Gardner 1965) both θ and water velocity vary with radius, and so should the diffusion coefficient. Therefore

$$\frac{\partial C_1}{\partial t} = D_G \frac{\partial^2 C_1}{\partial x^2} + \frac{1}{\theta} \frac{\partial (v\ C_1)}{\partial x}$$

is only approximate.

It can be concluded that the equations which have been proposed to describe the uptake of ions by plants from soil are limited in many ways. However Nye (1966b) has stressed the need for general theories "to provide a framework for discussion and experiment, and to indicate the parameters that need be measured for a complete quantitative description."

2.6 Conclusions

Despite the work of plant physiologists on the uptake of water and ions by plants, and that of soil physicists and chemists on the movement of water and ions in soils, little work has been done on the whole soil-plant system. One major reason for examining ion uptake is to understand better the mineral nutrition of whole plants in real environments. Under such conditions a number of transfer processes both within the soil and within the plant will contribute to the inorganic nutrient uptake of the plant or crop. It is unlikely that a single ion transfer process will serve the plant equally well at all times and under all environmental conditions.

The volume of water transpired by plants is large, but it is not known precisely how water movement in the soil affects the quantity of ions brought to and taken up by plants. In turn, it is not known how ion movement and uptake by the plant affects the uptake of water. Membranes exist in the plant which behave as quasi semi-permeable membranes and across which ion concentration gradients exist. This means that osmotic potential gradients can operate in moving water from the soil into and through the plant. Thus the steady state uptake of water and ions, if it ever occurs, follows upon even more complicated interactions between water and ion uptake in the transient state. The models so far proposed to describe the effects of water uptake on ion uptake by plants, do not consider the full extent of the interactions involved.

It is believed that the simplification of the physical features of the soil-plant system has been necessary to enable development of preliminary quantitative descriptions, but the interaction between convection and diffusion of ions both in the soil and in the plant can no longer be neglected.

3. EXPERIMENTAL PROGRAMME

3.1 Introduction

The aim of the experiments was to ascertain the importance of environmental variables upon the uptake of water and ions by plants.

The "plant" experiment, Section 3.2, was designed to assess the influence of aerial humidity upon water and ion uptake by wheat seedlings under various water and ion contents in the soil.

The physical study, Section 3.3, was designed to measure the effects of water flux density upon the radial axisymmetrical transport of ions across a soil bed.

3.2 Water and Ion Uptake by Wheat Seedlings

3.2.1 Experimental material and methods

Wheat seedlings were grown in pots of sand in a controlled environment cabinet. Three relative humidity levels were employed in three sequential experiments. Three soil water content treatments and three sodium chloride concentrations were used in the pots for each experiment. Harvests were made on two occasions and replications were composed of three replicates in space. Each run in the controlled environment cabinet therefore consisted of

1 humidity x 3 sodium chloride levels x 3 moisture levels x 2 harvests x 3 replicates

and 9 fallow pots, i.e., 3 moisture levels x 3 replicates.

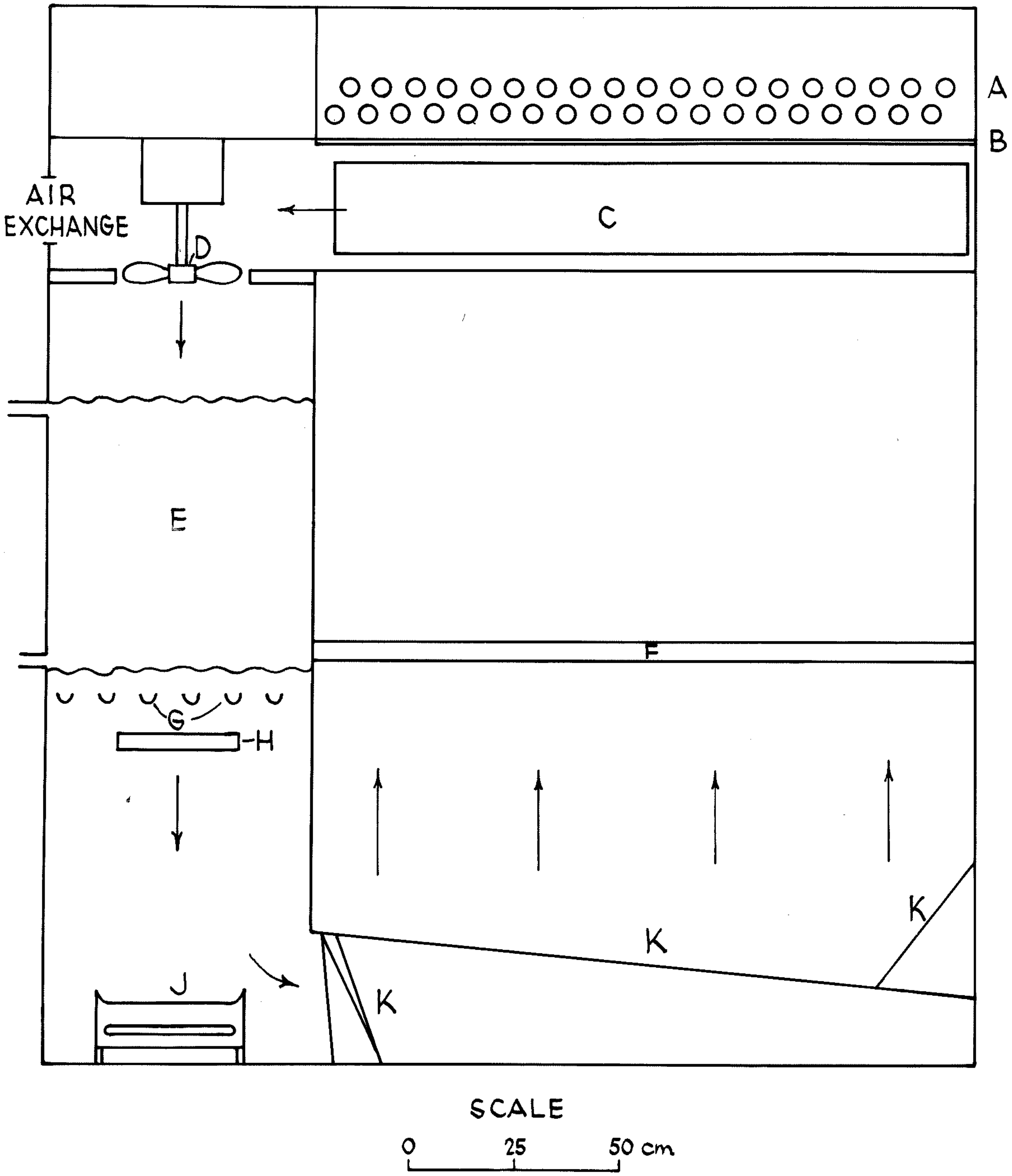
Controlled Environment Cabinet:

The design of the cabinet is shown in Figure 3. The cabinet was lit by 38 120-watt fluorescent tubes arranged in two banks at the top. A stippled glass screen separated the lights from the growth cabinet section giving uniform light distribution. A cooled air stream above the screen reduced the heat load from the lights, assisting in maintaining controlled temperatures

Figure 3. Design of Growth Cabinet

A. Light banks
B. Stippled glass screen
C. Wind baffles at sides on air outlet ducts.
D. Fan
E. Cooling coils
F. Moveable pot platform
G. Drip trays
H. Strip heaters
J. Humidifier
K. Wind reflector screens

Arrows indicate air path.



A
B
AIR EXCHANGE
C
D
E
F
G
H
J
K
K
K
K
SCALE
0
25
50 cm

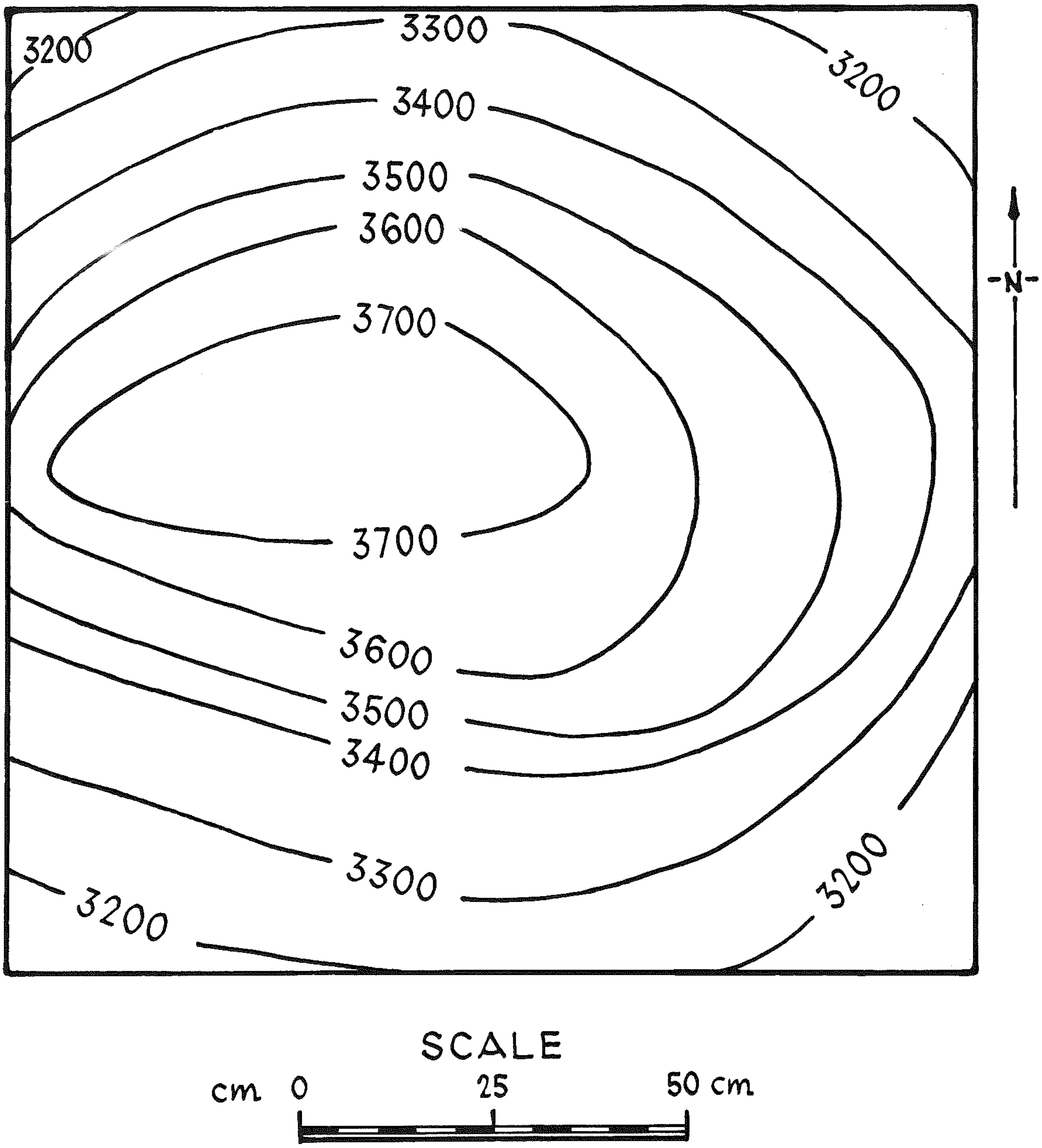
in the growth cabinet itself.

Light intensity varied with the age of the tubes, and as a relatively high level was desired (approximately 3,000 ft. candles), it was found necessary to renew the light tubes in the lower bank at the beginning of each run and to replace the tubes of the upper bank with those from the lower bank. The tubes moved from the lower to upper bank had each been used for a constant length of time. The tubes were lit for three days before the pots were placed in the growth cabinet. Change in light intensity at pot height (95 cm from the glass upper screen) both during and between runs was very small, dropping 200 foot-candles from the initial level. The initial distributions of light intensity at pot height are shown in Figure 4.

The "lights-on" period, or day length, was set at 16 hours and dark period was 8 hours.

The control of temperature and humidity was maintained as follows. The set dry bulb temperature was achieved by dry bulb control of the refrigeration system only. During the day, the radiant heat input from the lights was constant and constituted the major heat load. During the night cycle, black strip heaters in the air ducts replaced the heat load of the lights.

Figure 4: Initial Light Distribution in Growth Cabinet at Pot Height (ft.-candles)


3200
3300
3200
3400
3500
3600
3700
3700
3600
3500
3400
3300
3200
3200
N
SCALE
cm 0
25
50 cm

Humidity control was achieved with a Honeywell hair element humidistat. The control system was pneumatic and included a differential pressure control which actuated either black strip heaters or a pan humidifier in the air duct. When the humidity in the cabinet rose above the set point, the strip heaters, see Figure 3, switched in, resulting in a rise of dry bulb temperature. This was countered by refrigeration which continued until the set dry bulb temperature was attained. Accompanying this counter-cooling, water vapour was condensed on the coils and drained off. By varying the heat load of the "dehumidification" strip heaters with other components of the total heat load, a range of balanced conditions could be obtained, each characterized by a set relative humidity. When the relative humidity fell below the set point, the pan humidifier was activated.

The variation in temperature was only plus or minus 1°F over growth cabinet and with time, while relative humidity varied at the most plus or minus 4% either side of mean level.

Preliminary experiments had shown that at 71°F the widest range in relative humidity obtainable was 40 to 95%. The set values adopted were 42.5%, 67.5% and 92.5%. These preliminary experiments showed the need to redesign the humidification system to ensure it was safe and reliable(see Figure 5). A microswitch was installed to turn the humidifier off following a failure in water supply and modifications were made to eliminate condensation in the microswitch.

A uniform distribution of wind velocity was difficult to obtain with the design of the present cabinet. A fan, D Figure 3, with a variable speed control, provided satisfactory mean velocities. Relatively even distribution of wind velocity was achieved only after extensive trials (see Figure 6) using screens and baffles (see Figure 3). The baffles were situated on the return air ducts at the top of the cabinet.

Experience from this work has enabled a more efficient system to be designed in which the flow of air is forced through a mesh floor at several centimeters water gauge pressure into the growth cabinet section (Shaw 1964).

Pot Preparation:

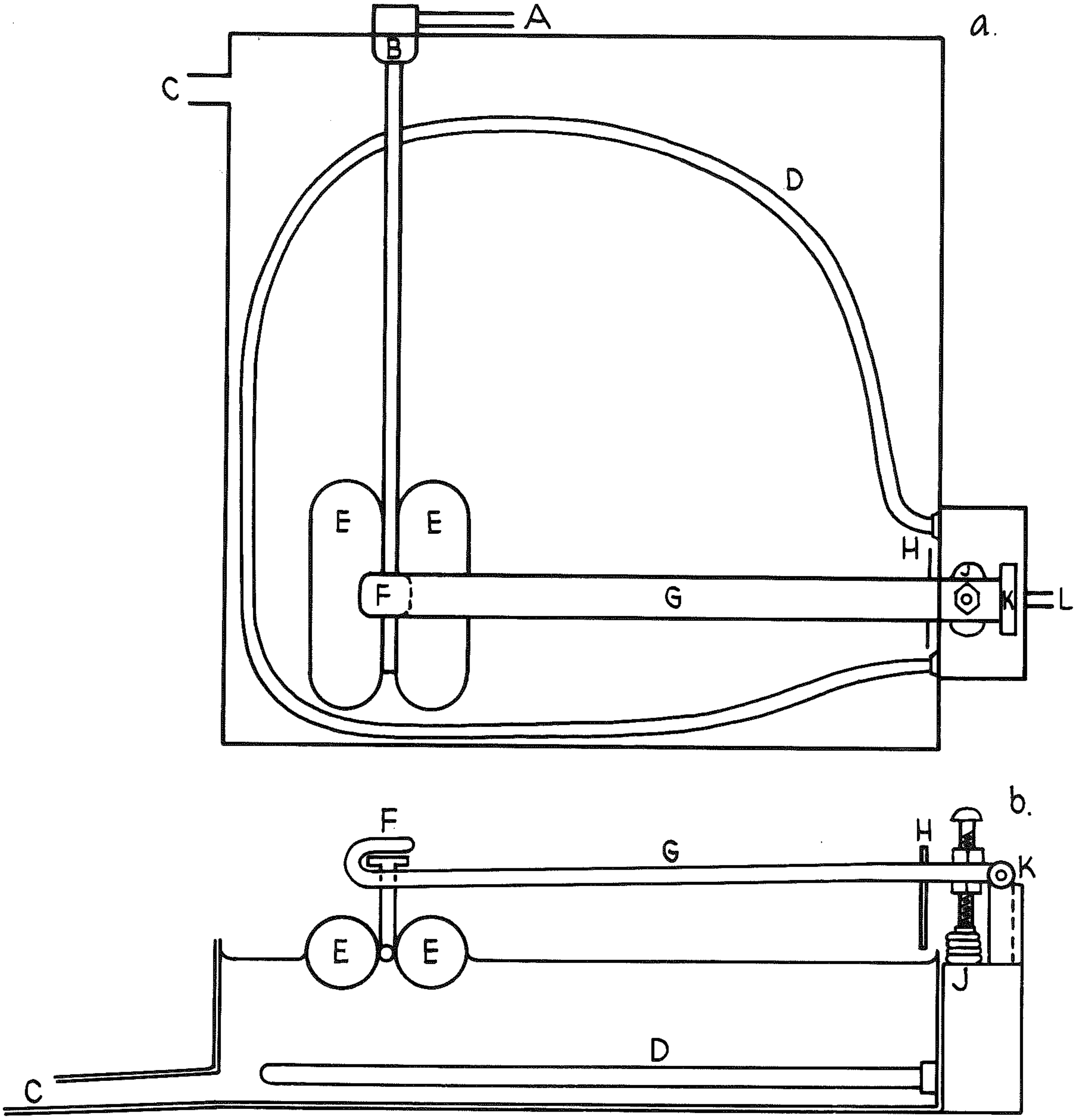
Three concentrations of sodium chloride were used, 0.14 mM (= 5 ppm of chloride and 3.2 ppm sodium), 2.82 mM (= 100 ppm of chloride and 64.8 ppm of sodium) and 28.2 mM (=1000 ppm of chloride and 644 ppm sodium). The highest

Figure 5: **Diagram of Humidifier with Essential Safety Devices**

a. Plane View

b. Vertical Section

A.	Hose from rain water source
B.	Needle valve controlling water level
C.	Drainage outlet for flushing humidifier daily
D.	Strip heater
E.	Floats of stainless steel
F.	Swivel attachment from floats to microswitch bar
G.	Microswitch bar
H.	Metal shelf to stop moisture running down arm and onto microswitch
J.	Microswitch
K.	Swivel for microswitch bar
L.	Power lead


A
a.
B
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E
H
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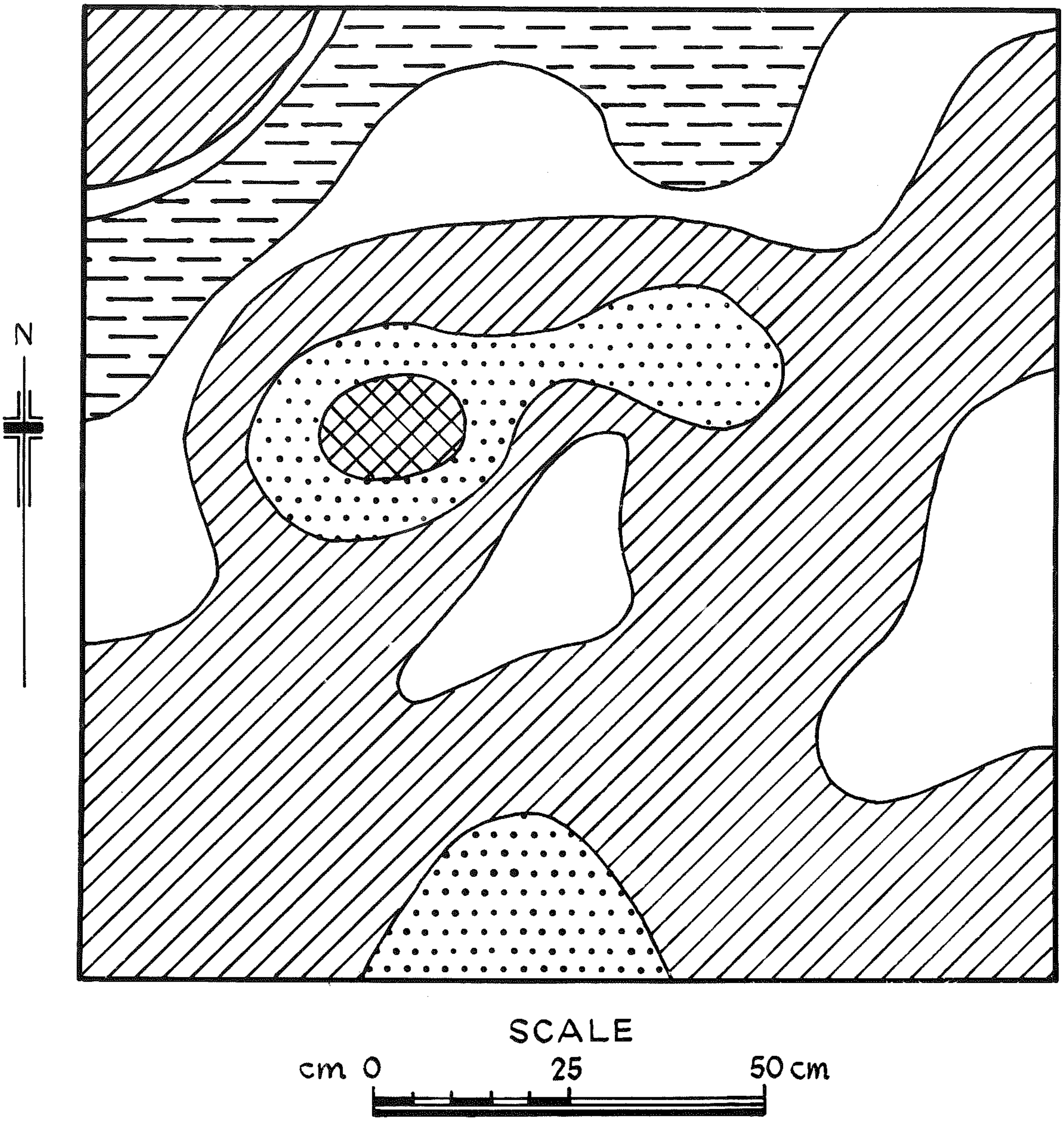
F
G
K
L
b.
F
G
H
K
E
E
J
D
C

Figure 6: Mean Wind Velocities at Pot Height
(ft/min)

▤	20 - 30
□	30 - 40
▨	40 - 50
⁙	50 - 60
▩	60 - 70


N
SCALE
cm 0
25
50 cm

level was used to ensure that under circumstances of high water flow not all of the chloride ions reaching the root surface would enter the root.

It was necessary to have the sand in the pots at a uniform initial moisture content and preliminary tests were carried out to devise techniques suitable for handling large quantities of soil and which would allow reproducible moisture contents and bulk density of the soil to be obtained. The most suitable technique was to spray the soil with required sodium chloride solution to a constant moisture content of 4% and then to compact the soil into the pots to the required bulk density of 1.46 gm/cc. For pots requiring higher moisture contents than 4%, sodium chloride solutions were added to the surface and a drainage period allowed before the pots were used.

The surface horizon of Golden Grove sand, a podsolized soil, was sieved to remove stones and other debris, washed and then leached under suction with five times its volume of deionized water. The treated soil was then dried, sieved again through a 1 mm sieve and stored in a sealed container. Both prior to storage and prior to use the sand was thoroughly mixed with a shovel and mechanical mixer. Samples, random in space and time showed that particle size distribution, chloride and sodium contents were uniform throughout the bulked sand. Analysis showed that the sand was low in essential nutrients, N, P, K and Ca, and contained very little clay or organic matter.

The plants were grown in tin plate containers 10.2 cm in diameter and 30.5 cm deep,coated prior to use with tar-epoxy resin, which did not release any nutrients to solutions in contact with it (Loneragan pers.comm.). The pot size used was smaller than that desired, but was dictated by the precision of balances available. The pot size was such that errors in the daily water loss measurement were less than 5%.

Batches of sand sufficient for one replicate plus four extra pots were mixed in a cement mixer. The sand in the mixer was sprayed with the required sodium chloride solution and,during the spraying, the mixer was continually in motion. After mixing thoroughly, the moistened sand was removed from the mixer and packed into the pots. The packing of each pot was done in three sections, each section occupying one third of the total pot. The required quantity of sand was added to the first section and packed to the required height with dumping and compression from a piston at the top. The smooth upper soil surface so formed was broken with a piece of wire before the next third was added. The same procedure was repeated to compress this section and to fill the remaining third of the pot. To obtain the other two moisture levels of 6% and 8% moisture, sodium chloride solutions were added to the surface at a rate such as not to damage the surface during pouring. A perforated lucite plate was used to protect the surface during pouring. Some small channels were formed as air escaped but these apparently did not interfere with the reproducibility of the wetting technique (see Appendix 1a). After addition of the extra solution, the pots were stored in a constant temperature room at 71°F for 15 days. It was found from preliminary experiments that there was very little water movement after 10 days and no detectable redistribution of water could be found between the 12th and 20th days. During the storage period, the pots were covered with black polyethylene covers 0.030 in. thick and a second cover of aluminium foil. No measurable loss of water occurred during the storage period. There was some variation within and between pots in the distribution of water and chloride and in bulk density (see Appendix 1 a,b,c - also see Appendix 1d for moisture characteristic of Golden Grove sand).

Plant Preparation:

The experimental work was designed to enable sufficiently precise measurements to be obtained which would permit examination of ion uptake in a system where diffusive and convective transfer of ions occurred. In particular, nutrient effects upon plant growth were minimized by growing the plants without the addition of any nutrients to the soil. Initial experiments had shown that, without addition of nutrients and in particular nitrogen, the tips of the first leaves turned yellow after about thirteen days and by the end of eighteen days the whole of the first leaf and half of the second leaf were yellow. Addition of various nutrient solutions, via split root technique, eliminated some of this yellowing. However, it was also found that with split root feeding, most of the water transpired by the plants was taken up through the roots in the nutrient solution and only a small amount from the roots in the sand.

To overcome this yellowing, without using split root feeding, wheat seeds of high nitrogen content were germinated on a nutrient solution. Wheat seeds, variety Gabo, with a nitrogen percentage of 3.5 (on dry weight basis) were used as these had the highest nitrogen content of all seed available. To reduce variation between plants, only seeds whose weights were 38.0 to 41.9 mgm were used. It was desirable to use seeds of more uniform weight but this was not possible due to the restricted availability of seeds with this high nitrogen content. Only 0.3% of the original seeds produced suitable seedlings.

The composition of the nutrient solution which was found most suitable in the preliminary experiments is given in Appendix 2.

The selected seeds were rinsed for two minutes in 0.1% mercuric chloride solution, containing a wetting agent, then washed thoroughly in deionized water. The washed seeds were placed with the embryo upwards on stainless steel mesh over aerated nutrient solution. The mesh was lowered until a film of nutrient solution covered the seeds. After 24 hours, at 71°F, the seeds had swelled, and the level of the nutrient solution was lowered until only a thin film of nutrient solution covered the lowest portions of the seed. After 120 hours soaking, seeds with the centre root between 1.5 and 2.0 cm long were taken. Three replicates, each of three seedlings were washed in distilled water and dried between blotting paper. These formed the initial samples for wet weight, dry weight, chloride content and sodium content determinations.

Others of the seeds were encapsulated in waxed cylinders (see Figure 7). The cylinders ensured that only one root grew down into the sand. This was done to maximize the uptake of water per unit length of root and also to reduce competition between roots for water and ions in the pots. The cylinders were cast in two sections from plaster of paris. The upper half was drilled to make a cavity for the seed and a smaller escape hole for the coleoptile and later the "stem" to grow out of the cylinder. The lower half was drilled with a small cavity and a small hole approximately 0.65 cm in diameter. Both halves were soaked in hot paraffin wax to seal the cylinders against water and salt entry. The small hole in the lower half was also sealed with wax and then re-bored to give a hole 0.6 mm in diameter. This diameter permitted one root to fill the hole and did not allow any of the other roots confined in the seed cavity to grow down and out of the cylinder into the sand.

In sowing the plants in these small cylinders, the centre root of the three present at five days, and which was between 1.5 and 2.0 cm long was carefully slipped through the wetted hole in the lower half of the

Figure 7: Vertical Section through Planting Capsule

A - Coleoptile

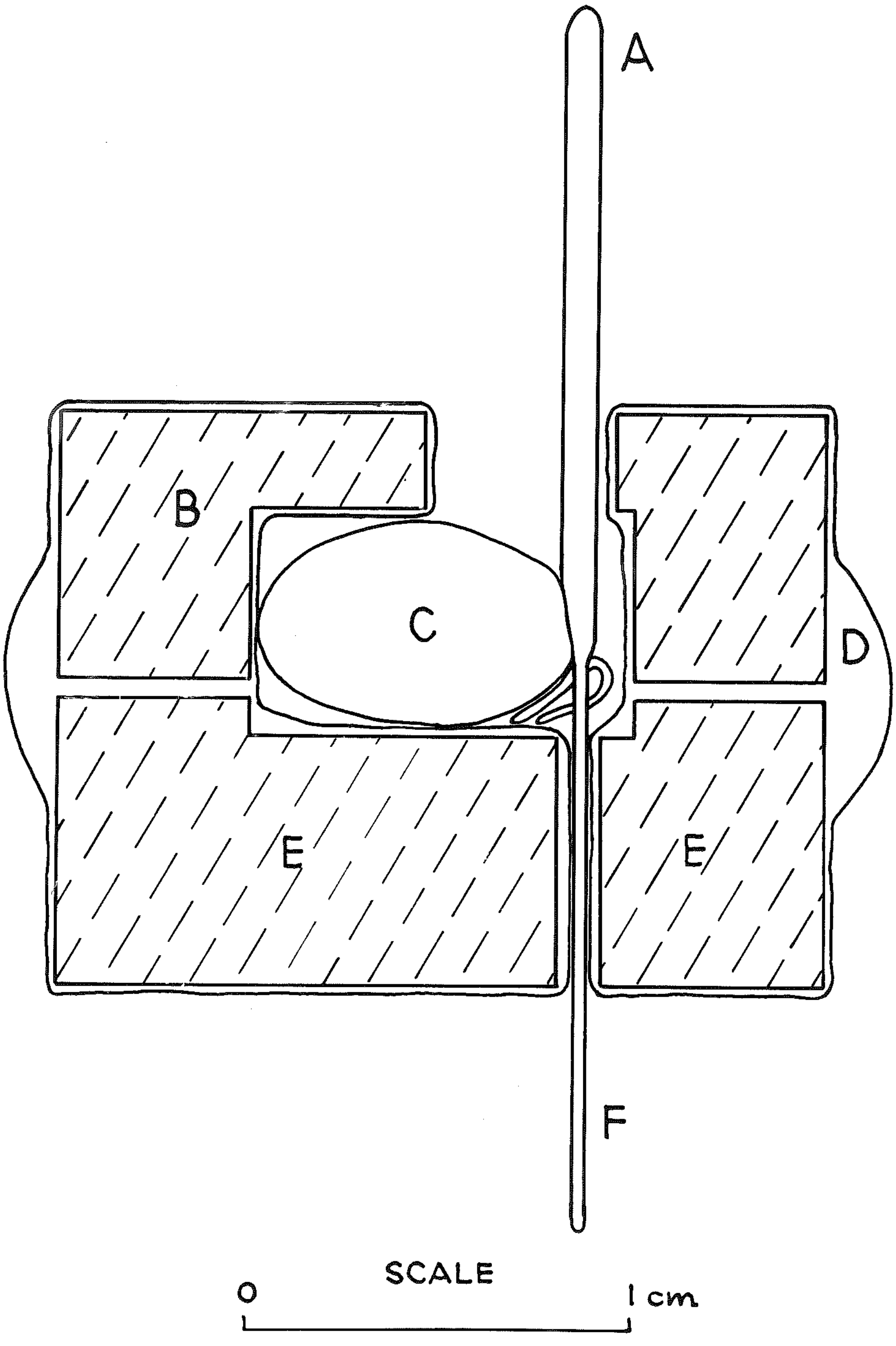
B - Upper half of Plaster of Paris body

C - Seed

D - Wax seal

E - Lower half of Plaster of Paris body

F - Root.


A
B
C
D
E
E
F
SCALE
0
1 cm

cylinder. The top half was lowered over the seed ensuring that the coleoptile was free to grow through the prepared hole. The two halves were sealed together with paraffin wax and the cylinder sunk into a specially prepared hole in the sand.

A seeding plate and tube (Figure 8) were used to ensure even spacing and depth of sowing for each of the three plants in each pot.

After sowing, each pot was covered with 0.003 in. black polyethylene containing three holes (matching the planting pattern) which were plugged with cotton wool. Oxygen cathode measurements (Shearer et al. 1966) revealed that the oxygen content of the space between the polyethylene and sand surface was the same as that in the ambient air during the eighteen days growth. Twenty-four hours after sowing, the coleoptiles reached the level of the polyethylene covers, 2.3 cm above the surface of the sand and were led through the plugged holes of the pot cover.

With each run, nine fallow pots, treated in the same way as sown pots, were used to measure evaporation of water direct from the soil. Chloride content did not affect the quantity of water evaporated from the pots, but soil water content had some effect at the two lowest humidities (see Appendix 3).

Figure 8: Special Seeding Plate

a. Cross Section

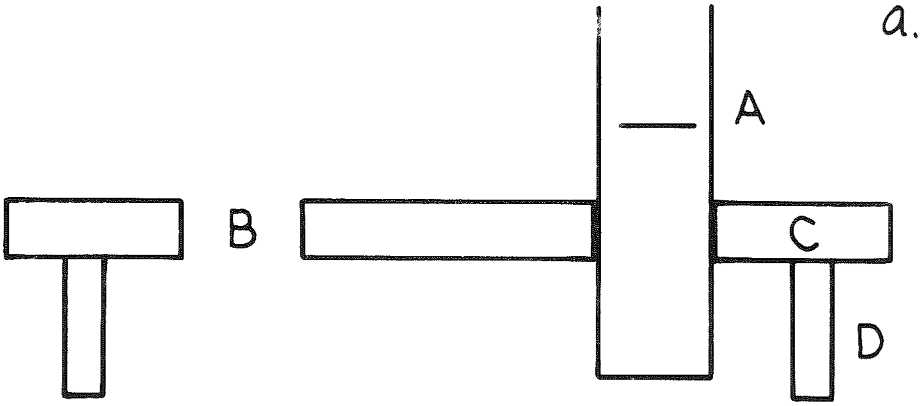
b. Plane View

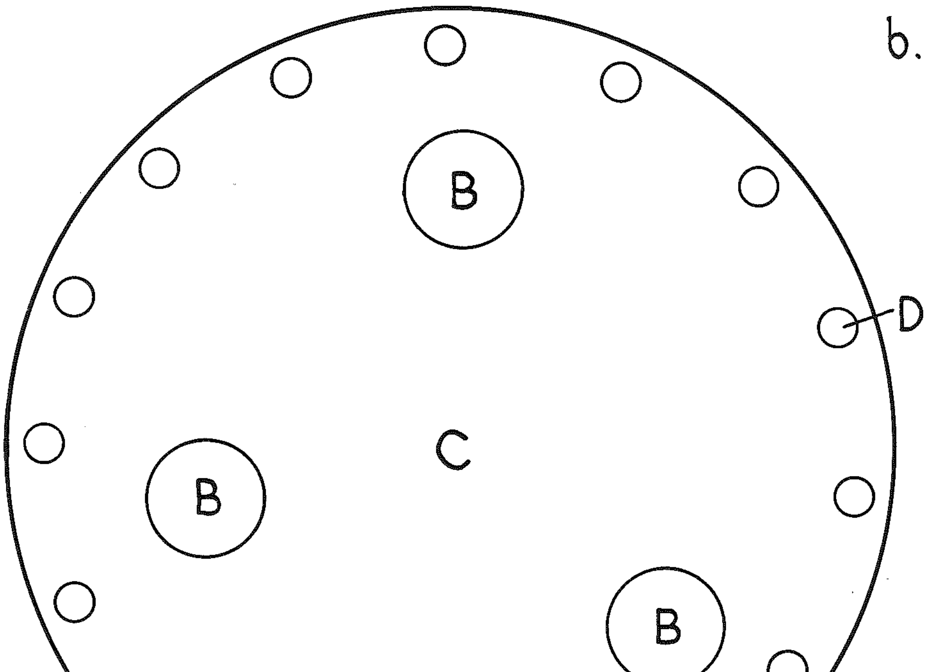
A. Boring tube, marked to give constant sowing depth

B. Holes for boring tube

C. Plate

D. Legs which fitted just inside of pots ensuring even distribution of holes in each pot


a.
A
B
C
D


b.
B
D
C
B
B

Pot Randomization:

Randomization of the pots was made in relation to the distribution patterns of the light, temperature, wind velocity and humidity in the cabinet (see Figures 4 and 6). From these distribution patterns, it was decided to run replicates in an east-west direction in the cabinet with each replicate being two rows by nine columns (see Figure 9). Harvests were made after nine and eighteen days, which allowed the pots of each harvest to be randomized using a latin square of nine positions (in rows) x nine days. The pots were moved to new positions within the replicate every twenty-four hours and each pot of the first harvest (9 days) occupied every column once during the first nine days,while those of the second harvest (18 days) occupied every column twice. The row that each pot of a replicate occupied in a particular column was decided by randomizing the pots of the first harvest between row one or two. The row in which the pots for the second harvest were placed, during days 1 - 9, was that row not occupied by a first harvest pot in that column. For days 10 - 18, the pots were randomized in column positions as above but their row position was that which they had not occupied during days 1 - 9 while in that column.

Figure 9: a. Plane View of Pot Distribution in Growth Cabinet

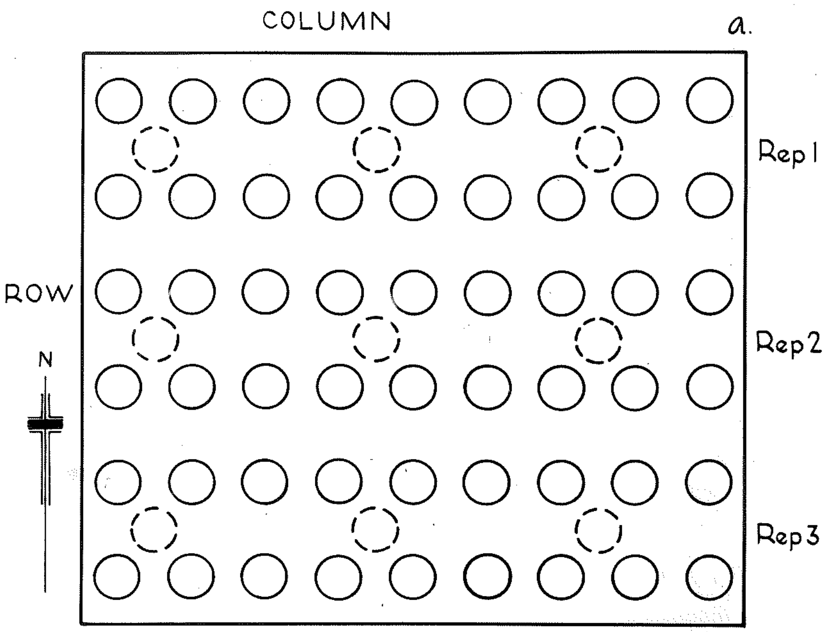
○ Positions of pots containing plants

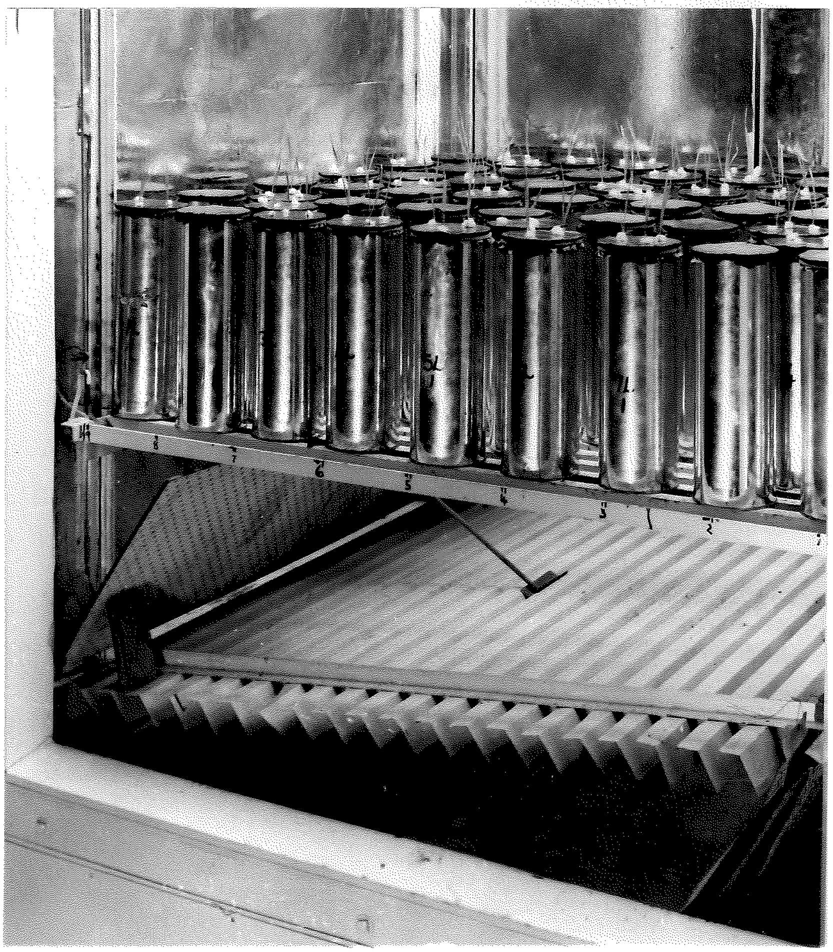
◌ Positions of fallow pots

b. Photograph of Pots in Growth Cabinet

Note the position of wind reflector screens on bottom of growth cabinet.

a.





After the pots for the first harvest were removed at nine days they were replaced by similar but empty pots occupying positions not filled by the pots for the second harvest.

The fallow pots were placed in positions shown in Figure 9. These pots were randomized using a 3 (places) x 3 (days) latin square.

Harvests:

At the completion of sowing and before placing in the growth cabinet, the pots were weighed. At various intervals during the nine or eighteen days further weighings were made to measure water loss. The pots were weighed at harvest and the plants washed onto a fine sieve from the pots with a stream of tap water. This washing out process occupied less than thirty seconds. The plants on the sieve were immediately rinsed with distilled water and dried between two sheets of blotting paper. The roots were excised by cutting them off flush with the bottom of the planting capsule. The remaining portions of the plant were removed from the cylinder and the seeds and suppressed roots excised from the tops. After a second rinsing of the separated plant parts with distilled water, surface water was removed with blotting paper. The wet weights of the plant parts were obtained and the seeds placed into an oven at 65°C for 72 hours, by which time constant dry weights were obtained. Root systems were taken, placed into a shallow bath of distilled water, brushed apart to display individual roots and photographed (see Figure 10). The roots were then transferred to individual beakers of distilled water, and rinsed three times. The lapsed time in the shallow bath and the beakers was 20 minutes for each sample. The roots were then placed into tared weighing bottles and dried for 72 hours at 65°C. The leaves were taken, placed onto "Ozalid" light-sensitive paper, covered with glass slides, and exposed to 3,000 foot-candles of light for 170 seconds to obtain leaf prints. The leaves were then removed from the sheets and dried for 72 hours at 65°C.

Analytical Techniques:

The photographs of the roots (Figure 10) were made into slides. These slides were projected onto white matt paper, the root numbers noted and root lengths measured with an opisometer (Figure 11). Each photograph contained a standard length to permit conversion of observed root length to actual length of the roots. Preliminary photographs had revealed that with the

Figure 10: Photograph of Roots

a. Roots taken at nine day harvest.

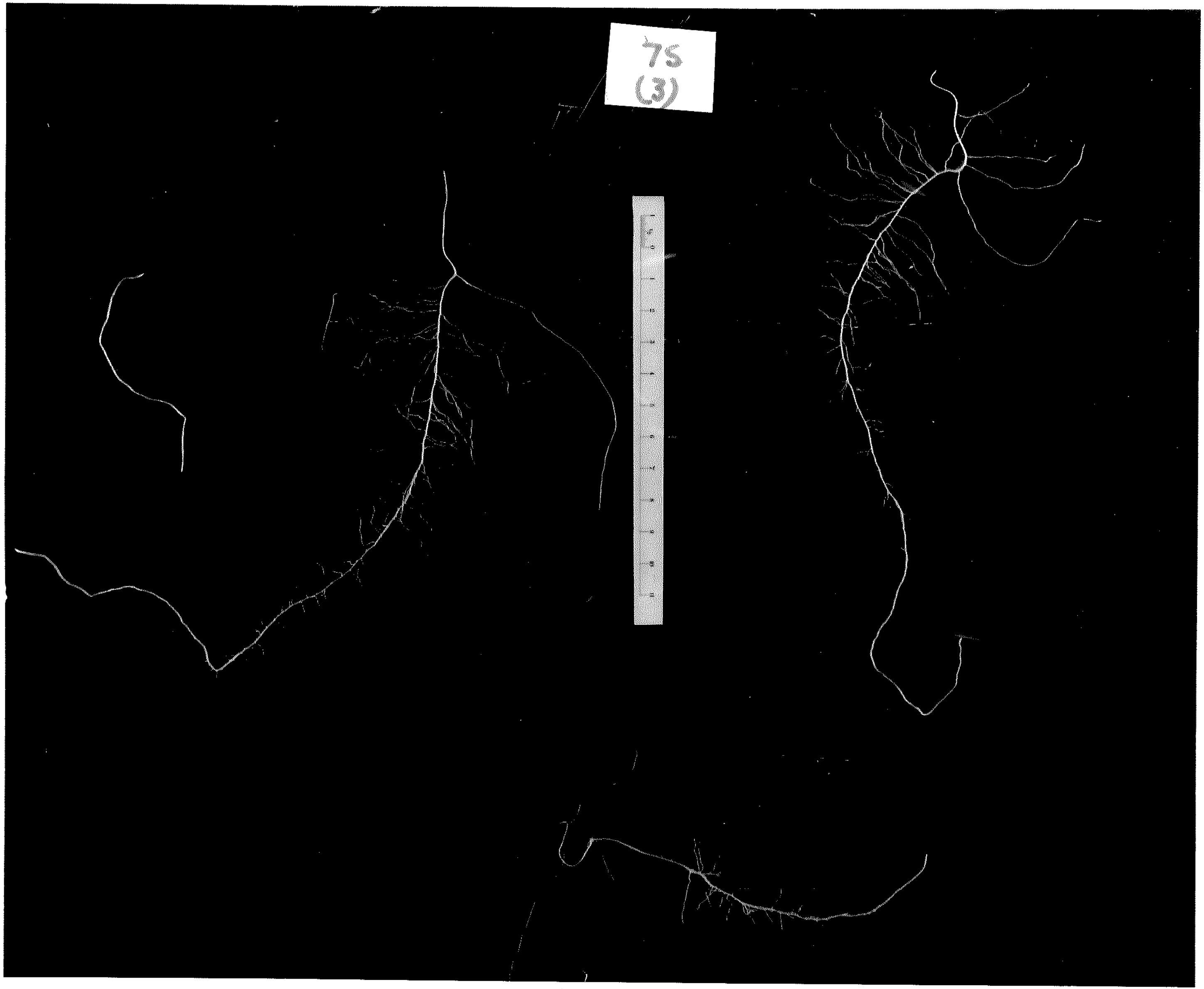

75
(3)

Figure 10: b. Roots taken at eighteen day harvest.

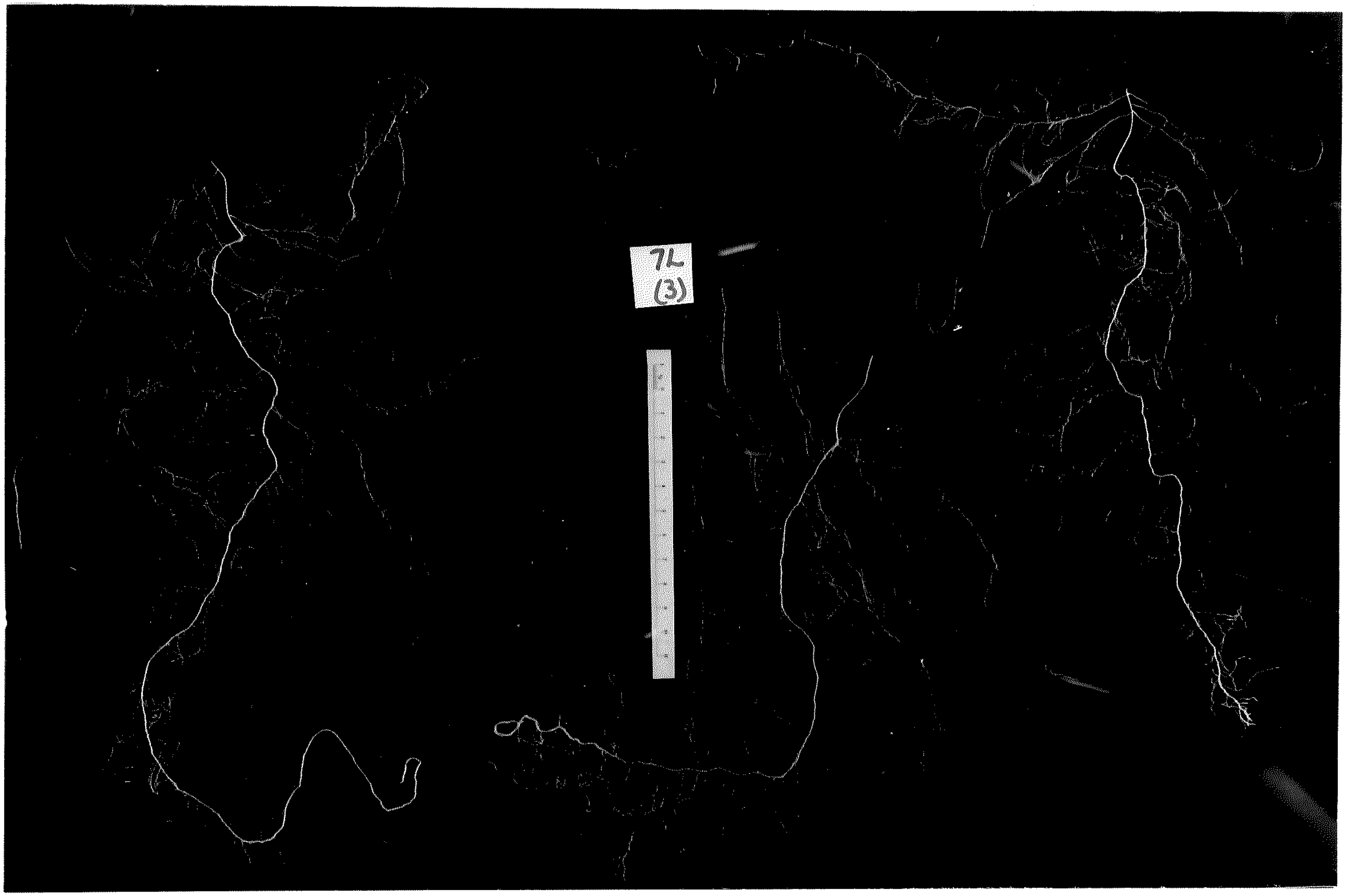

7L
(3)

Figure 11: Photograph of Opisometer Used for Measuring Root Lengths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GERMANY
36 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34
12 2 4 6 8 10 12 2 4 6 8 10

particular equipment used there was negligible distortion of standard lengths scattered throughout the bath.

The area of the leaves was most conveniently and accurately measured by cutting out the leaf silhouettes developed on the light-sensitive paper, drying them in an oven at 65°C for 48 hours, and then weighing them. The regression of area on weight was obtained from standard areas. Other techniques for measuring leaf areas were investigated, including silhouette planimetry and a direct-measuring electronic planimeter (Wilkinson and Silsbury 1966) but these methods required too many replicate readings to obtain the precision required.

The dried plant portions were ground and boiled in distilled water for 40 minutes. After cooling to 21°C, the containers plus solution and plant debris were placed onto a balance and contents diluted with distilled water to a known weight. The solutions were then shaken thoroughly for an hour and the supernatant poured off into storage bottles.

Chloride contents were determined in a darkened constant-temperature room at 21°C, using a modification of the electrotitrimetric method of Best (1929). Supporting electrolyte, 1 cc per 10 cc of solution, and titration to a zero point enabled more accurate measurement of the low chloride concentrations (Kolthoff and Kuroda 1951, Johnson and Ulrich 1959).

Apparatus was set up as in Figure 12a. The silver-silver chloride electrode system was constructed and is shown in Figure 12b. The silver wire was polished with fine emery cloth and cleaned by successive immersions in alcohol, ammonia and 3 N nitric acid. Between each immersion, the wire was rinsed with distilled water. Approximately 5 cm of the silver wire was immersed in 0.1 N HCl and connected to the positive pole of a 2 volt dry-cell battery. A platinum wire was placed into the same solution and connected to the negative pole of the battery. The current was adjusted by means of resistances until 3 milliamperes flowed through the circuit. After the immersed section of the silver wire was covered with a deposit of brown silver chloride (i.e., after about 30 minutes), the wire was removed from the solution, rinsed with distilled water and then connected to the galvanometer. The electrode was stored with the silver wire immersed in distilled water.

The reference electrode is shown in Figure 12b. About 0.1 gm of quinhydrone was added to the centre glass tube and the tube filled with buffer solution (see

Figure 12: Chloride-Measuring Apparatus

a. Photograph of apparatus

A - Microburette

B - Electrodes

C - Stirring mechanism separated from solution and stirrer by asbestos mat to reduce heat conduction to solution

D - Switch key

F - Galvanometer

E - Laboratory jack

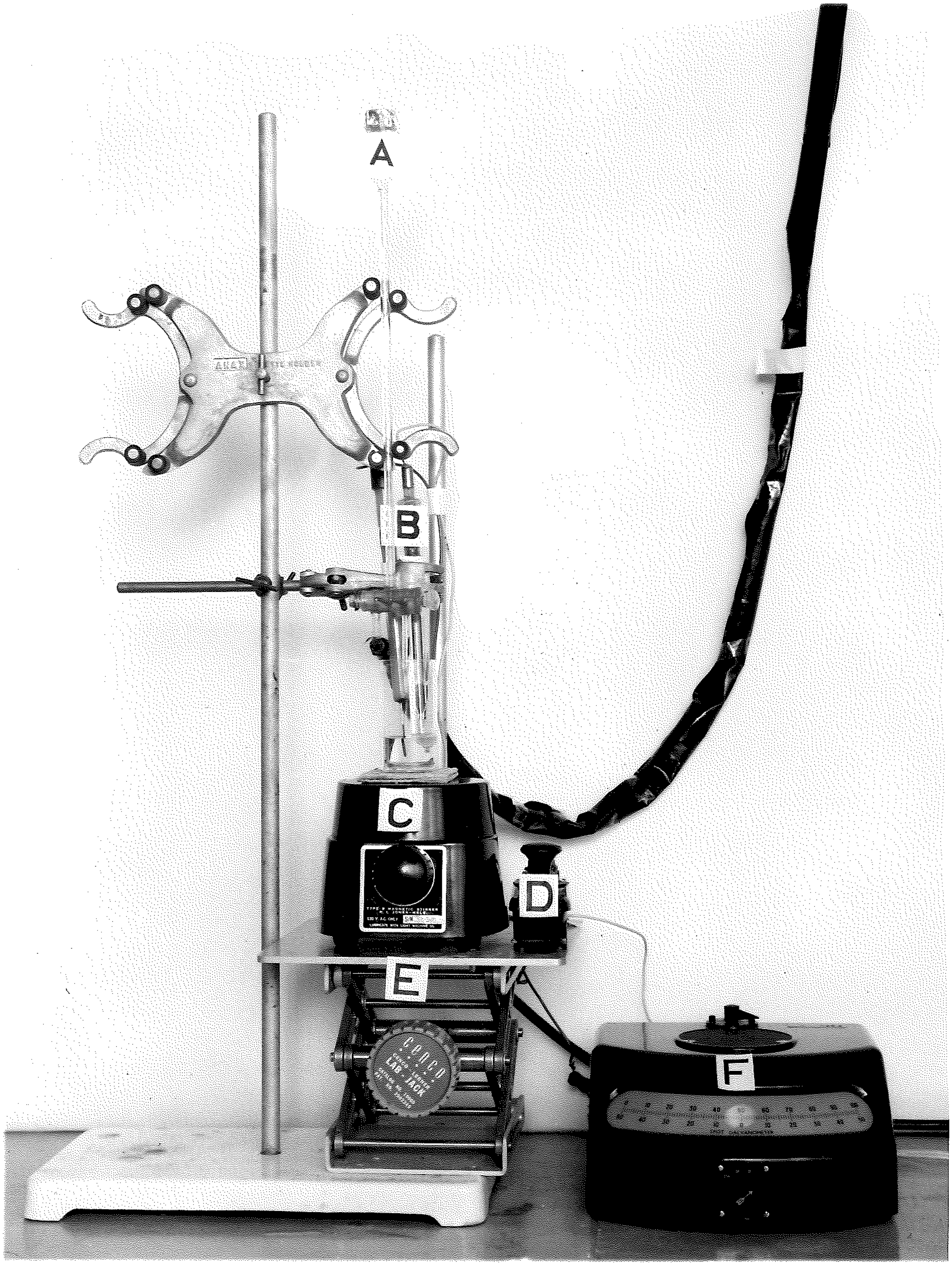

A
B
C
D
E
F
cenco
LAB-JACK

Figure 12: b. Design of electrodes and salt bridge

(1) Silver-silver chloride electrode

G. Lead to electrical circuit

H. Araldite-filled body

J. Silver wire

(2) Reference electrode and salt bridge

K. Ground glass joints sealed with sealing grease

L. Platinum wire

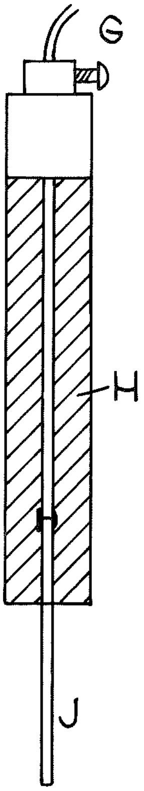
M. Cavity of reference electrode filled with 0.1 gm of quinhydrone and buffer solution

N. Salt bridge filled with saturated KNO_3 solution

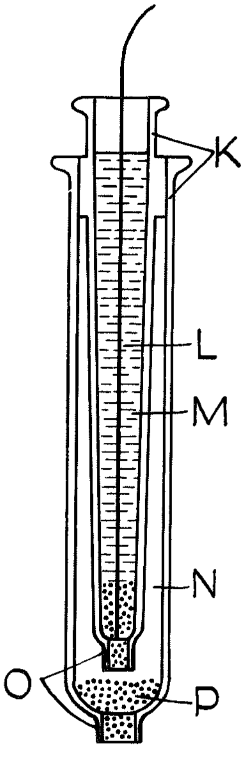
O. Glass sinters

P. Solid KNO_3

(1)



(2)



Appendix 4a for composition). The cap containing the platinum wire was then pushed into position and the tube sealed after ensuring there were no air bubbles entrapped in the tube. The ground-glass joints were smeared with a chloride-free sealing grease to ensure an air-tight seal. The outer glass tube, or salt bridge, was filled with a chloride-free saturated potassium nitrate solution. Due to the design of the apparatus, it was found necessary to place a small quantity of solid potassium nitrate (A.R. grade) in this tube. The reference electrode was then pushed into the salt bridge and sealed in place by use of sealing grease on the ground-glass joint. This was connected into the circuit with the silver-silver chloride electrode galvanometer and a switch key. The electrode was stored in a saturated potassium nitrate solution to reduce the need for refilling the salt bridge.

When the apparatus had been assembled the silver-silver chloride electrode was allowed to age for four days before it was used.

Duplicate chloride determinations were made on each solution. The appropriate volume of solution at 21°C was pipetted into a beaker and made up to 50 cc with distilled water, and 5 cc of supporting electrolyte added (see Appendix 4b for preparation). The two electrodes were placed into a zero-point solution at 21°C which contained 50 cc of distilled water plus 5 cc of supporting electrolyte and 2 drops of a standard silver chloride suspension. The stirrer was started, and the key depressed for short periods of a second or so, and reading of the end point taken after 95 sec. This delayed reading was found to be essential to obtain both the zero point and end point for any titrations, as it was found that the reading changed rapidly with stirring, only becoming steady after about 60 sec. After another 60 sec. the reading again began to change. It appeared that the initial decline was associated with the electrode coming to equilibrium, while the later change was associated with a temperature rise in the solution evidently due to heat conducted from the stirrer motor. After the zero point was determined, the silver nitrate solution was calibrated against standard KCl solutions. Consistent titration figures for the standard KCl solutions could be obtained only in a darkened room, no doubt because the dilute silver nitrate was affected by light. Once the zero point and standard were checked a run of 20 unknown solutions x 2 replicates were titrated. Each titration could be completed within 90 sec with no significant variation in the zero point from run to run. Nevertheless the determination of the zero point and the normality of the silver nitrate were always carried out with each run, to check the equipment. The chloride content of the plant-material was calculated from normality, titre and dilution data.

The sodium content of the solutions was determined with a Techtron AA-4 Atomic Absorption Spectrophotometer, using a coal gas flame. Direct analysis of solutions was practical in most cases but it was necessary to dilute some solutions for analysis.

The harvesting, extraction and analysis techniques were checked experimentally to ensure high precision in the determination of the chloride and sodium contents of the plant parts. The design of this experiment was

$$\underset{3}{\begin{bmatrix}\text{Chloride}\\ \text{concn.}\end{bmatrix}} \;\text{x}\; \underset{2}{\begin{bmatrix}\text{Initial}\\ \text{washing}\\ \text{treatment}\end{bmatrix}} \;\text{x}\; \underset{4}{\begin{bmatrix}\text{Duration of}\\ \text{second wash}\\ \text{in distilled}\\ \text{water}\end{bmatrix}} \;\text{x}$$

$$\underset{3}{\begin{bmatrix}\text{Duration of}\\ \text{extraction}\\ \text{treatment}\end{bmatrix}} \;\text{x}\; \underset{2}{\begin{bmatrix}\text{Harvest}\end{bmatrix}}$$

Roots from three plants were used for each treatment-variant. The design for analysis of top and seed material was the same as the above except that only one second wash with distilled water was made. Tops and seeds from three plants were used for each variant.

Treatments for the roots were

Chloride concentration,	(a) 5 ppm
	(b) 100 ppm
	(c) 1000 ppm
Initial washing,	(a) in distilled water for 30 sec.
	(b) in tap water for 30 sec.
Duration of second wash,	(a) dipped twice
	(b) 5 minutes
	(c) 10 minutes
	(d) 30 minutes
Duration of extraction period,	(a) 5 minutes in boiling distilled water
	(b) 15 minutes in boiling distilled water
	(c) 30 minutes in boiling distilled water
Harvests,	(a) after 9 days growth
	(b) after 18 days growth.

For tops, the treatments were the same except for the second washing treatment which was a standard single rinse in distilled water for all treatment variants.

The seeds were germinated by the standard method and at 120 hours transferred to stainless-steel grids over the various sodium chloride solutions. The samples from each harvest were dried at 65°C for 72 hours, weighed, ground and the supernatant from each extract analysed for sodium and chloride.

The results showed

(a) no significant differences between the initial washing treatments after a second wash of 10 minutes or 30 minutes in distilled water,

(b) 15 minutes extraction in boiling distilled water was adequate, giving the same results as 30 minutes extraction,

(c) there were no chloride concentration x treatment interactions for plants mentioned in (a) above.

3.2.2 Results

Water loss from pots:

Table 2 shows the amount of water evaporated from the soil surface, Ev, and the quantity of water transpired by the plants, Tr. Table 1 gives the code for the treatments.

Table 1

Code Used for Treatments in Tables 2-9

Code	Treatment		
	Humidity of aerial environment (%)	Water content of sand (%)	Chloride content of solution (ppm)
1	42.5	4	5
2			100
3			1000
4		6	5
5			100
6			1000
7		8	5
8			100
9			1000
10	67.5	4	5
11			100
12			1000
13		6	5
14			100
15			1000
16		8	5
17			100
18			1000
19	92.5	4	5
20			100
21			1000
22		6	5
23			100
24			1000
25		8	5
26			100
27			1000

Table 2

Water Loss from Pots - gm per pot

(Mean of three replicates)

Treatment	Water lost at time of harvests			
	9 day		18 day	
	Ev	Tr	Ev	Tr
1	3.8	6.4	7.9	30.3
2	3.8	5.3	7.9	29.5
3	3.8	4.9	7.9	35.4
4	3.9	9.7	8.3	52.1
5	3.9	8.5	8.3	46.2
6	3.9	5.5	8.3	46.4
7	3.6	7.0	8.2	51.8
8	3.6	9.4	8.2	59.7
9	3.6	6.8	8.2	47.7
10	3.1	2.2	5.3	28.3
11	3.1	3.0	5.3	23.4
12	3.1	2.2	5.3	28.5
13	3.2	4.5	5.6	38.4
14	3.2	2.4	5.6	36.0
15	3.2	3.1	5.6	31.9
16	2.9	3.0	5.3	37.1
17	2.9	3.4	5.3	38.7
18	2.9	3.9	5.3	33.1
19	1.3	1.4	2.5	12.3
20	1.3	1.5	2.5	14.8
21	1.3	1.6	2.5	17.4
22	1.3	2.0	2.7	23.5
23	1.3	2.1	2.7	20.2
24	1.3	1.7	2.7	20.4
25	1.2	2.7	2.6	18.8
26	1.2	2.3	2.6	19.5
27	1.2	2.5	2.6	20.5

The effects of the relative humidity and time on the amount of water evaporated and transpired can be seen (also see Appendix 5a for significance of treatments on these variables). The significant reduction in the amount of water transpired at 4% water-content as compared with 6% and 8% can also be seen.

Root lengths:

Table 3 summarizes the root lengths obtained from the slides of the roots.

Table 3

Root Lengths - cm per pot

(Mean of three replicates)

Treatment	Root Length	
	9 day	18 day
1	355	1347
2	347	1551
3	339	1840
4	426	1867
5	428	1951
6	345	2274
7	289	1964
8	382	2313
9	351	2443
10	186	1318
11	213	1368
12	192	1516
13	239	1604
14	138	1662
15	239	1736
16	146	1614
17	176	1782
18	257	1841
19	115	895
20	102	980
21	119	1166
22	114	1207
23	114	1317
24	130	1535
25	144	1048
26	114	1152
27	163	1287

The effect of relative humidity and time on the root length should be noted as this has considerable bearing in the analysis of the results (see Appendix 5b for significance of treatments on the root length).

Root numbers:

Table 4 summarizes the numbers of roots obtained from the slides of the roots.

Table 4

Number of Roots per Pot

(Mean of three replicates)

Treatment	Numbers of roots	
	9 day harvest	18 day harvest
1	239	829
2	198	746
3	216	1311
4	221	1241
5	226	1077
6	206	1242
7	163	1026
8	207	1290
9	209	1427
10	73	835
11	102	825
12	116	1035
13	123	970
14	66	912
15	117	808
16	87	951
17	95	976
18	160	991
19	77	433
20	60	514
21	64	723
22	65	652
23	53	760
24	68	800
25	98	542
26	57	625
27	86	622

See Appendix 5c for significance of treatments on the number of roots.

Areas of leaves:

Table 5 summarizes the total upper-surface area of leaves in each pot. It must be noted that the yellow areas formed only parts of whole leaves.

Table 5

Total Upper-Surface Area of Leaves (cm^2 per pot)

(Means of three replicates)

Treatment	Harvest 9 day		18 day	
	green area	yellow area	green area	yellow area
1	8.4	0.6	12.4	0.8
2	8.9	0	13.0	0.9
3	7.1	0	15.7	0.4
4	11.1	0	17.4	0.6
5	10.9	0.1	16.9	0.7
6	8.1	0	17.9	0.7
7	9.1	0	16.9	1.0
8	11.7	0	19.8	1.1
9	8.6	0	18.4	0.8
10	4.9	0.2	12.9	0.7
11	5.5	0.1	12.1	1.4
12	4.3	0	16.0	0.2
13	7.2	0	16.1	0.7
14	5.2	0	15.8	0.7
15	6.4	0	15.1	0.4
16	5.0	0	15.3	0.4
17	6.7	0	16.9	0.4
18	7.4	0	16.6	0.2
19	5.3	0	8.8	1.4
20	4.7	0	10.1	2.1
21	5.1	0	12.8	0.6
22	5.8	0	15.2	1.6
23	6.3	0	14.4	1.6
24	5.6	0	14.8	0.8
25	6.4	0	12.2	1.3
26	5.5	0	13.4	2.1
27	6.3	0	15.4	1.3

See Appendix 5d for significance of treatments on the leaf area.

Weights of plant material:

Table 6 summarizes the wet weights of plant material and Table 7 the dry weights.

Table 6

Wet Weights of Plant Material (mg per pot)

(Means of three replicates)

Treatment	Harvest					
	9 day			18 day		
	tops	seeds	roots	tops	seeds	roots
1	285	113	508	426	72	1035
2	305	112	387	418	71	1050
3	263	119	471	566	73	1527
4	340	135	568	585	100	1560
5	328	134	549	579	94	1676
6	288	126	483	614	89	1968
7	295	145	444	575	110	1621
8	347	125	560	643	113	2221
9	297	134	477	614	93	1887
10	214	128	283	422	83	1162
11	240	142	345	399	73	1042
12	215	122	313	460	93	1480
13	273	172	389	496	98	1672
14	230	173	255	485	96	1556
15	273	130	396	467	93	1445
16	218	164	282	474	113	1548
17	254	146	318	516	96	1690
18	286	174	469	486	95	1782
19	229	182	240	290	98	670
20	212	172	244	335	96	891
21	214	172	265	405	103	1158
22	208	147	218	453	129	1232
23	242	192	265	444	160	1224
24	258	212	292	450	114	1361
25	238	167	317	361	133	1009
26	225	190	259	418	135	1109
27	241	175	357	487	122	1253

Initial wet weight of treatments 1 - 9 = 359
Initial wet weight of treatments 10 - 18 = 420
Initial wet weight of treatments 19 - 27 = 386

See Appendix 5e for significance of treatments on the wet weight of plant material.

Table 7

Dry Weights of Plant Material (mg per pot)

(Means of three replicates)

Treatment	Harvest					
	9 day			18 day		
	tops	seeds	roots	tops	seeds	roots
1	41	23	30	86	28	74
2	43	22	24	81	26	70
3	36	24	27	95	26	95
4	47	25	32	104	26	92
5	47	23	31	107	28	99
6	38	24	27	114	27	105
7	39	27	25	103	26	84
8	46	24	30	113	27	118
9	40	28	26	109	27	105
10	26	23	24	70	25	71
11	27	25	17	63	26	72
12	29	24	20	69	26	77
13	28	25	21	82	27	79
14	26	28	13	82	25	81
15	31	23	20	74	24	73
16	24	27	17	72	26	72
17	30	24	16	77	28	80
18	32	27	22	77	24	80
19	33	35	18	48	25	32
20	29	34	19	55	24	41
21	29	31	23	57	25	50
22	28	31	12	63	25	53
23	34	32	17	62	29	55
24	36	36	20	53	30	58
25	35	27	19	53	29	41
26	30	33	16	57	25	48
27	33	33	19	67	26	52

Initial dry weight of treatments 1 - 9 = 96
Initial dry weight of treatments 10 - 18 = 95
Initial dry weight of treatments 19 - 27 = 101

See Appendix 5f for significance of treatments on the dry weight of plant material.

Sodium and chloride content of plant material:

Table 8 summarizes the sodium content of the plant material and Table 9 the chloride content.

Table 8

Sodium Content of Plant Material (mg x 10^2 per pot)

(Means of three replicates)

Treatment	Harvest 9 day			18 day		
	tops	seeds	roots	tops	seeds	roots
1	3.9	4.4	9.0	3.8	5.3	29.2
2	2.4	2.7	22.0	4.0	6.5	48.5
3	13.4	8.3	37.8	24.4	8.4	84.5
4	5.2	5.6	13.0	4.5	5.6	44.4
5	6.7	4.9	31.4	6.0	7.5	80.7
6	22.4	10.1	41.5	24.8	8.7	98.1
7	2.7	4.8	7.6	4.5	6.1	51.6
8	3.9	5.9	35.4	6.2	6.6	106.2
9	17.5	9.6	39.0	31.2	10.1	97.9
10	4.2	5.3	5.6	5.6	6.6	28.3
11	2.5	2.8	12.4	4.0	5.2	38.9
12	8.0	6.1	21.0	22.9	9.1	78.1
13	2.6	4.0	7.8	4.4	7.9	43.8
14	2.5	3.2	9.7	6.6	7.9	55.1
15	19.4	10.8	38.1	27.8	10.9	69.9
16	3.2	5.6	7.9	3.9	7.0	45.5
17	2.6	8.3	16.9	7.2	12.5	65.1
18	19.6	9.9	36.3	34.5	9.7	77.4
19	3.6	6.6	5.3	3.6	6.2	12.4
20	3.7	7.6	11.5	3.5	6.9	21.6
21	6.4	9.2	21.6	15.5	11.1	27.9
22	4.8	6.4	5.6	5.2	9.7	34.2
23	4.1	8.8	13.3	5.8	9.5	43.0
24	9.2	11.2	25.6	15.4	9.7	49.4
25	0.8	4.2	8.4	5.0	7.6	30.5
26	1.9	5.4	15.8	4.5	8.9	41.1
27	10.5	9.4	34.4	17.3	9.9	37.9

Initial sodium content of treatments 1 - 9 = 4.8
Initial sodium content of treatments 10 - 18 = 4.8
Initial sodium content of treatments 19 - 27 = 4.7

Table 9

Chloride Content of Plant Material ($mg \times 10^2$ per pot)

(Means of three replicates)

Treatment	Harvest					
	9 day			18 day		
	tops	seeds	roots	tops	seeds	roots
1	8.5	3.4	3.8	14.7	4.1	6.7
2	22.6	3.8	18.0	71.4	5.6	77.2
3	26.2	5.5	47.7	145.8	8.4	139.9
4	11.7	6.0	4.7	22.5	4.7	9.0
5	27.0	4.4	34.3	94.6	5.6	136.9
6	34.2	5.3	52.6	144.0	6.7	186.2
7	8.5	4.5	4.4	31.7	5.6	15.2
8	20.6	4.9	35.9	132.0	7.8	199.4
9	28.0	6.5	41.4	142.0	11.1	194.4
10	6.9	4.5	4.9	14.3	4.2	10.2
11	15.5	4.3	18.2	72.4	4.3	69.9
12	18.7	4.8	22.7	124.2	5.2	139.8
13	8.0	4.2	3.2	19.4	4.2	14.4
14	13.1	3.9	10.5	87.3	5.5	102.1
15	23.4	5.5	36.7	104.7	6.0	132.3
16	8.8	4.5	3.4	13.1	3.5	13.0
17	18.1	4.5	16.2	95.3	5.2	132.2
18	20.2	5.9	45.9	98.1	6.2	150.8
19	8.8	5.2	4.2	32.1	4.1	6.8
20	16.4	6.8	10.6	65.3	4.9	44.3
21	20.4	7.7	28.8	92.8	9.2	30.1
22	9.1	6.8	7.9	45.6	6.8	25.7
23	13.0	9.4	12.0	84.4	7.1	90.5
24	22.4	13.1	31.9	91.6	9.8	106.1
25	9.7	5.4	8.1	42.5	6.1	13.8
26	13.5	6.3	16.3	57.2	6.8	70.9
27	20.5	9.6	33.4	77.7	8.4	74.8

Initial chloride content of treatments 1 - 9 = 5.5
Initial chloride content of treatments 10 - 18 = 5.4
Initial chloride content of treatments 19 - 27 = 5.5

See Appendices 5 g and h respectively for significance of treatments on sodium and chloride contents of the plant material.

3.2.3 Discussion

Previous investigators have examined the effects of water uptake by plants upon uptake of ions using a variety of methods including plants growing under controlled environments but in culture solutions, detopped plants and plants growing in the field under naturally varying but often unknown environmental conditions. However it was believed that better analysis of the effects of water flow on ion uptake could be obtained by studying plants growing in soils under known and controlled environmental conditions.

The design of this experiment was such as to remove the effects ascribable to uptake of nutrients essential to plant growth, by using a single salt, sodium chloride, whose anion and cation are believed to be non-limiting for growth even at the lowest concentration to be used.

Sodium is essential for only a limited number of plants and the quantity required is so small that sufficient is supplied from the air or from the seed (Brownell and Wood 1957), i.e. from extrinsic sources. It has not yet been found to be essential for wheat and so a sodium deficiency is unlikely to be limiting growth in this experiment.

Chloride is essential for growth of higher plants as demonstrated by Broyer _et al_. (1954) and Johnson _et al_. (1957) and its role in the photoproduction of oxygen in chloroplasts has been determined by Arnon _et al_. (1961). Chloride deficiency in tomato plants, with a high requirement from nutrient solutions, can be corrected with a solution concentration of only three ppm. Therefore it is unlikely to be limiting the growth of wheat in this experiment.

Uptake of both sodium and chloride can result in toxic levels of these ions in the plants with consequent retardation of growth. It can be seen in Figure 13 that dry weights of tops, roots and the total dry weights were not reduced at high concentrations of sodium chloride in the soil solution. The use of a single salt solution might affect plant growth, but there has been little study of this point.

It is obvious from Figure 14 that as the total quantity of water transpired increased so did the total quantity of chloride taken up by the plants. However it is seen in Figure 15 that dry weight changes were coupled with changes in the quantity of water transpired by the plants. Thus changes in the growth of the plant itself did result from changes in its environment, which gave rise to variations in the total quantity of water transpired by it.

Figure 13: Dry Weight of Plant Material as a Function of Concentration of External Solution

Relative humidity (%)

● 42.5
▲ 67.5
× 92.5

Growth period (days)

——— 0 - 9
- - - 9 - 18

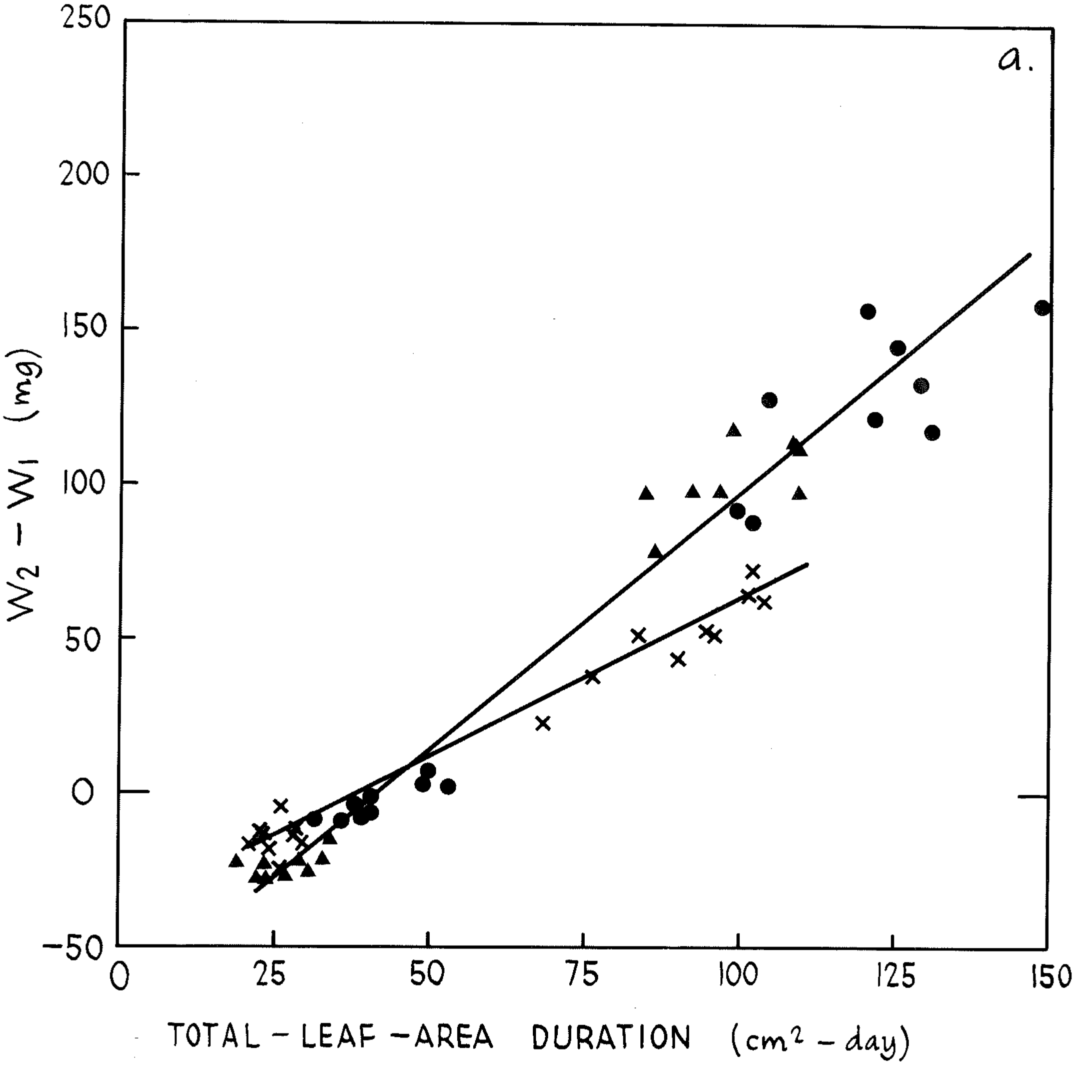
Figure 14: Total Quantity of Chloride taken up by Plants as a Function of Water Transpired

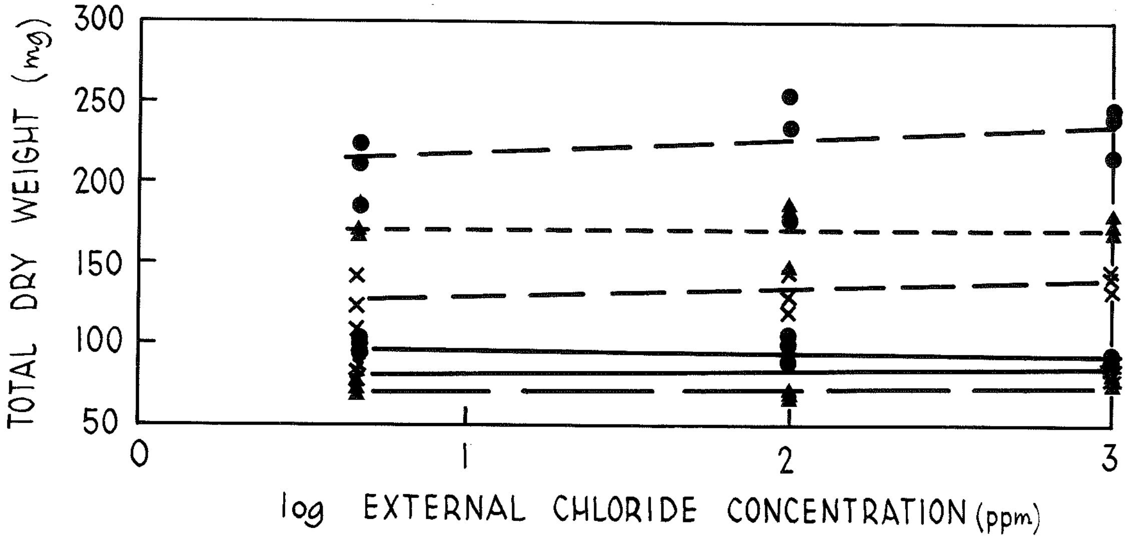
Relative humidity (%)

● 42.5
▲ 67.5
× 92.5
☒ 92.5, external chloride 1000 ppm

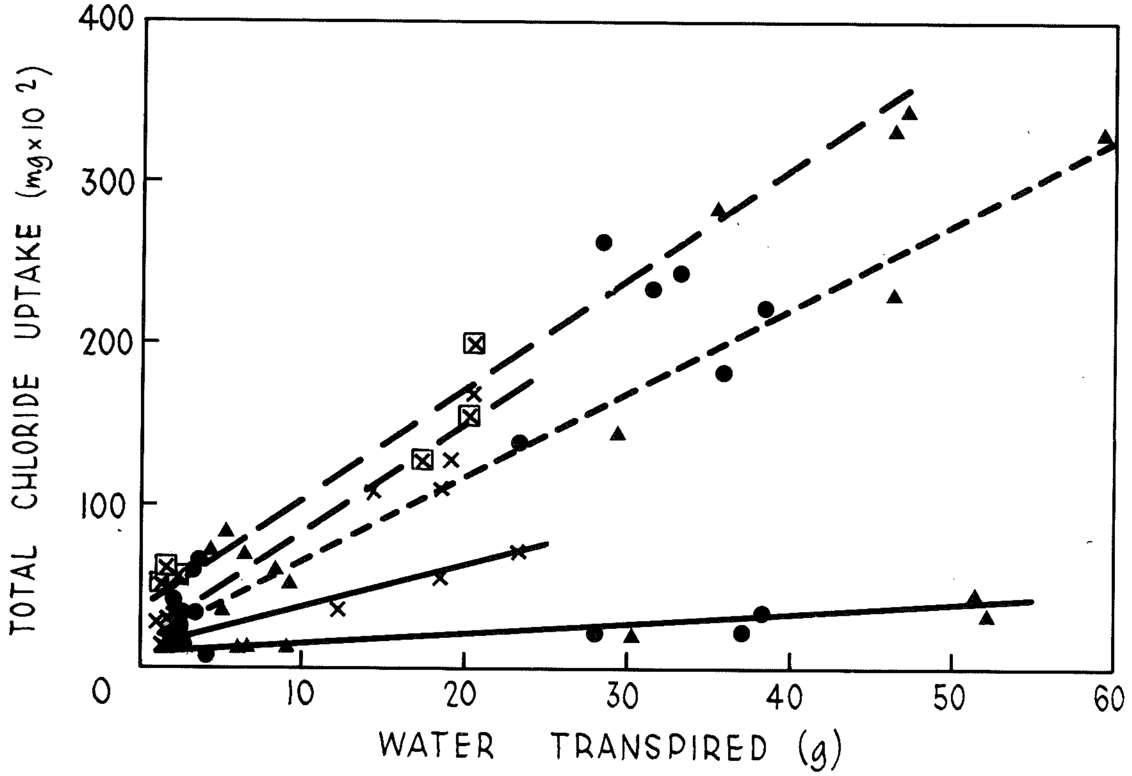
External chloride concentration (ppm)

——— 5
- - - 100
— — 1000


a.
250
200
150
100
50
0
−50
$W_2 - W_1$ (mg)
0
25
50
75
100
125
150
TOTAL - LEAF - AREA DURATION (cm² - day)



TOTAL DRY WEIGHT (mg)
300
250
200
150
100
50
0
1
2
3
log EXTERNAL CHLORIDE CONCENTRATION (ppm)



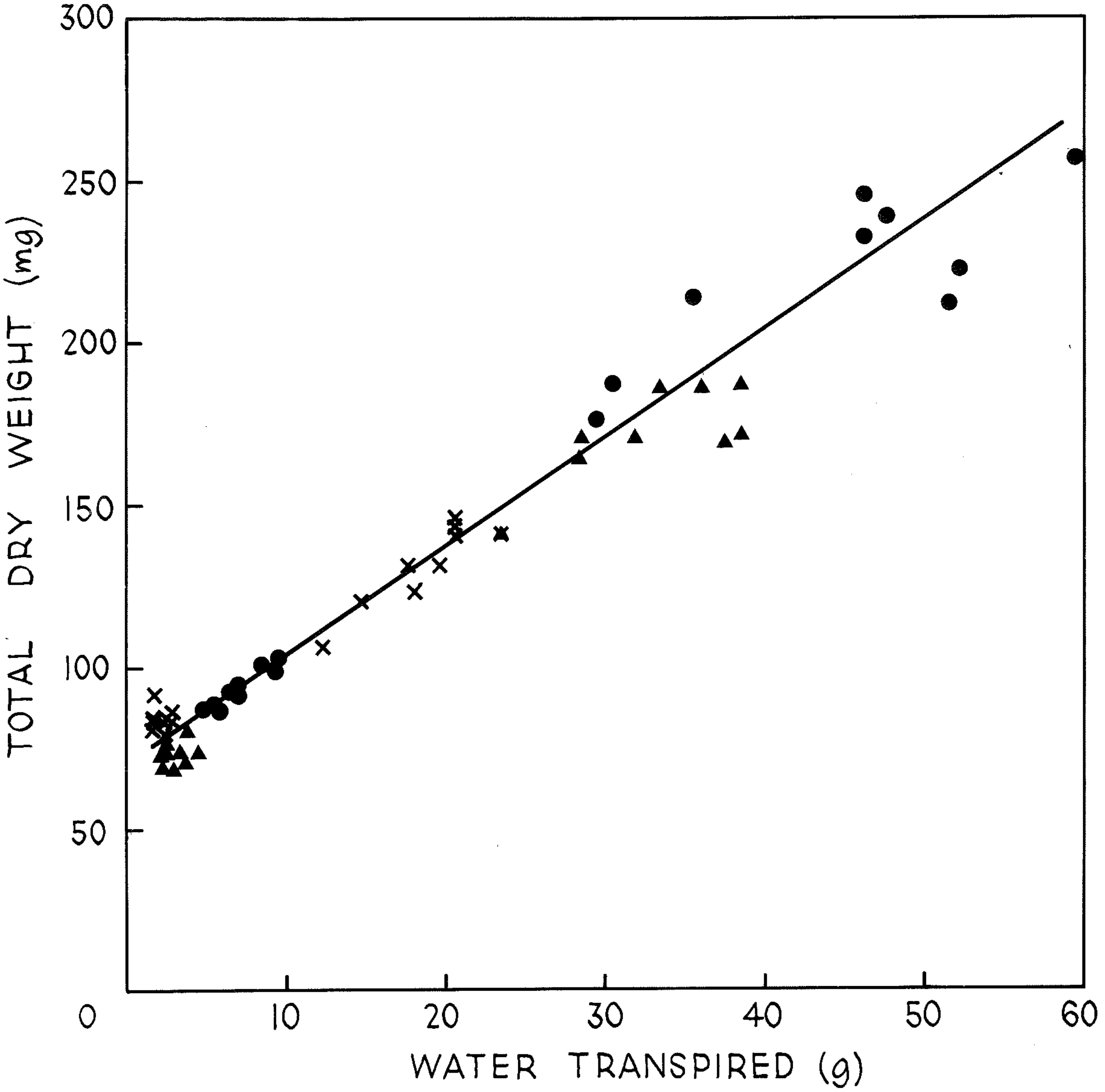
TOTAL CHLORIDE UPTAKE (mg x 10 2)
400
300
200
100
0
10
20
30
40
50
60
WATER TRANSPIRED (g)

Figure 15: Dry Weight of Plant Material as a Function of Quantity of Water Transpired

Relative humidity (%)

● 42.5
▲ 67.5
× 92.5

$y = 3.26x + 70.6$, $r = 0.982^{xxx}$


300
250
200
150
100
50
0
10
20
30
40
50
60
TOTAL DRY WEIGHT (mg)
WATER TRANSPIRED (g)

The three environmental conditions varied in this experiment were the saturation deficit of the aerial environment, the moisture content of the soil and the sodium chloride concentration of the soil solution. The effects of these treatments and their interactions upon the various measured factors are considerable (see Appendix 5) but in this discussion only several effects will be discussed. The presentation is divided into three sections. The first deals with the effects of the treatments upon the growth of the plant and the amount of water transpired; in the second the effects of water movement upon the uptake of chloride ions are examined; in the third the effects of water uptake upon the uptake of sodium ions are studied.

Dry weight growth and transpiration:

An increase in dry weight of plants largely results from the excess production of photosynthate in the leaves compared with the losses due to respiration in the whole plant. The rate of increase in dry weight of a plant, dW/dt, can be taken as the product of its leaf area, La, and the nett photosynthetic rate per unit leaf area. The latter is defined as the Nett Assimilation Rate or NAR (Williams 1946) and therefore

$$\frac{dW}{dt} = NAR.La \qquad \ldots\ldots (54)$$

If the NAR is constant, integration of equation (54) over the time interval $t_1 - t_2$ gives

$$W_2 - W_1 = NAR \int_{t_1}^{t_2} La\ dt \qquad \ldots\ldots (55)$$

where $\int_{t_1}^{t_2} La\ dt$ is termed the Leaf-Area Duration, LaD. Only two harvests were made in the present experiment and to calculate LaD the growth in leaf area was assumed to be linear from time zero to day nine and from day nine to day eighteen. Leaf area growth however is generally curvilinear, the slope increasing with time (at least to eighteen days) and consequently LaD was overestimated by the procedure adopted here. The increase in dry weight over the periods 0 - 9 and 9 - 18 days is linear with total LaD (Figure 16a), i.e. the NAR is constant. It must be appreciated however that during the very early period of growth there is little or no photosynthate production and differences in initial weight and weight at nine days were negative in most treatments. Thus it would appear that after some short initial growth period the NAR reaches a constant value. In Figure 16a it is shown that at 92.5% RH the NAR is lower than that for plants growing in an aerial environment of 67.5% and 42.5% relative humidity.

Figure 16: a. Dry Weight Differences as a Function of Leaf-area Duration

Relative humidity (%)

● 42.5
▲ 67.5
× 92.5

For relative humidites of 42.5% and 67.5%

$$y = 1.63x - 67.2, \quad r = 0.962^{***}$$

For relative humidity of 92.5%

$$y = 1.03x - 41.4, \quad r = 0.983^{***}$$

Difference in slopes was significant at $p = 0.001$.

It is well known that the NAR of yellowing or senescent leaves is lower than that of younger full green leaves. In Figure 16b the change in dry weight of the plants during days 0 - 9 and 9 - 18 against green leaf-area duration reveals that not all of the difference between the NAR at 42.5% relative humidity (or 67.5%) and 92.5% is accounted for by the yellowing of leaves. The plot used in Figure 16b assumes that the NAR of the yellow leaves is zero which is not necessarily so, therefore corrections are at a maximum. It is clear that the aerial humidity has influenced the dry weight growth of plants and, using growth analysis concepts, this effect is ascribable to a depression in NAR by high humidity, resulting partly from yellowing of leaves and partly from some unknown cause.

The relative humidity of the atmosphere can affect the growth of plants through effects upon the transpiration rate and leaf energy balance. Linacre (1964) has assessed the relation between humidity and leaf surface temperatures. Leaf temperatures are dependent not only upon nett radiation and ambient dry bulb temperatures (which were constant in this experiment), but also upon the internal vapour-diffusion resistance of the leaf, the boundary layer heat-diffusion resistance (a function of leaf-air temperature differences, wind

Figure 16: b. Dry Weight Differences at Various Green-Leaf-area Durations

Relative humidity (%)

● 42.5
▲ 67.5
× 92.5

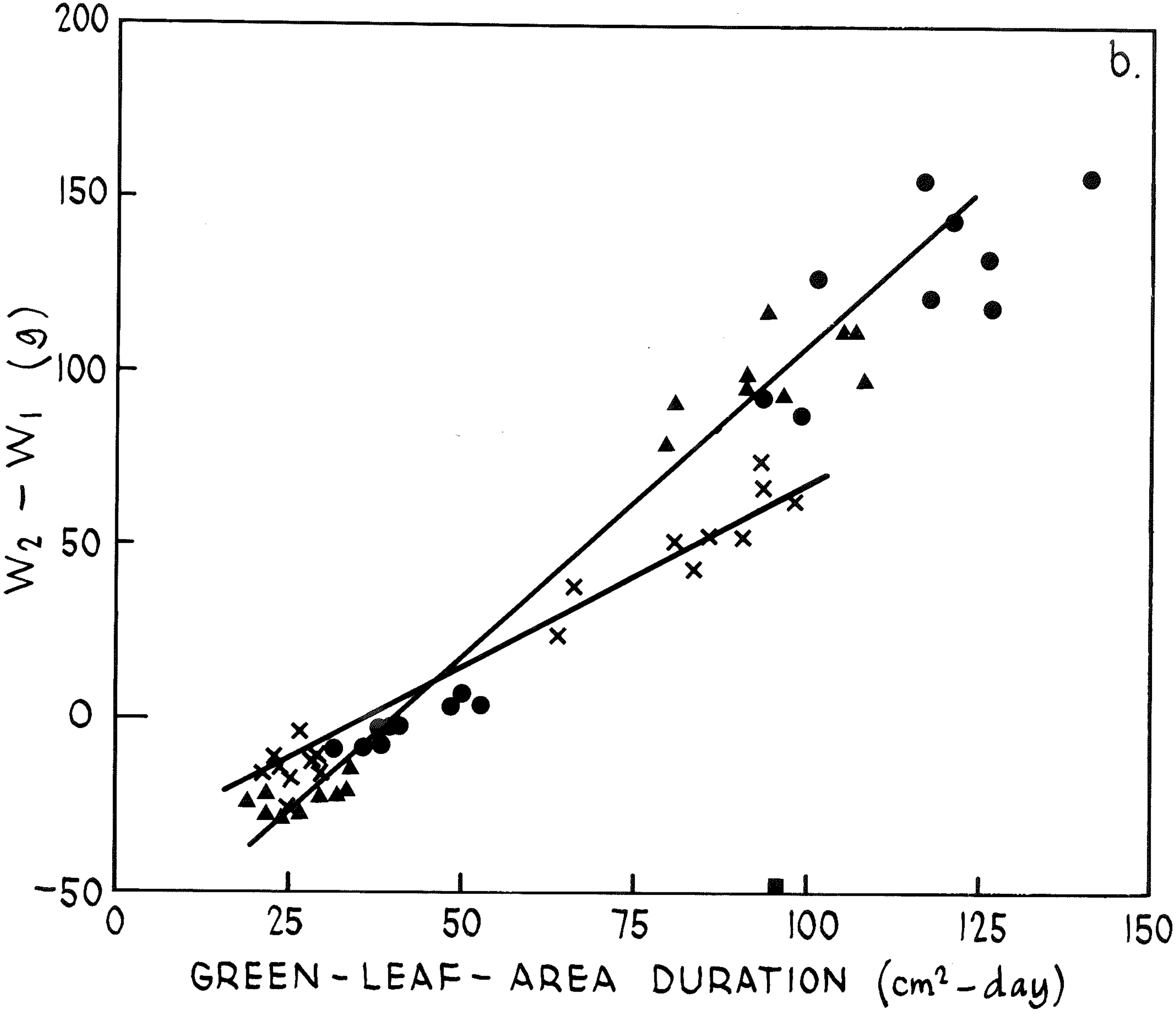
For relative humidities of 42.5% and 67.5%

$$y = 1.69x - 68.4, \quad r = 0.981^{***}$$

For relative humidity of 92.5%

$$y = 1.13x - 43.6, \quad r = 0.982^{***}$$

Difference in slopes was significant at $p = 0.001$.


b.
200
150
100
50
0
−50
0
25
50
75
100
125
150
$W_2 - W_1$ (g)
GREEN - LEAF - AREA DURATION (cm² - day)

speed and leaf form), and the ambient humidity of the aerial environment. In this work wind speeds were constant and no apparent variation in leaf form, i.e. in leaf roll or curl, was observed between treatments. Therefore the depression in NAR at high humidities is probably associated with a change in leaf temperature resulting from the effects of relative humidity and/or from changes in the vapour-diffusion resistance within the leaf. Other factors, such as transfer of carbon dioxide and oxygen transfer at the plant surfaces, may also vary with treatment but it is not possible with the present data to conclude precisely the mechanism through which the humidity affects the NAR.

The amount of water transpired, Tr, can be proportional to the leaf area over short periods of time, provided that no "internal" factors are limiting the loss of water from the plants,

$$\text{i.e.} \qquad \frac{dTr}{dt} = \delta \, La \qquad \ldots\ldots (56)$$

The coefficient of proportionality, δ, will then depend on temperature, light intensity, day length, wind velocity and relative humidity of the environment.

Over an extended period of time, as with this experiment, the leaf area is continually enlarging and it is appropriate to analyse water loss in terms of leaf-area duration (LaD). Thus integrating equation (56)

$$Tr_2 - Tr_1 = \delta . LaD \qquad ..... (57) \quad ,$$

assuming that δ is a constant. In this experiment, the coefficient, δ, should be a function only of the relative humidity, as all other aerial environmental conditions were constant, and will be termed the potential unit transpiration rate, UTR_p. In Figure 17 is shown the relation between the amount of water transpired and the LaD over the periods 0 - 9 days and 9 - 18 days. At low values of LaD the actual UTR falls below the potential UTR. It appears that some factor prevents the attainment of the maximum possible UTR (UTR_p), when LaD is small. Also in Figure 17, it may be seen that the potential UTR of plants growing in a relative humidity of 67.5% and 42.5% is the same, though larger than that of plants growing in a relative humidity of 92.5%. Therefore some factor prevented the UTR_p from increasing further when relative humidity was reduced below 67.5%.

Gardner (1960) has suggested that root length could limit the ability of plants to absorb a sufficient quantity of water to meet the demand set by the aerial environment. In Figure 18 (see also Appendix 5), the effects of the treatments on root lengths is given. In

Figure 17: Amount of Water Transpired as a Function of Total Leaf-area Duration

a. Over periods 0 - 9 and 9 - 18 days.

	Relative humidity (%)
●	42.5
▲	67.5
×	92.5

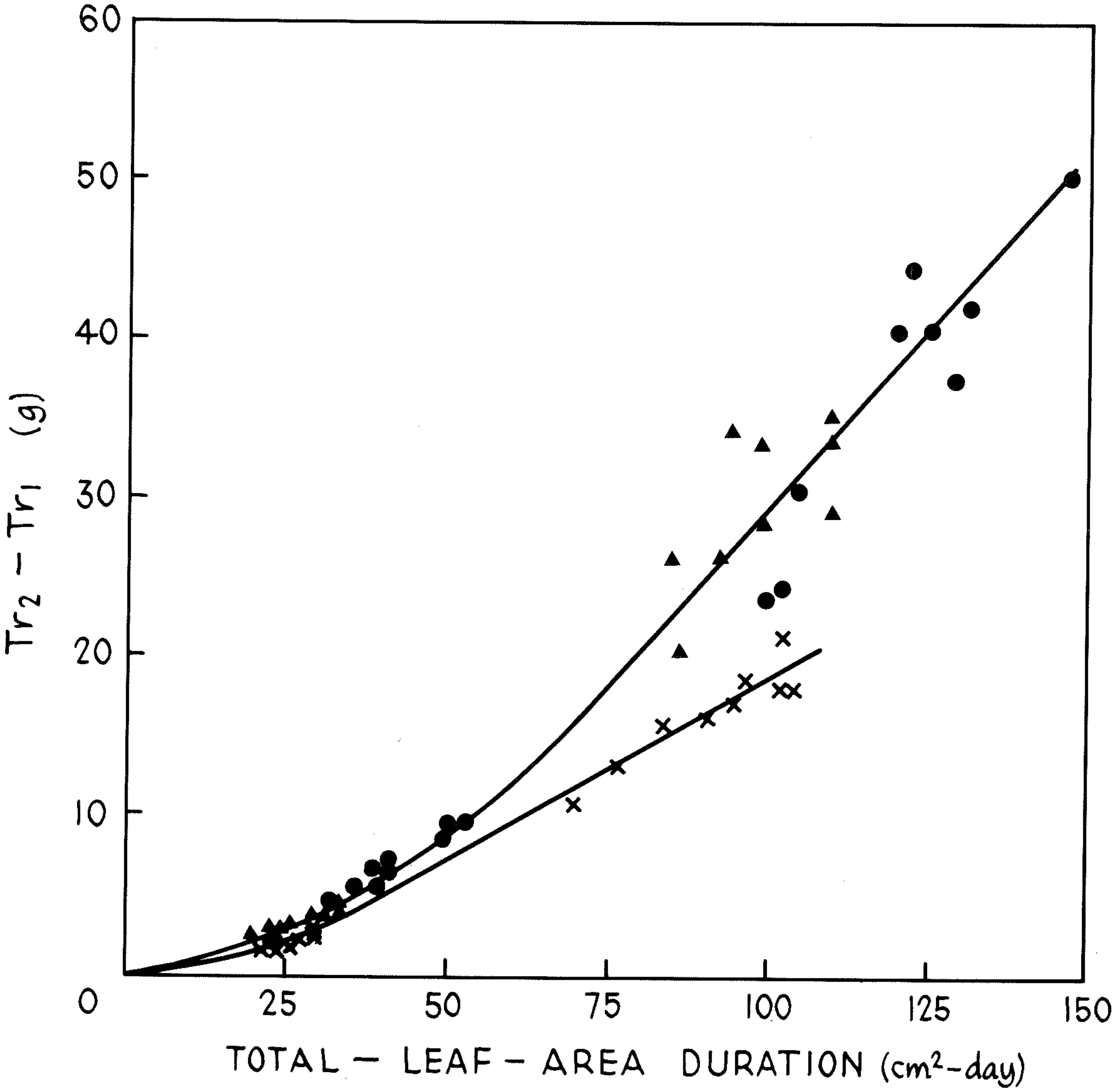

60
50
40
30
20
10
0
25
50
75
100
125
150
$Tr_2 - Tr_1$ (g)
TOTAL – LEAF – AREA DURATION (cm²-day)

Figure 17: b. Over period 0 - 9 dyas

	Relative humidity (%)	Water content of sand
●	42.5	4
◉	42.5	6
▣	42.5	8
▲	67.5	4
▲⃝	67.5	6
▲⃞	67.5	8
×	92.5	4
⊗	92.5	6
⊠	92.5	8

Subscripts indicate chloride concentration (ppm) of soil solution

1 = 5
2 = 100
3 = 1000.

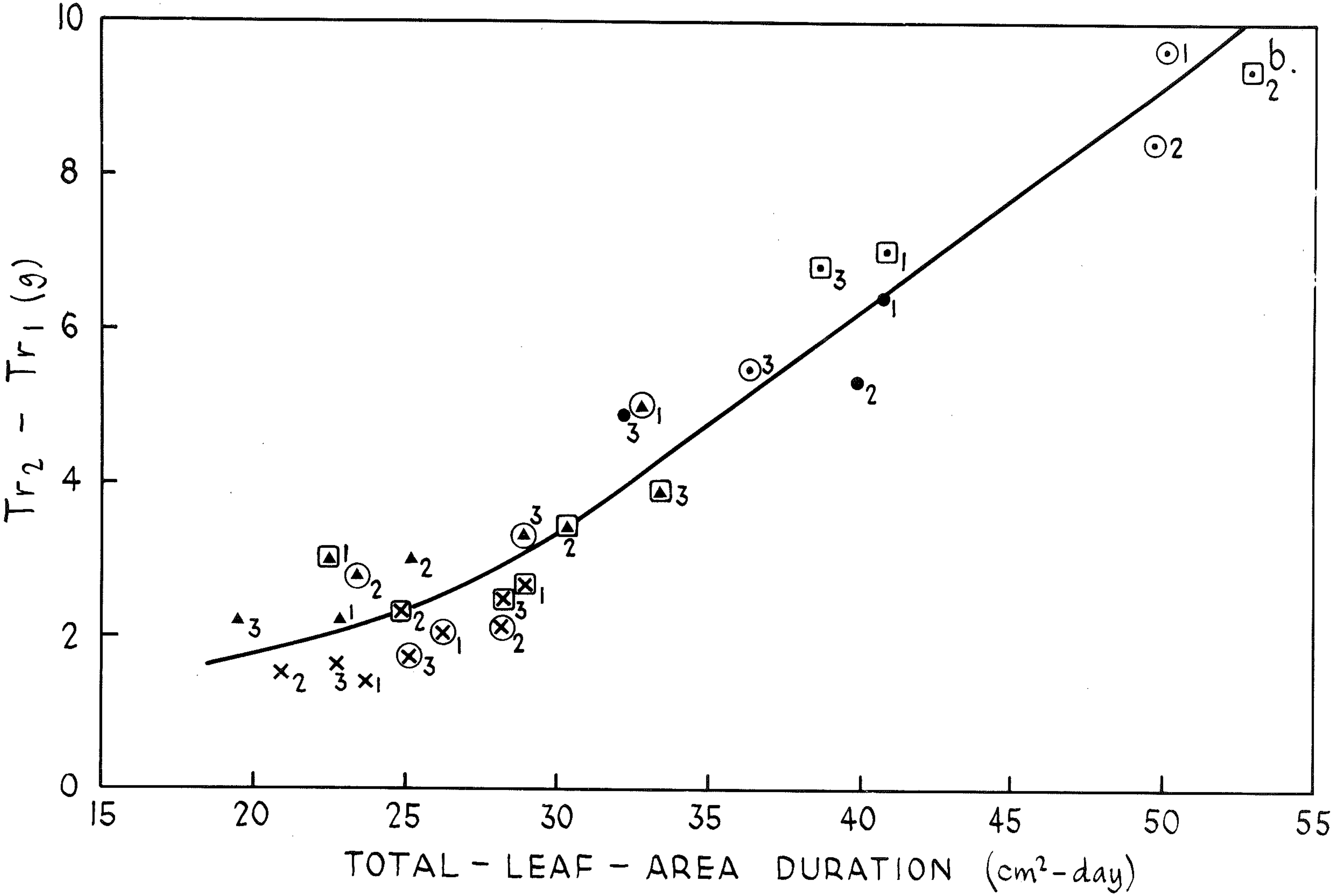

b.
Tr₂ - Tr₁ (g)
0
2
4
6
8
10
15
20
25
30
35
40
45
50
55
TOTAL - LEAF - AREA DURATION (cm²-day)
1
2
3

Figure 18: Effect of Treatments on Root Length

—— 18 day

— — 9 day

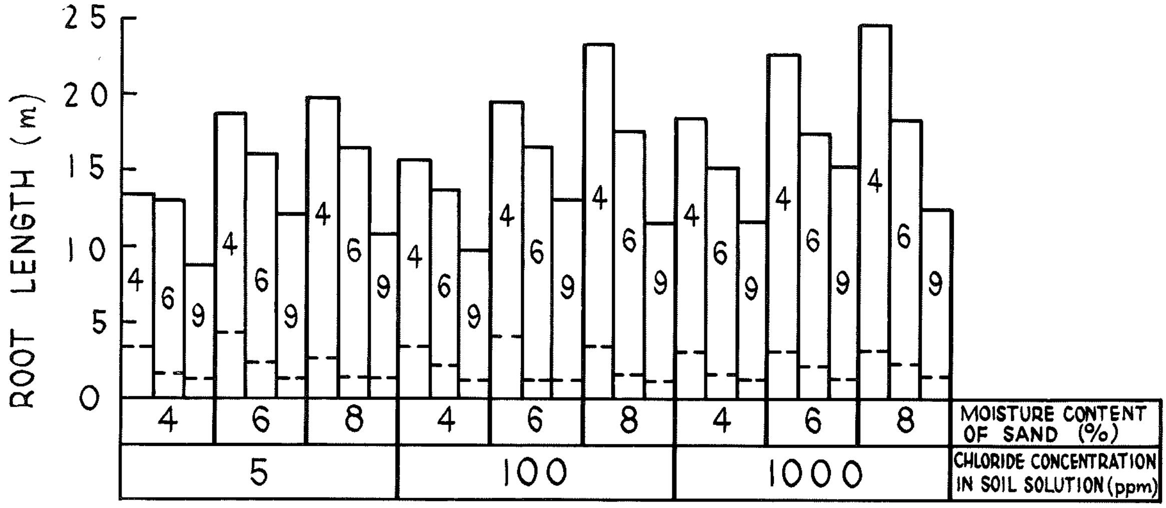
Numbers in histogram indicate relative humidity

4	42.5%
6	67.5%
9	92.5%

Figure 19: Effect of Root Length upon the Value of Unit Transpiration Rate

Relative humidity (%)

●	42.5
▲	67.5
×	92.5


ROOT LENGTH (m)
0
5
10
15
20
25
4
6
9
MOISTURE CONTENT OF SAND (%)
4
6
8
CHLORIDE CONCENTRATION IN SOIL SOLUTION (ppm)
5
100
1000

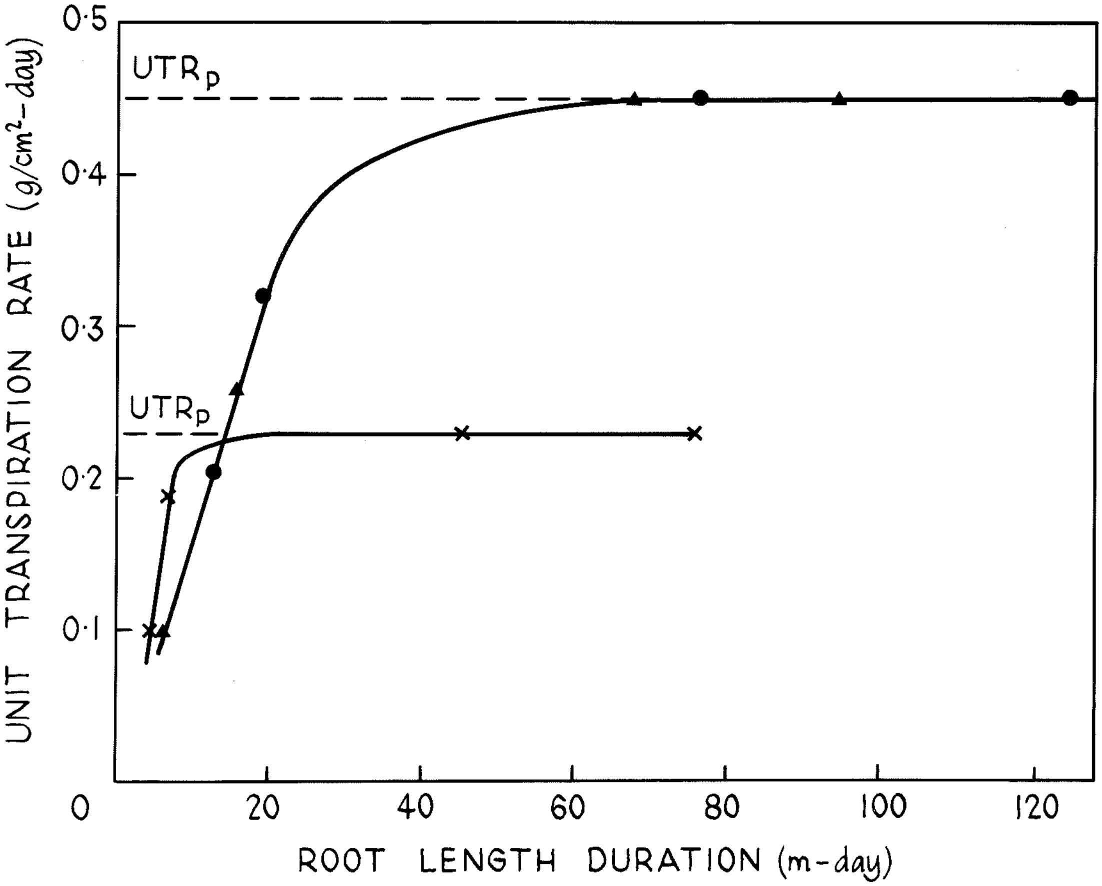

UNIT TRANSPIRATION RATE (g/cm²-day)
0·1
0·2
0·3
0·4
0·5
UTR$_p$
UTR$_p$
0
20
40
60
80
100
120
ROOT LENGTH DURATION (m-day)

Figure 19 the dependence of the UTR (calculated from slopes in Figure 17) on the root length duration is given and it can be concluded that the root length prevents the plants during days 0- 9 from attaining their potential UTR. This limiting root length probably caused the total water potential within the plant to become more negative (Gardner and Ehlig 1962) with a subsequent reduction in the water loss per unit of leaf area (see Ehlig and Gardner 1964). The fact that root length is limiting the quantity of water transpired per unit leaf area, implies that, under the water potential gradients around the roots, insufficient water can be transmitted to the root surface (Gardner 1960). Thus it should be expected that the value of the UTR at any limiting root length, should be greatest at the highest soil water content and least at the lowest water content. Figure 17b reveals the general tendency for this to occur.

The water uptake per unit root-length duration (URLD) data (see Table 10) shows only small variation with treatment. However the data are in keeping with the above discussion on the limiting effects of root length, provided that water uptake per unit root-length duration is indicative of the water potentials surrounding the roots.

Table 10

Water Uptake per Unit Root-length Duration

(g/m-day)

(Means of three replicates)

Relative Humidity (%)	Chloride Concentration soil solution (ppm)	Water Content of Soil (%)	Days	
			0 - 9	9 - 18
42.5	5	4	0.43	0.32
		6	0.53	0.42
		8	0.57	0.46
	100	4	0.37	0.29
		6	0.47	0.36
		8	0.60	0.43
	1000	4	0.36	0.32
		6	0.38	0.36
		8	0.48	0.34
67.5	5	4	0.29	0.40
		6	0.46	0.42
		8	0.54	0.45
	100	4	0.35	0.30
		6	0.44	0.43
		8	0.50	0.42
	1000	4	0.25	0.36
		6	0.33	0.34
		8	0.39	0.32
92.5	5	4	0.32	0.25
		6	0.46	0.38
		8	0.47	0.31
	100	4	0.38	0.28
		6	0.46	0.30
		8	0.52	0.32
	1000	4	0.36	0.30
		6	0.35	0.27
		8	0.38	0.29

Further discussion on the treatment effects on the UTR is made difficult by the few harvests. Therefore any further investigations along the above lines should involve at least three harvests.

As expected, the potential UTR for plants growing in a relative humidity of 92.5% is lower than that for plants growing in relative humidites of 67.5% and 42.5%. However as the potential UTR of plants in relative humidities of 67.5% and 42.5% are the same and not increasing with increased root length, some factor other than root length is preventing the UTR_p at 42.5% relative humidity from exceeding the UTR_p at a relative humidity of 67.5%. Thus it would appear that under certain circumstances the ability of the plant to transmit water from the roots and up through the plant to the leaves could also limit the amount of water which can be transpired by wheat plants.

The evaporation rate from a free water surface per unit area, E_o, may be described by the equation

$$E_o = f(u).(P_o - P) \qquad ..... (58)$$

where f(u) is a function of the horizontal wind velocity, P_o is the vapour pressure at the evaporating surface, or the saturated vapour pressure at the temperature of the water in the pan, and P is the vapour pressure of water in the atmosphere above the free water surface (Penman 1948). It is also found that a linear relation exists between the amount of water transpired by plants, per unit time per unit leaf area, and the rate of evaporation from a free water surface, i.e.

$$Tr = \gamma E_o \qquad \ldots\ldots (59)$$

where γ is mainly determined by the hours of possible sunshine (Penman 1948). In the present experiment f(u), P_o and γ should be constant and since $P = H.P_o/100$, equation (59) can be written in the form

$$Tr = b_2(100 - H)$$

where Tr is the amount of water transpired over a period of time per unit leaf area and b_2 is the proportionality constant. With non-limiting water supply Tr is the theoretical potential UTR. Thus the potential UTR for the three relative humidity treatments of 92.5%, 67.5% and 42.5% would be expected to be in the proportions 1:4:8 respectively. In fact, the experimentally determined proportions were 1:2:2. This might indicate the limitation of water supply for the transpiration process not only in the 42.5% relative humidity treatment but also in the 67.5% relative humidity treatment.

Other factors than that above may cause a reduction in the theoretical ratios. Leaf form changes with treatment could reduce the functional leaf area but observations in the present experiment eliminate this cause. The yellowing of the leaves might have some effect upon the measured ratios, but Figure 20, which is based on green-leaf area, when compared with Figure 17 shows that the measured ratios of the potential UTR are not affected by the yellowing of the leaves. Changes in leaf temperature could also have a pronounced effect on the amount of water transpired. Assuming that the relative humidity at the leaf surface is 100% or very nearly so, the water vapour pressure at the leaf surface will vary with temperature as shown in Table 11. In addition, considering that all plant environmental factors are constant except for leaf temperature and the relative humidity of the air, the quantity of water transpired per unit leaf area should be proportional to the difference in the saturated vapour pressure at leaf temperature and the vapour pressure of the air. Table 11 shows the difference in vapour pressure between the air, 92.5% = 18 mm Hg, 67.5% = 13.2 mm Hg and 42.5% = 8.3 mm Hg at 71°F, and that at saturation at various temperatures. It is possible from this Table to find various temperatures at which a ratio of 1:2:2 could be obtained, e.g. those marked with an asterisk. Consequently in the present experiment changes in leaf

Table 11

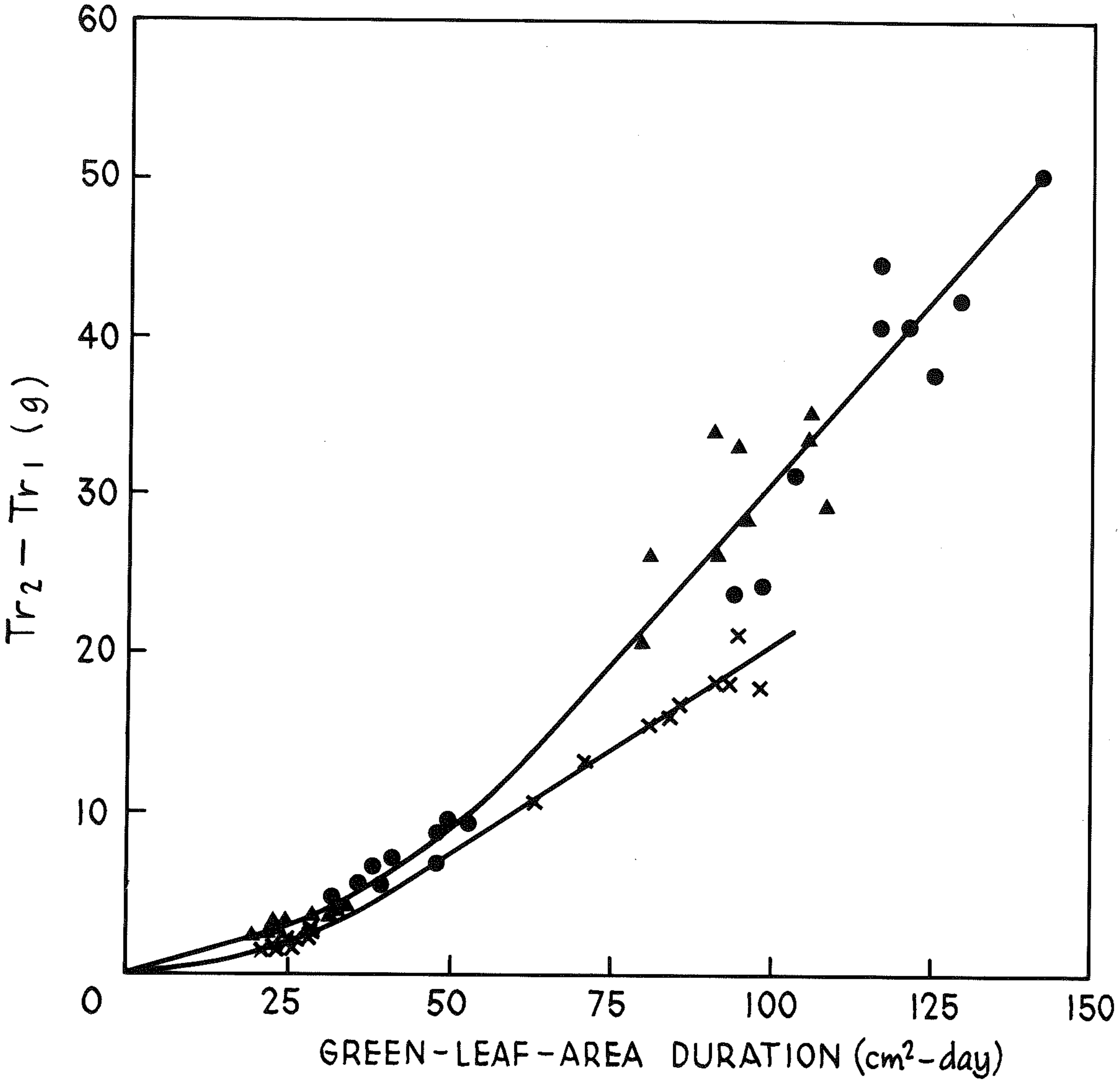
The Difference between Ambient Vapour Pressures of the Experiment and the Saturation Water Vapour Pressure at a Range of Possible Leaf Temperatures

Temperature (°F)	Saturation Vapour Pressure (mm Hg)	Vapour Pressure Difference		
		Ambient 18 mm Hg (92.5% at 71°F)	Ambient 13.2 mm Hg (67.5% at 71°F)	Ambient 8.3 mm Hg (42.5% at 71°F)
59	12.8	-	-0.4	4.5 *
60	13.3	-	0.1	5.0
61	13.7	-	0.5	5.4
62	14.3	-	1.1	6.0
63	14.7	-	1.5	6.4
64	15.3	-	2.1	7.0
65	15.7	-	2.5	7.4
66	16.4	-	3.2	8.1
67	16.9	-	3.7	8.6
68	17.5	-0.5	4.3 *	-
69	18.2	0.2	5.0	-
70	18.8	0.8	5.6	-
71	19.5	1.5	6.3	-
72	20.1	2.1 *	6.9	-
73	20.8	2.8	7.6	-

Figure 20: Transpiration as a Function of Green-Leaf-Area Duration

Relative humidity (%)

● 42.5
▲ 67.5
× 92.5


60
50
40
30
20
10
0
25
50
75
100
125
150
$Tr_2 - Tr_1$ (g)
GREEN-LEAF-AREA DURATION (cm²-day)

temperature probably gave rise to the measured ratios of potential UTR.

Combining equations (54) and (56) one obtains that

$$\frac{dW}{dt} = \frac{NAR}{\delta} \frac{dTr}{dt}$$

or upon integration and assuming NAR/δ is constant,

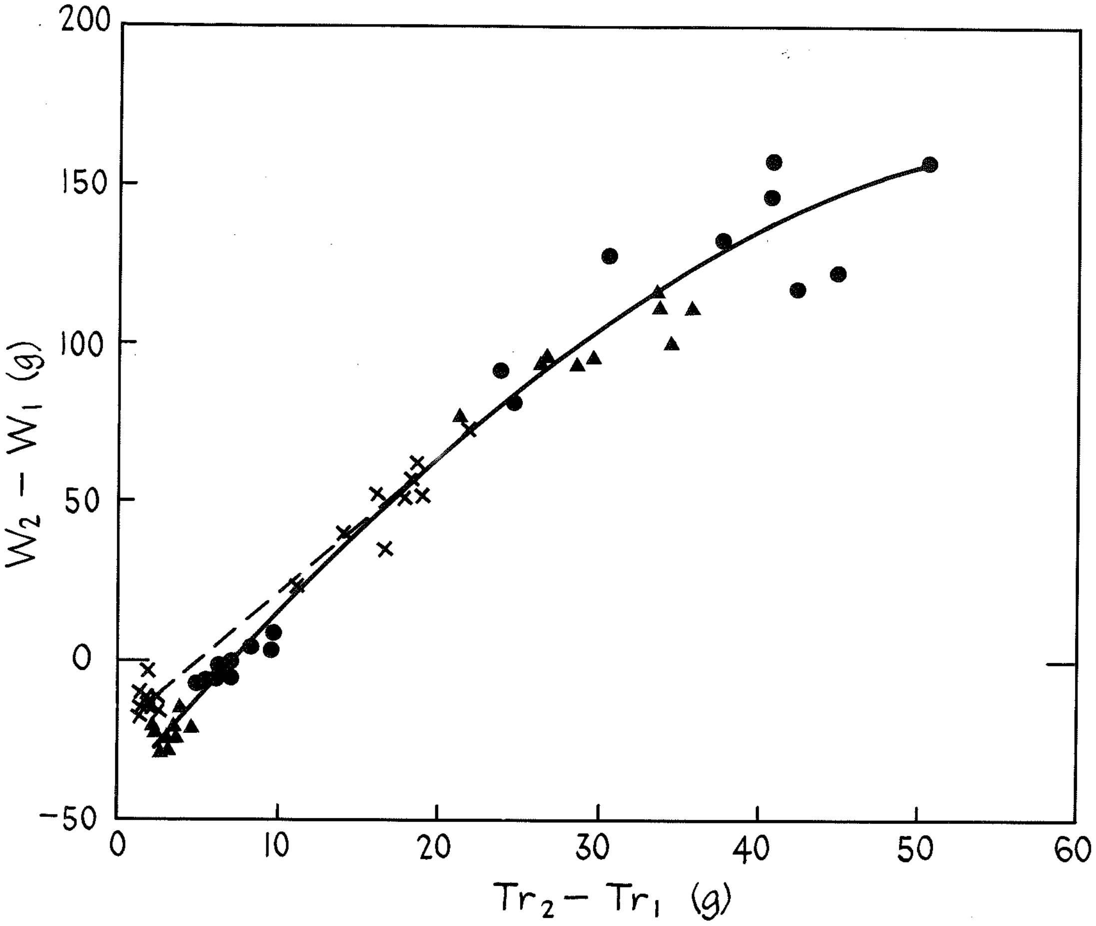
$$W_2 - W_1 = \frac{NAR}{\delta} (Tr_2 - Tr_1) \qquad \ldots\ldots (60)$$

In Figure 21, c.f. Figure 15, is shown the relation between $W_2 - W_1$ and $Tr_2 - Tr_1$, the slope being the ratio NAR/δ. The relations found are the same in contrast to the separate relations of water loss to leaf-area duration and dry weight production to leaf-area duration. In the latter cases it was found that both NAR and UTR were lower in the 92.5% relative humidity treatments. It is clear that the relative effect of humidity is the same for NAR and UTR over a wide range of conditions. However it is not clear why the slope lessens for large values of $W_2 - W_1$ and $Tr_2 - Tr_1$.

Arkley (1963) found a linear relation between yield of dry matter and the amount of water transpired, for several cereal crops at several sites. By plotting data in the form of yield, Y, against the amount of water

Figure 21: Total Dry Weight Production as a Function of Water Transpired during periods of 0 - 9 days and 9 - 18 days

	Relative humidity (%)
●	42.5
▲	67.5
×	92.5


200
150
100
50
0
−50
0
10
20
30
40
50
60
$W_2 - W_1$ (g)
$Tr_2 - Tr_1$ (g)

transpired, Tr, divided by (100-mean daily relative humidity of the atmosphere, H) he found the same linear relation for all sites for a single crop species. Figure 22 shows that the regression coefficient of Arkley is not constant in the present work but is dependent upon the relative humidity. Arkley recognized that the coefficient should be dependent upon the dry bulb temperature variation and concluded that the common regression for a number of sites resulted from some unknown compensation of dry bulb variation.

In the present work variation in NAR and UTR with relative humidity treatments contributes to the variation in dry matter accumulation and can account for the divergence of the regression in Figure 22 (c.f. Figure 15). The regression equation for Figure 15 is

$$Y = 3.26\ Tr + 70.6, \qquad r = 0.982^{***}$$

Similarly, linear relations were obtained between the dry weight of tops or roots and Tr/(100 - H) or Tr, see Figures 23 and 24. The regression equation for Figure 24a, the relation between dry weight of tops and quantity of water transpired is

$$Y = 1.55\ Tr + 27.9, \qquad r = 0.977^{***}$$

The slope of 1.55 mg/cc approximates to that given by

Figure 22: **Total Yield (Dry Weight) of Plants as a Function of the Quantity of Water Transpired/(100 - Mean Relative Humidity)**

Relative humidity (%)

●	42.5
▲	67.5
×	92.5

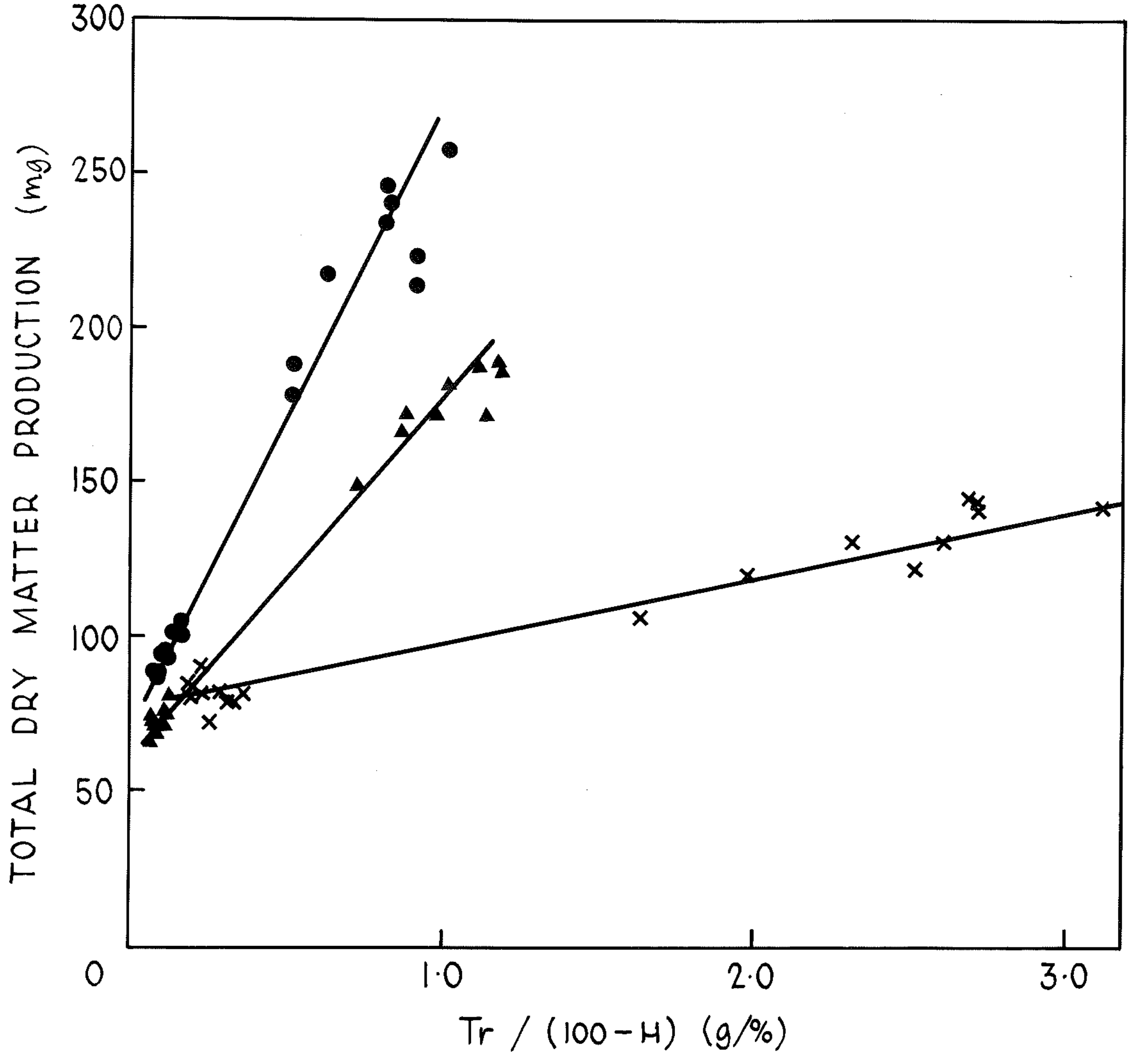
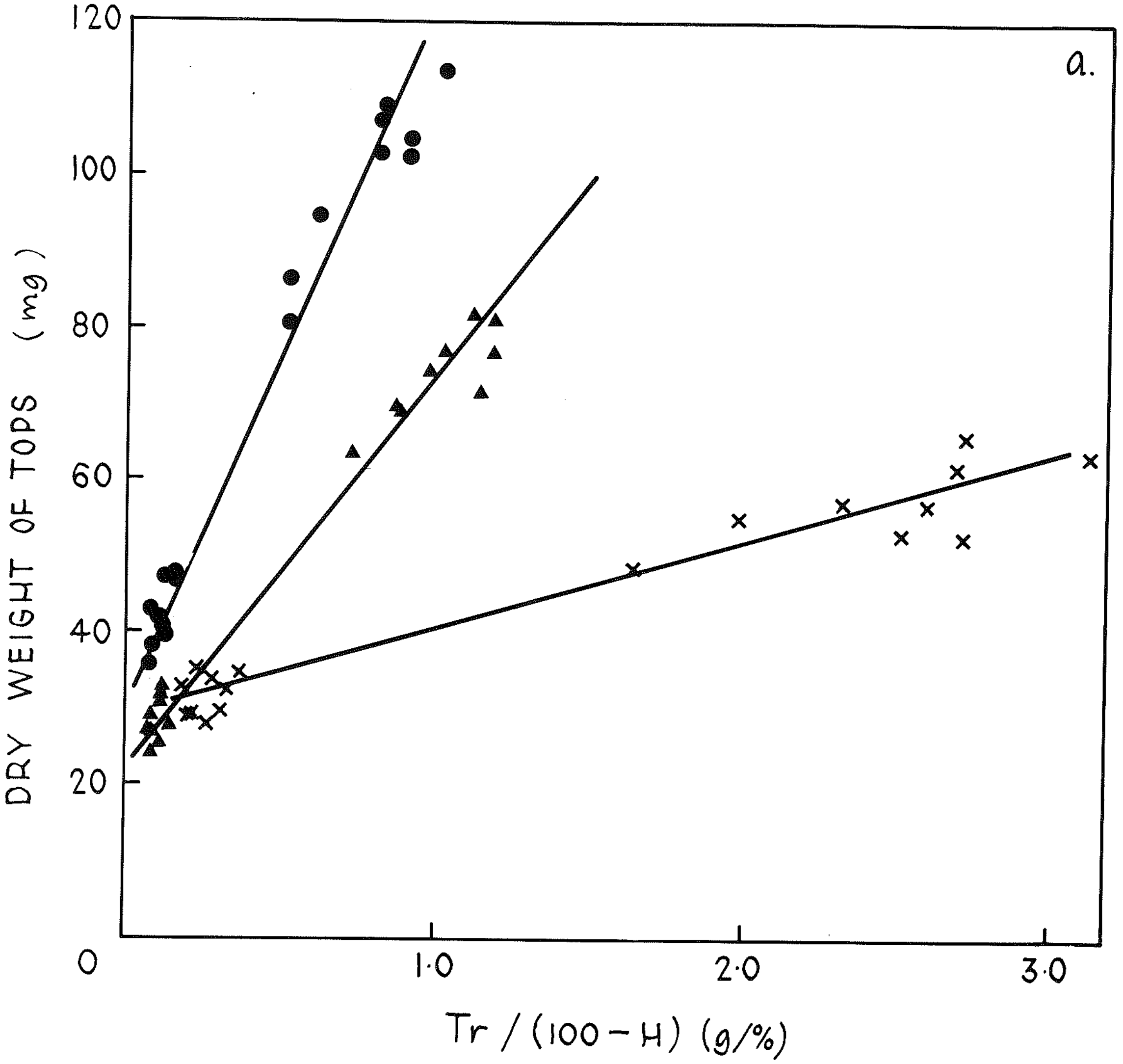

TOTAL DRY MATTER PRODUCTION (mg)
300
250
200
150
100
50
0
1·0
2·0
3·0
Tr / (100 – H) (g/%)

Figure 23: a. Dry Weight of Tops, as a Function of the Quantity of Water Transpired/(100 - H)

Relative humidity (%)

●	42.5
▲	67.5
×	92.5


a.
DRY WEIGHT OF TOPS (mg)
120
100
80
60
40
20
0
1·0
2·0
3·0
Tr / (100 − H) (g/%)

[illegible]

[illegible]

[illegible]

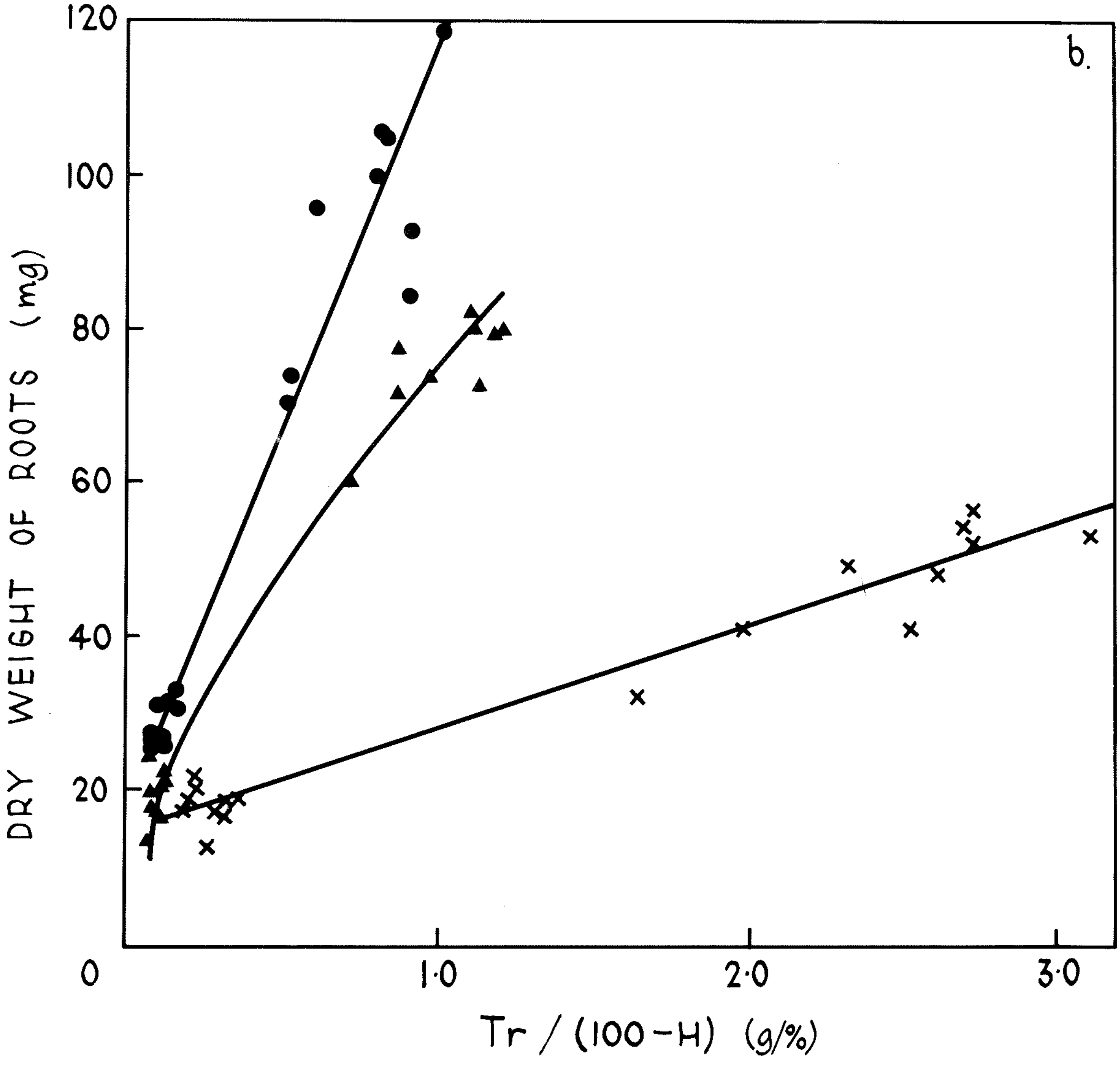
[illegible]

[illegible]

Figure 23: b. Dry Weight of Roots, as a Function of the Quantity of Water Transpired/(100 - H)

Relative humidity (%)

●	42.5
▲	67.5
×	92.5


b.
DRY WEIGHT OF ROOTS (mg)
120
100
80
60
40
20
0
1·0
2·0
3·0
Tr / (100 − H) (g/%)

[illegible]

[illegible]

[illegible]

[illegible]

Figure 24: a. Dry Weight of Tops, as a Function of the Quantity of Water Transpired

Relative humidity (%)

●	42.5
▲	67.5
×	92.5

$y = 1.55x + 27.9, \quad r = 0.977^{***}$

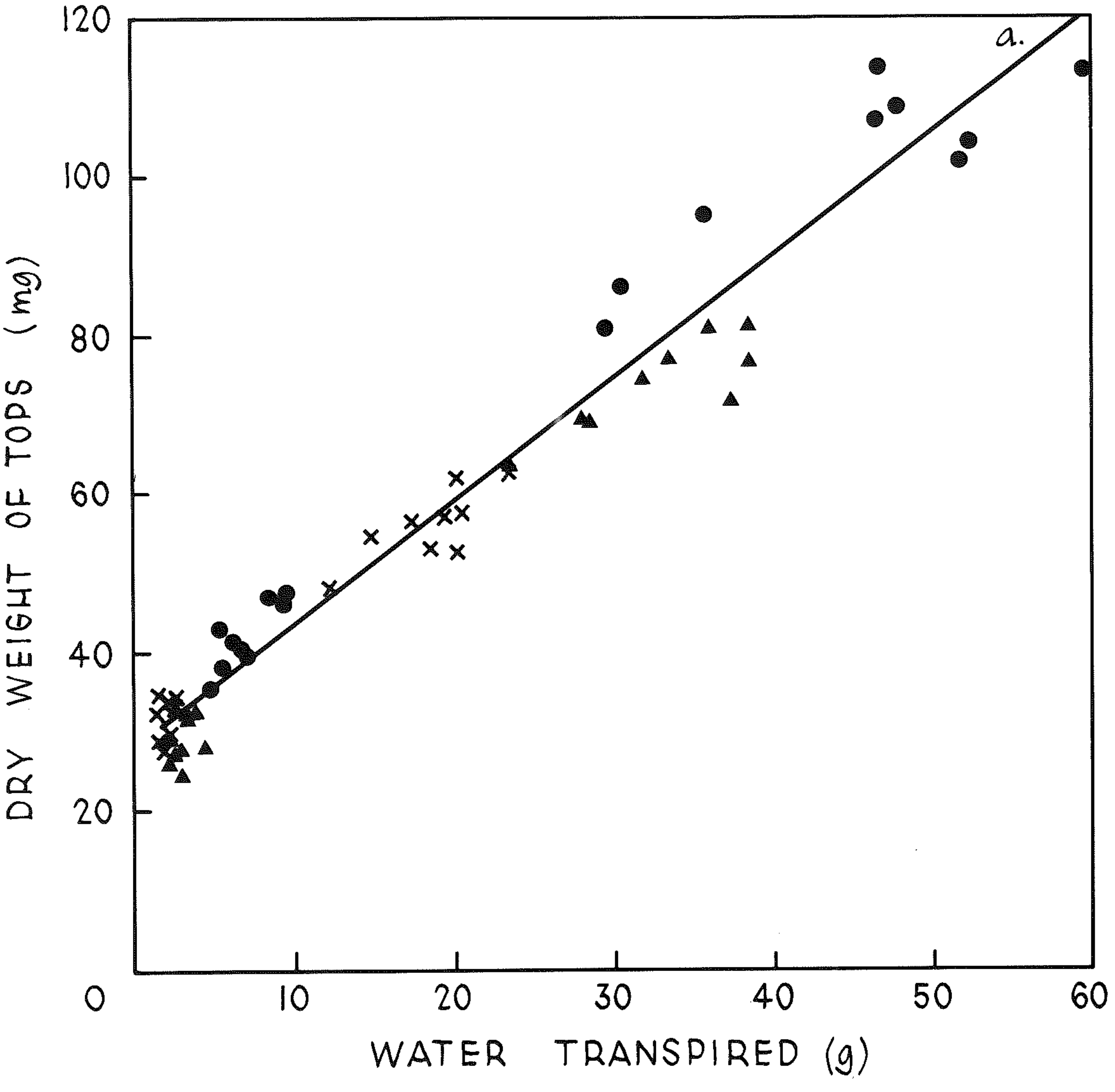
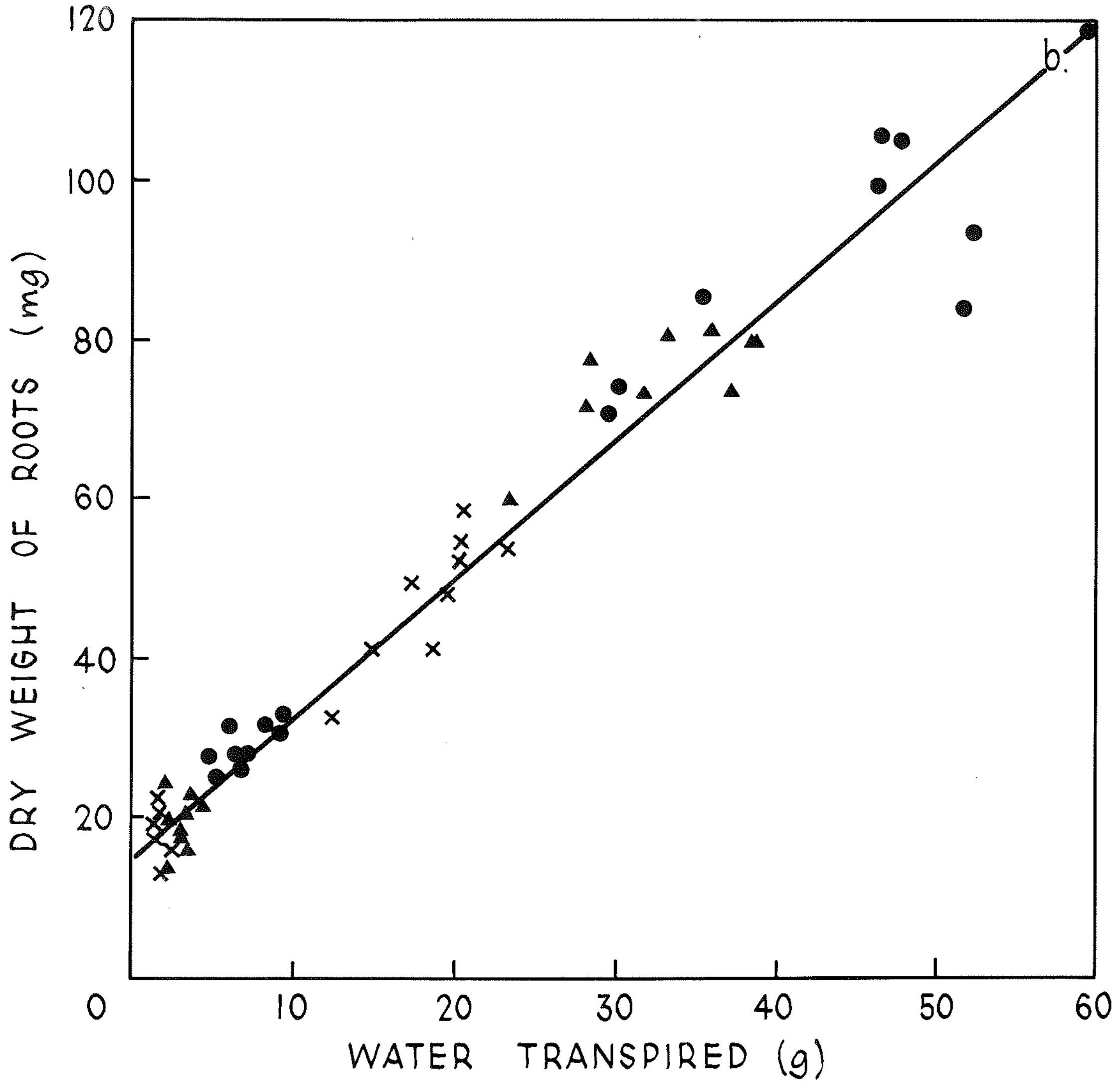

a.
DRY WEIGHT OF TOPS (mg)
WATER TRANSPIRED (g)
0
10
20
30
40
50
60
20
40
60
80
100
120

Figure 24: b. Dry Weight of Roots, as a Function of the Quantity of Water Transpired

	Relative humidity (%)
●	42.5
▲	67.5
✖	92.5

$y = 1.74x + 15.5, \quad r = 0.977^{xxx}$



b.
DRY WEIGHT OF ROOTS (mg)
120
100
80
60
40
20
0
10
20
30
40
50
60
WATER TRANSPIRED (g)

Arkley (1963) for the yield (dry weight of tops) of oats, i.e. 1.63 g/l, but is somewhat lower than that obtained for wheat on unfertilized soil where the slope was equivalent to 1.87 g/l.

Summary of Dry Weight Growth and Transpiration

The uptake of chloride increased with the amount of water transpired and the dry weight yield showed a simple linear increase in relation to water transpired. Increase in chloride uptake with increased transpiration could be due simply to the larger plants offering a greater storage capacity for ions.

However although all treatments fell on a common regression of dry matter yield on water transpired, separate regressions of chloride uptake on water transpired were found for the three humidity treatments and the three salt concentration treatments.

The higher the external salt concentration the greater was the chloride uptake per unit of water transpired. This result scarcely requires comment.

However chloride uptake per unit of water transpired was greatest in the 92.5% relative humidity treatment for external concentrations of 5 and 100 ppm of chloride. When the chloride was 1000 ppm humidity treatments had no effect.

Since total dry weight gain was depressed by the high relative humidity treatment relative to that found at 42.5% and 67.5% relative humidity, it appears that the higher salt uptake with respect to water uptake is not readily ascribed to greater size of plants and enhanced storage capacity. Further discussion of chloride uptake is given in the next section.

Reduction in dry weight yield with increased relative humidity was ascribable to depression in nett assimilation rate. Variation in unit transpiration rate was not in proportion to the imposed variation in relative humidity. The results suggest that higher leaf temperature associated with reduced unit transpiration rate was coupled with reduced nett assimilation rate. The stronger dependence of respiration rate, compared with photosynthesis rate, on leaf temperature would give rise to lower nett assimilation rate athigher leaf temperatures.

The dominating effect of relative humidity treatments compared with soil water content treatments on unit transpiration rate is due possibly to the different action of each on the total evaporation process at the foliage surfaces plus the dominating effect of the humidity treatment upon the length of roots. The importance of root length in the analysis of water uptake by plants is discussed.

Provided plant water potential differences have little effect on the resistance within the plant and provided the first effect of stress is on leaf expansion itself, then unit transpiration rate will vary largely with evaporative demand. It has been shown by Luxmoore (1962) that soil water content had little effect on unit transpiration rate over 60 days but leaf-area duration was substantially reduced by soil water stress.

Nevertheless plant (or plant-soil) resistance to water flow was significant in limiting unit transpiration rate. It was shown that unit transpiration rate was dependent on root-length duration in some circumstances. At the highest relative humidity, unit transpiration rate reached a plateau, called the potential unit transpiration rate at a lower root-length duration than that required to achieve the higher potential unit transpiration rate characteristic of the lower two humidity treatments.

The similar unit transpiration rates found in the 42.5% and 67.5% relative humidity treatments was due either to compensatory effects of more rapid decline in soil water content and hence hydraulic conductivity in the former and lower evaporative demand in the latter or due to increased resistance in the plant associated with a more negative value of the total water potential within the plant. This domination of plant resistance to water movement over that of the soil is possible at lower soil water potentials (Gardner and Ehlig 1962b).

The near-linear relation between dry weight yield and water transpired was examined in relation to Arkley's (1963) and Penman's (1948) work. Some deviations from linearity could be ascribed to leaf yellowing or senescence which affected NAR but had little effect on UTR.

Uptake of chloride ions

A major difficulty in assessing the effects of water uptake upon ion uptake is to separate those effects due directly to convective transport of ions due to mass flow of water, from indirect effects, arising within the plant and themselves contributing to the different rates of ion uptake. The direct effects of convection can occur in the soil as well as within the plant and some discussion of these has already been given in the literature review. In the first part of this section it has been shown that the nett assimilation rate and unit transpiration rate changed with the relative humidity of the aerial environment. There was not only variation in the rate of the physical process of evaporation at the leaf surface but there were indirect effects on growth and presumably metabolic activity of the plant itself.

The effects of treatments and their interactions upon the total chloride ion uptake and the root and shoot components are given in Appendix 5. In Figure 25 the dominant effect of chloride concentration in the soil solution upon the uptake of chloride ions by the plant is clearly shown and this result has been found by many workers. The relation between total water uptake and the total uptake of chloride ions is shown in Figure 26, where total water uptake is equal to the sum of the water transpired plus the water content of the plant minus the water initially present in the seedlings. At soil solution concentrations of 5 ppm and 100 ppm of chloride, the effect of high humidity was to increase the ratio of the ion flux to water flux compared with that found at lower humidities. The effect of high relative humidity was to reduce the water loss per pot to about half that found at 42.5% and 67.5% relative humidity. Root growth in meters per pot was reduced to about 60% of that found in the lower humidity treatments. Water flux per unit root-length duration (see Figure 27) thus shows little variation with relative humidity and the difference in ratio of ion flux to water flux is then due to enhanced

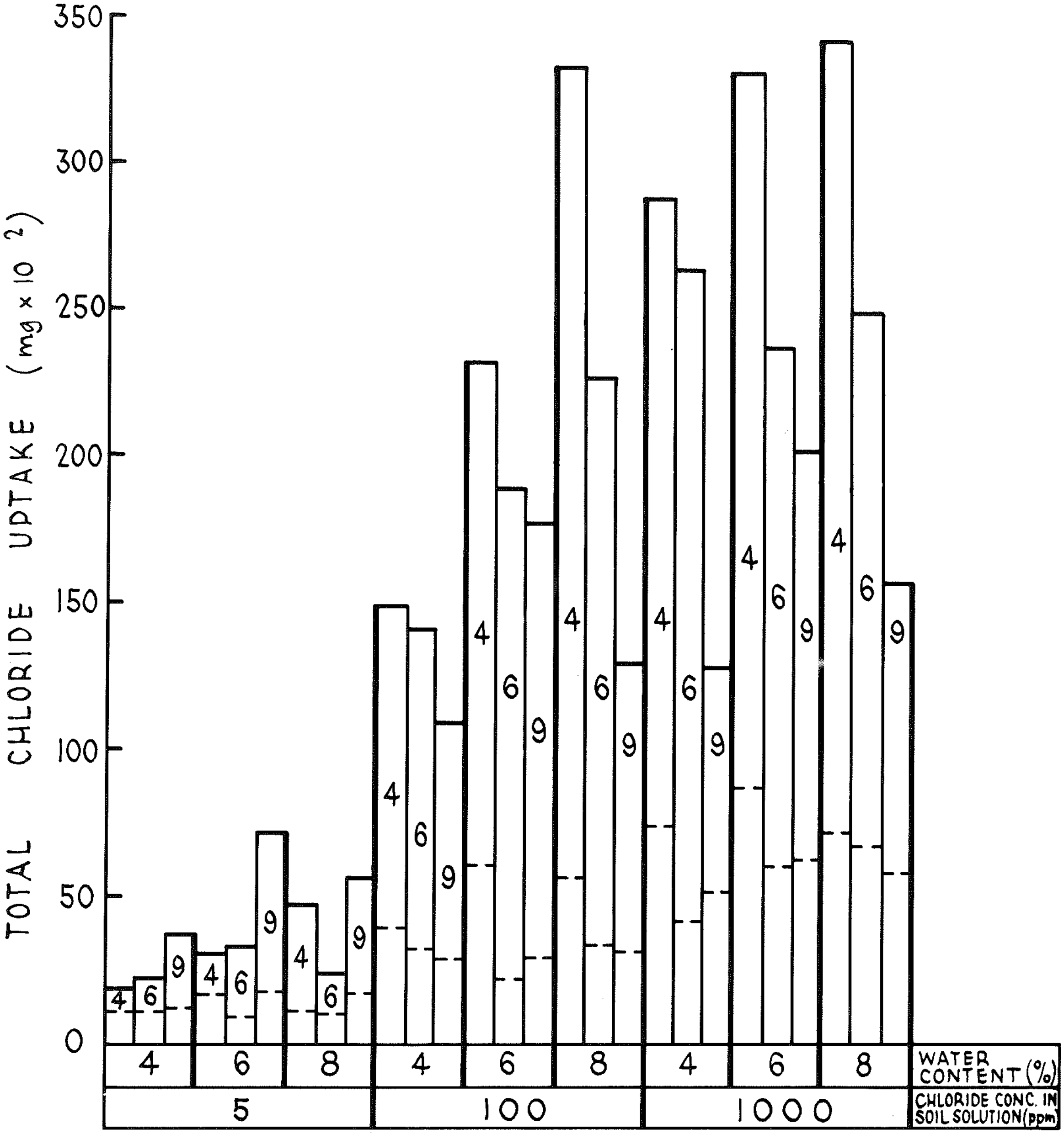
Figure 25: Total Chloride Uptake by Plants under Various External Environmental Conditions

——— 18 days

— — 9 days

Numbers in histogram refer to relative humidity

4	42.5%
6	67.5%
9	92.5%



TOTAL CHLORIDE UPTAKE (mg × 10 2)
350
300
250
200
150
100
50
0
4
6
9
WATER CONTENT (%)
4
6
8
4
6
8
4
6
8
CHLORIDE CONC. IN SOIL SOLUTION (ppm)
5
100
1000

Figure 26: Total Chloride Uptake as a Function of Total Water Uptake

Relative humidities (%)

● 42.5
▲ 67.5
× 92.5

Chloride concentration of soil solution (ppm)

——— 5
— — 100
- - - 1000

Subscripts 5, 10, 1000 refer to chloride concentration (ppm) of soil solution.

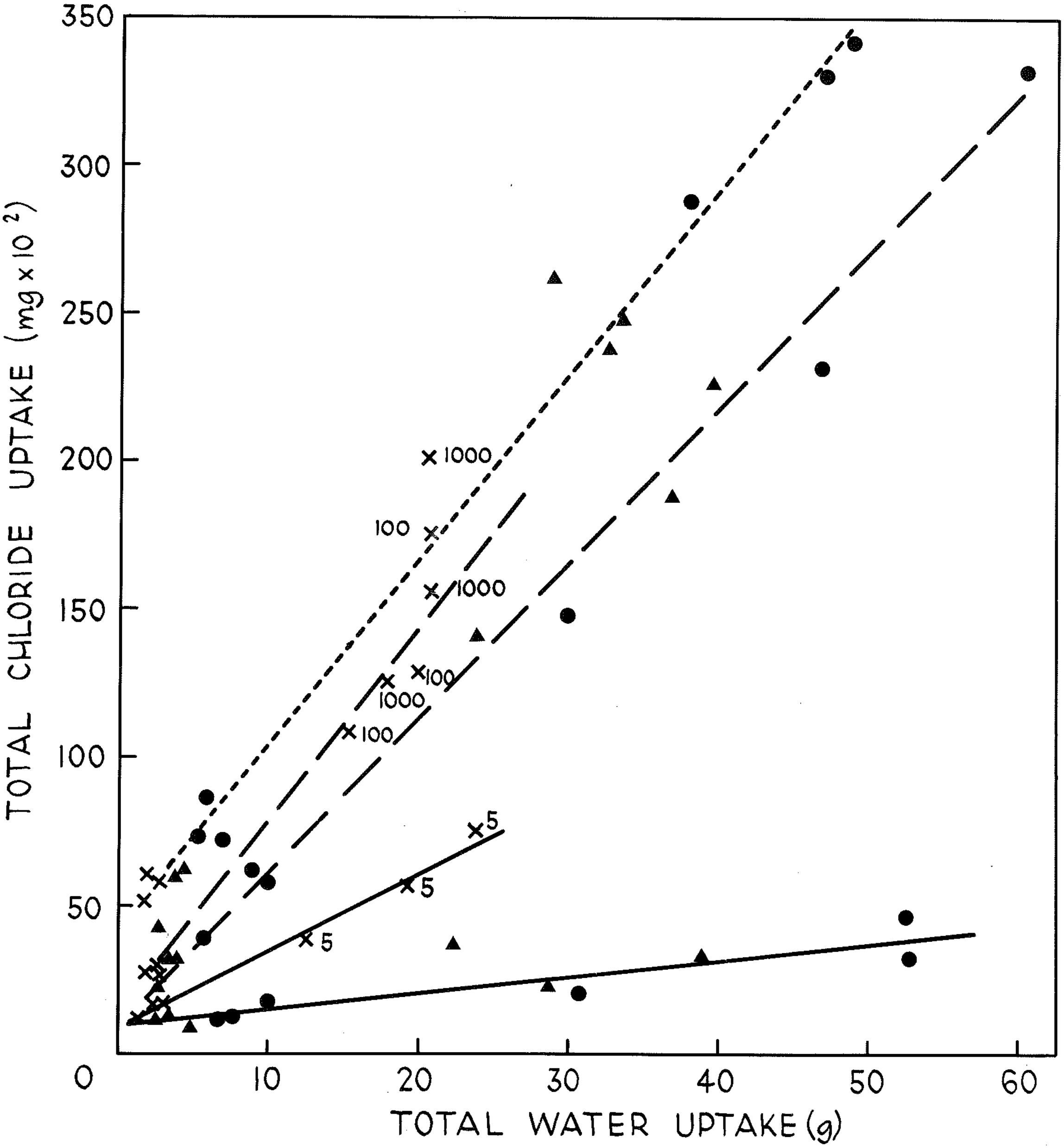

350
300
250
200
150
100
50
0
10
20
30
40
50
60
TOTAL CHLORIDE UPTAKE (mg × 10²)
TOTAL WATER UPTAKE (g)
1000
100
1000
100
1000
100
5
5
5

Figure 27: Total Chloride Uptake as a Function of Water Uptake

(Both variables normalized to unit root-length duration)

Relative humidity (%)	Period of growth (days)	
	0 - 9	9 - 18
42.5	⊙	●
67.5	◬	▲
92.5	⊗	×

a. At a soil solution concentration of 5 ppm of chloride

b. At a soil solution concentration of 100 ppm of chloride.

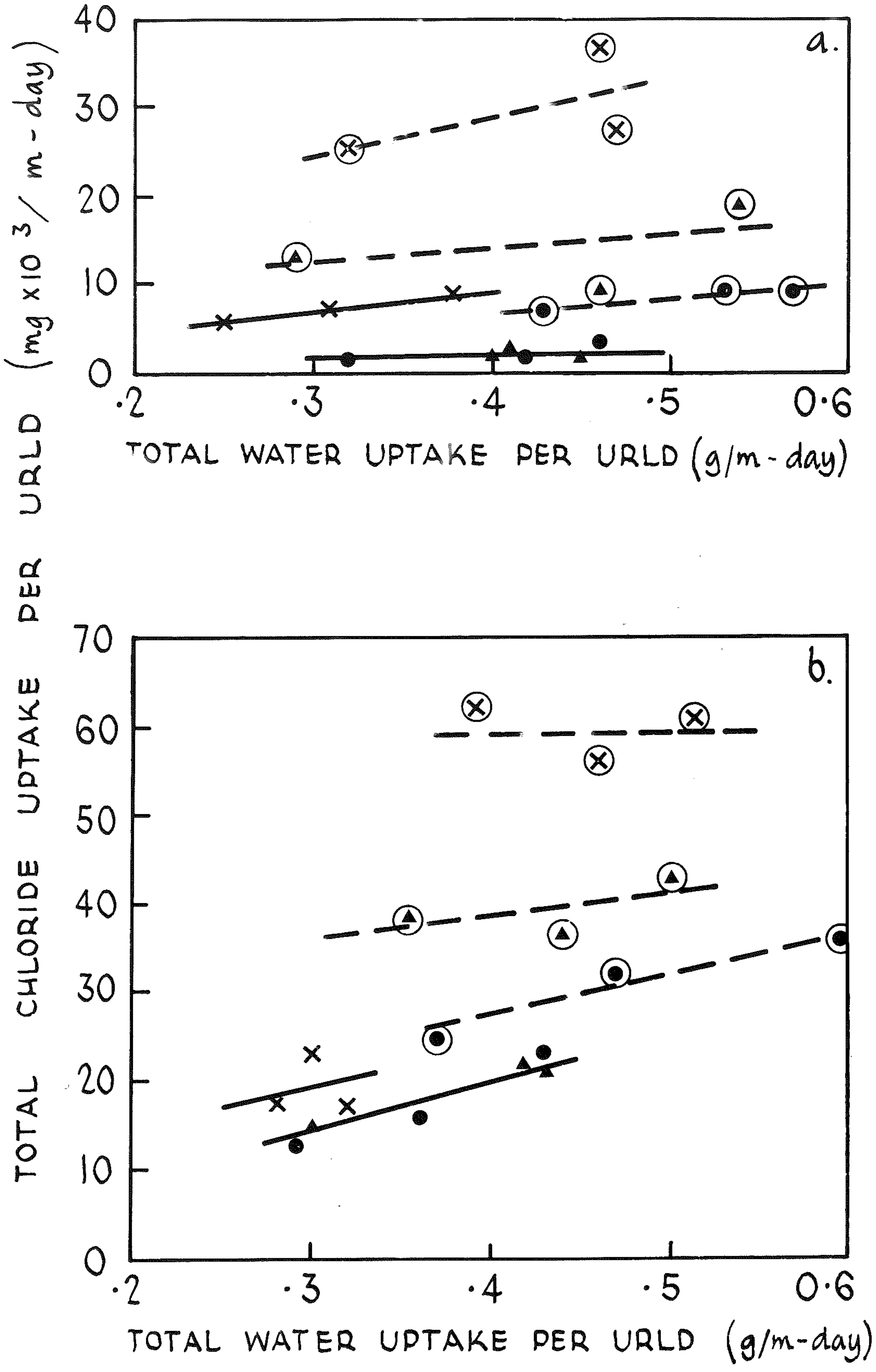
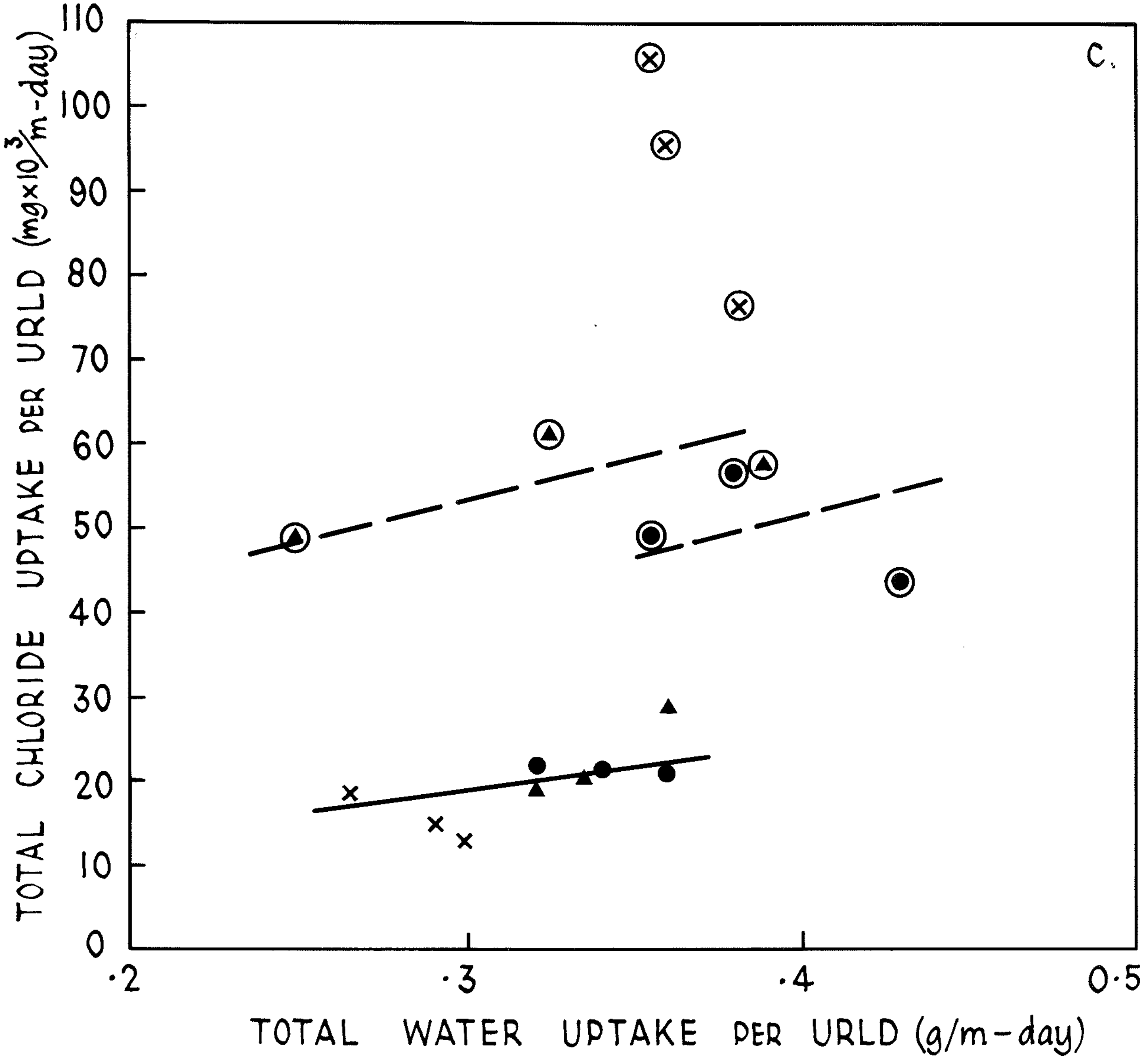

a.
b.
40
30
20
10
0
70
60
50
40
30
20
10
0
·2
·3
·4
·5
0·6
TOTAL WATER UPTAKE PER URLD (g/m-day)
TOTAL CHLORIDE UPTAKE PER URLD (mg x 10 3/ m-day)

__Figure 27:__ c. At a soil solution concentration of 1000 ppm of chloride.


C.
TOTAL CHLORIDE UPTAKE PER URLD (mg×10^3/m-day)
0
10
20
30
40
50
60
70
80
90
100
110
·2
·3
·4
0·5
TOTAL WATER UPTAKE PER URLD (g/m-day)

ion flux at the highest humidity.

In defining fluxes based on root-length duration it is implied that all of the root length is equally available for water and ion uptake or that a constant but not specified proportion of root length participates in the uptake of ions. It has already been pointed out in the literature review that not all of the root length need be equally functional in the uptake of water or ions at all times. It might be assumed that the functional root length (RL_f) is a product of some constant length (l) and the number of root tips (NR), that is

$$RL_f = l.NR$$

However it is shown in Figure 28 that a linear relationship exists between the root length and the root number and no further insight is gained by use of this variable. The results will therefore be discussed only in terms of root-length duration.

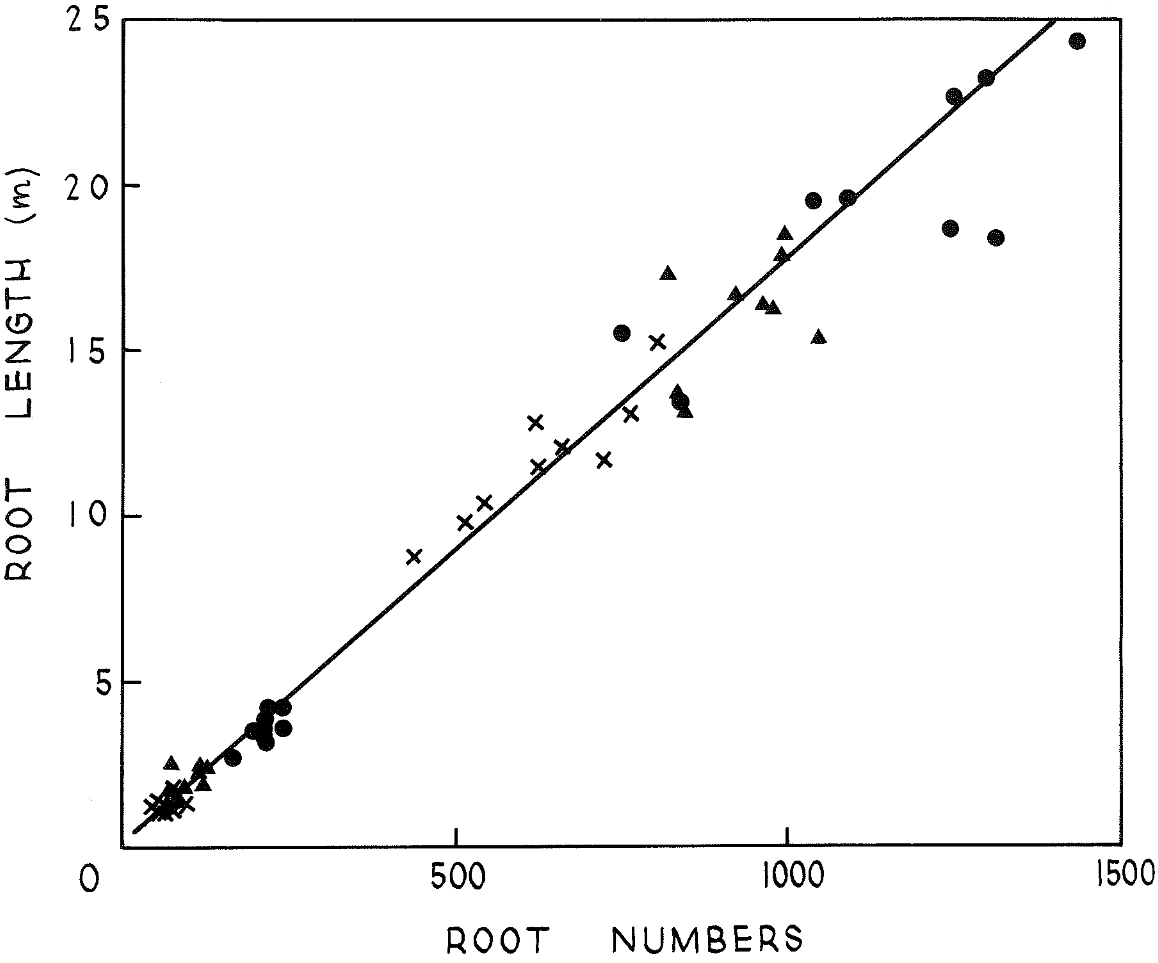
The narrow range of water uptake rates, shown in Figure 27 reduces the effectiveness of the experiment in assessing the direct effects of water flux on ion flux through the soil and into the plant. The lines drawn in Figure 27 and other subsequent figures are therefore drawn where possible to indicate trends only.

Figure 28: Root Length as a Function of Root Number.

Relative humidity (%)

●	42.5
▲	67.5
×	92.5

$y = 1.70x + 33.4, \quad r = 0.985^{xxx}$


25
20
15
10
5
0
500
1000
1500
ROOT LENGTH (m)
ROOT NUMBERS

At all soil water content treatments, lower water flux implies lesser gradients in water potential about the roots and therefore lesser gradients in water content. Ion diffusivity is a function of water content and although lower water fluxes imply relatively less convection of ions to the roots, diffusion of ions should occur with greater facility.

Provided the ion concentration at the root surface differs from that at some distance from the root, both diffusion and convection of ions occur with transpiring plants. Increase in water flux therefore can result in contrary effects on each process, provided the ion concentration increases with distance from the root. Increased water flux will cause increased ion transfer by convection but the steeper water content gradient will be accompanied by reduction in the 'mean' ion diffusivity about the root and lessened transfer by diffusion although concentration boundary conditions could conceivably remain unchanged.

When the plant cannot accept chloride at the rate of transfer to the root surfaces by convection, then the chloride concentration gradient will be in the reverse direction, that is, the root surface concentration will become greater than that of the bulk solution. In this situation, increase in water flux, again associated with steeper water content gradients about the roots, is coupled with a reduction in 'mean' diffusivity of ions about the roots but lessened facility for transfer of ions by diffusion <u>away</u> from the roots.

At any particular soil solution concentration, absence of an effect of water flux on ion flux into the roots could be interpreted as due to equal and opposing effects of water flux on the convective and diffusive components of transfer. A positive effect, that is an increase in ion flux, might imply a dominance of convective over diffusive transfer with or without ion accumulation at the outer surface of the root. A negative effect would therefore imply a dominance of diffusive transfer over convective transfer.

The general trends shown in Figure 27 could therefore be interpreted as indicating that under the water potential gradients existing around the roots the ion transfer to the roots is predominantly by mass flow.

The process of ion uptake however is neither a simple passive process alone, nor is it solely the result of complex, metabolic, active processes. Over a range of concentrations of the external solution there is dependence of ion uptake (flux) on external concentration whether the uptake mechanism is active or passive. This root surface-soil concentration boundary condition is determined by both plant and soil characters and is the resultant of complex interacting transfer processes.

It is shown in Figure 27 that, at the same water uptake rates per URLD, the total uptake of chloride varies with the time of harvest as well as with the external environment. As discussed earlier the effects of increasing humidity upon the plant included a reduction in the nett assimilation rate and unit transpiration rate as well as root growth. However the reduced total plant weight (sink size) is apparently offset by the relatively smaller decrease in root length and root-length duration, allowing greater ion flux/water flux ratios in the high humidity treatment. The greater uptake during days 0-9 as compared to days 9-18 could be associated with the well-documented phenomenon of greater uptake in plants of low chloride status. This same pattern of uptake was found in chloride transport to the tops and chloride accumulation in the roots (see Figures 29 and 30 respectively). The similar pattern of total uptake and transport to the tops with total water uptake and water uptake to the tops(water transpired plus water taken up and stored in the tops) results from the dominant effect of chloride transport to the tops on the total chloride uptake (see Table 9). The only major difference in Figures 27, 29 and

Figure 29: Chloride Ion Transport to the Tops as a Function of Water Uptake

(Both variables normalized to unit root-length duration)

Relative humidity (%)	Period of growth (days)	
	0 - 9	9 - 18
42.5	◉	●
67.5	◬	▲
92.5	⊗	×

a. At a soil solution concentration of 5 ppm of chloride.

b. At a soil solution concentration of 100 ppm of chloride.

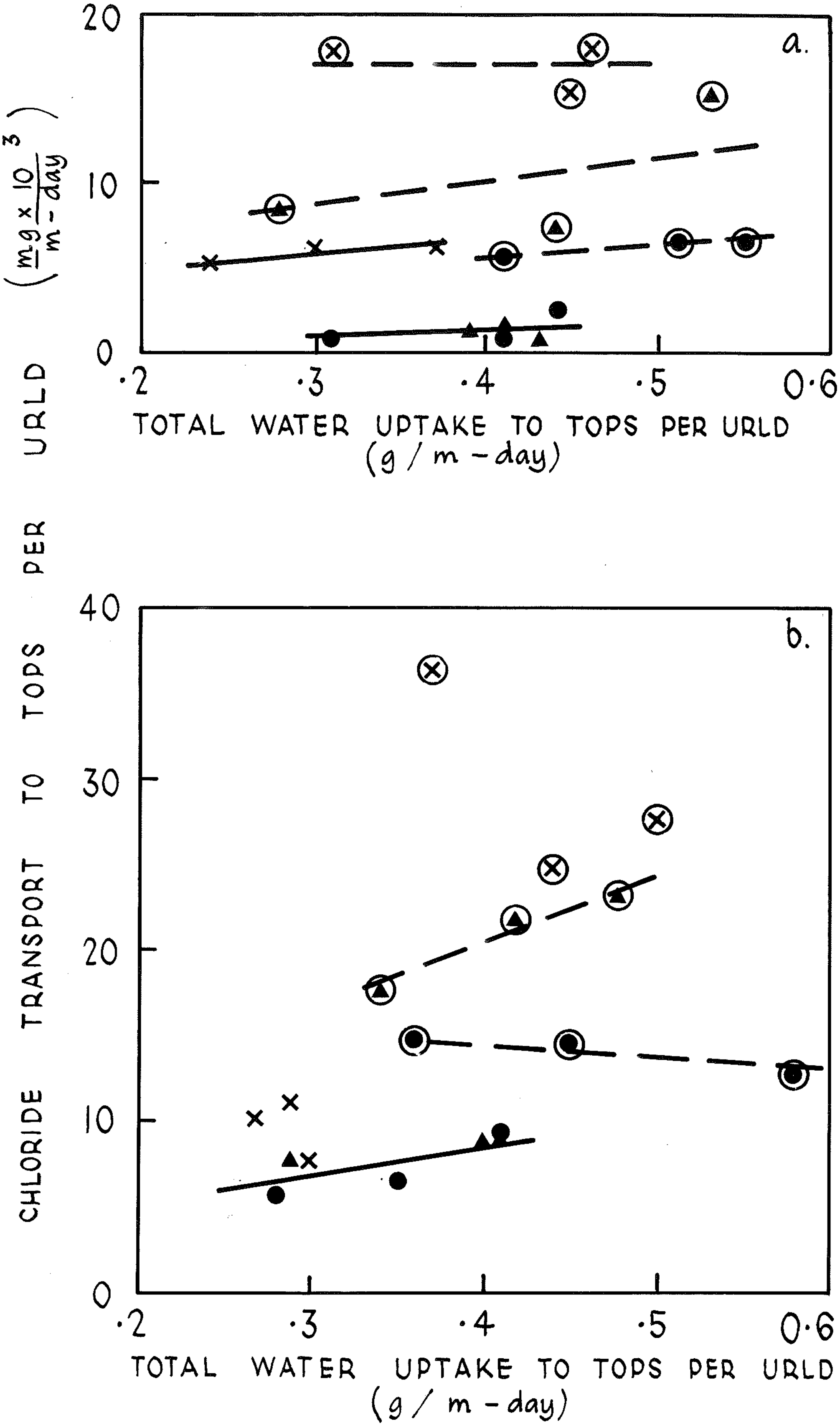

a.
b.
20
10
0
40
30
20
10
0
·2
·3
·4
·5
0·6
TOTAL WATER UPTAKE TO TOPS PER URLD
(g / m - day)
CHLORIDE TRANSPORT TO TOPS PER URLD
(mg x 10^3 / m - day)

Figure 29: Chloride Ion Transport to the Tops as a Function of Water Uptake

(Both variables normalized to unit root-length duration)

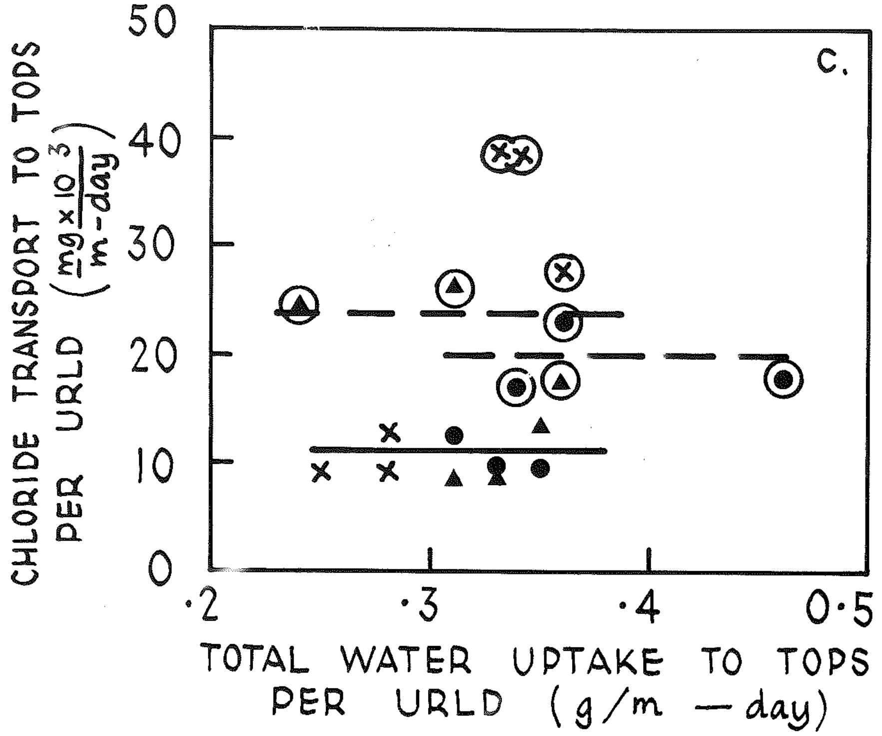
c. At a soil solution concentration of 1000 ppm of chloride.

Figure 30: Chloride Ion Accumulation in Roots as a Function of Water Uptake

(Both variables normalized to unit root-length duration)

Relative humidity (%)	Period of growth (days)	
	0 - 9	9 - 18
42.5	(●)	●
67.5	(▲)	▲
92.5	(×)	×

a. At a soil solution concentration of 5 ppm of chloride.


c.
CHLORIDE TRANSPORT TO TOPS PER URLD $\left(\frac{mg \times 10^{3}}{m-day}\right)$
0
10
20
30
40
50
·2
·3
·4
0·5
TOTAL WATER UPTAKE TO TOPS PER URLD (g/m — day)

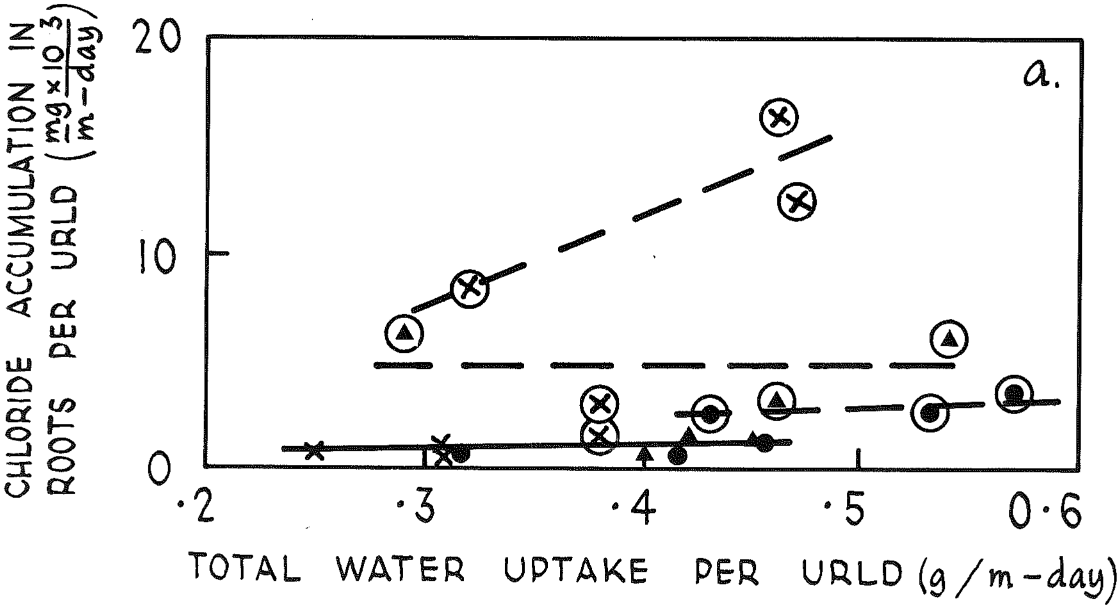
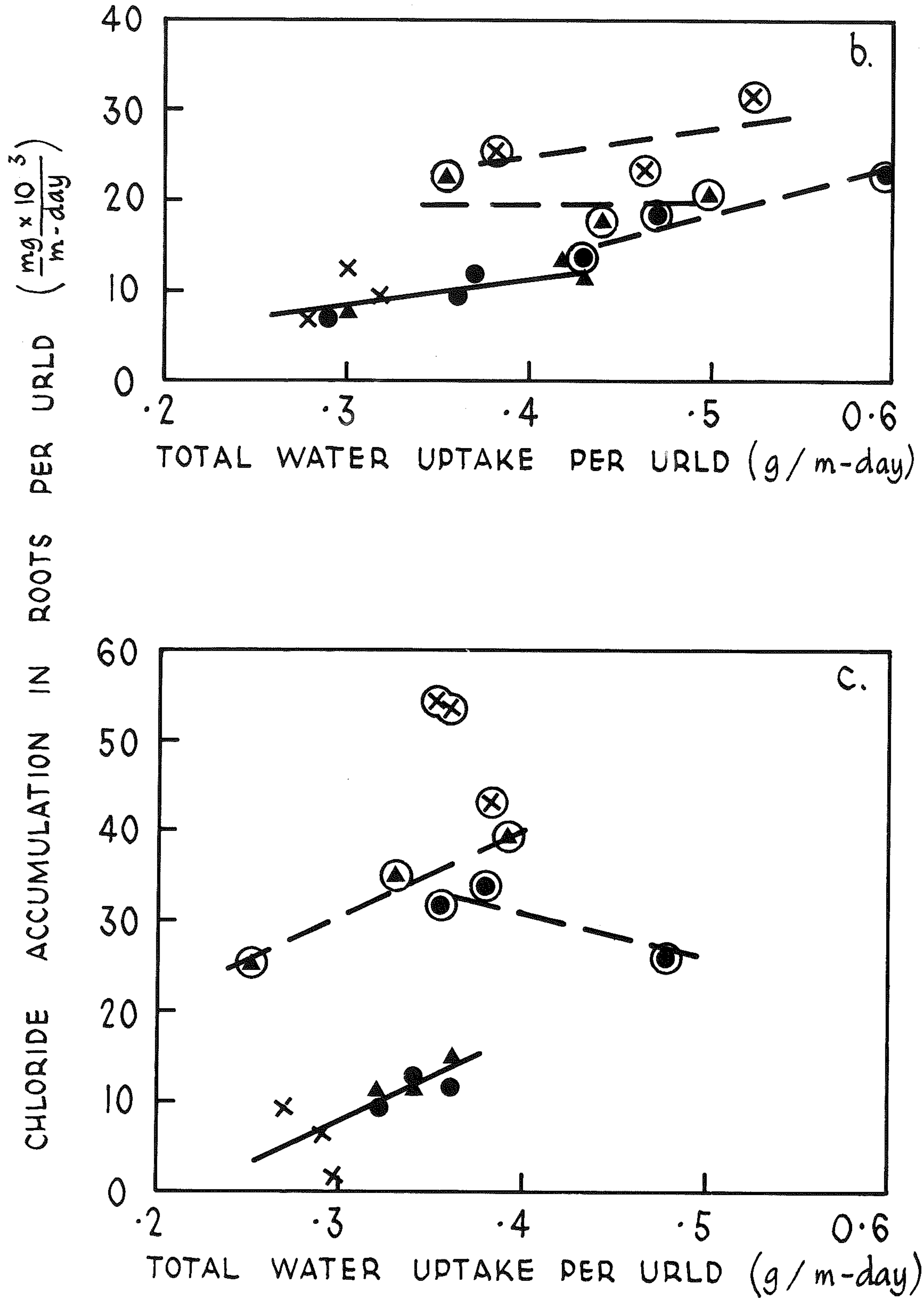

a.
CHLORIDE ACCUMULATION IN ROOTS PER URLD $\left(\frac{mg \times 10^{3}}{m-day}\right)$
0
10
20
·2
·3
·4
·5
0·6
TOTAL WATER UPTAKE PER URLD (g/m-day)

Figure 30: b. At a soil solution concentration of 100 ppm of chloride.

c. At a soil solution concentration of 1000 ppm of chloride.


b.
40
30
20
10
0
·2
·3
·4
·5
0·6
TOTAL WATER UPTAKE PER URLD (g/m-day)
CHLORIDE ACCUMULATION IN ROOTS PER URLD $\left(\frac{mg \times 10^{3}}{m\text{-}day}\right)$
c.
60
50
40
30
20
10
0
·2
·3
·4
·5
0·6
TOTAL WATER UPTAKE PER URLD (g/m-day)

30 is that the accumulation of chloride in the roots during days 9 - 18 is constant for all three humidity treatments.

Assuming that the water uptake per unit root-length duration is indicative of the water potential gradients around the roots, the higher ion flux/water flux ratios in Figures 27, 29 and 30 would indicate, with the present proposals on active ion uptake, that the respiration rate is highest in plants growing in a relative humidity of 92.5%, lowest for plants growing in a relative humidity of 42.5% and intermediate for plants growing in a relative humidity of 67.5%. The reasons for a decline in the NAR for the highest humidity treatment have already been discussed in the previous section, as has the possibility that this is due to a higher respiration rate due to higher leaf temperature. The lower moisture stress within the plant as compared to plants in the other humidity treatments may also contribute to a higher leaf temperature. This would mean that, at least for the plants in 67.5% and 42.5% relative humidity treatments, the photosynthetic rate must also have changed correspondingly to keep the NAR constant.

When the soil solution concentration is low, it is unlikely that the ion uptake processes of the plants would become saturated, consequently any increase in water flux should cause enhanced ion flux into the plant. At some higher concentration in the external solution, saturation of the uptake processes or storage available in the plant could limit entry into the plant. Saturation of accumulation mechanisms appears to have occurred (see Figure 30) at the three humidity and chloride treatments for days 9- 18 and consequently any further increase in chloride ion uptake with increased water uptake would have to result from some indirect effect within the plant. The saturation of the uptake process at an external chloride ion concentration of 5 ppm (Figure 30 a) is in agreement with the proposals of Torii and Laties (1966) who have shown that at solution concentrations approximating 5 ppm of chloride the relation between the quantity of chloride accumulated and the external concentration reaches a plateau stage. Thus small variations of concentration about this level cause no change in the quantity of ions accumulated by the plant. Comparison of the accumulation at 5 ppm for days 9- 18 with the product of water flux and initial concentration of the soil solution reveals that the concentration at the root surface is very close to 5 ppm. At concentrations above 10 ppm of chloride in the external solution the rate of accumulation again increases with external concentration and a second and different uptake mechanism probably accounts for this behaviour (Torii and Laties 1966). A comparison between accumulation rate in the roots at 5 ppm with that at 100 and 1000 ppm of chloride in solution shows a shift in the absolute rate of accumulation. However at the higher concentrations the concentration at the root surfaces is greater than that initially in the soil solution. It cannot be said how high these concentrations are but it is striking that the accumulation rate is the same per unit of water uptake.

Summary

Compensating responses of the plants to the imposed treatments resulted in a narrow range of variation in water flux per unit root-length duration. Nevertheless there was an apparent trend that the flux of ions into the plants increased with increase of the water uptake rate. However closer analysis has revealed that the process of ion transport to the tops and ion accumulation behaved in a similar manner and that for initially low salt status plants some change in the plant, possibly leaf temperature, caused differences in the uptake of ions with different relative humidity treatments. This variation in leaf temperature has been ascribed to variation in the water loss from the leaf resulting from the different relative humidities (water demand). In addition, the leaf temperature may have depended upon the apparent resistance offered by the plants to water movement through the vascular system, supply of water to mesophyll tissues of the leaves and consequent development of leaf water stress. This indirect effect of water stress on ion uptake could likewise apply to the effects of increased water flow on ion uptake i.e. by decreasing leaf temperatures. Consequently any future studies on the effects of water flux on ion flux must be able to distinguish between direct and indirect effects.

Uptake of sodium ions

The effects of treatments and treatment interactions on sodium uptake by the whole plant, roots and shoots are given in Appendix 5. The data for total sodium uptake is given in Figure 31. All treatments affected sodium uptake which increased with soil solution concentration, decreased with increase in relative humidity and increased with soil water content. However some of the interactions were significant.

The relation between total sodium uptake and total water uptake is shown in Figure 32. As with chloride, at the lowest external ion concentration, the

Figure 31: Total Sodium Uptake under Various External Environmental Conditions

——— after 18 days

— — after 9 days

Numbers in histogram refer to relative humidity (%)

4 ≡ 42.5

6 ≡ 67.5

9 ≡ 92.5

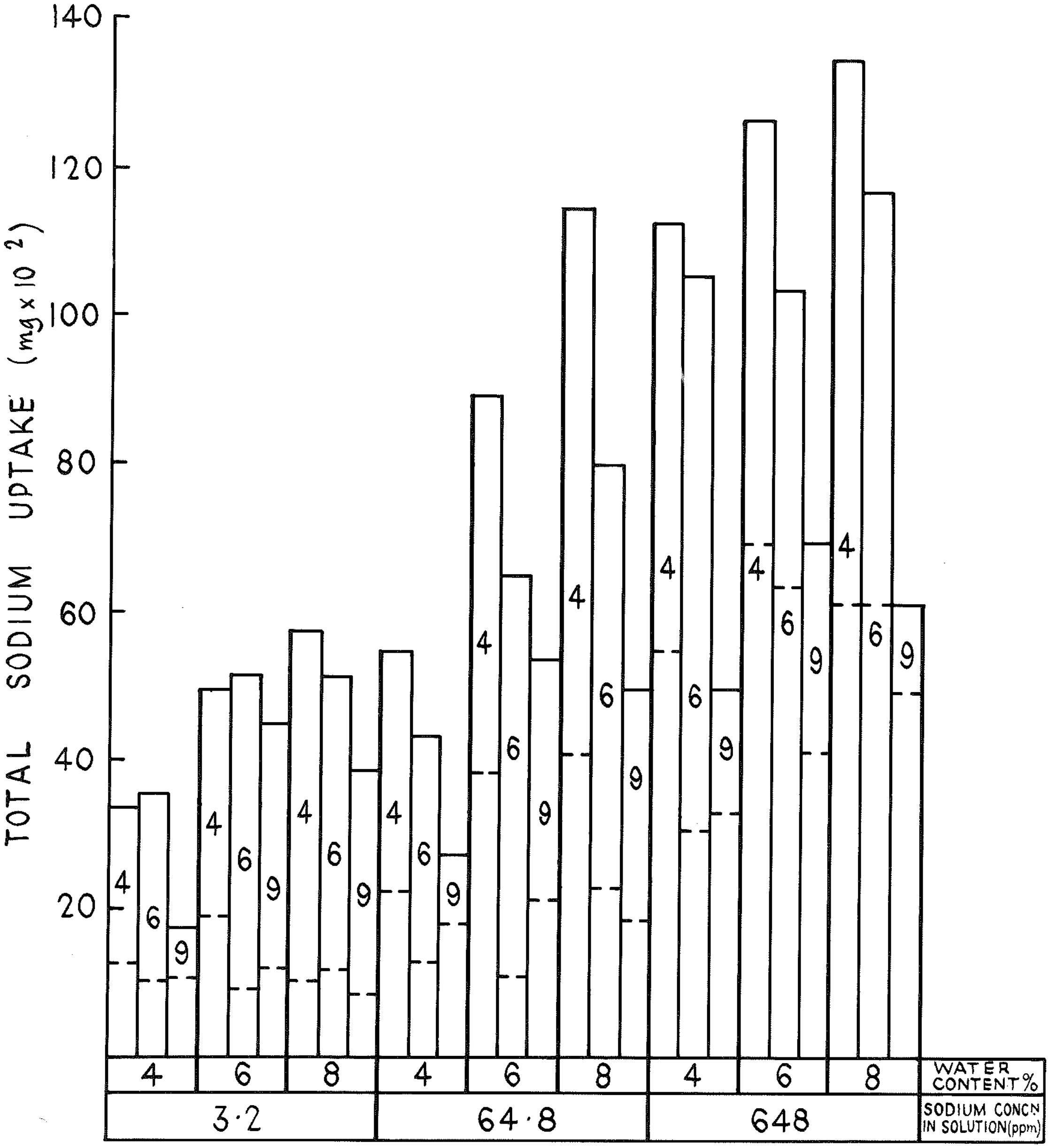

TOTAL SODIUM UPTAKE (mg x 10 2)
140
120
100
80
60
40
20
4
6
9
WATER CONTENT %
4
6
8
4
6
8
4
6
8
SODIUM CONCN IN SOLUTION (ppm)
3·2
64·8
648

Figure 32: Total Sodium Uptake as a Function of the Total Water Uptake

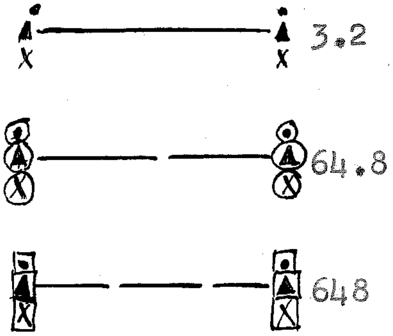
Relative humidities (%)

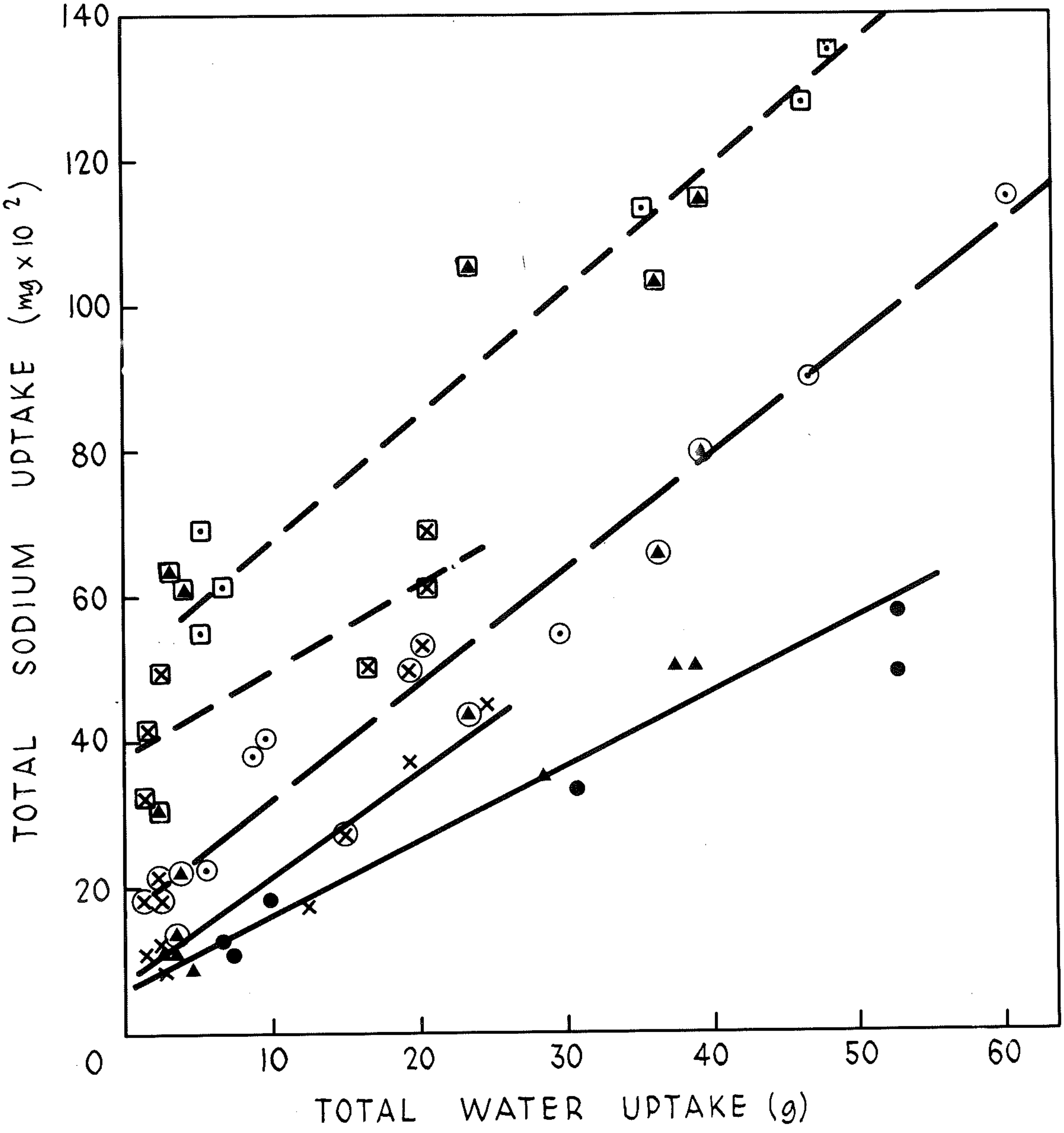
● 42.5

▲ 67.5

X 92.5

Sodium concentration of soil solution (ppm)




TOTAL SODIUM UPTAKE (mg x 10 2)
0
20
40
60
80
100
120
140
10
20
30
40
50
60
TOTAL WATER UPTAKE (g)

total uptake was higher at 92.5% relative humidity. However unlike chloride uptake, the uptake at the highest external sodium concentration was lower at 92.5% relative humidity than that for relative humidities of 42.5% and 67.5%. Also at the intermediate sodium concentration of 64.8 ppm the sodium uptake was the same at all humidity treatments.

In Figures 33 a, b and c, the relations between total sodium uptake per URLD and total water uptake per URLD are given. In Figures 34 and 35 the component transport to the tops and accumulation are shown in relation to the uptake of water to the tops per URLD and total water uptake per URLD, respectively. ~~are given~~. These figures reveal the importance of normalizing the results on a root-length duration basis, for although the results portrayed in Figure 32 appear to give an entirely different picture of sodium uptake as compared to chloride uptake, Figure 33 shows that the total sodium uptake per URLD behaves in a similar manner to total chloride per URLD uptake. One major difference between the figures for total chloride uptake and total sodium uptake lies in the close association of total sodium uptake to that of sodium accumulation in the roots, (Table 8 reveals that the dominating component in sodium uptake is the accumulation in the roots) while the total chloride uptake is

Figure 33: Total Sodium Uptake as a Function of Water Uptake

(Both variables normalized to unit root-length duration)

Relative humidity (%)	Uptake period (days)	
	0-9	9-18
42.5	◉	●
67.5	◬	▲
92.5	⊗	×

a. At a soil solution concentration of 3.24 ppm of sodium.

b. At a soil solution concentration of 64.8 ppm of sodium.

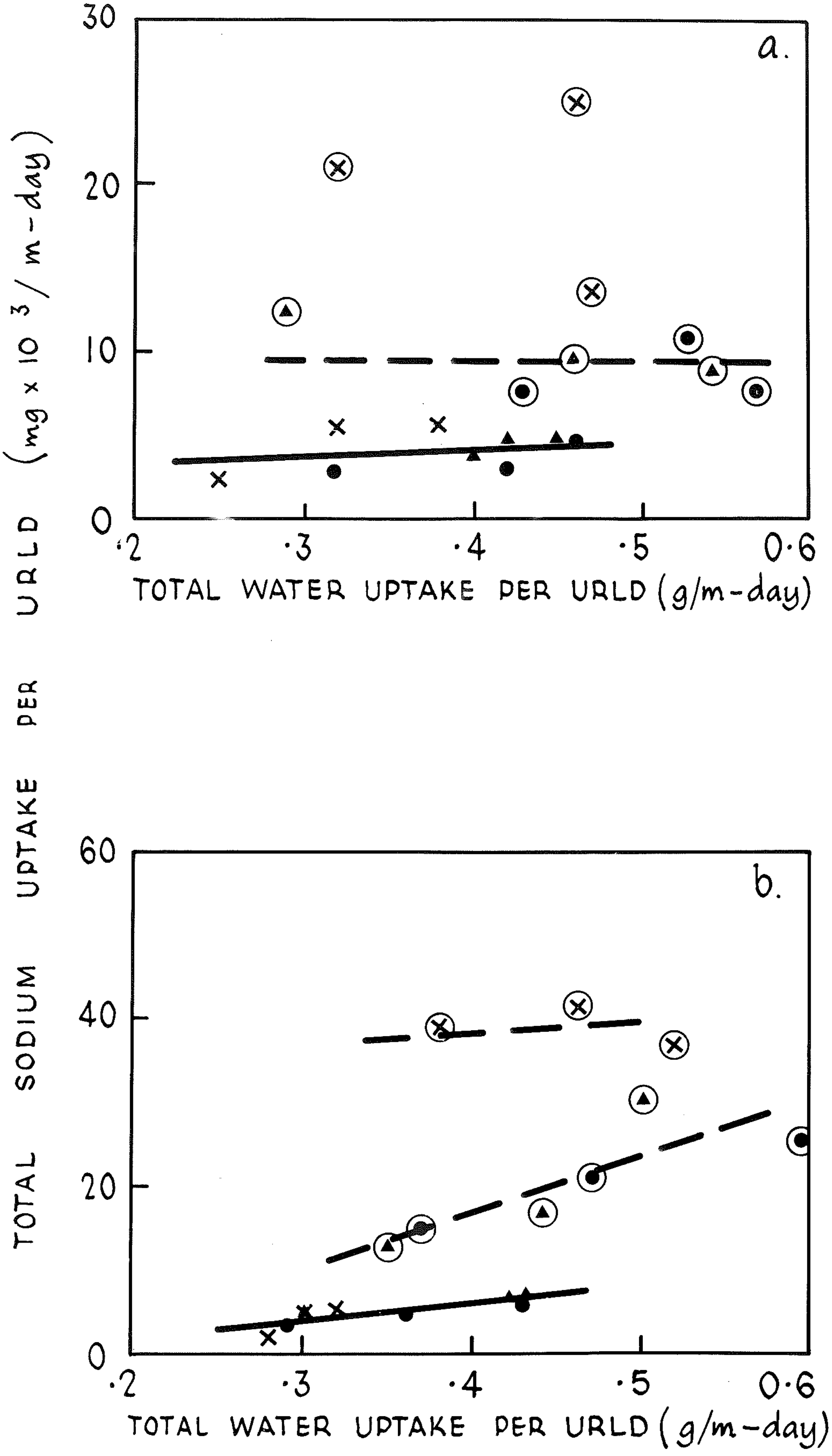

TOTAL SODIUM UPTAKE PER URLD (mg x 10 3 / m-day)
a.
30
20
10
0
·2
·3
·4
·5
0·6
TOTAL WATER UPTAKE PER URLD (g/m-day)
b.
60
40
20
0
·2
·3
·4
·5
0·6
TOTAL WATER UPTAKE PER URLD (g/m-day)

Figure 33: c. At a soil solution concentration of 648 ppm of sodium.

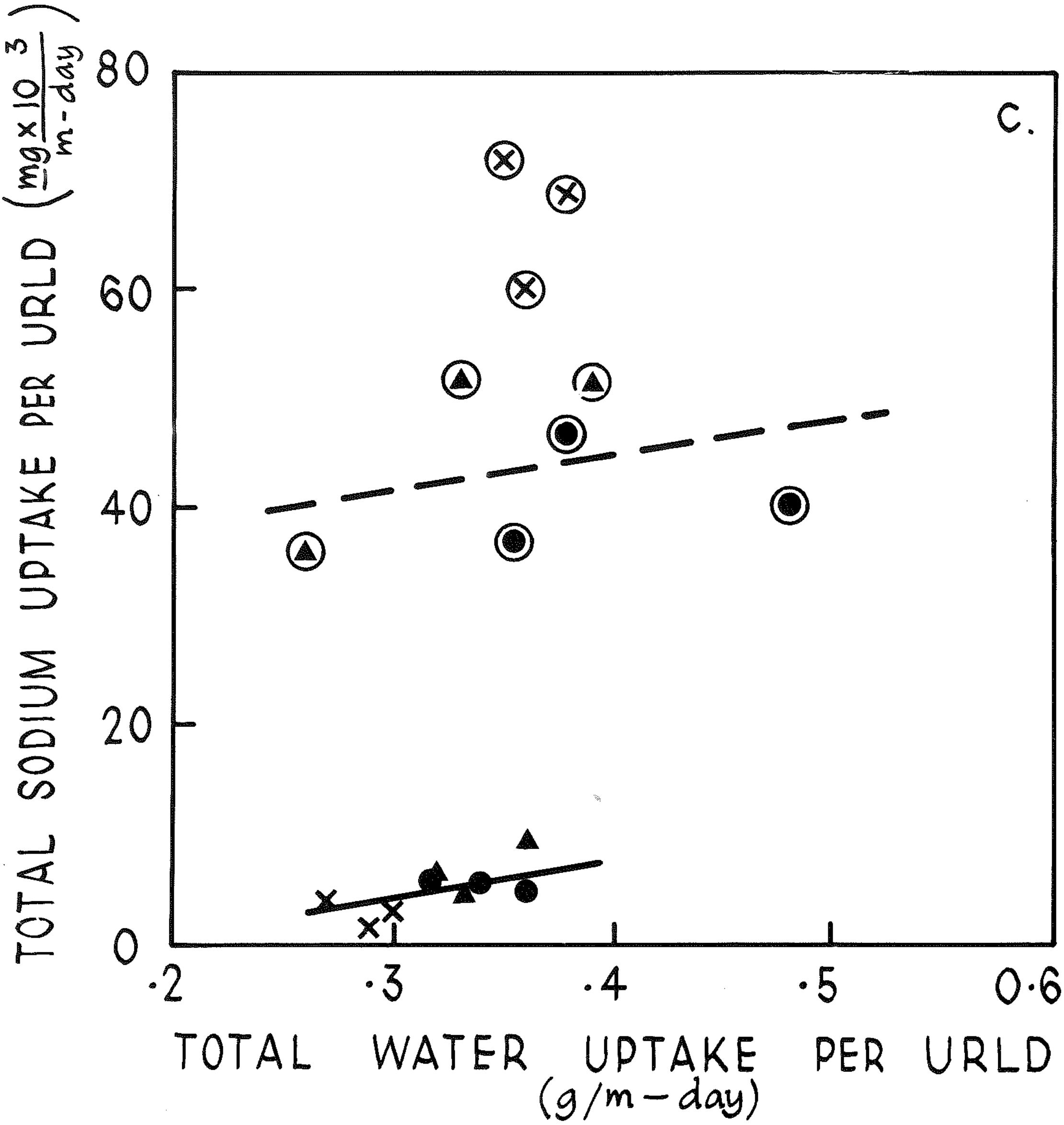

c.
TOTAL SODIUM UPTAKE PER URLD $\left(\frac{mg \times 10^{3}}{m\text{-}day}\right)$
0
20
40
60
80
·2
·3
·4
·5
0·6
TOTAL WATER UPTAKE PER URLD
(g/m – day)

Figure 34: Sodium Accumulation in Roots as a Function of Water Uptake

(Both variables normalized to unit root-length duration)

Relative humidity (%)	Uptake period (days)	
	0 - 9	9 - 18
42.5	⊙	●
67.5	▲⃝	▲
92.5	⊗	×

a. At an external sodium concentration of 3.24 ppm.

b. At an external sodium concentration of 64.8 ppm.

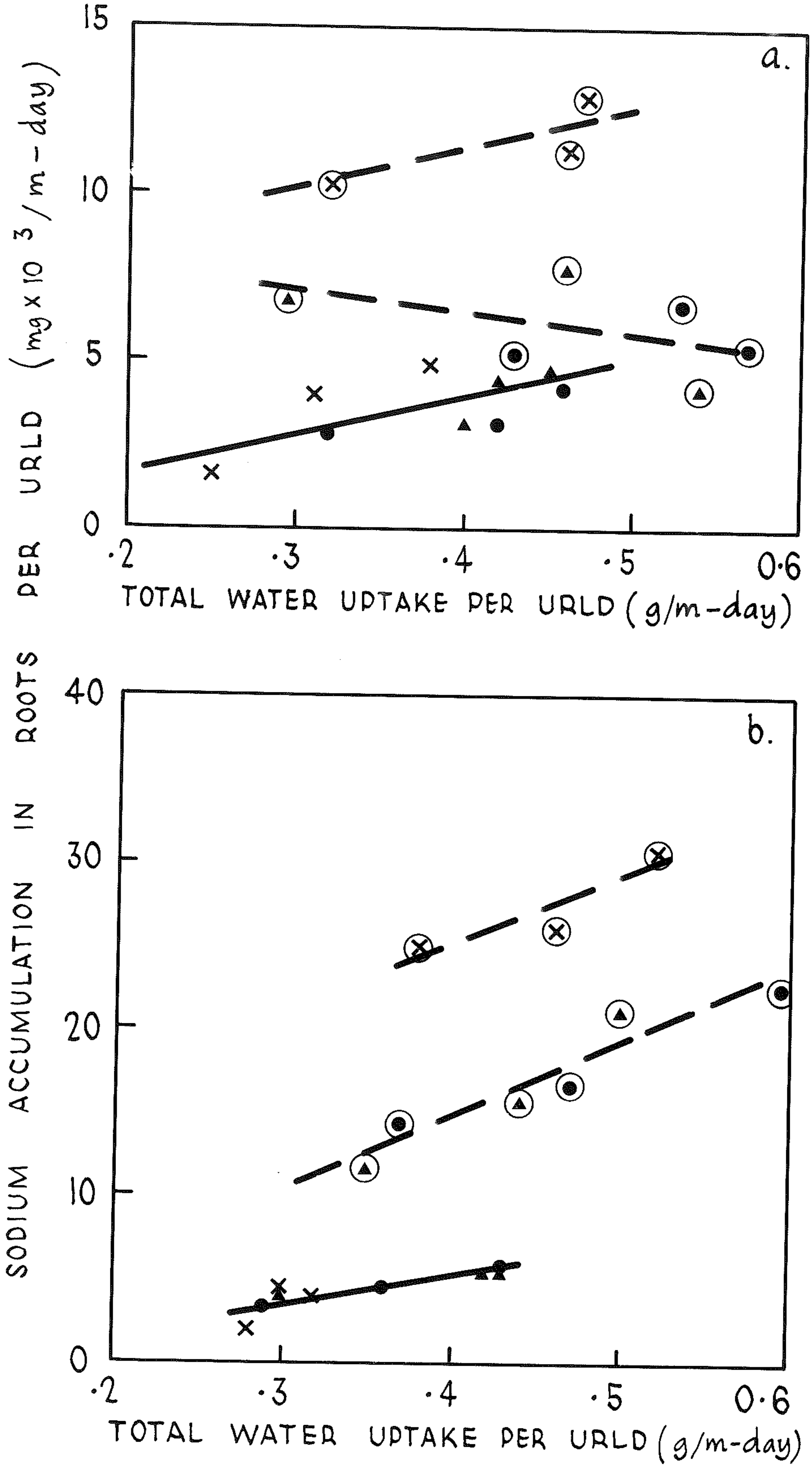

a.
b.
SODIUM ACCUMULATION IN ROOTS PER URLD (mg x 10 3 / m - day)
15
10
5
0
40
30
20
10
0
·2
·3
·4
·5
0·6
TOTAL WATER UPTAKE PER URLD (g/m-day)

Figure 34: c. At an external sodium concentration of 648 ppm.

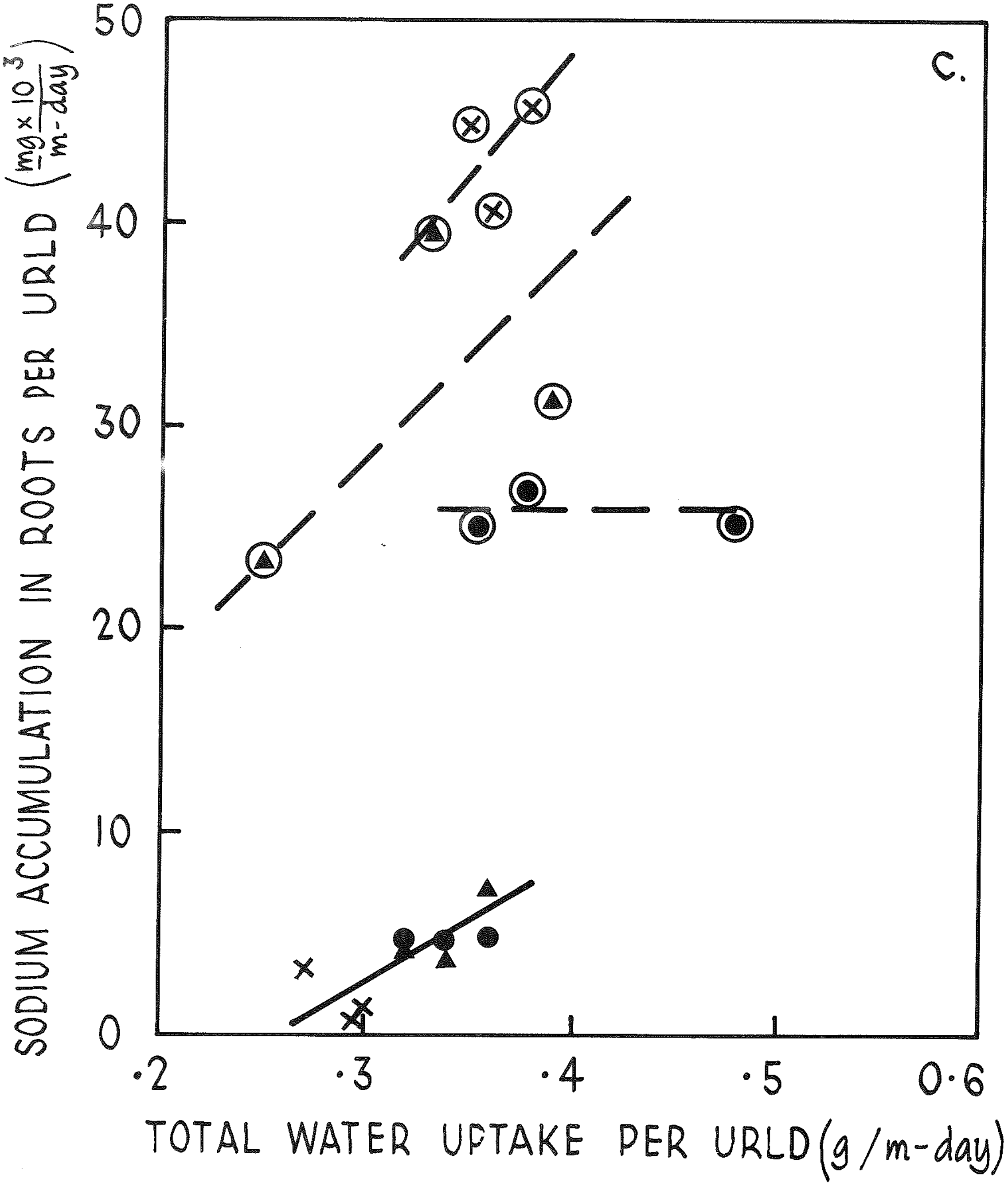

c.
SODIUM ACCUMULATION IN ROOTS PER URLD $\left(\frac{mg \times 10^3}{m\text{-}day}\right)$
0
10
20
30
40
50
·2
·3
·4
·5
0·6
TOTAL WATER UPTAKE PER URLD (g/m-day)

Figure 35: Sodium Ion Transfer to Tops as a Function of Water Uptake

(Both variables normalized to root-length duration)

Relative humidities (%)	Uptake period (days) 0- 9	9- 18
42.5	⊙	●
67.5	▲⃝	▲
92.5	⊗	×

a. At external solution concentration of 3.24 ppm of sodium.

b. At external sodium concentration of 64.8 ppm of sodium.

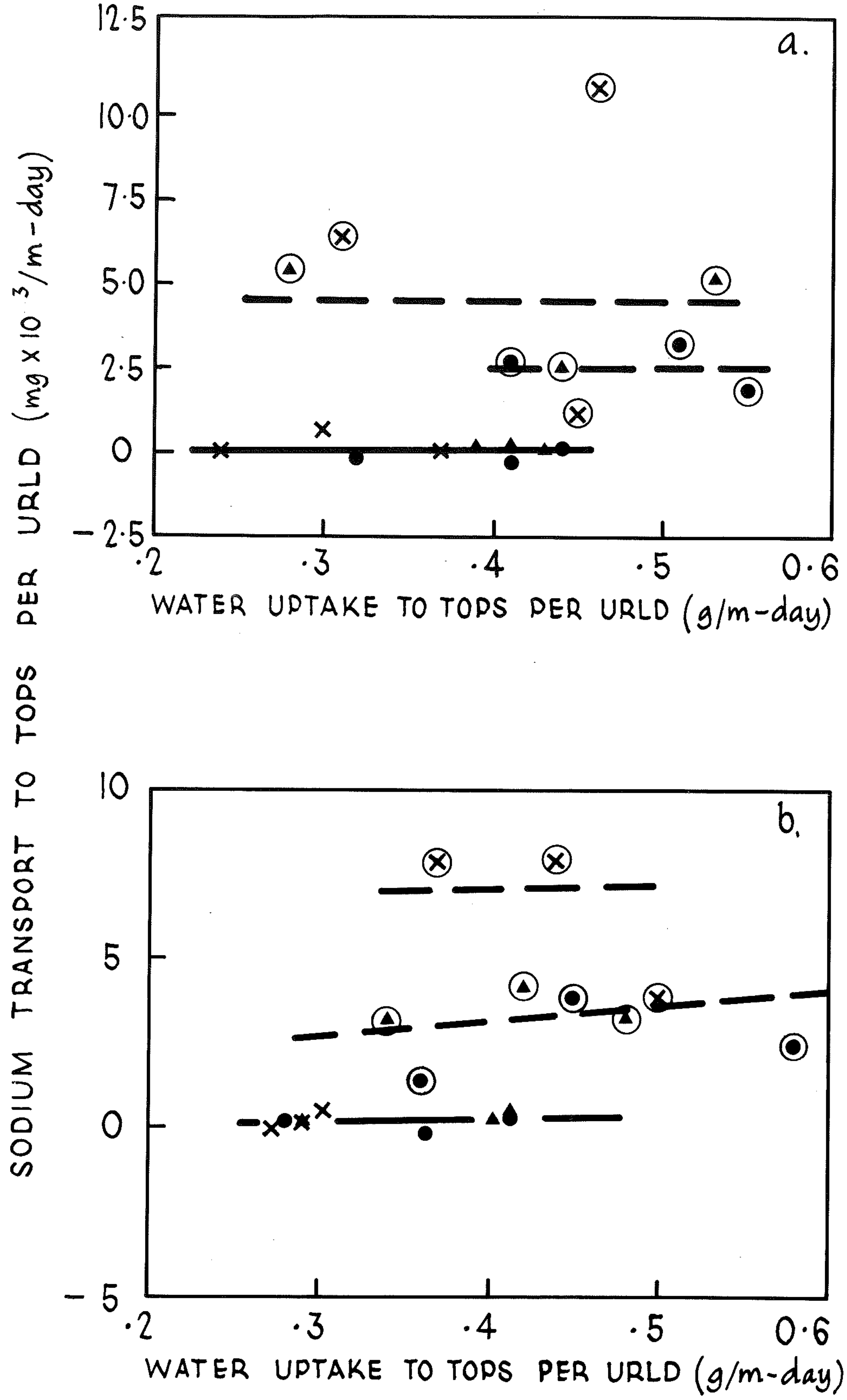
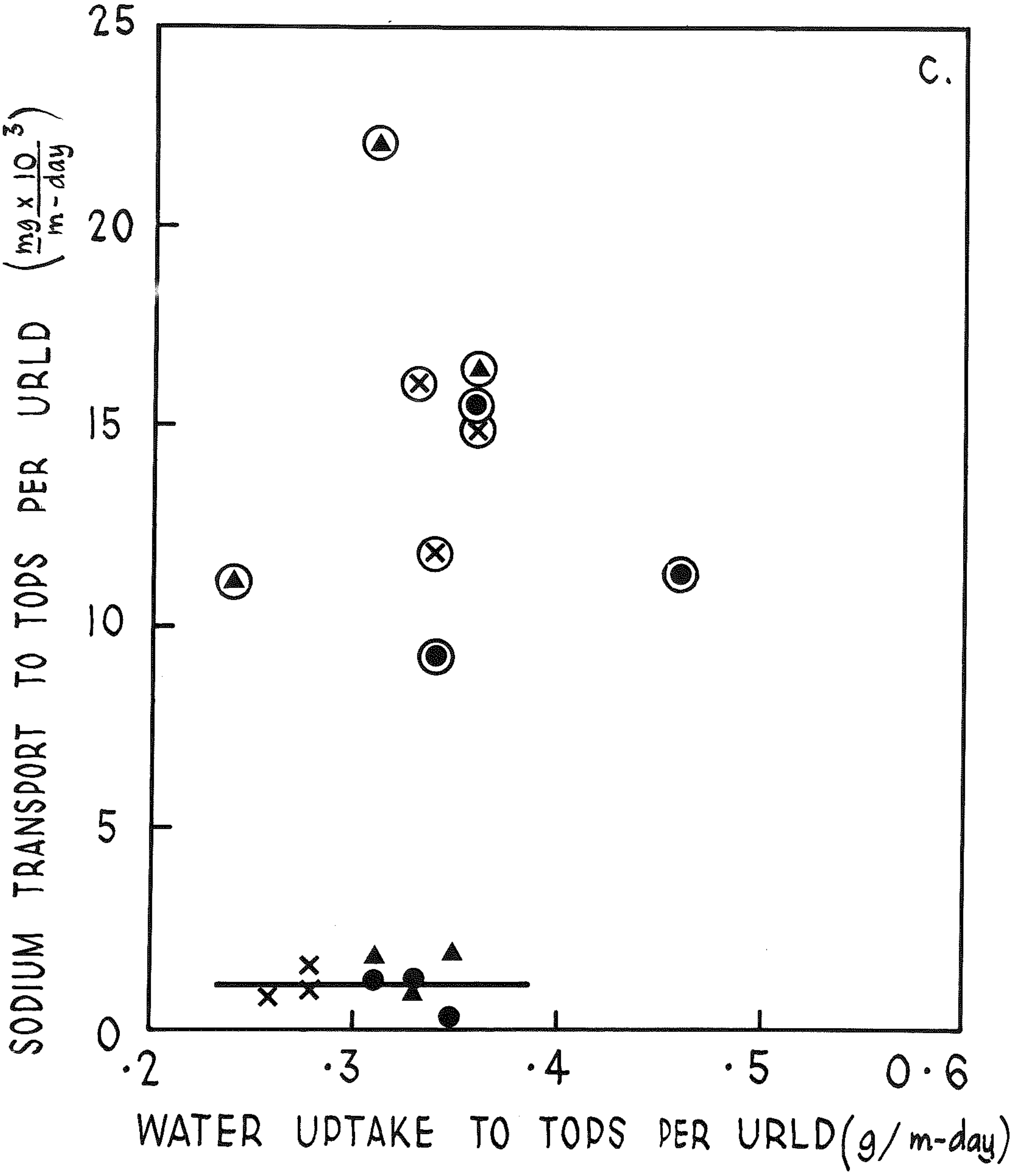

a.
b.
SODIUM TRANSPORT TO TOPS PER URLD (mg x 10 3/m-day)
12·5
10·0
7·5
5·0
2·5
0
−2·5
10
5
0
− 5
·2
·3
·4
·5
0·6
WATER UPTAKE TO TOPS PER URLD (g/m-day)

Figure 35: c. At an external sodium concentration of 648 ppm.


C.
25
20
15
10
5
0
SODIUM TRANSPORT TO TOPS PER URLD $\left(\frac{mg \times 10^3}{m\text{-}day}\right)$
·2
·3
·4
·5
0·6
WATER UPTAKE TO TOPS PER URLD (g/m-day)

influenced considerably by the uptake to the tops (see Table 9). The reduced transfer of sodium ions to the tops is a well known phenomenon and indicates that roots are able to act as restrainers to the movement of sodium ions.

It would appear that at least for the first nine days the relationship between sodium transfer to the tops and water uptake is not as well defined as that for chloride although some similarities do occur, e.g. at external concentration of 100 ppm. The almost complete lack of transfer from days9 - 18 suggests that once the tops and associated transfer systems are saturated little extra sodium is transferred to the tops. This saturation appears to occur very readily, for transfer to the tops is identical at 3.2 ppm and 64.8 ppm of sodium (Figures 35aand b) for days 9 - 18. The complete lack of effect of water uptake on the transfer of sodium to the tops is also apparent. However at the highest soil solution concentration (Figure 35 c, c.f. Figures 35 a and b) uptake increases again indicating that a second transport mechanism is operating which again shows little or no response to water uptake.

Sodium accumulation in the roots (Figure 34) behaves in a similar manner to chloride accumulation in roots and therefore will not be reiterated.

Summary:

Comparison of the relations between total sodium uptake per URLD and total water uptake per URLD, and total sodium uptake and water uptake and likewise with total chloride uptake reveal the importance in any ion uptake experiments of including treatment effects upon the root length. This therefore throws some doubt on the interpretation of experiments where treatment effects could have caused some change in root length, but no account of this change is given.

The restraining power of the root to sodium transport to the tops is demonstrated and it is concluded that there are two different concentration dependent mechanisms. The first mechanism which operates at low concentrations is readily saturated at very low levels and it is not until the exterior soil solution concentration is raised considerably that further transfer of sodium ions occurs. The transfer mechanisms would appear to be independent of water flux but this may be due to the saturation of the transfer mechanisms such that any further transport to the transfer site has no effect on the quantity of ions moving to the tops.

The accumulation mechanism behaves in the same way as the chloride accumulation mechanism and it appears that

both are affected by the demand for water by the atmosphere and the ability of the plant to supply water to meet this demand. Thus water stress within the plant could have a pronounced effect upon ion accumulation in the roots.

3.3 Effect of Water Flow on Ion Transport to a Cylindrical Sink

There is no data available on the effect of radial flow of water upon the transport of ions to a central sink. This is approximately the geometry of convective transport of ions to plant roots and for these reasons work was initiated on the problem. One feature of convective transport in porous solids which has not been resolved, even in the linear case, is the nature of the relation between water flux density (or mean solution velocities) and the diffusion coefficient for the particular ions.

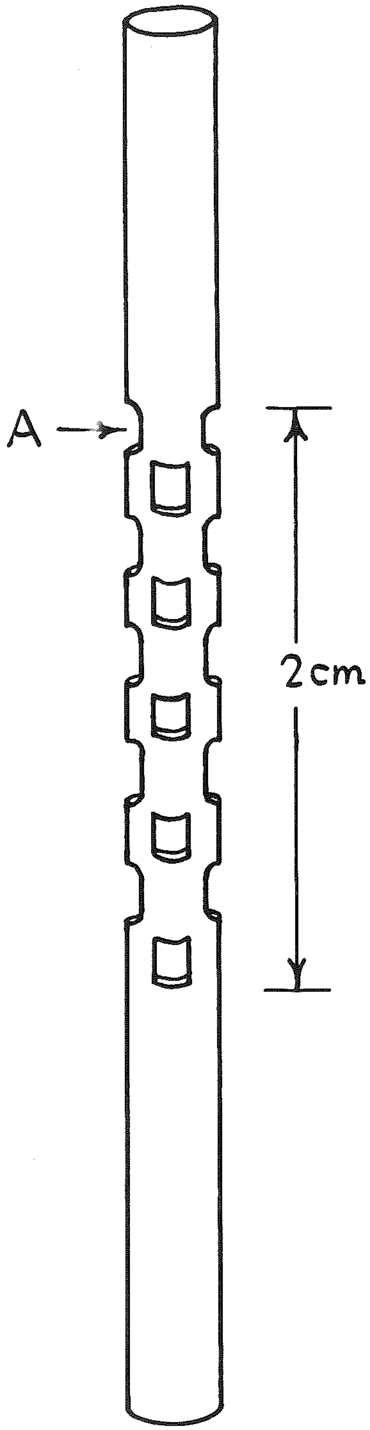
3.3.1 Experimental materials

There are many problems inherent in the development of apparatus to measure simultaneous radial water and ion movement through soils. Firstly some means must be obtained to measure the flux of water and ions out of the axial sink. Next, the physical characteristics of the sink and the outer boundary membrane enclosing the soil can greatly modify the flows if they have significant resistances to water or ion flow. The calculation of the diffusion coefficient of the ion in the soil solution becomes difficult when inner and outer boundaries offer appreciable resistances. In this work both the membranes were highly permeable to water and ions. The outer membrane was of Porvic grade S and was readily obtained. However the inner cylindrical sink had a further requirement which limited the availability of suitable materials. It was desirable that the sink be of a small diameter, comparable with that of roots themselves. The only material found which satisfied all requirements was a cylindrical "Millipore" filter approximately 4 cm long with an external diameter of 0.29 cm and an internal diameter of 0.21 cm. This material lacked rigidity, was very fragile and required extreme care in handling. It was supported in position on a 15 gauge hypodermic needle modified as in Figure 36, which was slipped inside the filter. The millipore filter was cemented to the hypodermic needle with special cement ("Millipore" Cement Formulation 1) and the remainder of the filter either side of the perforated section of the supporting needle was sealed with the same cement.

Minute particles of clay or organic matter moving

Figure 36: Supporting Tube for Millipore Filter

A. - Holes cut in hypodermic needle

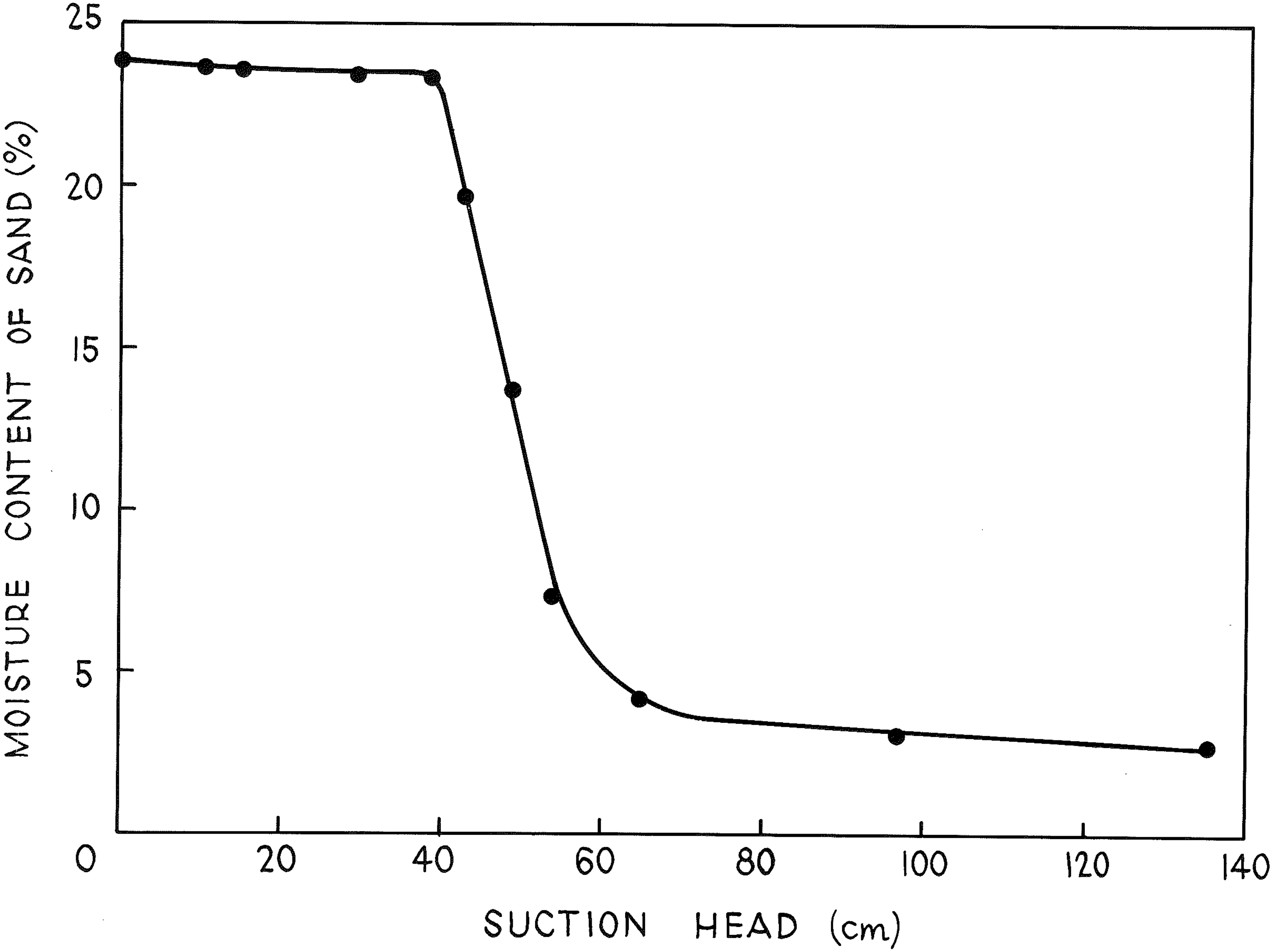

A
2cm

with the water could block the filter so altering its permeability. To reduce this hazard the prepared soil used in the plant experiment was taken and treated to remove small size fractions. The soil was shaken in 1% sodium hexametaphosphate solution for 8 hours. The sodium hexametaphosphate and suspended clay was decanted. The sand was then transferred to large containers filled with water. These were thoroughly shaken end-over-end, the sand allowed to settle for 4 minutes and the water and suspended material poured off. After a further shaking in 1.0% sodium hexametaphosphate, settling for 4 minutes was allowed and the supernatant was again poured off. These procedures were repeated until the supernatant was free of clay. As many as three or four full treatments as above were required. The sand was then leached with distilled water until no sodium or chloride could be detected in the filtrate. The sand was transferred from the leaching apparatus to a muffle furnace and heated to 550°C for four hours to oxidize all the organic matter. The samples were cooled and stored in a closed vessel. The moisture characteristic of the sand is given in Figure 37.

The cell for measuring the radial movement of the chloride ion was prepared in sections (see Figure 38).

Figure 37: Moisture Characteristic of Prepared Sand

(Desorption curve)



MOISTURE CONTENT OF SAND (%)
25
20
15
10
5
0
20
40
60
80
100
120
140
SUCTION HEAD (cm)

Figure 38: Sections of Cells before Assembly

A - Upper lucite plate

B - Porvic outer membrane

C - Lucite cylinder

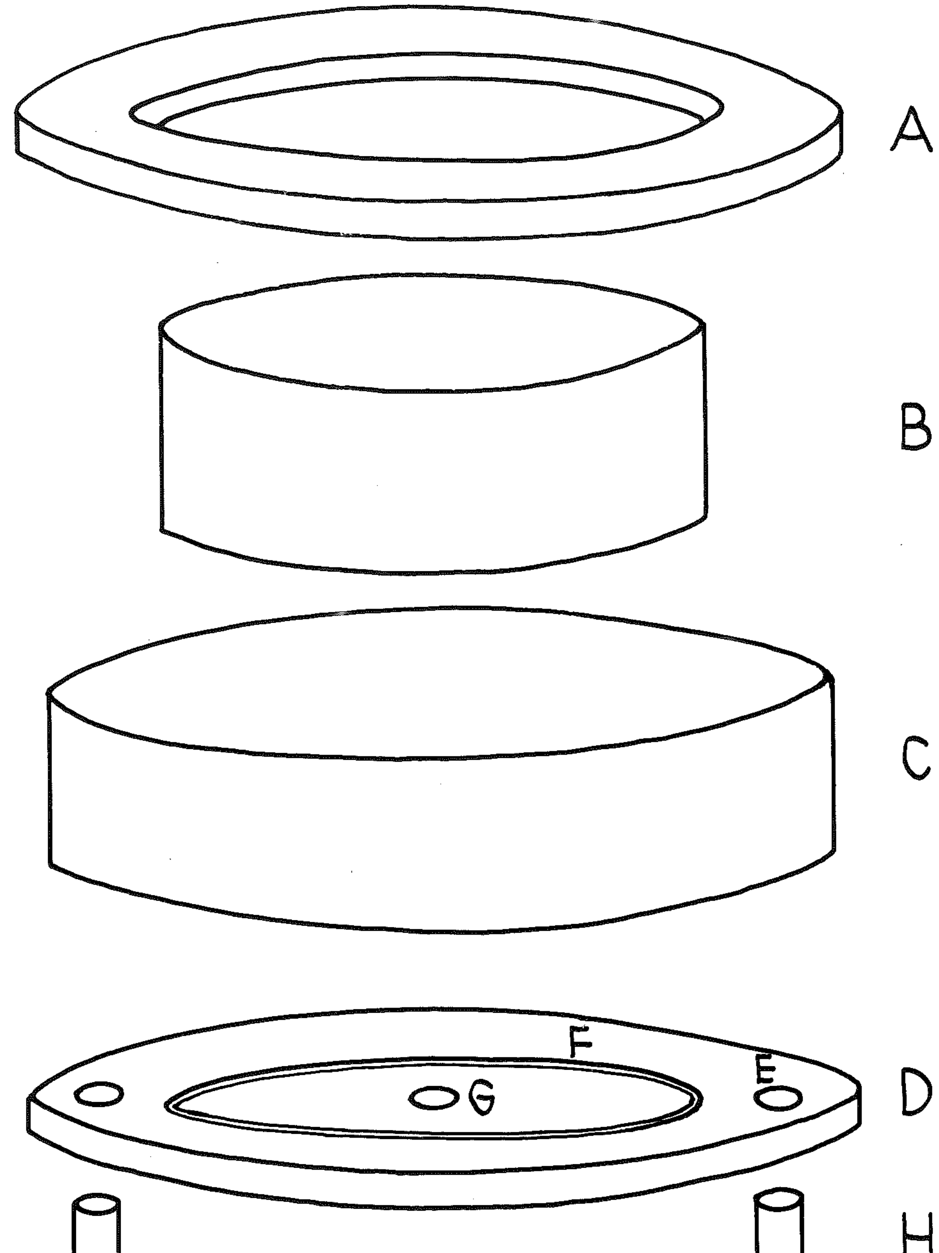
D - Lucite base plate

E - Holes for outlet tubes

F - Groove cut in base plate for porvic cylinder

G - Hole to take rubber bung containing Millipore sink

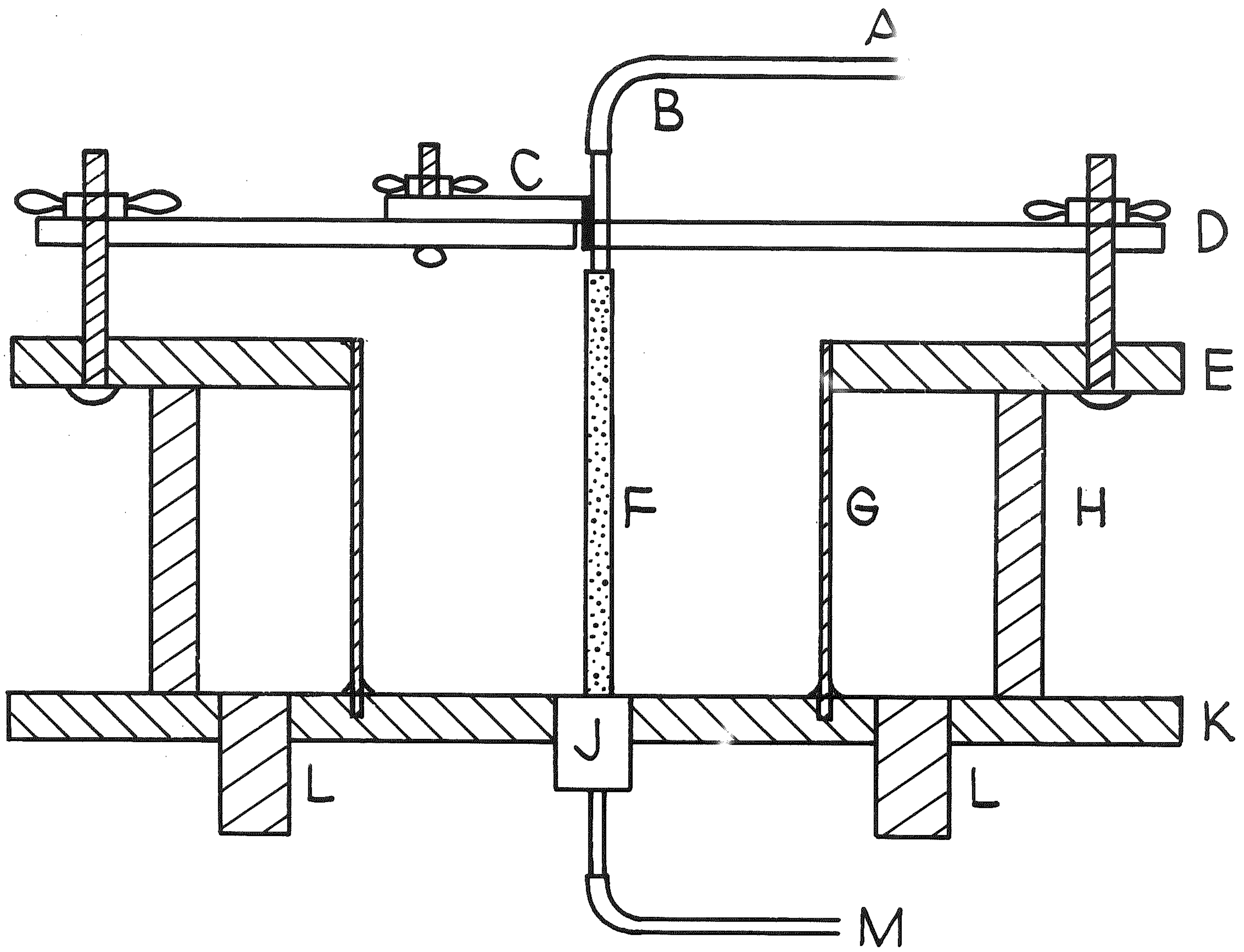
H - Lucite outlet tubes.


A
B
C
F
E
G
D
H

The sections were annealed by heating in an oven at 86°C for 24 hours to stop crazing. The lucite cylinder, C, was cemented onto the lucite base plate, D, with "Tensol" cement No. 7, the whole inverted and a heavy weight placed upon the base until set. Next the porvic outer membrane, B, was cemented, with the same cement as above, into the groove, F, in the base and finally the upper lucite plate, A, with the inside of the hole smeared with cement, lowered into position and cemented to the lucite cylinder, C. Clamps were applied until the whole was dry and then all seals checked to ensure they were water tight. Generally a further cementing of the porvic membrane to the upper plate was found to be necessary. Finally, the lucite outlet tubes, H, were cemented into the holes, E, in the base plate. The above procedure was important to ensure the whole was sealed and that at the same time the porvic membrane was not damaged. The following procedure for the assembly of the sink or "root" was likewise most important and for the same reasons. A rubber plug, J, in Figure 39, was made and a small hole drilled through the centre of it with a 16 gauge hypodermic needle. A larger hole, 0.5 cm in diameter and 0.3 cm deep was then cut into the upper surface of the bung. A 15 gauge needle with perforated walls and with two marks, one

Figure 39: Assembled Cell

A - Connection tube
B - Fine plastic tube from sink needle
C - Clamp slide to hold sink in position
D - Clamp supporting plank
E - Upper lucite plate
F - Millipore filter
G - Porvic outer membrane
H - Lucite cylinder
J - Rubber bung supporting sink
K - Lucite base plate
L - Lucite outlet tubes
M - Tube to collecting vessel.

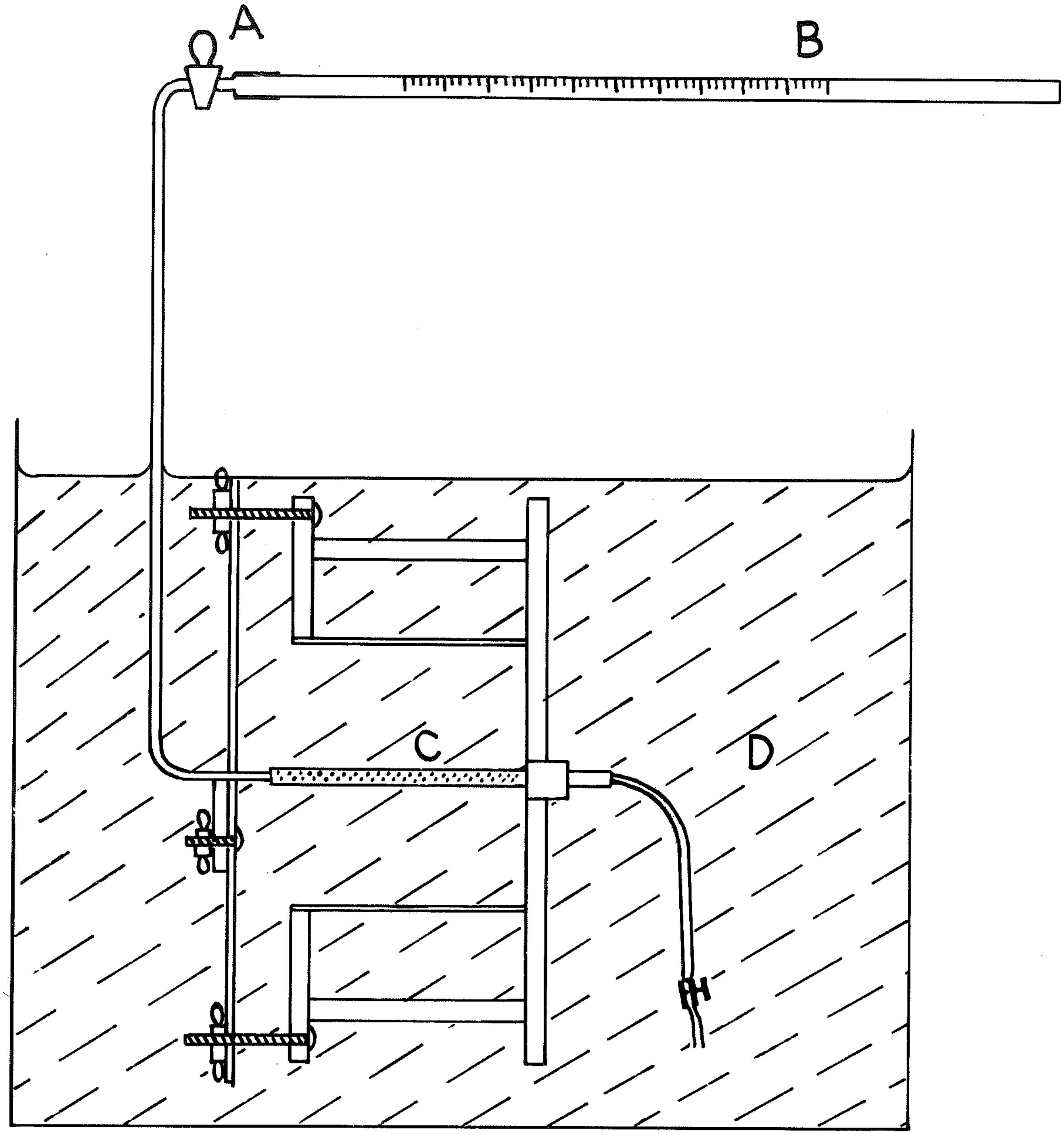

A
B
C
D
E
F
G
H
K
J
L
L
M

0.3 cm below the bottom of the holed area and another the measured length of the filter above the other mark was gently pushed into place in the hole in the bung. The bung was then placed into position in the base of the cell with the needle vertical. The bung was always inserted so that its top was level with the top surface of the base plate of the cell. The filter was lowered over the needle until its top was 1 cm below the upper mark on the hypodermic needle. Small-bore plastic tubing was connected to the ends of the needle at this time. The 1 cm of needle between the filter and the top mark was smeared with the millipore cement and the filter raised over this until the bottom of the filter was level with the bottom of the perforated section of the needle. The annular space in the bung was almost filled with cement and the portion of the needle below the filter was smeared with cement. The filter was pulled down so that the top was level with the upper mark on the needle. Finally the needle was lowered until the lower end of the filter rested on the bottom of the well in the bung. The upper portion of the filter was covered with cement almost down to the level of the first hole in the needle, and the top of the needle supported in a clamp (see C, Figure 39). It was found to be essential that the needle be made vertical and outlet tubes be connected at the stages described for if any movement of the filter occurred after the cement was dry, the filter crinkled and cracked. After the cement was dry the well in the bung was filled to the upper surface of the base plate with cement and the remaining portion of the filter above the perforated section of the needle sealed with cement. The final sealing was carried out after the cement was allowed to thicken to a very heavy paste.

The cell was suspended in a vacuum desiccator over boiled distilled water. After ensuring that one of the tubes from the filter was open to the air in the desiccator, so that no differential pressures would occur across the filter, the vessel was evacuated and the cell then lowered into the water. When all compartments were saturated, the cell was placed onto its side in a container of distilled water. The upper tube was connected to a calibrated capillary tube, B, Figure 40, and filled with boiled distilled water by applying a slight suction to the calibrated tube. When the system was filled with water, Tap A (Figure 40) and the tube connected to the bottom of the filter were sealed. The graduated tube was raised approximately 5 cm above the "root", at time zero the tap opened, and the water flow

Figure 40: Apparatus for Measuring Hydraulic Conductivity of Sink

A - Tap
B - Calibrated tube
C - Sink
D - Water filled vessel.


A
B
C
D

through the filter measured with the calibrated tube. From measurements of applied hydraulic head, the hydraulic conductivity for water in the filter under the described conditions was calculated.

The cell was disconnected from the above and connected to an air pressure line and the air entry value of the filter determined to check for air leaks and to see if filters could be used for unsaturated soils if necessary. In all cases it was found that suctions of at least 100 cm of water could be applied without exceeding their air entry value.

Problems associated with the collection of solution from the filter were such that only the steady-state condition of water and ion transfer were studied. Radial flow and axial inflow were measured by calibrated tubes, while axial outflow was measured by weighing collection vessels.

Because the velocity of the water changed with radial distance from the sink, it was necessary that soil samples be taken from the bed in a series of annuli and measurements of chloride concentration changes with distance be made on these annuli. The radial distance across each annulus should be as small as practical and a compromise was therefore necessary to ensure that the chloride contents of the zones could be measured. The most practical width of the annuli was found to be 0.5 cm. The sampler (see Figure 41) consisted of concentric brass rings or steel rings (used for the larger diameters, for which brass was not available) soldered onto a brass plate. The rings were 3.2 cm high with a wall thickness of about 0.5 mm, and were let into grooves in the brass plate before soldering. The heights of the rings were trimmed in the lathe and the whole assembly finally tested for leaks from one annulus to the next.

One point which became most important was the length of the calibrated tubes attached to the filter and the cell. During preliminary experiments it was found necessary to refill the "flushing" tube (the tube measuring the axial inflow of water) after some period of time. When this was done the axial water flow through the filter and the radial flow through the sand bed changed for a period, although both rates eventually returned to the original rates. Therefore it became essential that the length of this tube be long enough to completely flush the filter and outlet tube on it, i.e. from the filter to the collection vessel (which therefore had to be as small as possible) and to have adequate in reserve to permit sufficient steady state flow measurements to be

Figure 41: Photograph of Soil Sampler Showing Sampling Rings and Air Outlets

Note seal on one air outlet.

obtained. Uniform bore capillary tubing was used both for the inlet tube to the filter and the inlet tube to the outer boundary reservoir. Such uniform bore tubing was only selected after mercury calibration of numerous lengths of stock tube under constant temperature conditions. Using a sliding scale, lengths of mercury columns could be measured to 0.01 mm and weights were measured to 0.0001 g.

3.3.2 Experimental method

It was decided that investigations would be made into three aspects, namely the effect of water flow rates, the effect of concentration gradients, and the effects of positive and negative concentration gradients away from the sink. In all cases the direction of water flow was from the outer boundary towards the sink. Unfortunately duplicate runs were not possible, although they were highly desirable, because of the difficulties in controlling water flow rates.

The combinations used were:-

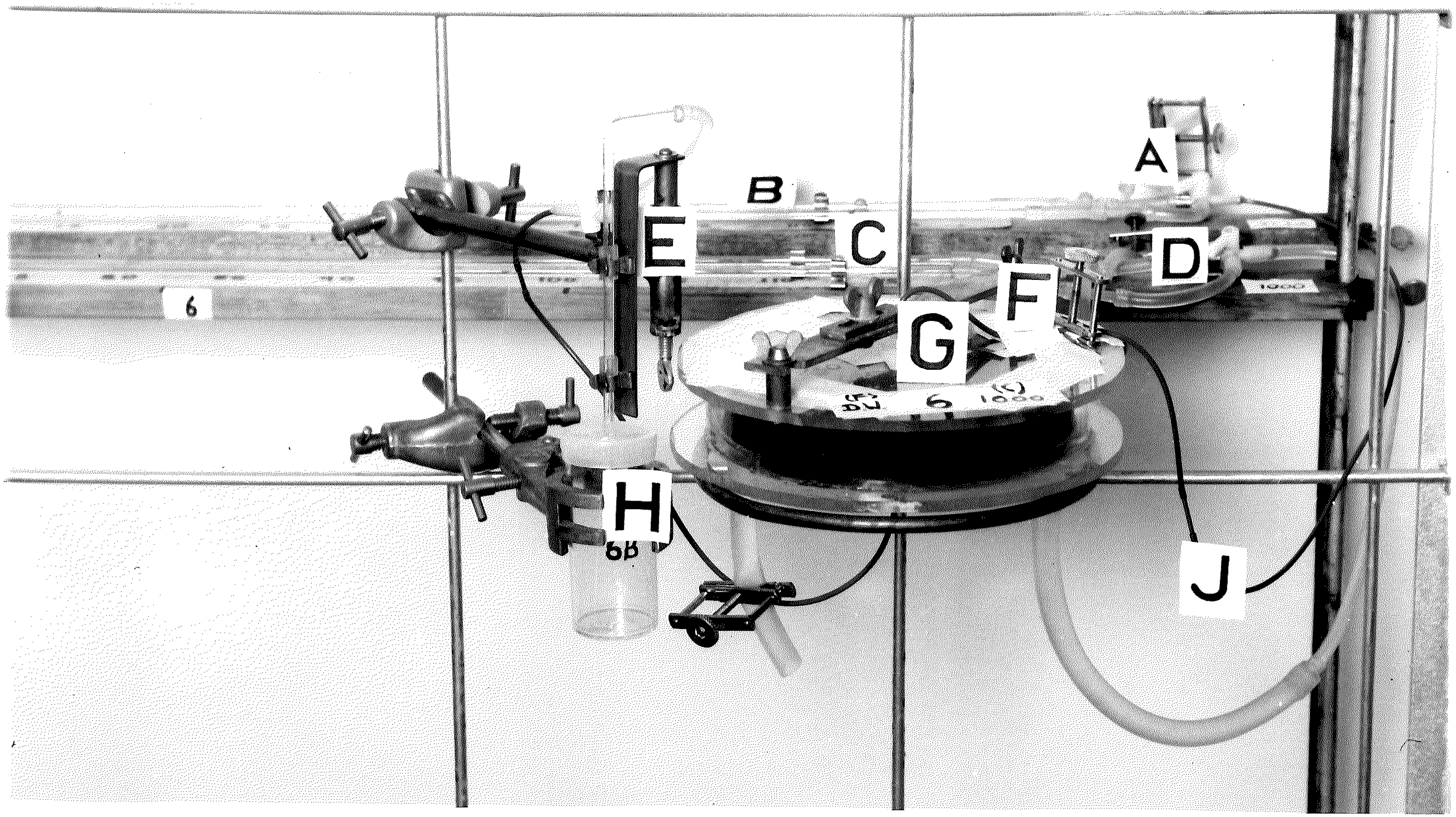
1. Distilled water flushing the sink, 1000 ppm of chloride at the outer boundary and at a low water flow across the bed.
2. Distilled water flushing the sink, 100 ppm of chloride at the outer boundary and at a low water flow across the bed.

3. Distilled water flushing the sink, 1000 ppm of chloride at the outer boundary and at a high water flow across the bed.
4. 1000 ppm of chloride flushing the sink, distilled water at the outer boundary and at a low water flow across the bed.
5. 1000 ppm of chloride flushing the sink, 100 ppm of chloride at the outer boundary and at a low water flow across the bed.

The cell was dried after the air entry test and placed into the vacuum vessel over the required sodium chloride solution. The vessel was filled with the required solution as already described in section 3.3.1. When the cell was saturated and the cell chamber sealed, it was removed from the vacuum vessel and connected up as shown in Figure 42. The cell was mounted above the level of the cell-chamber tubes so that, when the sealing clip was removed from the outlet tube, the sodium chloride solution flowed back and filled the cell-chamber tubes. Checks were made to ensure that no air was entrapped in the lines. The two-way tap was closed and the cell was lowered until the tubes were a little above the top of

Figure 42: Photograph of Complete Cell Assembly

A. Side tubes for filling calibrated tubes
B. Axial inflow (or flushing) tubes
C. Cell-chamber tubes
D. Three-way taps
E. Slide for control of collection head
F. Screw valve
G. Lucite covering plate
H. Collecting vessel
J. Connecting tube.


A
B
E
C
D
F
6
G
6
1000
1000
H
6B
J

the cell. The axial inflow tubes were filled with the required solution, made from boiled distilled water, by applying a small suction on the outflow end of the system. All taps on this line were closed after the level of the outlet tube was made equal to that of the bottom of the cell. The required weight of the specially prepared sand was poured into the bed section of the cell, which had been filled with solution, and levelled to give a bulk density of 1.46 g/cc and a depth of 2 cms. The excess solution in the bed section was removed and the calibrated tubes lowered so that the axial inflow tubes were 5 cm below the centre of the sand bed while the tubes connected to the cell chamber were placed 0.9 cm below the "flushing" tubes, this height difference plus levelling of the tubes being done with a cathotometer. The collection outlet was also lowered to about 0.2 cm below the cell-chamber tubes. The bed section was covered with a thin lucite plate (see Figure 42, G) which was sealed into place with adhesive tape. All taps were then turned to required positions and flows allowed to proceed. The collection head was lowered until radial water flow through the sand bed occurred, at which time the screw valve (F, Figure 42) on the flushing tube was closed until the water-flushing rate was approximately that required, i.e. about 10 times water flow rate through the sand bed. By further readjustment of the collection-head and the screw clip on the flushing tube compromise flow rates were obtained. It took a considerable time to reach steady-state water flow and further time and check analyses of outflow to ensure that steady-state ion flow was also attained. It should be noted that the sample taken from the collection vessel was in fact that which had existed in the sink some hours previously and possibly modified by the effects of flow through the collection tube. Thus it was essential that the steady-state flow of water and chloride ions be maintained over a considerable period of time to ensure that solution collected and soil sampling were indicative of the same situation. Thus refilling of tubes during this period was not possible.

During the sampling checks, it was found that unless the head slide was fixed by means of adhesive tape some minor twisting of the slide occurred which caused minor changes in the head and therefore flow rates. Consequently once the required flow rates were obtained the head slide was securely fixed, so that further changes of the collection vessel in no way affected the flow rates.

When all elements of the system were in a steady state, the cover over the bed was removed, the flushing tube closed between the connecting tube (J, Figure 42) and sink and immediately all other taps closed. Shut-down of the system was carried out in this order as it was noticed that during sealing of the axial inflow tube, as indicated, a small amount of solution was forced down the tube. Therefore it was felt that by leaving the collection tube open momentarily, this displaced water could flow out of the collection tube and not back into the sand bed. The axial inflow tube was immediately broken at the connecting tube, the clamp for the sink removed and the sampler carefully pushed over the axial inflow tube and through the sand bed onto the base plate. A circle had been marked on the cell to ensure that the sampler was centrally placed. Seals were placed over the air escape tubes of the sampler and the sampler and cell inverted. This entire process from shut-down to inversion took 20 seconds at the most. It is felt therefore that only a very small and insignificant change in concentration would occur in this time.

The sampler was removed from the cell and the open face covered with a sheet of "Parafilm". This sheet was pushed onto the sampling rings with the finger, starting from the centre of the sampler, until seals were obtained. A large rubber bung was placed over the sampler to keep the film in place. Immediately this was completed the sand remaining on the porvic outer boundary was removed with a palette knife and placed into a sample bottle. Samples of solution from the outer boundary cell were also taken. The Parafilm covering the outer annulus was removed by running a scapel along the outside edge of the next ring and lifting the out section away. The sampler was tilted and the sand scraped out of the outer annulus with a fine blade into a sample bottle. The film over the remaining annuli therefore fulfilled three purposes; firstly it sealed the soil zones so stopping any evaporation from them, secondly it prevented any soil from falling out and thirdly it eliminated any risk of cross contamination. The remaining annular samples were removed in a similar manner, although as the distance of the sample annulus from the centre decreased, so the size of the bung held against the film was reduced.

The soil samples were weighed in tared bottles and dried in an oven at 105°C for 48 hours, after which no loss of water could be detected. Twenty five cc of distilled water were added to each bottle and the whole shaken for 1 hour. Aliquots of supernatant were removed and titrated for chloride. Procedures for chloride sampling and analysis followed those described in section 3.2.

3.3.3 Results

In the following tables, the annulus number refers to the annulus whose internal and external radii from centre of sink are as given in Table 12. The direction of water flow in all cases was towards the Millipore sink.

Table 12

Annulus Number and Corresponding Internal and External Radii

Annulus No.	Internal Radius (mm)	External Radius (mm)
1	5.0	10.0
2	10.0	15.0
3	15.0	20.0
4	20.0	25.0
5	25.0	30.8
6	30.8	36.2
7	36.2	40.5
8	40.5	45.0

The results for the first combination of 1000 ppm of chloride at the outer boundary, distilled water flushing the sink and at two rates of water flow radially across the sand bed are given in Tables 13 and 14.

Table 13

Measured Water Flows and Flux of Chloride Ion

(means of three four-hourly samples)

Set	Rate of Axial water Flow (cc/hr)	Rate of Radial water Flow (cc/cm/hr)	Total water collected (cc/hr)	Radial Chloride Flux through Bed ($mg \times 10^2/cm/hr$)
1	0.1995	.0077	0.2151	1.55
2	0.2563	.0177	0.2917	2.66

Samples taken did not vary by more than 0.5% from mean.

Table 14

Means of Duplicate Determinations of Chloride Ion Concentrations Across the Sand Bed ($mg \times 10^2$ per cc of solution)

Set	Annulus No.							
	1	2	3	4	5	6	7	8
1	62.1	70.0	77.0	81.3	85.1	88.3	90.8	92.6
2	63.0	70.8	76.9	81.6	85.7	89.1	92.1	94.1

Duplicates did not vary by more than 0.2% from mean.

The results for the combination of 100 ppm of chloride at the outer boundary, and distilled water flushing the sink are given in Tables 15 and 16.

Table 15

Measured Water Flows and Flux of Chloride Ion

(means of three four-hourly samples)

Rate of Axial Water Flow (cc/hr)	Rate of Radial Water Flow (cc/cm/hr)	Total Water Collected (cc/hr)	Radial Chloride Flux through Bed ($mg \times 10^2/cm/hr$)
0.2408	0.0081	0.2573	0.155

Samples taken did not vary by more than 0.5% from mean.

Table 16

Means of Duplicate Determinations of Chloride Ion Concentrations Across the Sand Bed ($mg \times 10^2$ per cc of solution)

Annulus No.							
1	2	3	4	5	6	7	8
6.02	6.72	7.20	7.80	8.10	8.58	8.94	9.17

Duplicates did not vary by more than 0.2% from mean.

The results for the combination of distilled water at the outer boundary and 1000 ppm of chloride flushing the sink are given in Tables 17 and 18.

Table 17

Measured Water Flows and Flux of Chloride Ion

(means of three four-hourly samples)

Rate of Axial Water Flow (cc/hr)	Rate of Radial Water Flow (cc/cm/hr)	Total Water Collected (cc/hr)	Radial Chloride Flux through Bed (mg x 10^2/cm/hr)
0.3046	0.0083	0.3211	0.880

Samples taken did not vary by more than 0.5% from mean.

Table 18

Means of Duplicate Determinations of Chloride Ion Concentrations Across the Sand Bed (mg x 10^2 per cc of solution)

Annulus No.							
1	2	3	4	5	6	7	8
36.90	27.20	21.05	18.15	14.65	12.15	10.20	8.66

Duplicates did not vary by more than 0.2% from mean.

The results for the combination of 100 ppm of chloride at the outer boundary and 1000 ppm of chloride flushing the sink are given in Tables 19 and 20.

Table 19

Measured Water Flows and Flux of Chloride Ion

(means of three four-hourly samples)

Rate of Axial Water Flow (cc/hr)	Rate of Radial Water Flow (cc/cm/hr)	Total Water Collected (cc/hr)	Radial Chloride Flux through Bed (mg x 10^2/cm/hr)
0.2339	0.0111	0.2563	0.64

Samples taken did not vary by more than 0.5% from mean.

Table 20

Means of Duplicate Determinations of Chloride Ion Concentrations Across the Sand Bed (mg x 10^2 per cc of solution)

Annulus No. 1	2	3	4	5	6	7	8
45.70	34.85	30.00	27.15	23.95	20.40	18.80	17.35

Duplicates did not vary by more than 0.2% from mean.

The mean measured water content at saturation was 0.45 cc/cc of bed. The variation about this mean was less than 0.5%.

3.3.4 Discussion

Following the corrected procedure of Gardner (1965), as indicated in section 2.5,

$$Q = 2 \quad rD \frac{dC_1}{dr} + wC_1 \qquad \ldots\ldots \ (61)$$

where Q is the quantity of ion taken up by the sink per unit length of sink, w is the water uptake per unit length of sink and D is the diffusion coefficient defined by

$$J = - D \frac{dC_1}{dr}$$

The radial distribution of chloride concentration was graphed using the mid-point of each annular section as the radial coordinate. From this curve the change of concentration with radius was derived and apparent diffusion coefficients at the various radii calculated from equation (61). These are given in Table 21. Such diffusion coefficients include the effects of soil factors, i.e. hydrodynamic dispersion, moisture content, etc. The data show that D is a function of radius from the sink, and therefore models which are proposed to describe radial ion flow through porous media, where both diffusion and convective transport occur, must include D as a function of radius. It has already been discussed in the literature review that with transient ion or water

Table 21

Diffusion Coefficients at Various Radii from Sink

(x 10^6 cm^2/sec)

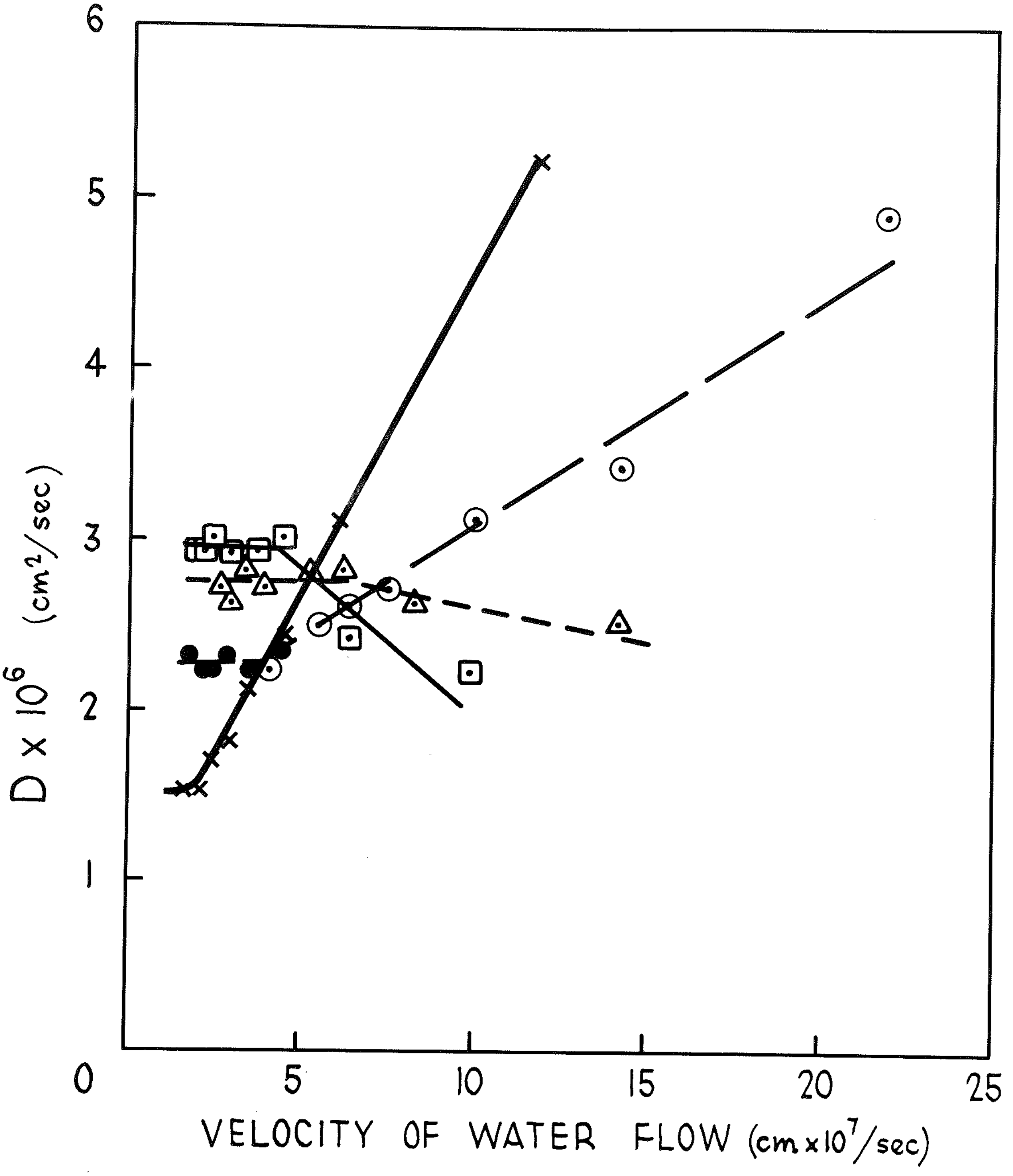
Outer Boundary Concentration (mg x 10^2)	Axial Inflow Concentration (mg x 10^2)		D							
			Annulus No.							
			1	2	3	4	5	6	7	8
1000	0	Set 1	3.0	2.6	2.3	2.2	2.3	2.2	2.2	2.3
		Set 2	4.9	3.4	3.1	2.7	2.6	2.5	2.4	2.2
0	1000		2.2	2.4	3.0	2.9	2.9	3.0	2.9	2.9
100	1000		2.5	2.6	2.8	2.8	2.7	2.8	2.7	2.8
100	0		5.2	3.1	2.4	2.1	1.8	1.7	1.5	1.5

fluxes the velocity of the water flow can influence the observed diffusion coefficient through the effects of miscible displacement. When the diffusion coefficients above are plotted against the velocity of water at the radius concerned, one obtains the relations shown in Figure 43. The effects of water flow velocity are to increase the diffusion coefficient when water flow is in the direction of the diffusional movement of ions, but to reduce the value of the coefficient when the water movement is in the reverse direction to the diffusional movement of ions. The increase in the diffusion coefficient as described above has also been found during linear movement of water and ions (Day and Forsythe 1957, Biggar and Nielsen 1964). However, to the author's knowledge, water flow against the diffusional movement of ions has not been previously investigated. This situation is significant in soil-plant relations since ion accumulation can occur at root surfaces and therefore where convective transport of ions is against the diffusional movement of ions.

Another noticeable feature of Figure 43 is the apparent difference in the diffusion coefficients at low water-velocities at different concentrations of the boundary conditions. These results appear hard to reconcile with present tabular data of the dependence of diffusivity on concentration. It could be suggested

Figure 43: Effect of Water Flow Velocity on the Apparent Diffusion Coefficient

	External Chamber Concn. ppm of Chloride	"Flushing" Concn. ppm	Water Flow Velocity
●— —●	1000	0	Low
⦿— —⦿	1000	0	High
▲- - -▲	0	1000	Low
▣——▣	100	1000	Low
×——×	100	0	Low


6
5
4
3
2
1
0
D x 10^6 (cm^2/sec)
5
10
15
20
25
VELOCITY OF WATER FLOW (cm x 10^7/sec)

that variation in concentration has resulted in these minor differences in the measured diffusion coefficient at or near zero water flow, which has been recorded. Moreover the variation observed in the value of the diffusivity at zero water flux (obtained by extrapolation) does not follow any obvious pattern. It is felt that limitations of the technique contributed to this variation at zero flux rather than any physical phenomenon. The techniques employed in this experiment lacked some precision for comparisons between samples under different boundary conditions although it is suggested as being useful for studies within one sample.

One of the more obvious modifications to enhance precision would be to reduce the width of the sampling zones to at least half that employed above and so obtain more accurate estimates of concentration gradients. The use of the computer to calculate the curve of best fit and the concentration gradients would also aid analysis of the results. Radioautography could possibly ~~also~~ be of considerable use in studies like that above.

3.3.5 Summary

In any one "run", that is for one radial water flow rate and from one set of concentration boundary conditions, the existence of the steady state of flow was determined with precision, as were the concentration distribution data. Within this one set of data, the calculated values of D at each radius gave an internally consistent set on which to establish the relation between D and velocity.

Relation of D to velocity has been found not to remain constant at all water velocities. If water flow occurs in the same direction as the diffusional movement of ions the apparent diffusion coefficient increases with increased water flow velocities above about 4×10^{-7} cm/sec. If water flow occurs in the opposite direction to the diffusional movement of ions, the apparent diffusion coefficient decreases with increased water flow velocities above about 4×10^{-7} cm/sec.

4. GENERAL DISCUSSION

Nye (1966b) stressed the need for general theories or models to describe the uptake of ions by plants from soils in order "to provide a framework for discussion and experiment, and to indicate the parameters that need be measured for a complete quantitative description". Paul (1965) and Clarke (1966) have shown that the uptake of chloride ions and nitrate ions by wheat plants is correlated with the diffusion coefficient of chloride and nitrate in the soils. However their procedures were such as to eliminate any ion uptake effects due to the uptake of water. It is believed that models based on diffusion only have limited applicability to very special circumstances. The real situation in the field requires that models must also account for the effects of water uptake by the plants on ion movement and uptake.

All models so far have assumed that the influence of water uptake by plants on the transfer of ions through soils can be assessed by summing the flux contribution due to diffusion with that due to convection. It is shown in this work that the coupled transfer can not be treated in this way when D is constant and that an interaction occurs between the two, due to hydrodynamic effects within pores. The overall effect, or miscible displacement, gives rise to a situation where the diffusion coefficient is not a constant but varies with the water flow velocity and therefore radius. As the water flow increases so does the apparent diffusion coefficient, i.e. the equation for steady-state flow of ions

$$J = - D \frac{dC_1}{dr} + v\ C_1 \qquad \ldots\ldots (62)$$

does not fully describe the transfer process across the bed. An additional equation defining the functional relation of D and v is necessary. Further work upon this point will decide the most practical approach to the problem.

When D is considered as a function of v (at rate comparable with those of Gardner 1960) and therefore a function of r, substitution of equation (62) into the equation of continuity must show this dependence of D on r.

The influence of water flow on D found in section 3.3 has not been extended to unsaturated systems where water-flow velocity varies in a complex manner with radius due to water-content gradients around the root or sink. Marked water content gradients may occur around the root and microscopic water-flow velocities within the pores near the root surface, may be relatively high indeed. This aspect requires considerable investigation before models can be adequately used, for even with the same water-uptake by two plants, (i.e. the value of w may be the same for both) the moisture gradient and root radius differences may result in very different water flow velocities around the roots.

It is believed that clarification of the above points provides a more useful starting point for development of ion uptake models more appropriate than those presently in use.

The first part of the experimental work (Section 3.2) has shown that definition of the root surface boundary conditions offers the greatest challenge to the use of any model. The quantity of ions taken up by the plant is not simply a function of the ion concentration at the root surface but is also a function of other environmental conditions which give rise to variation in water-uptake rate. These "indirect" effects of water uptake upon ion uptake were evident in this work and it is necessary to obtain data on a broader scale with fewer restrictions than those imposed on the plants used here. The indirect effects of other environmental conditions upon ion uptake through their effects on water uptake deserve further study.

The development of concepts in any field requires progress through the testing of existing hypotheses and substitution of new hypotheses, if necessary, based upon more soundly established premises. The development of thought in the field of endeavour of the present study, has proceeded rapidly over the last five years. Although it was deemed practical to neglect some features of the systems to facilitate early progress, this situation no longer holds.

Further development and understanding of nutrient uptake by plants in real environments will come only from fuller recognition of the complexity of the systems. So much progress has been made that each succeeding forward step requires inclusion of those features of the system previously neglected because of the complexity they carried with them.

APPENDIX 1

Code for Samples Used in Appendix 1

Code	Sample		
	Desired Water Content of Pots (%)	Chloride Content of Solution (ppm)	Depth (cm)
i	4	5	0-5
ii			5-10
iii			10-15
iv			15-20
v			20-bottom
vi		100	0-5
vii			5-10
viii			10-15
ix			15-20
x			20-bottom
xi		1000	0-5
xii			5-10
xiii			10-15
xiv			15-20
xv			20-bottom
xvi		5	0-5
xvii			5-10
xviii			10-15
xix			15-20
xx			20-bottom

xxi	6	100	0-5
xxii			5-10
xxiii			10-15
xxiv			15-20
xxv			20-bottom
xxvi		1000	0-5
xxvii			5-10
xxviii			10-15
xxix			15-20
xxx			20-bottom
xxxi	8	5	0-5
xxxii			5-10
xxxiii			10-15
xxxiv			15-20
xxxv			20-bottom
xxxvi		100	0-5
xxxvii			5-10
xxxviii			10-15
xxxix			15-20
xl			20-bottom
xli		1000	0-5
xlii			5-10
xliii			10-15
xliv			15-20
xlv			20-bottom

APPENDIX 1a

Changes in Water Content of Stored Fallow Pots with Time

Sample	Replicates								
	1			2			3		
	Day 5	Day 10	Day 20	Day 5	Day 10	Day 20	Day 5	Day 10	Day 20
i	4.0	3.9	4.0	4.0	4.0	3.9	4.1	4.0	4.0
ii	3.9	3.9	4.0	4.1	4.0	4.0	4.0	3.9	3.9
iii	4.0	4.0	3.8	3.9	4.1	3.8	4.1	4.1	4.0
iv	4.1	4.0	4.0	4.0	3.9	4.0	4.0	4.0	4.0
v	3.9	4.1	4.0	4.1	4.0	4.0	4.0	4.0	3.8
xvi	8.8	7.3	7.2	8.6	7.5	7.3	8.8	7.5	7.5
xvii	7.2	6.2	6.2	7.4	6.1	6.2	7.0	6.3	6.3
xviii	6.7	6.0	5.8	6.9	6.0	5.9	6.7	6.1	6.0
xix	4.2	6.0	5.9	5.9	6.1	5.8	4.5	5.9	6.0
xx	4.0	5.5	5.7	4.1	5.3	5.5	3.9	5.1	5.4
xxxi	7.2	7.1	7.3	7.4	7.3	7.4	7.1	7.3	7.2
xxxii	8.5	8.4	8.4	8.2	8.5	8.1	8.5	8.3	8.6
xxxiii	7.6	8.2	8.3	8.4	8.2	8.2	8.4	8.2	8.1
xxxiv	7.9	8.1	7.8	8.0	8.1	7.9	8.2	8.1	7.8
xxxv	10.4	10.4	10.1	10.2	10.4	10.3	10.3	10.4	10.4

The variation in the remaining samples was similar to that above and therefore they were not tabled.

APPENDIX 1b

Chloride Content of Stored Fallow Pots

Code	Sample								
	Rep 1			Rep 2			Rep 3		
	Day 5	Day 10	Day 15	Day 5	Day 10	Day 15	Day 5	Day 10	Day 15
i	5.0	5.1	5.0	4.9	4.9	5.1	5.0	4.9	4.9
ii	4.9	4.9	5.1	5.0	5.1	5.0	4.9	5.2	5.1
iii	5.2	5.1	5.1	5.0	4.8	4.9	5.0	5.0	5.0
iv	4.9	4.9	4.9	5.1	5.0	5.0	5.1	4.9	4.9
v	5.0	5.0	4.9	4.9	5.1	5.1	4.9	5.0	5.1
xvi	98	105	95	102	100	98	99	103	101
xvii	104	101	102	99	97	99	101	101	104
xviii	101	100	101	97	102	103	101	98	99
xix	97	99	101	102	101	100	104	103	101
xx	100	99	99	103	99	101	100	100	100
xxxi	997	1007	1021	986	976	999	1000	1009	1017
xxxii	1023	998	1001	1000	997	1007	1008	1019	1006
xxxiii	987	1017	987	965	1004	978	987	992	1001
xxxiv	1006	1027	975	1035	1048	1023	1036	1004	1000
xxxv	993	995	1026	1004	1001	1004	1007	1003	1005

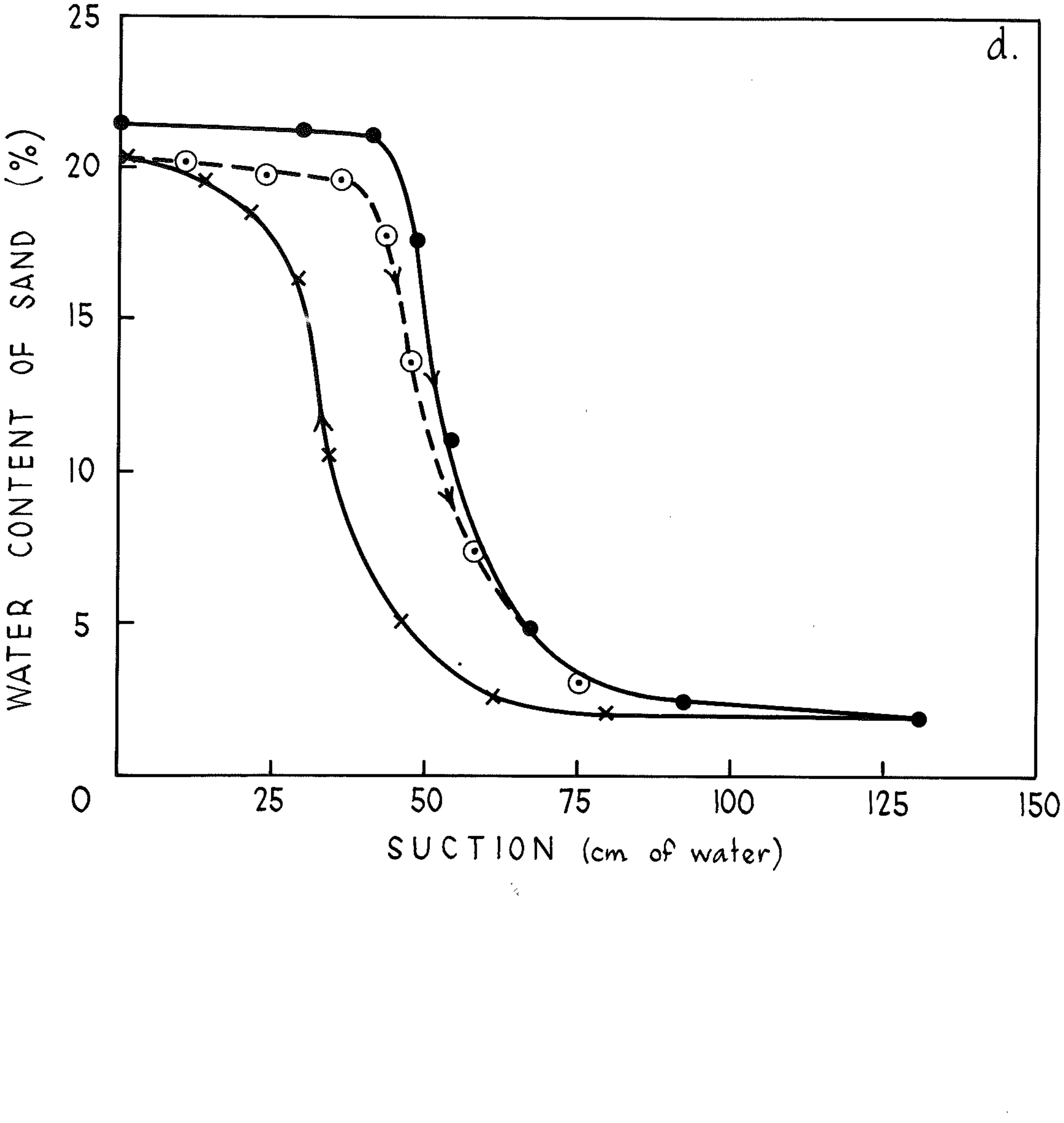
Results for other moisture contents are not given as these gave similar results to those above with variations no greater than 5% from desired value and with no time trends.

APPENDIX 1c

Variation in Bulk Density of Prepared Pots

Code	Sample								
	Rep 1			Rep 2			Rep 3		
	Rep a	Rep b	Rep c	Rep a	Rep b	Rep c	Rep a	Rep b	Rep c
i	1.46	1.47	1.48	1.48	1.49	1.43	1.49	1.45	1.46
ii	1.45	1.42	1.45	1.40	1.41	1.41	1.41	1.42	1.49
iii	1.36	1.44	1.38	1.39	1.42	1.45	1.46	1.47	1.42
iv	1.41	1.47	1.42	1.39	1.45	1.47	1.46	1.43	1.46
v	1.46	1.43	1.39	1.40	1.45	1.48	1.45	1.44	1.43
xvi	1.47	1.49	1.50	1.48	1.48	1.49	1.45	1.46	1.46
xvii	1.44	1.38	1.43	1.44	1.44	1.43	1.43	1.45	1.42
xviii	1.43	1.43	1.39	1.43	1.43	1.41	1.41	1.44	1.43
xix	1.37	1.49	1.46	1.47	1.47	1.49	1.48	1.47	1.46
xx	1.52	1.49	1.48	1.41	1.41	1.45	1.46	1.42	1.48
xxxi	1.52	1.48	1.48	1.48	1.49	1.48	1.50	1.50	1.47
xxxii	1.43	1.44	1.41	1.42	1.42	1.44	1.39	1.40	1.45
xxxiii	1.44	1.46	1.43	1.46	1.42	1.42	1.48	1.48	1.42
xxxiv	1.35	1.36	1.40	1.41	1.44	1.39	1.41	1.40	1.43
xxxv	1.48	1.46	1.48	1.48	1.47	1.49	1.44	1.46	1.48

Appendix 1: d. Moisture Characteristic of Sand


d.
25
20
15
10
5
0
25
50
75
100
125
150
WATER CONTENT OF SAND (%)
SUCTION (cm of water)

APPENDIX 2

Composition of Nutrient Solution

Ten cc of each of the following solutions were added to distilled water and the whole made up to one litre.

Solution 1:	K_2SO_4	40.087 gm/l
	$MgSO_4.7H_2O$	20.167 gm/l
Solution 2:	$FeC_6H_5O_7.3H_2O$	8.925 gm/l
Solution 3:	KH_2PO_4	2.796 gm/l
Solution 4:	$Ca(NO_3)_2$	18.457 gm/l
	NH_4NO_3	181.652 gm/l

Solution 2 was always stored in a refrigerator and used as required because after some time in the whole nutrient solution precipitation occurred. However no precipitation occurred during period of seed germination.

APPENDIX 3

Water Loss from Fallow Pots after Nine and Eighteen Days

Relative Humidity (%)	Water Content of Pot (%)	Chloride Content of Solution (ppm)	Water loss (gm)					
			9 days			18 days		
			Rep 1	Rep 2	Rep 3	Rep 1	Rep 2	Rep 3
42.5	4	5	4.0	4.2	3.3	7.9	8.8	7.0
		100	4.1	4.3	3.3	7.9	8.7	7.1
		1000	4.0	4.3	3.4	7.8	8.8	7.1
	6	5	4.2	4.3	3.2	8.4	9.2	7.1
		100	4.1	4.2	3.3	8.5	9.0	7.2
		1000	4.0	4.2	3.1	8.3	9.1	7.1
	8	5	4.0	4.0	3.1	8.5	9.0	7.1
		100	4.1	4.3	3.2	8.4	9.0	7.2
		1000	4.0	4.2	3.2	8.5	9.1	7.1
67.5	4	5	2.8	3.6	2.8	5.4	6.3	4.4
		100	2.8	3.7	2.8	5.3	6.2	4.4
		1000	2.7	3.7	2.7	5.3	6.1	4.3
	6	5	3.6	3.5	2.6	6.6	5.9	4.4
		100	3.5	3.5	2.6	6.5	5.7	4.3
		1000	3.6	3.5	2.5	6.5	5.9	4.3
	8	5	3.0	3.4	2.4	5.9	5.8	4.3
		100	3.0	3.2	2.4	6.0	5.9	4.1
		1000	3.0	3.4	2.5	6.0	5.8	4.3
92.5	4	5	1.5	1.1	1.1	3.1	2.1	2.2
		100	1.6	1.1	1.1	3.1	2.3	2.3
		1000	1.5	1.2	1.1	3.2	2.3	2.2
	6	5	1.6	1.1	1.1	3.6	2.5	2.0
		100	1.5	1.2	1.1	3.6	2.6	2.1
		1000	1.7	1.2	1.1	3.6	2.6	2.1
	8	5	1.5	1.2	1.1	2.8	2.6	2.6
		100	1.3	1.0	1.2	2.7	2.5	2.5
		1000	1.4	1.1	1.2	2.8	2.6	2.6

APPENDIX 4

a. Preparation of Buffer Solution for Reference Electrode

10.21 gm of potassium hydrogen phthalate were dissolved in 500 cc of distilled water and 148 cc of 0.1 N H_2SO_4 added to this. Contents then diluted to one litre and stored in a stoppered pyrex bottle.

b. Preparation of "Supporting Electrolyte"

101 gm of chloride free KNO_3 were dissolved in water and to this 62 cc of concentrated HNO_3 were added. The whole was then made up to one litre.

APPENDIX 5

A split plot randomized block analysis was carried out on the data using the Wellesbourne-Waite general statistical computer program (Genstat) of Nelder, J.A., Wilkinson, G.N., *et al* (to be published). When this analysis revealed the need for a general randomized block-analysis involving the summation of errors this was carried out using Genstat.

In all cases the data was transformed into logarithms, to the base e, so as to make the model additive and to make the variance between the treatment homogeneous.

Abbreviations used in Tables below:

C - Soil solution concentration
H - Harvest
R - Relative humidity
W - Water content of soil
DF - Degrees of freedom
MS - Mean square
NS - Not significant
EMS - Error mean square
* - Significant at 5% level
** - Significant at 1% level
*** - Significant at 0.1% level.

a. i Effects of Treatments upon the Quantity of Water Transpired (g)

	Component	DF	MS or Significance
Reps:	Total	2	2.179
Runs:	R	2	**
	EMS	4	0.3204
Pots:	H	1	***
	W	2	***
	C	2	NS
	WxC	4	NS
	HxW	2	NS
	HxC	2	NS
	RxH	2	***
	RxW	4	NS
	RxC	4	NS
	HxWxC	4	NS
	RxHxW	4	NS
	RxHxC	4	NS
	RxWxC	8	NS
	RxHxWxC	8	NS
	EMS	102	0.0687

ii Effect of Treatments upon Quantity of Water Evaporated from Pots (g)

	Component	DF	MS or Significance
Reps:	Total	2	0.9068
Runs:	R	2	***
	EMS	4	0.2290
Pots:	H	1	***
	W	2	***
	HxW	2	**
	RxH	2	***
	RxW	4	NS
	RxHxW	4	NS
	EMS	138	0.0049

b. Effect of Treatments upon Root Length (cm)

	Component	DF	MS or Significance
Reps:	Total	2	0.9184
Runs:	R	2	***
	EMS	4	0.0882
	Total	6	8.4568
Pots:	H	1	***
	W	2	***
	C	2	**
	WxC	4	NS
	HxW	2	NS
	HxC	2	NS
	RxH	2	NS
	RxW	4	***
	RxC	4	NS
	HxWxC	4	NS
	RxHxW	4	NS
	RxHxC	4	*
	RxWxC	8	NS
	RxHxWxC	8	NS
	EMS	102	0.0453

c. Effect of Treatments upon Root Numbers

	Component	DF	MS or Signficance
Reps:	Total	2	2.3510
Runs:	R	2	***
	EMS	4	0.2976
Pots:	H	1	***
	W	2	NS
	C	2	*
	WxC	4	NS
	HxW	2	NS
	HxC	2	NS
	RxH	2	***
	RxW	4	NS
	RxC	4	NS
	HxWxC	4	NS
	RxHxW	4	NS
	RxHxC	4	NS
	RxWxC	8	NS
	RxHxWxC	8	NS
	EMS	102	0.1089

d. i Effect of Treatments upon Total Leaf Area (cm^2)

	Component	DF	MS or Significance
Reps:	Total	2	0.0865
Pots:			
	R	2	***
	H	1	***
	W	2	***
	C	2	NS
	WxC	4	*
	HxW	2	NS
	HxC	2	*
	RxH	2	***
	RxW	4	NS
	RxC	4	NS
	HxWxC	4	NS
	RxHxW	4	NS
	RxHxC	4	NS
	RxWxC	8	NS
	RxHxWxC	8	NS
	EMS	106	0.0255

ii Effect of Treatments upon Green Leaf Area (cm^2)

	Component	DF	MS or Significance
Reps:	Total	2	0.0860
Pots:			
	R	2	***
	H	1	***
	W	2	***
	C	2	NS
	WxC	4	*
	HxW	2	NS
	HxC	2	**
	RxH	2	***
	RxW	4	NS
	RxC	4	NS
	HxWxC	4	NS
	RxHxW	4	NS
	RxHxC	4	NS
	RxWxC	8	NS
	RxHxWxC	8	NS
	EMS	106	0.0260

d. iii Effect of Treatments upon Yellow Leaf Area (cm^2)

As there were no significant differences at nine days only the results for eighteen days are given below.

	Component	DF	MS or Significance
Reps:	Total	2	0.1850
Pots:	R	2	***
	W	2	NS
	C	2	***
	WxC	4	NS
	RxW	4	NS
	RxC	4	NS
	RxWxC	8	NS
	EMS	52	0.385

e. i Effect of Treatments upon Total Wet Weight (mg)

	Component	DF	MS or Significance
Reps:	Total	2	0.2680
Pots:	R	2	***
	H	1	***
	W	2	***
	C	2	***
	WxC	4	NS
	HxW	2	***
	HxC	2	NS
	RxH	2	**
	RxW	4	NS
	RxC	4	NS
	HxWxC	4	*
	RxHxW	4	NS
	RxHxC	4	NS
	RxWxC	8	NS
	RxHxWxC	8	NS
	EMS		0.0176

e. ii Effect of Treatments upon the Wet Weight of Tops (mg)

	Component	DF	MS or Significance
Reps:	Total	2	0.1055
Pots:	R	2	***
	H	1	***
	W	2	***
	C	2	**
	WxC	4	NS
	HxW	2	*
	HxC	2	*
	RxH	2	NS
	RxW	4	NS
	RxC	4	NS
	HxWxC	4	*
	RxHxW	4	NS
	RxHxC	4	*
	RxWxC	8	NS
	RxHxWxC	8	NS
	EMS	106	0.0136

e. iii Effect of Treatments upon the Wet Weight of Roots (mg)

	Component	DF	MS or Significance
Reps:	Total	2	0.0791
Pots:	R	2	***
	H	1	***
	W	2	***
	C	2	***
	WxC	4	NS
	HxW	2	*
	HxC	2	NS
	RxH	2	***
	RxW	4	NS
	RxC	4	NS
	HxWxC	4	NS
	RxHxW	4	NS
	RxHxC	4	NS
	RxWxC	8	NS
	RxHxWxC	8	NS
	EMS	106	0.0441

f. i **Effect of Treatments upon the Total Dry Weight** (mg)

	Component	DF	MS or Significance
Reps:	Total	2	0.1306
Pots:	R	2	***
	H	1	***
	W	2	***
	C	2	*
	WxC	4	NS
	HxW	2	***
	HxC	2	NS
	RxH	2	***
	RxW	4	NS
	RxC	4	NS
	HxWxC	4	NS
	RxHxW	4	NS
	RxHxC	4	NS
	RxWxC	8	NS
	RxHxWxC	8	NS
	EMS	106	0.0098

ii **Effect of Treatments upon the Dry Weight of Tops** (mg)

	Component	DF	MS or Significance
Reps:	Total	2	0.0940
Pots:	R	2	***
	H	1	***
	W	2	***
	C	2	NS
	WxC	4	NS
	HxW	2	NS
	HxC	2	NS
	RxH	2	***
	RxW	4	NS
	RxC	4	NS
	HxWxC	4	NS
	RxHxW	4	NS
	RxHxC	4	**
	RxWxC	8	NS
	RxHxWxC	8	*
	EMS	106	0.0155

f. iii Effect of Treatments upon the Dry Weight of Roots (mg)

	Component	DF	MS or Significance
Reps:	Total	2	0.7945
Pots:	R	2	***
	H	1	***
	W	2	NS
	C	2	*
	WxC	4	NS
	HxW	2	**
	HxC	2	NS
	RxH	2	***
	RxW	4	NS
	RxC	4	*
	HxWxC	4	NS
	RxHxW	4	NS
	RxHxC	4	NS
	RxWxC	8	NS
	RxHxWxC	8	NS
	EMS	106	0.0436

iv Effect of Treatments upon the Dry Weight of Seeds (mg)

	Component	DF	MS or Significance
Reps:	Total	2	0.0655
Pots:	R	2	***
	H	1	NS
	W	2	NS
	C	2	NS
	WxC	4	NS
	HxW	2	NS
	HxC	2	NS
	RxH	2	***
	RxW	4	NS
	RxC	4	NS
	HxWxC	4	NS
	RxHxW	4	NS
	RxHxC	4	NS
	RxWxC	8	NS
	RxHxWxC	8	NS
	EMS	106	0.0248

g. i **Effect of Treatments upon Total Sodium Uptake**

(mg x 10^2)

	Component	DF	MS or Significance
Reps:	Total	2	0.4965
Pots:	R	2	***
	H	1	***
	W	2	***
	C	2	***
	WxC	4	NS
	HxW	2	NS
	HxC	2	***
	RxH	2	***
	RxW	4	NS
	RxC	4	**
	HxWxC	4	**
	RxHxW	4	NS
	RxHxC	4	NS
	RxWxC	8	NS
	RxHxWxC	8	NS
	EMS	106	0.0928

ii **Effect of Treatments upon Sodium Transfer to Tops**

(mg x 10^2)

	Component	DF	MS or Significance
Reps:	Total	2	0.030
Pots:	R	2	***
	H	1	***
	W	2	**
	C	2	***
	WxC	4	**
	HxW	2	**
	HxC	2	NS
	RxH	2	NS
	RxW	4	NS
	RxC	4	NS
	HxWxC	4	*
	RxHxW	4	NS
	RxHxC	4	NS
	RxWxC	8	NS
	RxHxWxC	8	NS
	EMS	106	0.167

g. iii Effect of Treatments upon Sodium Accumulation in Roots (mg x 10^2)

	Component	DF	MS or Significance
Reps:	Total	2	1.055
Pots:	R	2	***
	H	1	***
	W	2	***
	C	2	***
	WxC	4	NS
	HxW	2	NS
	HxC	2	***
	RxH	2	***
	RxW	4	NS
	RxC	4	*
	HxWxC	4	NS
	RxHxW	4	*
	RxHxC	4	NS
	RxWxC	8	NS
	RxHxWxC	8	NS
	EMS	106	0.108

h. i Effect of Treatments upon the Total Chloride Uptake (mg x 10^2)

	Component	DF	MS or Significance
Reps:	Total	2	0.7470
Pots:	R	2	***
	H	1	***
	W	2	***
	C	2	***
	WxC	4	NS
	HxW	2	NS
	HxC	2	***
	RxH	2	NS
	RxW	4	*
	RxC	4	***
	HxWxC	4	NS
	RxHxW	4	**
	RxHxC	4	***
	RxWxC	8	NS
	RxHxWxC	8	NS
	EMS	106	0.0481

h. ii Effect of Treatments upon Chloride Transfer to Tops (mg x 10^2)

	Component	DF	MS or Significance
Reps:	Total	2	0.5985
Pots:	R	2	***
	H	1	***
	W	2	**
	C	2	***
	WxC	4	NS
	HxW	2	NS
	HxC	2	***
	RxH	2	*
	RxW	4	NS
	RxC	4	***
	HxWxC	4	*
	RxHxW	4	**
	RxHxC	4	***
	RxWxC	8	NS
	RxHxWxC	8	NS
	EMS	106	0.0476

iii Effect of Treatments upon Chloride Accumulation in Roots (mg x 10^2)

	Component	DF	MS or Significance
Reps:	Total	2	0.9765
Pots:	R	2	***
	H	1	***
	W	2	***
	C	2	***
	WxC	4	NS
	HxW	2	***
	HxC	2	***
	RxH	2	***
	RxW	4	***
	RxC	4	***
	HxWxC	4	NS
	RxHxW	4	**
	RxHxC	4	NS
	RxWxC	8	**
	RxHxWxC	8	**
	EMS	106	0.0806

j. 1 Effect of Treatments upon Total Quantity of Water Held in Plants (mg)

	Component	DF	MS or Significance
Reps:	Total	2	0.2885
Pots:	R	2	***
	H	1	***
	W	2	***
	C	2	***
	WxC	4	NS
	HxW	2	***
	HxC	2	NS
	RxH	2	**
	RxW	4	NS
	RxC	4	NS
	HxWxC	4	*
	RxHxW	4	*
	RxHxC	4	NS
	RxWxC	8	NS
	RxHxWxC	8	NS
	EMS	106	0.0197

ii Effect of Treatments upon Quantity of Water Held in the Roots (mg)

	Component	DF	MS or Significance
Reps:	Total	2	0.8035
Pots:	R	2	***
	H	1	***
	W	2	***
	C	2	***
	WxC	4	NS
	HxW	2	*
	HxC	2	NS
	RxH	2	***
	RxW	4	NS
	RxC	4	NS
	HxWxC	4	NS
	RxHxW	4	NS
	RxHxC	4	NS
	RxWxC	8	NS
	RxHxWxC	8	NS
	EMS	106	0.0452

j. iii Effect of Treatments upon the Quantity of Water Held in the Tops (mg)

	Component	DF	MS or Significance
Reps:	Total	2	0.1105
Pots:	R	2	***
	H	1	***
	W	2	***
	C	2	**
	WxC	4	NS
	HxW	2	*
	HxC	2	*
	RxH	2	NS
	RxW	4	NS
	RxC	4	NS
	HxWxC	4	**
	RxHxW	4	NS
	RxHxC	4	NS
	RxWxC	8	NS
	RxHxWxC	8	NS
	EMS	106	0.0146

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