THE ROOT GROWTH OF A WHEAT CROP IN RELATION TO ITS USE OF WATER AT VARYING SEEDING RATES AND RATES OF APPLIED NITROGEN

A thesis submitted

by

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LIST OF ABBREVIATIONS AND SYMBOLS USED

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

N	Nitrogen
S	Seeding rate
A	Plane area (cm^2)
B	Weight of soil at a specified depth per unit area of horizontal plane
C	Flux of sensible heat into the crop
D	Diffusivity of soil water (cm^2 min^{-1})
E	Evapotranspiration (cm), latent heat flux
E_c	Transpiration (cm)
E_o	Potential evaporation
E_s	Evaporation from the soil surface
F	Matching factor
G	Pneumatic potential
H	Total hydraulic head (cm)
H_{L1}	Hydraulic head of water at the upper end of the xylem (cm)
H_{L2}	Hydraulic head of water in cell walls of the mesophyll (cm)
H_L	$H_{L1} - H_{L2} = H_L$
H_{r1}	Hydraulic head of water at the root surface (cm)
H_{r2}	Hydraulic head of water at the start of the xylem (cm)
H_r	$H_{r1} - H_{r2} = H_r$

H_s	Hydraulic head of water in a volume element of soil (cm)
I	Rainfall (cm)
K	Hydraulic conductivity of soil (cm min^{-1})
L	Lamina area index
M	Photosynthesis
P	Pressure potential
Q	Net radiant energy
Q_a	Flux of sensible heat
R	Root length (cm)
R_a	Root length per unit area of ground surface (rooting density) (cm^{-1}) abundance
R_p	Root length per plant (cm, m)
R_v	Root length per unit volume of soil (root density abundance) (cm^{-2})
S	Flux of heat into the soil
U	Flow of water across the lower boundary of the root zone
V	Volume flow of water across unit cross section of soil
W	Gravimetric water content (g)
W_a	Root weight per unit ground area (mg cm^{-2}, kg ha^{-1})
W_p	Root weight per plant (g)
W_v	Root weight per unit volume of soil (g cm^{-3})
Y	Run off of water from the soil surface
Z	Depth of root zone (cm)
a	Equivalent radius of a root
b	Radial distance from which water flows to a root

d	Plant density, number of centres of plants per unit area of ground surface (m^{-2})
$\underline{g}$	Acceleration due to gravity
h	Component of H
h_m	Matric head (cm)
h_p	Pressure head (cm)
h_g	Gravitational head (cm)
k	Capillary conductivity of soil (cm min^{-1})
l	Length (cm)
$l.$	Litre
n	Number
q	Rate of water uptake per unit length of root (cm^2 min^{-1})
r	Radius
t	Time
w	Gravimetric water content of soil
x	Number of tillers per unit ground area (m^{-2})
z	Depth (cm)
A	Resistance to water flow through the soil pores and the plant ($A_s + A_r = A$)
A_r	Resistance to water flow into and along roots
A_s	Resistance to water flow in the soil pores
Φ	Total potential of soil water
Ψ	Chemical potential
Ψ_m	Matric potential
Ψ_p	Pressure potential

Ψ_z	Gravitational potential
Ψ_π	Osmotic potential
α	Pore pressure coefficient
β	A function of number and size of roots
ε	Flow across unit cross sectional area of pore
η	Viscosity of water
θ	Volumetric soil water content
μ	$\Sigma \mu m$
ν	Withdrawal of water by roots per unit volume of soil
λ	Derived value of ν
ρ	Density (g cm^{-3})
ρ_b	Bulk density of soil (g cm^{-3})
σ	Surface tension of water
τ	Radius of capillary pore

SUMMARY

The growth of the root system, the water use, and the pattern of water uptake of a wheat crop (*Triticum aestivum* L. cv. Heron) grown in the field on a sandy red-brown earth were examined at intervals during two growing seasons. Changes in the growth of the tops were measured also. In the main experiment conducted in the second season, treatments consisted of three seeding rates - 10, 55, and 280 kg ha^{-1} of seed; S_1, S_2, and S_3 - in factorial combination with three rates of nitrogen fertilizer applied at seeding - 0, 35, and 170 kg ha^{-1} of nitrogen; N_0, N_1, and N_2.

The total dry weight of tops increased at the higher levels of S and N. Sowing rate S_2 produced the highest grain yield, but there was no significant difference in yield between the N rates.

Variation in S rate affected root growth more than did variation in N rate. During early growth, the root length per unit area of ground surface R_a (cm^{-1}) was related positively to S, but differences were not detected at maturity when R_a reached its maximum values of 400 to 500 cm^{-1}. At maturity root length per unit volume of soil R_v (cm^{-2}) ranged from 12 at 5 cm through 5 at 50 cm, 1 at 100 cm, to 0.1 at 150 cm. Increasing rates of N increased total root length in the topsoil and reduced the length in the lower horizons. These statistical differences were not always apparent in the qualitative photographs of unreplicated root profiles. Radioisotope uptake studies indicated that the extreme depth of rooting was greater at S_2 than at S_1 and S_3, and that lateral spread of roots within the row was related negatively to S. Root growth in length continued to maturity, and the highest mean rates of root elongation per tiller occurred during the period 18 to 20 wk.

Water withdrawal occurred mainly from the top metre of the soil. The soil within the root zone dried more rapidly at the higher rates of S and N; differences between the treatments were greatest at 10 to 100 cm depth and were most pronounced during the middle of the growing season.

The rate of water withdrawal by the roots, calculated as a function of depth and time, was influenced mainly by R_v and the volumetric water content of the soil θ. Before the root system was well developed and when θ was high, the rate of water withdrawal from various depths depended mainly on the distribution of R_v. Later, with a well developed root system and a drying soil, the rate of withdrawal was determined mainly by θ and hence by k. At 13 wk the rate of water withdrawal by the root network was highest at S_3 – $S_1 = 1.0 < S_2 = 1.6 < S_3 = 1.8$ mm day^{-1} –; by 20 wk the upper part of the root zone had dried, and the withdrawal was slowest at S_3 – S_1, S_2, $= 1.5$, $S_3 = 0.7$ mm day^{-1}.

The mean rates of water uptake per unit length of root ranged from $1\cdot10^4$ to $1\cdot10^3$ cm^2 day^{-1}. The mean rates expressed per unit length of hair bearing zone were one order of magnitude higher. The maximum rate of water uptake for the hair bearing zone – $6.6\cdot10^{-2}$ cm^2 day^{-1} – occurred at 100 to 125 cm depth 20 wk after emergence. The time trend analysis of θ for each sampled depth for the period 8 to 22 wk after emergence showed significant negative trends to a depth of 75 – 100 cm at S_1, 125–150 cm at S_2 and 100 – 125 cm at S_3. On the N treatments the trends were significant to a depth of 125 – 150 cm at N_0, 100 – 125 cm at N_1, and 75 – 100 cm at N_2. Cumulative evapotranspiration for the whole season increased with S rate – $S_1 = 36$ cm $< S_2 = 40$ cm $<$ $S_3 = 42$ cm –; there was no significant difference between the N rates.

STATEMENT

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

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INTRODUCTION

1. INTRODUCTION

Water supply is the most important factor that influences the variation in wheat (*Triticum aestivum* L.) yields in South Australia (Cornish 1950). Although the cultivars used commercially in Australia are early maturing, water stored under fallow is important in most seasons and water shortage often occurs after anthesis. In order to conserve water during the first half of the growing season, the seeding rates are low ranging from 50 to 60 kg ha^{-1} of seed. Although the soils of the wheat belt tend to be deficient in nitrogen, the application of fertilizer nitrogen tends to increase growth and water use before anthesis, and, in drier years, plant water stress may be severe later in the season with a resulting reduction in grain yield (Barley and Naidu 1964).

There is a growing fund of information pertaining to the influence of seeding rate and rate of nitrogen on the top growth and grain yield of wheat crops in South Australia. However no information has been published on the influence of seeding rate and rate of nitrogen on the growth and development of the root system of wheat crops in the field in southern Australia.

The present study is designed to complement earlier Adelaide studies on the effects of seeding rate and rate of nitrogen on the growth and yield of wheat in the field. The first section of the thesis reviews the literature on the growth and development of the wheat crop, the retention and movement of water in soils, water uptake by plants, and the influence of seeding rate and rate of nitrogen on plant growth and plant water relationships. The experimental work examines the growth and water use of a wheat crop (*T. aestivum* L. cv. Heron) grown in the field at varying seeding rates and rates of nitrogen. Emphasis has been placed on the growth and development of the root system and seasonal evapotranspiration. Measurements have also been made to determine whether significant amounts of water flow upward to the root zone toward the end of the season, when the water content of the topsoil is low, or if it is necessary for the crop to root deeply in order to utilize water stored in the deeper layers of the sub-soil.

LITERATURE REVIEW

2. LITERATURE REVIEW

2.1. The growth of the wheat crop with emphasis on root growth

The morphological development of cereal plants has been described by Percival (1921), Hector (1936) and Hayward (1948). More recently, the morphological and physiological development of the temperate cereals has been the subject of a symposium (Milthorpe and Ivins 1966) and of reviews edited by Quisenberry and Reitz (1967). Earlier investigations of the morphology and distribution of cereal roots in the soil have been reviewed by Weaver *et al.* (1922), Weaver (1926), Kutschera (1960) and Troughton (1962). Recent studies of the morphology and physiology of roots, and their relation to the growth of the plant as a whole, have been discussed at a symposium (Whittington 1969). Only those aspects of plant growth and development that are relevant to the present study will be discussed here.

2.1.1. Introductory comments on top growth

The above ground parts of cereal plants show a well defined sequence of development. After germination there is a vegetative phase during which tillers and leaves are initiated.

Vegetative growth is curtailed when the apical meristems become reproductive, and after this no more leaves are initiated. Ear emergence occurs shortly after enlargement of the flag leaf and subsequently grain development becomes the dominant growth process. In wheat (*Triticum* spp.), small amounts of stored carbohydrates are translocated from the stems to the grain, but most of the dry matter in the grain is derived from photosynthesis after ear emergence (Thorne and Watson 1955, Watson *et al.* 1958, 1963, Thorne 1965, 1966, Welbank *et al.* 1966).

The vegetative phase has important effects on grain yield by determining the number of fertile tillers and the size of the organs in which photosynthesis takes place after ear emergence (Bunting and Drennan 1966). A large photosynthetic area will increase grain yield only when there are effective 'sinks' for storage of carbohydrate. The potential maximum number of grains, which are the sinks, is determined during spikelet formation and is controlled mainly by photoperiodism (Rawson 1970). Adverse growing conditions after spikelet formation reduce the number of ovules that develop and the final yield is determined by grain setting and by the growth of the grains after anthesis.

2.1.2. The growth and development of the wheat root system

(i) The main morphological components

Cereal plants produce fibrous root systems that consist of two chief types of roots, the seminal roots that develop from the embryo, and the nodal roots that develop adventitiously from the basal nodes of the stem.

(a) The seminal roots. The number of seminal root primordia in the embryo is governed by genetic factors (Pavlychenko 1937, 1942, Pope 1945, Derera *et al.* 1969). In wheat, the number that develop varies from three to eight (Weaver 1926, Manner 1957), and, within the genetic limitations, the number is related directly to the carbohydrate and mineral reserves of the grain (McCall 1934, Taylor and McCall 1936, Pope 1945). Generally five seminal roots develop consisting of the radicle and two pairs of laterals (Robins 1931, Hayward 1948). Further seminal roots can develop later (Percival 1921, McCall 1934) but they are often less vigorous than the earlier roots (Pinthus and Eshel 1962).

Reduced development and survival of seminal roots occur with deep planting (Percival 1921, Taylor and McCall 1936), germination on the soil surface (Pavlychenko 1942), intense competition in communities of one or more species (Pavlychenko 1937), low soil water content (Weaver *et al.* 1922, Pavlychenko and Harrington 1934), and low soil temperature (Taylor and McCall 1936).

(b) The nodal roots. The nodal roots arise endogenously in whorls at the basal nodes of the stem (Hector 1936, Hayward 1948). Each tiller usually produces a nodal root system and the number of main nodal roots per plant is related positively to the number of tillers (Weaver 1926, Manner 1957, Pinthus 1969, Black 1970). In wheat, the main tiller usually produces two and the other tillers one root at each of several nodes (McCall 1934). The number of main nodal roots per tiller decreases as the order of tillering increases (Pinthus 1969). The main tiller of wheat (McCall 1934, Taylor and McCall 1936) and barley (*Hordeum distichum* L.) (Hackett 1968) sometimes produces one to three early nodal roots which are morphologically similar to the seminal roots. In barley, these two types of roots are easily distinguished by the anatomy of the stele (Hackett 1968).

(ii) Development of the root system

From germination until the onset of tillering the seminal roots grow downwards (Weaver *et al.* 1922). Krassovsky

(1926) cites early opinion that the seminal roots gradually cease to function as the nodal roots develop, and that the seminal roots sometimes decay before the plants mature, but Krassovsky's own investigations and other studies have shown that the seminal roots may function throughout the life of the plant (Percival 1921, Krassovsky 1926, McCall 1934, Balasz 1954). Sometimes the seminal roots are the only ones that survive in adverse conditions such as intense plant competition and a dry topsoil (Locke and Clarke 1924, Pavlychenko and Harrington 1935, Pavlychenko 1937).

The main nodal roots begin to appear during the second or third week after seedling emergence and their production is correlated positively with tillering (Weaver 1926). In wheat, the production of the main nodal roots is most rapid during the period from spike initiation to ear emergence (Pinthus 1969, Black 1970) but may continue at a slow rate to maturity (Pinthus 1969). The seminal roots continue to elongate and to branch as the nodal roots are produced (Weaver *et al.* 1922). Toward the end of tiller enlargement, the nodal roots elongate and branch intensively (Pavlychenko 1937); the seminal roots continue growing, but at reduced rates, and mostly at the lower depths (Derera *et al.* 1969). As the plant matures, the growth rate of all roots is reduced considerably (Weaver *et al.* 1922).

Pinthus and Eshel (1962) and Pinthus (1969) found significant varietal differences in the production and growth of the main nodal roots of wheat. *T. turgidum* produced a larger number of main nodal roots per tiller than *T. aestivum*, and late maturing cultivars of both varieties produced larger numbers than their early maturing cultivars. At ear emergence, the late cultivars had formed 90 per cent of their final number of main nodal roots but the early cultivars had formed only 60 per cent. Initiation of main nodal roots was reduced during the period immediately preceding ear emergence but was renewed thereafter. This renewed growth, together with root initiation by the young tillers, continued to maturity.

The dry weight of the root system often increases to maximum values just before ear emergence and then declines to maturity. This has been shown in sand cultures for wheat (Ballard *et al.* 1936) and corn (Turner 1922), in pots of soil for wheat (Brenchley and Jackson 1921), and in the field for barley (Kamel 1959, Welbank and Williams 1968) and wheat (Harris 1914, Bohne and Grieffenberg 1954, Schuurman 1959). In contrast, in a field experiment conducted by Stucker and Frey (1960), the root weight of oats (*Avena sativa* L.), increased to a maximum at ear emergence and then remained constant to maturity.

There are relatively few data on changes in the total length of cereal root systems over the growing season. Pavlychenko and Harrington (1934, 1935) and Pavlychenko (1937, 1942) measured the total root length of wheat (*T. aestivum* L.), rye (*Secale cereale* L.), and wild oats (*Avena fatua* L.) at intervals during growth in the field in spring at Saskatchewan, Canada. Table 1 shows the mean rates of root elongation for wheat. The data show the importance of the seminal roots throughout the 80 day season, and the rapid growth of the nodal roots during the latter half of the season.

Table 1

The elongation rate of the wheat root system at 4 stages of growth* (after Pavlychenko 1937)

Days after emergence	Root elongation per plant (cm per day)		
	Seminal	Nodal	Total
1 - 5	35	0	35
5 - 22	340	20	360
22 - 40	960	25	985
40 - 80	520	120	640

* 400 plants per sq. m. at establishment in rows 15 cm apart.

The vector rate of root penetration, or downward extension of the rooting front, is often confused with increase in the length of individual roots. Rates of 1.3 cm day^{-1} reported for wheat during the first 70 days (Weaver *et al.* 1924), 5.1 cm day^{-1} for corn (*Zea mays* L.) during the period 10 to 30 days after planting (Linscott *et al.* 1962), and 1.9 to 5.1 cm day^{-1} for sorghum (*Sorghum* spp.) (Nakayama and van Bavel 1963) refer to rates of downward extension. Failure to distinguish between downward extension and increase in the total length of roots has caused confusion in the literature (Hurd 1964, 1968), and may have given the mistaken impression that the roots cease to elongate at ear emergence. It is now known that the length of roots per plant of wheat can continue to increase until the plants mature (Hurd 1964, Pinthus 1969).

2.1.3. Root abundance, rooting density and root distribution in the field

(i) Methods of investigation

(a) Direct methods. The trench method is most commonly used to investigate the gross morphology of root systems. Vertical or horizontal trench faces are prepared and the soil is carefully removed to expose the larger roots. Many of the higher order laterals are lost, as it is seldom possible to separate them from the soil. This method was used by Weaver (1919, 1920, 1925, 1926) in extensive descriptive studies and has been described by Weaver and Bruner (1927) and Weaver and Darland (1949). A more complete picture of the root system may be obtained by excavating blocks of soil ('monoliths') and washing away the soil to expose the roots (Pavlychenko 1937, Kmoch *et al.* 1957, Fehrenbacher *et al.* 1969). Schuurman and Goedewaagen (1965) and Nelson and Almaras (1969) give detailed descriptions of the soil block technique. The trench face and the soil block methods are laborious and require large samples; they provide useful qualitative descriptions of the root system rather than quantitative, statistical data. Quantitative data may be obtained with careful work but the methods are so laborious that replication is usually inadequate.

Soil cores or auger samples may be taken for root separation to measure the rooting density and the distribution of roots in different soil horizons or at specific depths and distances from isolated plants (Fehrenbacher and Alexander 1955, Bloodworth *et al.* 1958, Kmoch 1961, Linscott *et al.* 1962, Welbank and Williams 1968). With adequate replication reliable quantitative data can be obtained. Methods for the separation of roots from soil by washing have been given by Fehrenbacher and Alexander (1955), Williams and Baker (1957) and McKell *et al.* (1961). Barley (1955) separated roots by elutriation after the soil had been fragmented and then dispersed in a high-speed disperser. After separation, the total length of the root in each sample can then be obtained by intercept counting (Newman 1966, Evans 1970, Reicosky *et al.* 1970). Torssell *et al.* (1968) have combined root separation from soil cores and intercept counting to obtain quantitative data of changes in the rooting density (root length per unit volume of soil) R_v and in the root abundance (root length per unit ground area) R_a, with time and depth during the growth of a crop in the field. The techniques of Barley (1955) and Newman (1966) have been adapted to measure root length in the present study and are described in Section 3.3.2.

Rooting density can also be described by counting the number of roots that intersect a plane of known area (Fitzpatrick and Rose 1936, Barley and Sedgley 1961, Melhuish and Lang 1968). If the roots are distributed randomly, the number that intercept three mutually perpendicular planes can be related to R_v (Melhuish and Lang 1968). If it is assumed that the segments of roots can be represented by random straight lines, the mean length of the secants intersecting unit cube is $^2/_3$ (Kendall and Moran 1963).

R_v (cm^{-2}) is then given by

$$R_v = 2\,\bar{m}$$

where $\bar{m}$ (cm^{-2}) is the arithmetic mean number of root axes intercepted per unit area for the three planes (Barley 1970). For non-random root distribution, as in the early seedling stage or in anisotropic soils where the roots have preferred angular directions, R_v can be found from the anisotropy and the sum $m_1 + m_2 + m_3$ for the three planes (Lang and Melhuish 1970).

(b) Indirect methods. Tracer methods used in uptake studies provide indirect data on root distribution. The methods consist of locating a chemical or radioactive tracer in the soil and detecting it in the foliage. In a pioneer study, Sayre and Morris (1940) used lithium chloride to measure the extent of corn root systems. More recently, Hall *et al.* (1953) demonstrated the utility of ^{32}P in root system investigations, and subsequently, radioactive isotopes, in particular ^{32}P, have been used extensively in attempts to assess the distribution and the activity of roots in different parts of the soil profile (Murdoch and Englebert 1958, Nye and Foster 1960, 1961, McClure and Harvey 1962, Nakayama and van Bavel 1963, Cooper and Ferguson 1964).

When using the tracer method, the rooting volume is divided into a number of imaginary compartments the sizes of which are determined by the degree of resolution desired and by previous knowledge or preliminary exploration of the soil properties and the gross rooting characteristics of the plant. The usual proceedure is to make a series of injections into each compartment at standard depths and distances from the base of randomly chosen plants (Nye and Foster 1961). When the roots are well distributed, a more economic alternative is to place the tracer at randomly chosen locations for each depth and then sample plants at various specified lateral distances from the point of application. In order to avoid interference, the points of application must be separated by more than twice the lateral spread of the roots.

Depending on the material used, the tracer may be placed in the soil at the beginning of the growing season (Nye and Foster 1960, 1961, Nakayama and van Bavel 1963) or several days before sampling the tops (Bray *et al.* 1969, Lavy and Eastin 1969). Requirements are that the tracer remains at the location where placed for the duration of the study, be readily absorbed and translocated to the tops, and easily identified in the plant material.

The availability of the isotope for plant uptake varies with the chemical and physical properties of the soil and the size of the labile pool must be measured and taken into account (Nye and Foster 1960). Plant uptake may also be influenced by soil disturbance during application and by radioactive damage to the roots (Nye and Foster 1960, Penner 1954). Isotope uptake data tend to be excessively variable (Burton *et al.* 1954, Cooper and Ferguson 1964), and the quantitative distribution of root activity has seldom been obtained in the field by tracer methods.

An alternative to soil injection is to label the plant top with a suitable radioisotope and, after equilibration throughout the plant (two to five days), soil samples from the rooting zone are assayed without the roots being separated (Racz *et al.* 1964, Russell and Ellis 1968, Subbiah *et al.* 1968). Although the root tips usually contain higher levels of radioactivity than other sections of the root, comparisons of the radioactivity in different soil zones and root weights obtained directly by root separation have shown good agreement when ^{86}Rb was used (Ellis and Barnes 1968). Variable results have been obtained with ^{32}P (Racz *et al.* 1964). The roots of individual plants growing in a community can be identified by labelling the tops of selected plants followed by autoradiography of either the labelled roots in separates (Nielson 1964) or the labelled root intercepts on soil sections.

(ii) Experimental data

As noted in Section 2.1.2., each species and cultivar of cereal shows distinctive rooting characteristics. The data in Table 2 illustrate the variations that may occur between the rooting densities of cereal species in one environment.

Table 2

Rooting density ($\bar{R}_a$) for mature crops
in the field* (after Pavlychenko 1937)

Species	Cultivar	$\bar{R}_a$ (cm^{-1}) Seminal	Nodal	Total
Barley	Hannchen	460	170	630
Rye	Prolific spring	370	160	530
Wheat	Marquis	330	80	410
Wild Oats		250	370	620

* 400 plants per sq. m. at establishment in rows 15 cm apart.

Reported root weights of different cereals are shown in Table 3. The differences in the root weight found by different authors for the same species may be attributed to varietal differences, variations in experimental conditions and techniques, and also in the length of the growing season; in general winter-sown cereals produce a larger weight of roots than spring-sown cereals (Gericke 1946, Goedewaagen and Schuurman 1950, 1951).

Table 3

The root weight of temperate cereals at maturity

Author	Dry weight (kg per ha)			
	Barley	Oats	Rye	Wheat
Gericke (1946)	1170	2100	1930	1970
Goedewaagen and Schuurman (1950, 1951)	2100	2800	3100	2600
Kmoch *et al.* (1957)	-	-	-	1920
Haidu (1959)	-	-	-	1350
Welbank and Williams (1968)	650	-	-	-
McNeill and Frey (1969)	-	3040	-	-

Variations in rooting density and root distribution have been observed between cultivars of wheat (Janssen 1929, Webb and Stephens

1936, Worzella 1932, Hurd 1964, 1968), barley (Hass 1949, Lee 1960, Hackett 1968), oats (Derick and Hamilton 1942) and corn (Kiesselbach and Weihnig 1935). Extensive descriptive studies (Weaver *et al.* 1922, Weaver 1926, Kutschera 1960) have shown that gross genotypic variations in rooting tend to be preserved in contrasting environments. Nevertheless, the depth and lateral spread of roots are greatly modified by soil conditions, plant density, and mineral nutrition (Russel 1961, Black 1968, Schuurman 1965).

A densely consolidated or chemically adverse state of subsoils restricts roots to the topsoil (Brenchley and Jackson 1921, Wiersma 1959, Schuurman 1965). In near saturated soils Goedewaagen and Schuurman (1956) found that lowering the water-table promoted deeper rooting. In semi-arid areas Weaver and Crist (1922) and Kmoch *et al.* (1957) have observed a direct relation of the wetting front and the rooting depth of cereals.

Maximum rooting depths of 230 cm for rye, 210 cm for wheat, 200 cm for barley, and 150 cm for oats under field conditions have been reported by Weaver (1926). Kmoch (1961) reported 160 cm for both wheat and rye. Under favourable conditions wheat roots have been observed at 290 cm (West 1934) and even at 400 cm depth (Kmoch *et al.* 1957).

The lateral spread of roots has been found to vary from 15 to 30 cm on all sides of the plants in oats and barley, 15 to 25 cm in wheat, and 12 to 14 cm in rye when grown at crop densities (Weaver 1926). Linscott *et al.* (1962) found that rectilinear planting produced an oblong rooting pattern in corn with roots spreading 50 cm between the rows and 20 to 25 cm within the row. When the depth of rooting is restricted, lateral spread may be increased (Weaver and Crist 1922, Elliot 1924).

When measured by weight, the larger part of cereal root systems is found in the top 30 cm of the soil profile and root dry weight per unit volume of soil W_v decreases rapidly with increasing depth (Kmoch *et al.* 1957, Foth 1962, Welbank and Williams 1968, McNeill and Frey 1969). Bloodworth *et al.* (1958) measured the vertical distribution of oat roots in the field. Their data are shown in Table 4.

Table 4

The dry weight of roots per cc of soil under oats[*] 12 wk after emergence (after Bloodworth *et al.* 1958)

Depth (cm)	W_v (mg per cc)
0 - 7	0.95
7 - 15	0.26
15 - 22	0.08
22 - 30	0.09
30 - 45	0.06
45 - 60	0.05
60 - 90	0.03
90 - 120	0.03
120 - 150	0.01

[*] cv. Victor-Grain.

The number of root intercepts per unit planar area is also highest in the topsoil. Fitzpatrick and Rose (1936) found 0.5 visible wheat roots per sq. cm of horizontal section in the top 75 cm of the soil profile; the number fell to 0.3 at 90 cm, 0.6 at 120 cm, and 0.02 at 135 cm, the maximum depth at which roots were visible.

The data in Table 5 show that in contrast to root weight, the specific length (length per unit weight of dry root material, cm per g) is higher for roots at deeper depths. The greater specific length suggests that they may be more important in uptake than their weights indicate. Burton *et al.* (1954) reported a lack of correlation between root weight distribution and the uptake of N, P, and K from different soil depths.

Table 5

Specific length of wheat* roots at different depths (after Derera *et al.* 1969)

Depth (cm)	Specific length (cm per g)
0 - 15	420
15 - 30	510
30 - 60	590
60 - 90	700
90 - 120	630

* *T. aestivum* (L.) Thell. cv. Mengavi. Single plants in cylinders of soil 6.5 cm in diameter, 122 cm deep and housed in field growth cabinets.

2.2. The uptake of water by cereal crops

2.2.1. Soil water

This section deals with the factors that especially affect the storage, flow, and availability of soil water, its uptake by crops, and the effects of water deficits on crop growth.

(i) Storage and retention

Most of the water absorbed by plant roots has been stored in the soil for some time, either within or beyond the rooting zone, before it moves to the roots. Water is retained in the pore space by liquid-air interface forces involving the surface tension of water (capillarity) and by liquid-solid interface forces which result from the nature of, and charge on, the particles that form the solid matrix. The mechanisms of water retention have been discussed in detail by Baver (1956), Childs (1957), Marshall (1959), and Day *et al.* (1967).

(ii) Energy potential

Because of the effects mentioned above, water in unsaturated soil is not 'free' in the thermodynamic sense, and the chemical potential, Ψ, of water in the soil is less than that of pure water in bulk (Edlefsen and Anderson 1943, Childs 1957).

The total potential, Φ, is 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 specified (datum) elevation and at specified (datum) pressure to the soil water at the point under consideration (International Society of Soil Science 1963).

The total potential $\Phi = \Psi + \Psi_z + \Psi_p$, where Ψ is the chemical potential, Ψ_z is the gravitational potential due to elevation, and Ψ_p is the potential due to the pressure imposed externally on the soil water.

For our purposes we define the chemical potential Ψ by $\Psi \equiv \Psi_m + \Psi_\pi$ where Ψ_m is the matric potential and Ψ_π is the osmotic potential. The matric potential $\Psi_m = \Psi_\sigma + \Psi_\alpha + \Psi_\omega$, where Ψ_σ is the capillary potential associated with the curved meniscus at the air-water interface and is given by $\Psi_\sigma = -2\sigma/r$ in which σ is the surface tension of the water and r is the radius of the capillary (soil pore). The component Ψ_α is the adsorption potential due to adsorptive forces acting on the first few molecular layers adjacent to the particle surfaces. The component Ψ_ω is due to the attraction between water molecules and ions in the electrical double layer at the charged surfaces of the clay particles. In relatively dry soil $\Psi_c << \Psi_a + \Psi_w$.

Because work has to be done to move water against gravitational forces, Ψ_Z increases with height above the datum.

The pressure potential $\Psi_P = G + P$ where G is the potential due to the external gas pressure and P is the potential due to the pressure the overburden or overlying soil exerts on the soil water. P is related to the weight per unit area of overburden B through a pore pressure coefficient α which takes account of the fact that the overburden is supported partly by the solid matrix of the soil through intergranular contact and partly by the pore water. B changes with depth z. If $z = 0$ at the soil surface and is positive downwards, the value of B at depth z (cm) is given by

$$B = \int_0^z (\rho_b + \rho\theta)\underline{g}\, dz \qquad \text{(dyne cm}^{-2}\text{)} \qquad (1)$$

where ρ_b is the profile bulk density (g per cc), ρ is the density of water (unity in c.g.s. units), θ is the volumetric water content of the soil, and $\underline{g}$ is the acceleration due to gravity (cm sec^{-2}). Change in Ψ_P affects Φ since work will have to be done in transferring water from a region at one pressure to a region at any other pressure. This term is positive if the pressure on the water is greater than the atmospheric datum, and negative if less.

The relationship between ϕ and θ is termed the soil water characteristic and is obtained experimentally by measuring ϕ prevailing in an external body of water in equilibrium with the soil water at specified values of θ. As θ decreases below saturation, ϕ decreases rapidly (Moore 1939). The ϕ, θ function depends on the pore size distribution, and any change in pore size distribution due to swelling or shrinking, compaction, or other change of soil structure alters the function. Also, the function is not unique but depends on whether the soil is being drained or wetted. The degree of hysteresis is greatest in coarse textured soils at high θ (Haines 1930, Cary 1967). Fine textured soils, particularly if they contain expanding lattice clays, retain more water than coarse textured soils at a given ϕ.

(iii) Flow through the soil

The main processes of water flow through soils are viscous flow in the liquid phase, which is dominant in moist soils, and molecular flow in the gaseous phase, which becomes increasingly important as the soil dries. In general, both processes contribute to flow, but soil water flow to plant roots occurs largely in the liquid phase (Slatyer 1967).

Water tends to flow in the direction of decreasing Φ, and in a closed system Φ will be uniform at equilibrium. Different components of Φ operate in different flow par~~t~~hs. In the soil Ψ_π does not affect liquid flow, as dissolved salts tend to move with water, but it affects liquid flow across the osmotic membranes in the root and mesophyll cells where gradients of Ψ_π often occur. Ψ_π does not affect flow through the xylem.

When dealing with water flow, it is convenient to express Φ as energy per unit weight of water; this quantity has the dimension of length and is related to the engineers' concept of 'hydraulic head'. For each component of potential we may in principle define an analogous component h of the total head H. However, as the engineer is essentially concerned with liquid flow in non-osmotic systems, H is usually defined by

$$H \equiv h_m + h_z + h_p \quad \text{(cm)} \tag{2}$$

For liquid flow in one dimension, it is known empirically from Darcy's classical work in 1856 that in saturated, uniform porous beds, the volume of water, V, that flows across unit cross-section of the soil in time t in the +x direction is proportional to the gradient of the hydraulic head, that is

$$V = -K\,\Delta H/\Delta x \qquad (3)$$

where K, the water-transfer coefficient, characteristic of the particular porous bed is known as the hydraulic conductivity.

Richards (1931) and Childs and Collis-George (1948, 1950) have shown that liquid flow through unsaturated porous media is also proportional to the hydraulic gradient. In unsaturated media however, the transfer coefficient is not a constant but is a function of θ and is designated the capillary conductivity, k.

The value of k decreases rapidly as θ decreases below saturation (Moore 1939). The contribution to flow per unit cross-sectional area of pore is proportional to the square of the pore radius as shown by the Poiseuille equation

$$\dot{x} = -(\pi r^2/8\eta)dH/dx \qquad (4)$$

$\dot{x}$ is the flow rate per unit cross sectional area of pore, r is the radius of the pore and η is the viscosity of the water. As θ decreases, the larger pores are emptied first, the total cross-sectional area of pores through which water can flow for a given

H decreases rapidly, and flow occurs through more tortuous channels. The k,θ function varies with the total liquid filled porosity and pore size distribution, and, in the case of swelling soils, with the swelling behaviour of the clay.

The continuity condition equates the charge in θ with time, t, at a given position, to the difference between inflow and outflow at that position. For one dimensional liquid flow in the +x direction, with $h_s = h_p = 0$, modifying the Darcy equation and combining it with the continuity condition gives

$$\partial\theta/\partial t = \partial/\partial x\ (k\ dh_m/dx) \tag{5}$$

or

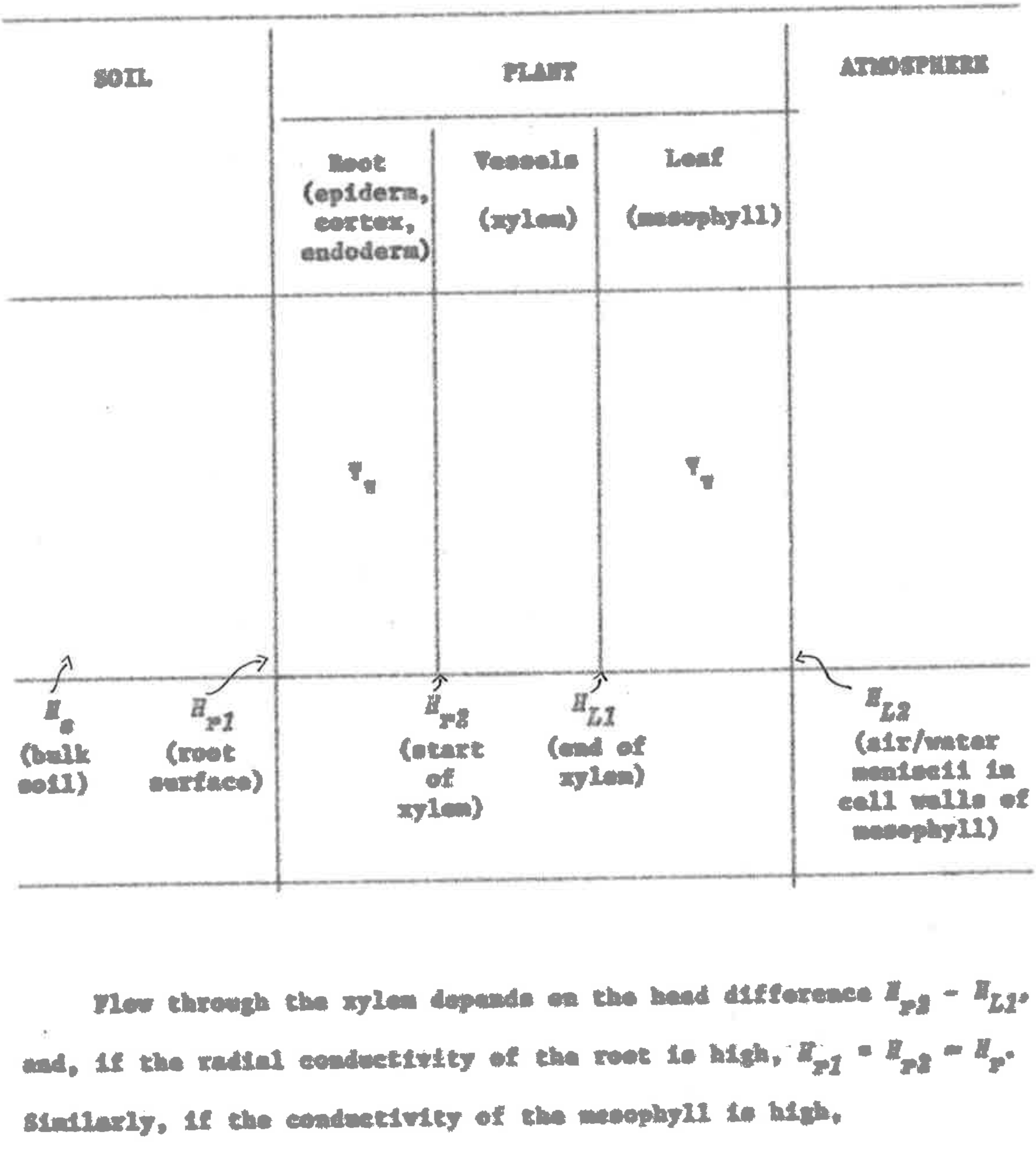
$$\partial\theta/\partial t = \partial/\partial x\ (D\ \partial\theta/\partial x) \tag{6}$$

where $D \equiv k\ dh_m/d\theta$ may be termed the soil water diffusivity (Klute 1952). Note that k, and $dh_m/d\theta$, and hence D are functions of θ.

In applying Eq. (6) the wetting and drying processes have to be considered independently because monotonic relations between h_m and θ, and between k and θ are implied. The diffusivity decreases with decreasing θ but less rapidly than does k. Most published data of k vary from 10 to 1×10^{-5} cm/day and of D from 1 to 1×10^{-4} cm^2/day. The data are often obtained from experiments with disturbed soil and can be different from the values obtained from undisturbed samples of the same soil.

(iv) The soil-plant-atmosphere continuum

Transfer of water in the plant is predominantly in the liquid phase, either across permeable membranes or as viscous flow in conducting vessels and channels. The transfer from the sites of evaporation in the sub-stomatal cavities to the atmosphere is chiefly by molecular diffusion of vapour. Because water can move freely across the soil-plant, soil-atmosphere, and plant-atmosphere interfaces, it is necessary to consider the water transfer system in soil, plant, and atmosphere as a continuum. van den Honert (1948) and Cowan (1965) suggest that the water pathways be represented as a number of resistances in series, though this is an oversimplification as flow occurs in series, in parallel, and in series-parallel combinations, and storage terms are also needed. The soil-plant-atmosphere continuum, and the paths along which the total hydraulic head H, and the osmotic potential Ψ_π affect flow can be represented diagramatically as:



Flow through the xylem depends on the head difference $H_{r2} - H_{L1}$, and, if the radial conductivity of the root is high, $H_{r1} = H_{r2} = H_r$. Similarly, if the conductivity of the mesophyll is high, $H_{L1} = H_{L2} = H_L$.

2.2.2. Soil-plant water relationships

(i) Atmospheric and canopy factors influencing evapotranspiration - the heat balance equation

Water use by crops is primarily an energy-controlled process modified by soil, plant and atmospheric factors. For a given soil and crop, the evapotranspiration rate is determined chiefly by the supply of radiant energy and the availability of water to the plant and at the soil surface (Tanner *et al.* 1960).

For vertical heat flux, the heat balance equation may be written as

$$\int_{t_1}^{t_2} \dot{Q}_{,z=z'} = \int_{t_1}^{t_2} [(\dot{E} + \dot{Q}_{\alpha} + \dot{C} + \dot{N}) + \dot{S}_{,z=0}], \; t_2 - t_1 >> 0 \qquad (7)$$

where $\dot{Q}$ is the net radiation intensity at canopy height z', $\dot{E}$ is the latent heat flux, $\dot{Q}_{\alpha}$ is the flux of sensible heat, the energy that heats the air, $\dot{C}$ is the flux of heat into the crop, $\dot{N}$ is the rate at which energy is used in photosynthetic processes, and $\dot{S}$ is the flux of heat into the soil (Penman 1948, Peters 1960, Tanner *et al.* 1960). In Eq. (7) $\dot{E}$, $\dot{Q}_{\alpha}$, $\dot{C}$, and $\dot{N}$ represent rates integrated over the height of the canopy and $\dot{S}$ is the flux of heat across the soil at $z = 0$. For infinitely large areas of dense, uniform crops, well supplied with water, in energy terms, E = 75–85% of daily Q; Q_a = 5–10%; $S + C$ = 5–10% and M about 5%. The errors of measurement are usually as large as 5–10% (Lemon 1963), and M is often ignored in heat-budget studies, but $\dot{M}$ can be as high as 12% of $\dot{Q}$ for short intervals of time (Loomis and Williams 1963).

The proportion of Q that is used for E is influenced by the length of time that the crop remains green and the extent of soil cover that it provides. The initial rate of evaporation $\dot{E}_s$ from a wet bare soil will be high but the rate is reduced as the soil dries. On the other hand, transpiration $\dot{E}_c$ increases as the plants produce larger leaf surfaces (Harrold *et al.* 1959), at least until the stomata start to close. Dense crops use a larger proportion of Q for E_c than sparse crops, and $\dot{E}$ can be maintained at high values for extended periods when the plant canopy is complete, provided water is available in the lower soil horizons (Tanner and Lemon 1962, Bowers *et al.* 1963).

Variations in the rate of water uptake at different phases of plant growth are determined mainly by the potential evaporation rate $\dot{E}_o$, the availability of water for uptake, the extent of plant cover, and by the resistance to water flow in the plant as governed by turgidity and leaf senescence. The value of $\dot{E}$ for wheat and barley (Erie *et al.* 1965), grown in climates with a relatively cool vegetative growing season and clear warm ripening period, increases in a sigmoid manner, attaining maximum rates when L and $\dot{Q}$ are high, and while the crop is still turgid. $\dot{E}_c$ decreases whenever turgidity decreases sufficiently to close the stomata, and as the leaves senesce.

(ii) The water balance equation

The water balance equation for the root zone can be written as

$$\Delta\int_0^Z \theta\, z = I - (E + U_Z + Y) \tag{8}$$

where Z is the depth of the root zone, E is now the evapotranspiration, I is rainfall, U_Z(+ve downwards) is flow across the lower boundary of the root zone and Y is net runoff from the soil surface. Storage in the plant is assumed to be negligible compared with the other terms over intervals of the order of weeks.

Water absorption by roots can be equated with $\Delta\int_0^Z \theta = -E_c$ only when $I - (E_c + U + Y) = 0$. Although the influence of the other terms is evident, it is sometimes forgotten that flow of water across the lower boundary of the root zone often occurs in response to gradients in H (Rose *et al.* 1965, van Bavel *et al.* 1968b), and, serious errors may be made if such transfers are neglected when estimating water uptake by crops (Robins *et al.* 1954, Wilcox 1960, Robins and Haise 1961). Even though θ for a certain layer of soil may remain constant, this does not in itself indicate the absence of water transfer through that layer.

After determining the net flow across the boundaries of successive layers of soil, and finding the change in θ in each layer, the water balance equation can be used to find the water uptake by roots from each layer (Rose and Stern 1967, van Bavel *et al.* 1968b). The instantaneous water balance equation is then expressed as

$$\dot{I} - (\dot{E}_s + \dot{U}_Z + \dot{Y}) - \int_0^Z \dot{\theta}\, dz = \int_0^Z \dot{\lambda}\, dz \qquad (9)$$

where $\dot{E}_s$ is the rate of evaporation from the soil surface (transpiration excluded), $\dot{U}_Z$ is the vertical flux (+ve downwards) across the lower boundary of the root zone at depth $z = Z$ (+ve downwards) and $\dot{\lambda}_{,z,t}$ is the rate of water withdrawal by the roots.

Considering the terms in Eq. (9), $\dot{I}$ is measured readily by standard methods, and Hudson (1957) has described structures and techniques for measuring $\dot{Y}$. For bare soil, $\dot{E}_s$ can be determined from water content profiles (Rose and Krishnan 1967). The flux $\dot{U}_{z,t}$ can be found from the Darcy equation, given $(k,H)_{z,t}$ and, provided the direction of flow is upwards $\dot{E}_s = |\lim U|_{z\to 0}$. The capillary conductivity k can be measured by outflow methods to be described later, and H can be derived from the soil water characteristic for measured values of θ and the overburden pressure (Rose *et al.* 1965). Given values of the other variables and parameters, Eq. (9) can be solved to find $\dot{\lambda}$ the rate of water uptake by the roots (Rose and Stern 1967).

(iii) Flow of water to a single root

A model has been proposed by Gardner (1960) to describe the dynamics of water flow to a single root. This model treats the root as an infinitely long cylinder of uniform radius and water absorbing properties so that soil water moves only in a radial direction towards the root. If water is absorbed by a cylinder of radius a, equivalent to the root, at a constant rate q per unit length from an initially uniform infinite body of soil, then, provided there is little depletion of water in the bulk of the soil

$$H_a - H_b = \Delta H = -(q/4\pi k)\ln(b^2/a^2) \qquad (10)$$

where b is the radial distance from which water is moving toward the root, H_a and H_b represent the hydraulic head of water at root surface and in the bulk soil.

In relatively wet soil, $h_m \geqslant -1{,}000$ cm, $/\Delta H/$ near the root is likely to be small even if q is large. As the wilting point is approached and k decreases to values of the order of 10^{-5} cm day^{-1} values of $/\Delta H/$ of the order of 10,000 cm of water are required for uptake of 0.01 ml cm^{-1} day^{-1}. Gardner (1960, 1964, 1968) considers cases for uptake of 0.1 ml cm^{-1} day^{-1} but this is anomalously high, being 10 times the maximum that can be expected. Gardner based his values of R_v on the data of Ogata *et al.* (1960), but their recovery of roots was incomplete and hence their values of R_v (0.33 to 0.45) were far too low.

(iv) Flow of water to a set of roots

When dealing with root systems (sets of roots) a steady rate of water uptake by the roots from a given volume element of soil may be represented conceptually by the equation

$$\Delta v/\Delta t = -(H_r - H_s)/(A_r + A_s) \qquad (11)$$

where v is the water uptake by the roots per unit volume of the element – by 'uptake' is meant the transfer of water out of the element by the root axes crossing the boundaries of the element –, where $H_{r1} = H_{r2} = H_r$ is the hydraulic head of water in the root (see p. 30) and is assumed to be uniform throughout the element, H_s is the hydraulic head of water in the bulk of the soil within the element, Λ_r is the resistance to water flow into and in the set of plant roots within the element, and Λ_s is the resistance to flow within the soil pores.

For root systems of 3 months old birdsfoot trefoil (*Lotus corniculatus* L.) grown in containers of fine sand, fine sandy loam, and clay, Gardner and Ehlig (1962a) concluded that Λ_s was relatively small in relation to Λ_r when the soil was moist, $h_m \geqslant -100$ cm, but Λ_s became predominant in dry soils, $h_m \leqslant -1{,}000$ cm. Gardner (1960, 1964) postulated that the resistance Λ_s is related inversely to k, and to R_v, and noting that, as, except in wet soils $\Lambda_s \gg \Lambda_r$,

$$\Lambda_{total} = \Lambda_s \equiv 1/Fk\,R_v \qquad (12)$$

where F is a matching factor for a given element of soil. Equation (12) assumes that any resistance at the boundary between the soil and root is either negligible or varies with $1/k$. Cowan (1965) and Cowan and Milthorpe (1968) take account of root length and radius by defining

$$A_s \equiv \beta/k$$

where

$$\beta \approx (1/8 \pi R_v) [(\ln 1/\pi a^2 R_v) - 3]$$

Newman (1969 a, b) questions the conclusions of Gardner and Ehlig (1962 a, b), Gardner (1960, 1964), and Cowan (1965) on the relative values of A_s and A_p at stated values of h_m. He considers the value of q = 0.1 cm^{-2} day^{-1} used in Gardner's (1960) model to be too high, and he points out that the maximum R_v (0.5 cm^{-2}) considered by Cowan (1965) is too low. Newman concluded that, given the high R_v in topsoils under herbaceous crops where $R_v \geqslant 5$ cm^{-2}, A_s will be too small to greatly influence water uptake from soils having properties similar to Pachappa sandy loam (Gardner 1960) until the soil water content approaches the permanent wilting percentage.

A basic assumption of the Gardner and Cowan models is that at any given moment, h_p is approximately uniform throughout the root system but this is not supported by experimental evidence (Hayward *et al.* 1942, Brouwer 1954). Newman's analysis implies that A_p generally provides the major resistance to water uptake. However, while this may apply in the upper soil horizons where R_v is high, A_s may be relatively large in subsoils where R_v is low. If there is little resistance within the root *or* in the soil why do plants lose turgor when the soil still contains 'available' water? If one were to accept Gardner's contention that A_r is small *and* Newman's contention that A_s is small, it would be difficult to explain why plants lose turgor progressively before they wilt.

(v) Flow of water through the root zone

Descriptive studies have shown that water uptake from different parts of the root zone is correlated positively with rooting density (Weaver 1926, Linscott *et al.* 1962). Root distribution is usually non-uniform, decreasing exponentially down the profile. During early growth, water is used more rapidly from the upper soil horizons, but, as growth proceeds and a larger root system is produced, roots enter fresh soil layers and water is absorbed at progressively lower depths and greater lateral distances from the base of the plant (Russell *et al.* 1940, Taylor and Haddock 1956, Linscott *et al.* 1962, Bauer *et al.* 1965). With the downward growth of the roots, and as the upper soil horizons dry, the zone of maximum water uptake often moves downwards.

Gardner (1964) described flow through root system profiles, and related the rate of water uptake per unit volume of soil to R_v. Vertical flow of water through the soil pores was assumed to be negligible. From Eqs. (11) and (12) for the ith layer in a set of layers or slabs

$$(\Delta v_i/\Delta t)\,(z_{i+1} - z_i) \;=\; -F(z_{i+1} - z_i)\,(H_p - H_{s_i})k_i R_{v_i} \qquad (13)$$

z_i is the depth to the top of the ith layer. The total rate of water uptake per unit area of ground surface, for the entire root zone is then

$$\sum_{i=1}^{N} [(\Delta v_i/\Delta t)(z_{i+1} - z_i)] \;=\; \Delta E/\Delta t \qquad (14)$$

H_p is taken to be uniform throughout the root system and storage in the plant is assumed to be negligible. If the initial θ of each layer is known, the water content can be determined as a function of depth and time given the values of the variables other than θ in Eq. (13) and Eq. (14). The solutions of Eq. (9) and Eq. (14) should yield similar numerical results when flow through the soil pores is negligible but the author is not aware of any published comparison. Equation (9) requires measurements of soil properties only and is less arbitrary. Both equations apply directly only to short (< 1 wk) intervals of time during which the change in θ and hence h_m and k at each depth is small. This presents a difficulty when using Eq. (9) as $\theta_{z,t}$ has to be measured precisely and precision is hard to achieve, particularly in the field.

The partition of water flow between the soil and roots depends on the relative resistance to flow in the two pathways. Studies of birdsfoot trefoil in containers of soil have shown that at high θ and low R_v, flow through the soil is relatively large but at low θ and high R_v, flow through the soil is relatively small (Gardner and Ehlig 1962a).

For grass sods on heavy clay, Wind (1955 a, b) and Visser (1964, 1965) found that the proportion of flow that took place through the roots decreased with increasing depth, and that upward flow of water from below 10 to 20 cm took place mainly through the soil although roots were present in depth. In Visser's experiment, the decrease in flow through the roots followed a geometrical progression with increasing depth.

Various plant factors contribute to reduce the flow of water through the deeper roots of most species: both R_v and the mean radius of the roots decrease with increasing depth, the conductivity of the xylem is proportional to the fourth power of the radii of the vessels, and, within a particular root system the mean radius of the vessels correlate positively with the external radius of the roots. Wind (1955b) estimated that in perennial ryegrass, flow through the deeper roots was restricted by the low number of roots.

In the upper soil horizons, there is less resistance to flow through roots because of the higher R_v and wider xylem vessels. On the other hand, a proportion of the incoming radiation reaches the soil surface causing evaporation directly from the soil, and reducing the amount of water that is available in the topsoil for plant uptake.

2.2.3. The influence of water deficits on crop growth, particularly root growth, and on water uptake

(i) Top growth

Water deficits affect cereal yield with varying intensity according to the stage of growth. Plant water stress during the period of rapid leaf enlargement decreases the number of fertile tillers (Slavik 1965); during the period of spikelet formation it decreases their number in the spike (Asana and Saini

1958, Asana *et al.* 1958), during anthesis it decreases the number of grains (van der Paauw 1949, Brouwer 1959, Martin 1960), and during grain filling, the weight per grain (Asana 1962, Day and Intalap 1970). In glasshouse experiments, Lehane and Staple (1962) and Campbell (1968) found that the grain yield of wheat subjected to water stress during early growth was reduced far less than that of plants subjected to stress during late growth. Similar results have been obtained for wheat in the field (Brown and Campbell 1966).

(ii) Root growth

Water availability influences the total length of roots, the orientation of the main roots, and hence the lateral extent and depth of rooting. Root growth is often affected adversely by low h_m, both because of direct effects of water shortage, and because of indirect effects of the high soil strength associated with low h_m in compact soils (Barley 1968).

In laboratory and greenhouse studies, the rate of radicle elongation in corn seedlings (Gingrich and Russell 1956), the length of the seminal roots of wheat seedlings (Salim *et al.* 1965, Ferguson and Boatwright 1968) and the root dry weight per unit volume of soil, W_v, of mature wheat plants (Campbell and Read 1968) decreased together with h_m.

In different soils, the same h_m may be associated with different levels of water availability and rates of flow to the root. In controlled environments Peters (1957) found that corn seedlings had higher rates of seminal root elongation when grown in soils with higher, than in soils with lower θ and k, even though the initial h_m was the same in all soils. However, different results may be obtained when older, branched roots are considered as root development is influenced by water supply. Jean and Weaver (1924) observed that the wheat and barley grown under dry conditions produced a larger number of branches per unit length of subtending root than plants grown under wet conditions. This may have been due partly to better soil aeration and increased N mineralization in the drier soil. In regions with low rainfall, the depth of rooting is usually limited by the depth to which the soil is wetted by rain (Cannon 1911, Weaver 1920, Weaver and Crist 1922, Kmoch *et al.* 1957). Weaver (1926) and Salim *et al.* (1965) noted that when the soil was wetted to shallow depths only, the lateral spread and branching of roots in the topsoil were increased. Maximov and Kruzilin (1936) found that frequent irrigation of wheat caused most of the roots (W_v) to be restricted to the top

40 cm of the soil but without irrigation high values of Ψ_p were measured at 40 to 60 cm depth. The restricted rooting at depth on the irrigated plots may have been caused by excessively wet subsoils.

In some studies wheat roots failed to elongate through soils with $h_m \leqslant -15{,}000$ cm of water (Robertson *et al.* 1934, Ferguson and Boatwright 1968). On the other hand, corn roots (Hunter and Kelly 1946), and wheat, oats and barley roots (Kmoch *et al.* 1957, Salim *et al.* 1965) are known to be able to elongate slowly in soils with $h_m \leqslant -15{,}000$ cm of water, when there is water available in other parts of the rooting zone.

(iii) Water uptake

Within the limit imposed by the potential evaporation rate $\dot{E}_o$, the rate of water uptake by plants is determined by the interplay of factors that affect water supply to the root surface and those which affect stomatal closure.

Models have been proposed by Philip (1957), Gardner (1960, 1964), Visser (1964) and Cowan (1965) to describe the effect of soil water status on water uptake by plants. These models consider that water flows through the soil as discussed earlier in this section, and that flow from the root to the transpiration sites in the leaves takes place along gradients of H. Cowan's (1965) model is the most detailed. It includes functions that describe the influence of k, H_v, H_s, H_r, H_L - see p. 30 - and A_r on stomatal aperture and hence on the capacity of the plant to transpire at the potential rate.

It is implicit in Cowan's model that $H_{r1} = H_{r2} = H_r$ and $H_{L1} = H_{L2} = H_L$ - see p. 30. The rate of water flow through the plant and hence E_o is taken to be proportional to the gradient $H_L - H_r$ and inversely proportional to the sum of the internal plant resistances. The model neglects the osmotically induced, respiratory dependent phenomena of root pressure and guttation, as indeed do most of the models concerned with water flow in the soil-plant-atmosphere continuum. Difference in H_r between and along roots (de Roo 1969), and the possibility of resistance at the root-soil boundary need to be considered also. As E_o from field crops is known to be largely 'passive', and highly dependent on the *external* supply of energy for evaporation, it is reasonable to simplify models by neglecting osmotic effects, especially as their inclusion may not greatly alter the results obtained. It should be remembered, however, that such models are incomplete.

The models referred to above indicate that in order to maintain E_o in a drying soil where k and H_r are decreasing, H_L must fall continually to provide the necessary gradient $H_L - H_r$ for water flow to the leaves. As R_v increases, a given rate of water uptake can be maintained until lower values of H_s are reached, smaller values of $/\Delta H/$ (Eq. 10) being adequate to sustain flow to the root. When k and H_r fall to certain levels, the accompanying decline in H_L may lead to a loss of turgor sufficient to cause partial or complete closure of the stomata. Consequently, the conductivity of the leaves is decreased and $\dot{E}_o$ declines. This decline will occur at relatively high values of H_s when $\dot{E}_o$ is high and k is low.

The general conclusions from such models have been confirmed in experiments. For a corn crop in the field, Denmead and Shaw (1962) found $\dot{E} < \dot{E}_o$ at progressively higher values of H_s as $\dot{E}_o$ increased. In a controlled environment (80% relative humidity, 18 hour photoperiod at 17 cal cm^{-2} min^{-1}), wheat grown in pots of soil at $H_s = -200$ to $-15{,}000$ cm of water had lower E values than wheat grown with adequate available water at $H_s = -200$ to $-1{,}400$ cm of water (Campbell and Ferguson, 1969). Gardner and Ehlig (1962a, 1963) and Ehlig and Gardner (1964) estimate that water uptake by plants decreases with H_s, but the proportion of upward flow that takes place within the root system increases.

(iv) Permeability of the plant

Loss of turgor and subsequent closure of the stomata are associated with reduced permeability of plants to water flow; in particular loss of turgor appears to decrease permeability of roots (Brouwer 1954). However, the effect of water stress on the permeability of plant tissues has not yet been adequately evaluated. Stocker (1960) has proposed a two stage reaction of protoplasm to water stress, in which an initial phase, associated with reduction in viscosity and increased permeability, is followed by an increase in viscosity and decrease in permeability.

Much more research is required in this field, and short-term effects of water stress on changes in permeability and the physiological function of the plant need to be separated from long-term effects on growth.

2.3. The influence of plant density on crop growth and water relations, with emphasis on root growth and water uptake

2.3.1. Top growth and grain yield

(i) General aspects of plant competition

The size and weight of most plant components are related inversely to plant density, the number of plants per unit area of ground surface *d* (Clements *et al.* 1929, Donald 1963). Measurements of top growth attributes have shown this relationship in wheat (Wassermann 1964, Puckridge and Donald 1967, Bremner 1969 a, b), barley (Kamel 1959) and corn (Lang *et al.* 1956, Allison 1969). The decrease in weight per plant with increasing *d* is determined by the intensity of competition for necessary resources.

Competition between plants arises when the immediate supply of any necessary resource falls below the combined demands of the plant community, and when the location of plants is such that there is interference in the growth of one plant by another (Clements *et al.* 1929). The factors for which cereal plants compete are essentially water, nutrients, light, oxygen and carbon dioxide. Donald (1961, 1963) discussed the nature of competition for different resources. Clements *et al.* (1929) and Donald (1961, 1963) conclude that competition for space seldom occurs.

The field density of cereal crops is such that, except in the earliest stages of growth, competition is intense; maximum dry weight per plant is attained at low *d* but maximum yield of dry matter per unit area is attained at a high *d* and high level of inter-plant competition (Donald 1961).

(ii) Total dry weight of tops

At germination and during the early growth of cereals dry matter per unit area is related directly to *d*. Subsequently, plant competition increases and the rate of increase in dry matter per unit area decreases at high *d*. In mature crops it is often found that dry matter per unit area rises to a maximum and then remains constant as *d* increases. These relationships have been found in wheat (Holliday 1960, Wassermann 1964, Bremner 1969b), barley (Rennie 1957) and maize (Haynes and Sayre 1956). At extremely high *d*, the total yield of tops of wheat (Puckridge and Donald 1967) and barley (Kamel 1959) have occasionally been decreased, possibly due to lodging. Reduced photosynthetic activity due to reduced use of assimilates at high *d* may also decrease the dry weight of tops (Moss 1962).

(iii) Tiller growth

During the early vegetative phase, the number of tillers per unit area is related directly to the seeding rate. Subsequent tiller mortality at the higher densities and continued tiller production at the lower densities have resulted in near constant tiller numbers at maturity for rice (*Oryza sativa* L.) (Kanda and Sato 1963), for perennial rye grass (*Lolium perens* L.) (Holliday

1953), and for sudan grass (*Sorghum sudanense* L.) (Burger and Campbell 1961) sown at widely varying seeding rates. In contrast, Kamel (1959) found that constancy of tiller numbers in barley was achieved only at moderate to high *d*, and Wassermann (1964), Puckridge and Donald (1967), and Bremner (1969 a, b) measured significant differences in the total number of tillers per unit area in mature wheat crops at moderate to high *d*.

The proportion of fertile tillers in wheat decreases as *d* is increased (Holmes and Tahir 1957, Wassermann 1964). An example of the effects of *d* on tiller survival, and the proportion of the maximum tiller number producing ears at maturity is given in Table 6 for wheat (cv. Insignia 49) grown at Adelaide, South Australia.

Table 6

Tiller and ear production of wheat
at widely varying densities (after Puckridge 1962)

Number per sq. m.			$\frac{\text{Number of ears}}{\text{maximum number of tillers}}$ (%)
Plants at emergence	Maximum tillers	Tillers at maturity	
1.4	57	46	72
7	210	150	62
35	490	350	47
185	1,010	510	35
1,100	1,400	540	23

(iv) Leaf growth

Leaf growth responds in a similar manner as tiller number to variations in *d*. This is to be expected as leaf production is dependent on tiller production. Wassermann (1964), and Puckridge and Donald (1967) found that as *d* increased in wheat, higher peak values of leaf area index *L*, were attained, less time was taken to attain L_{max}, and the subsequent decline to maturity was more rapid. Similar results have been obtained for barley (Kamel 1959).

(v) Grain yield

Unlike total dry matter, which tends to remain constant at moderate to high *d*, the grain yield per unit area usually but not always rises to a maximum and then declines as *d* is increased in wheat (Holliday 1960, Wassermann 1964, Puckridge and Donald 1967), barley (Kamel 1959), oats (Guitard *et al*. 1961), sorghum (Karper 1929), and corn (Haynes and Sayre 1956, Timmons *et al*.1966). The influence of *d* on yield components in cereals has been discussed in detail by Clements *et al*. (1929) and Donald (1963).

2.3.2. Root growth

In dense plantings of temperate cereals, the number of main roots per plant, the root length per plant, R_p and the root weight per plant W_p are generally less than 50 per cent of those for widely spaced plants (Clements *et al.* 1929, Sprague and Farris 1931, Pavlychenko and Harrington 1934, 1935, Pavlychenko 1937, 1942, Kamel 1959). However, the different members of the root system are not reduced to the same extent; the nodal roots are reduced more than the seminal roots and the initiation of higher order laterals is reduced more than that of first order laterals (Pavlychenko and Harrington 1934, 1935, Pavlychenko 1937).

Pavlychenko and Harrington (1934, 1935) and Pavlychenko (1937) provide the only detailed data describing the number and length of cereal roots at high and at low d. Further reference will be made to their data in the following sections. Although their data are derived from measurements of single plants, or means of five plants only, and were not analysed statistically, the differences observed between high and low d are sufficiently large to merit use of the data. It should be noted that Pavlychenko and Harrington's calculations of R_p were based on a constant number of plants per sq.m. at all times when root measurements were made. This indicates that either establishment counts or the number of seed sown per unit area were used rather than actual d. Seeding rate experiments are often reported incorrectly as density experiments.

(i) Number of main roots

(a) The seminal roots. Widely spaced wheat and oat plants usually, but not always, produce larger numbers of seminal roots than plants competing in dense communities of the same or other species (Simmonds and Sallans 1933, Pavlychenko and Harrington 1934, Pavlychenko 1937, 1942). The fifth and sixth seminal roots of wheat, which often appear much later than the first four seminal roots (McCall 1934, Pinthus and Eshel 1962), sometimes fail to survive the unfavourable conditions caused by intense competition particularly if this leads to early drying of the top soil (Locke and Clarke 1924, Pavlychenko 1942).

(b) The nodal roots. In temperate cereals, the number of tillers and main nodal roots per plant is generally related negatively to *d* (Weaver 1926, Simmonds and Sallans 1933, Pavlychenko 1937, Hurd 1964, Pinthus 1969, Black 1970). However, the number of main nodal roots per tiller is not always affected by *d*. Pinthus (1969) found that thinning uniformly spaced wheat plants immediately after spike initiation to vary *d* from 40 to 160 (m^{-2}) did not effect the number of main nodal roots per tiller at maturity. Pinthus' data show that *d* influences the number of main nodal roots per plant through its effect on tillering. In contrast, Pavlychenko and Harrington (1935) found that wheat and barley plants grown at *d* = 0.11 m^{-2} produced many more tillers but a smaller number of main nodal roots per tiller than plants grown at *d* = 400 m^{-2} (Table 7).

Table 7

Tillering and main nodal root formation in widely spaced and densely sown wheat (after Pavlychenko and Harrington 1935)

d (m^{-2})	Number of tillers per plant		Number of nodal roots per tiller		Number of nodal roots per plant	
	wheat	barley	wheat	barley	wheat	barley
0.11	27	127	3	0.7	89	83
400	1	1	6	4	6	4

Wheat = *T. aestivum* L. cv. Marquis; barley = *H. distichum* L. cv. Hannchen.

Varietal differences, variation in the environments, and in the relative importance of inter- and intra-plant competition, could have influenced nodal root initiation in these two experiments. Taken together, the experiments of Pavlychenko and Harrington (1935) and Pinthus (1969) suggest that the initiation and/or survival of the main nodal roots may be insensitive to changes in

d at moderate densities, but with extreme differences in d, their development may be affected. Multi-tillered plants tend to initiate main nodal roots above soil level, and it is likely that such roots will not survive where the top soil has been dried. This may be one reason why differences in the number of nodal roots per tiller between densities are relatively small.

(ii) Length of the main seminal and nodal roots

The mean length of the individual main seminal and nodal roots of wheat, barley, rye and wild oats is lower when the plants are grown at crop densities than when widely spaced (Pavlychenko and Harrington 1935, Pavlychenko 1934). The mean length of the main seminal roots of wheat decreased from 150 cm per root at $d = 0.11\ m^{-2}$ to 95 cm at $d = 400\ m^{-2}$ and that of the main nodal roots decreased from 55 to 25 cm. The nodal roots formed most of the total root length of the widely spaced plants, whereas in the dense community, most of the total root length consisted of seminal roots (Table 8). Similar relationships were observed in rye and wild oats (Pavlychenko 1937).

Table 8

Root length per plant of widely spaced and densely sown wheat (after Pavlychenko 1937)

d (m^{-2})	Root length per plant* (m)		
	Seminal	Nodal	Total
0.11	6,900	62,300	71,200
400	700	170	870

* including laterals.

(iii) Root branching

The frequency of root branching (number of laterals per cm of subtending root) in wheat, barley and rye tends to decrease as *d* is increased (Pavlychenko and Harrington 1934, 1935, Pavlychenko 1937, 1942); data for wheat grown at three densities are shown in Table 9.

Table 9

Frequency of root branching in wheat
grown at three densities (after Pavlychenko 1937)

d (m^{-2})	Frequency (cm^{-1})			
	First order branches		Second order branches	
	Seminal	Nodal	Seminal	Nodal
0.11	6	4	3	3
400	4	5	2	2
800	3	1	-	-

These data suggest that the frequency of branching is more sensitive to *d* on the nodal than on the seminal roots, probably because the nodal roots develop later when competition has increased.

(iv) Extent of the root system

Studies by Weaver (1925, 1926) and Clements *et al.* (1929) have shown that the maximum depth and the maximum lateral spread of cereal roots sown in closely spaced rows decrease as *d* is increased. Pavlychenko (1937) found that the rooting depth of widely spaced wheat, oats, and rye plants was 160 cm compared with

115 cm at crop densities. With increase in the number of corn plants per unit length of widely spaced rows, Haynes and Sayre (1956) found that spread of the roots of crowded plants decreased within the row, but the lateral spread into the inter-row spaces increased.

(v) Root growth rate

Pavlychenko's (1937) data show that the elongation rate per plant, over the entire growing season, of the root systems of wheat, wild oats, and rye grown in the field was 900, 1100, and 900 m day^{-1} at $d = 0.11$ m^{-2} and 11, 12, and 12 m day^{-1} at $d = 400$ m^{-2}. In a subsidiary trial, with the same variety in the same year, the mean rates of root elongation per plant for wheat at $d = 400$ and 800 m^{-2} were 4.5 and 4.0 m day^{-1} during the first 40 days after seedling emergence. These data for 40 day old wheat plants indicate that, above moderate values, d may not greatly influence R_p.

Clements *et al.* (1929) reported that root dry weight per plant W_p showed a mean increase of 1.7, 0.8, 0.5 and 0.4 mg day^{-1} for wheat grown for 40 days in pots of soil at $d = 20$, 90, 175, and 200 m^{-2}. Kamel (1959) reported rates of 1.8, 1.3, and 0.4 mg day^{-1} for barley grown to maturity in the field at $d = 125$, 250, and 500 m^{-2}; with the maximum rates of 9, 4, and 3 mg day^{-1} attained during the period 8 to 10 weeks after seedling emergence.

(vi) Rooting density

The root length per unit volume of the soil R_v (cm^{-2}), and the root length per unit ground area R_a (cm^{-1}), increase with d over a wide range. At 40 days after seedling emergence, the values of R_a at d = 400 and 800 m^{-2} were 700 and 1300 cm^{-1} for wheat and 1000 and 1600 cm^{-1} for barley. For mature wheat plants at d = 0.11 and 400 m^{-2} R_a was 80 and 3600 cm^{-1} (Pavlychenko 1937).

Clements *et al.* (1929) found that the root weight per unit ground area W_a of wheat seedlings grown in pots of soil for 21 days was related directly to d. In contrast, Kamel (1959) found that W_a of barley grown to maturity in the field at d = 125, 250 and 500 m^{-2} was 3, 4, and 2 mg cm^{-2}. In Section 2.3.1. (ii) it was noted that the dry weight of cereal tops has been found to decrease at high values of d in some experiments, but the proportional decrease in the weight of tops is not as large as that reported by Kamel for roots. This may be due to mutual shading, and reduced photosynthetic efficiency and translocation of carbohydrate to the roots as d is increased. From Kamel's report, it would seem that at $d = 500$ m^{-2} water was limiting during late growth. Campbell and Read (1968) have found that either increase in plant water stress or decrease in light intensity depressed W_a of wheat more than the weight of the tops.

2.3.3. Water use

(i) General

The relationship of water use and d is determined mainly by the availability of water. When water is readily available to the plant and at the soil surface to meet the evaporational demand, or when water is limited throughout the soil profile, changes in d have little influence on $\dot{E}$. In the first instance, E is limited by the income of net radiant energy Q, and in the second the amount of water available for E is limited.

If water is limited in the upper but not in the lower horizons, E may be increased at high d as resistance to water flow through the dry topsoil is much greater than resistance to flow through the plant. In relatively dry soil high R_v at high d reduces the resistance to flow through the soil-plant system (Gardner 1960, 1964, Newman 1969a). This may account for a reported positive correlation of water use and d for corn irrigated with intermittent drying of the topsoil (Carlson *et al.* 1959).

Plant density influences height in many crops, and E is correlated positively with plant height of corn (Tanner and Lemon 1962) and wheat (El Nadi and Hudson 1965). Plant height appears to influence $\dot{E}$ by greater interception of advected heat, and because air turbulence tends to be greater over the canopy of taller than of shorter crops (Lemon *et al.* 1957). Such effects are greater in small plots than within areas surrounded by an extensive fetch.

Field data relating E to d have generally been obtained from small-plot experiments. Without adequate fetch, $\dot{E}$ of small plots can be increased by horizontal advection of sensible heat from surrounding drier areas (Halstead and Covey 1957, Lemon *et al.* 1957, Tanner 1957). Graham and King (1961) estimated that advected energy accounted for 20 per cent of E from a corn crop, and McIlroy and Angus (1964) found $\dot{E} > \dot{Q}$ on plots with wide (100 m) borders. These results show that fetch may often be inadequate in density experiments.

(ii) Seasonal patterns

Clements *et al.* (1929) observed that in areas of low rainfall, wheat plants at high d showed signs of water stress at an earlier stage than those at low *d*. These early observations showed that rapid depletion of limited available water is an important factor in the relation of grain yield and the density of cereal crops. This is particularly so when the crop grows largely on water stored during fallows, or on rainfall that is concentrated at the start of the growing season. More recently, Timmons *et al.* (1960) and Bond *et al.* (1964) found that, during the first half of the growing season, the soil water content of plots of corn and sorghum at high *d* was depleted more than that of plots at low *d*; at maturity all available water had been used at both low and high *d*. In contrast, Shubeck and Caldwell (1955) found that the rate of soil water depletion for corn at high *d* was more rapid during late growth. In the experiments of Yao and Shaw (1964), widely varying densities of irrigated corn used similar amounts of water before full plant cover was attained as water use was mainly as E_s. During later growth, the high *d* planting used more subsoil water and its total water use over the whole season exceeded that of the low *d*. On unirrigated plots, both low and high *d* used the limited amount of water available.

If conditions are such that soil water use varies with *d*, optimum *d* of cereal crops increases with water supply (Brown and Shrader 1959, Timmons *et al.* 1966, Holt and Timmons 1968). With excessively high *d* and limited water supply, the available water may be depleted before the crop matures. Under such conditions, Bond *et al.* (1964) found that the grain yield of corn was significantly reduced, and Timmons *et al* (1966) found that the proportion of barren corn plants increased with *d*, reaching 96 per cent when excessively high *d* caused early depletion of limited soil water and extreme plant water stress after silking.

(iii) Uptake from different depths

As noted in Sections 2.2.2, water uptake per unit volume of soil usually decreases with increasing depth. No data describing the influence of *d* on plant water uptake from different soil depths are known to the author. Any change in *d* that alters R_p at different depths is also likely to alter the pattern of water uptake. Increasing *d* is likely to increase R_p and water uptake in the intermediate and lower soil horizons during mid- and late-season growth, due partly to the higher R_p and partly to the lowering of the hydraulic head of water in the topsoil causing increased upward flow through the soil pores.

2.4. The influence of nitrogen on crop growth and water relations, with emphasis on root growth and water uptake

2.4.1. Influence on top growth

(i) Duration of growth phases

Provided water supply is adequate, cereal leaves synthesise larger amounts of chlorophyll and remain green longer if they are adequately supplied with N than if they are N deficient (Mayer and Anderson 1961, Hewitt 1963). The greener colour is often mistakenly regarded as delayed maturity, but there are generally only small changes in the duration of distinct growth phases. In field experiments performed by Stackman and Aamodt (1924) floral initiation occurred as much as 10 days later, and ear emergence as much as 4 days later in N deficient wheat plants than in plants supplied with adequate N. In contrast, under laboratory conditions, Khalil (1956) found that the floral initiation of wheat was 2 days later in plants with more than adequate tissue N content. These two examples refer to extreme situations. Reduced light delays floral initiation in wheat (Khalil 1956) and barley (Kamal 1959), and N could, by increasing mutual shading, indirectly delay floral initiation of shaded tillers.

(ii) Dry matter production and nitrogen uptake

(a) Dry matter production. Plant N deficiency is associated primarily with reduced rates of protein synthesis, and, consequently, with numerous aspects of growth and function. Remedying N deficiency in field crops greatly increases total dry matter yield by increasing the growth of photosynthetic area rather than increasing the net assimilation rate (Watson 1952, Thorne and Watson 1955). Effects on net assimilation rates are important in severe deficiency in glasshouse experiments, but deficiencies are not often so severe in the field, apparently because of a larger rooting volume and continued N mineralization.

Increased availability of N tends to increase the dry weight of the foliage more than the grain yield of cereals (Weaver *et al.* 1924, Gregory 1937, Thorne and Watson 1955). Tiller production is increased with N availability (Thorne 1962, Aspinal 1963, Bunting and Drennan 1966, Langer 1967), and high levels of available N at all stages of growth lead to the initiation of late tillers. The late tillers are relatively inefficient in grain production but compete with early formed ears for carbohydrates and other resources (Thorne 1962, Bremner 1969a). Luxury supplies of N may increase vegetative growth but reduce the grain yield of wheat (Colwell

1963, Fischer 1963, Barley and Naidu 1964, Wassermann 1964), and barley (Luebs and Laag 1967).

If there is available water adequate N often maximises the duration of green leaf area after ear emergence (Thorne 1966), a factor that contributes to grain yield as noted in Section 2.1.

When the cereal plant has an overall deficiency of N, intra-plant competition occurs for N, and spikelet number and development are reduced, often with some compensation in grain size (Williams 1955, Single 1964). With adequate N, grain yield is increased mainly through the production of larger numbers of ears per plant (Watson 1936, Watson *et al.* 1958, Robins and Domingo 1962, Thorne 1962, Barley and Naidu 1964, Single 1964). The influence of N on the components of grain yield has been discussed by Milthorpe and Ivins (1966). The first increment of N usually produces the largest increase in the dry weight of cereal tops; not only lack of growth potential but also lack of other resources may limit dry matter production at the high end of the N range (Colwell 1946, Nicholson and Cooper 1956, Shepperd 1960, Gasser and Iordanou 1967). The level of N that produces maximum dry matter yield is higher for leaf and stem than for grain (Ramig and Rhoades 1963, McNeal *et al.* 1966). Some authors claim that in cereal plants supplied with more than adequate levels of N, carbohydrate is diverted into vegetative growth and grain yield is reduced (Brouwer 1962b) as shown by increased straw : grain ratios at high N. Generally, however, if other resources are not limiting, increased supplies of N will increase both total dry matter and grain yield (Gasser and Iordanou 1967). The increased straw : grain ratio at high N may be due mainly to the continued production of tillers, the latter of which fail to produce ears.

(b) Nitrogen uptake. Total N uptake of cereals is correlated positively with available supplies (Terman and Brown 1968, Reid *et al.* 1969). The rate of N uptake per plant is low during the seedling stage. As the root system develops, uptake increases, attaining a maximum rate during the period of rapid plant growth that precedes ear emergence, and then declines as the plants mature and as soil NO_3^--N and available water decrease (Richardson and Trumble 1928, McNeal *et al.* 1966, 1968, Storrier 1965, Gasser and Iordanou 1967). The N content of the grain is correlated positively with available N and also with the dry weight of the foliage, as 75 per cent of the N in leaves and stems may be translocated to the grain (McNeal *et al.* 1966, 1968). Uptake of N continues to maturity (Watson 1958), but a net loss of N from the tops may occur as the plants mature (Barley and Naidu 1964, Storrier 1965, Puckridge and Donald 1967, McNeal *et al.* 1966, 1968), particularly if the crop has had a luxury supply of N.

2.4.2. Influence on roots

(i) Physiological effects on root growth

Enhanced root growth due to N may result from increased synthesis of carbohydrates, proteins and other substances in the shoot, and increased translocation of carbohydrates to the roots. Assimilates transported to the roots are used in the formation of root tissue and also in the formation of labile organic acceptors for mineral elements. After the incorporation of assimilates with mineral elements, some of the materials formed are transported back to the tops where they are utilised.

Pristupa and Kursanov (1957) found that in the pumpkin plant, N deficiency caused marked reductions in the flow of amino acids and assimilates to the roots. After deficient plants were supplied with N the flow of assimilates to the roots was increased, and there was a close positive correlation of the rate at which assimilates flowed to the roots and the rate at which mineral elements were being absorbed.

The data of Turner (1922) and Reid (1929) show a combination of abundant carbohydrate and low N concentration in the tops of cereal plants to be correlated positively with high root : shoot ratios. Loomis (1953) and Brouwer (1962 a, b) attribute the effects of N on the relative weight of plant parts to intra-plant competition for N (and other nutrients) and for carbohydrates. There is usually an excess of carbohydrates in the tops of N deficient plants due to reduced protein synthesis. In such circumstances, the uptake and transport of nutrient elements by the roots is slow, and top growth may be reduced more than root growth as the roots have first call on the nutrients absorbed from the soil.

Wiersum (1958) found that pea plants (*Lepidium sativum* L.) grown in nutrient solutions of low N concentrations produced long, thin, and sparsely branched roots but plants grown in solutions of high N concentrations produced short, thick, and well branched roots. Growth in length and frequency in branching were related negatively. Similar results have been obtained for wheat (Gericke 1921, Burstrom 1950, Bosemark 1954, Williams 1968). In addition to the general effect, there is an effect of localized supply of N on root growth which is discussed in Section 2.4.2.(iii).

(ii) Abundance

Relatively few reports deal with the influence of N on the growth and development of cereal root systems. Most of the available data relate to measurements of root weight and those which refer to root length deal mainly with seedlings grown in sand and solution cultures.

In field experiments, additional N has been found to increase the dry weight of roots at maturity in wheat (Brenchley and Jackson 1921, Kmoch *et al.* 1957, Kahari and Elonen 1969), barley (Crist and Weaver 1924), oats (Grunes and Krantz 1958, McNeill and Frey 1969), and corn (Ferenbacher and Snider 1954, Duncan and Ohlrogge 1958).

(iii) Density and distribution

Early studies by Weaver *et al.* (1922) and Crist and Weaver (1924) indicated that surface applications of N often increase the *proportion* of the total weight of cereal roots in the upper soil horizons and decrease the proportion in the lower horizons. This has been confirmed recently for wheat (Kmoch *et al.* 1957), barley (Welbank and Williams 1968), and corn (Fehrenbacher and Snider 1954, Fehrenbacher *et al.* 1960) grown in the field. In these recent studies, it was found that rooting depth and W_a were increased relative to unfertilized plants. In contrast McNeill and Frey (1969) found that N broadcast and disced into the topsoil increased the weight of oat roots at 30 to 45 cm more than at any other depth. Heavy rains could have leached the N to lower depths as the response to K, which is also easily leached, was also greatest at 30 to 45 cm whereas the root growth response to relatively immobile P was greatest in the topsoil. Linscott *et al.* (1962) found that surface application of N did not affect W_{d} or root distribution at maturity. During early- and mid-season growth, the depth of root penetration, W_{d}, and the proportion of the total root weight in the top 30 cm of the soil were higher on the N-fertilized than on the controls. During late season growth the depth of root penetration and the root weight in the lower soil horizons increased more on the unfertilized than on the N-fertilized plots.

In low fertility soils, root branching and elongation are often increased in localized zones of relatively high N concentration (Weaver 1926, Wiersum 1958); and the N concentration is often highest in the topsoil (Pearson and Simonson 1939, Russell 1961, Black 1968). However, as noted in Section 2.1.3, the high rooting density found in topsoils may also reflect the normal pattern of root distribution or a less favourable environment in the subsoils for root growth. Weaver *et al.* (1922) and Crist and Weaver (1924) observed that localizing NO_3^- in the subsoil promoted the growth of barley roots in the fertilized zone and inhibited root elongation into the soil below; however, adequate controls (no applied NO_3^-) were not included, and no quantitative measurements of root growth were made in these experiments.

Split-root experiments with corn seedlings in solution cultures (Brouwer and Loen 1962) have shown that lack of a N supply to *any one* main seminal root does not affect its elongation rate and branching if the remainder of the root system is supplied with adequate NO_3^-. This shows that when the N nutrition of the whole plant is adequate, there is no *obligate* need for a local supply of N for root elongation and branching.

2.4.3. Availability of nitrogen at different soil depths

Crops usually obtain most of their NO_3^- from the top 30 to 50 cm of the soil profile (Russell 1961, Foth 1962, Storrier 1962), but barley and maize plants have been found to absorb NO_3^- readily from a depth of 75 cm (Crist and Weaver 1924). Dancer and Peters (1969) found that corn grown in the field with adequate water throughout the rooting zone absorbed similar amounts of NO_3^- from sources placed at depths varying from 0 to 75 cm. During periods of high rainfall, NO_3^- is usually leached from topsoil, but it remains available for plant uptake if it is not leached beyond the root zone (Doughty *et al.* 1954).

When NO_3^- is applied to a dry soil surface, uptake by plant roots is dependent largely on rain or irrigation water to move the NO_3^- into the rooting zone. If the soil surface is wet, significant amounts of surface-applied NO_3^- diffuse into the soil and uptake can be expected before effective rain is received (Stewart and Eck 1958).

The processes that limit the uptake of N from the soil by plant roots may be located either in the soil or in the plant. The important soil factors are the NO_3^- and NH_4^+ concentrations, and, at least at low rates of water flow, the diffusity of these ions in the soil (Clarke and Barley 1968). In the plant, the rate of ion uptake may be limited either at the sites in the root where nitrate is absorbed, or, uptake to the plant tops may be limited by the rate of flow through the xylem.

2.4.4. Influence of nitrogen on plant-water relationships

(i) Water use and grain yield

Leaves constitute the major proportion of the transpiring area of cereal crops, and as noted previously any factor such as N nutrition, that increases leaf area is likely to increase

E if the soil surface is dry, the canopy is not closed, and water is available in the lower horizons.

Reviews by Kelly (1954), Haise *et al.* (1960), and the data of Colwell (1963), Barley and Naidu (1964), and Luebs and Laag (1969) suggest that an increased supply of N early in the growing season is likely to increase the E of cereal crops. Greater E on N-fertilized plots may result from increases in crop height or bulk (Section 2.2.2.), from increased R_v reducing the resistance to water flow through the soil-root system (Section 2.2.2.), or from changes in the foliar characteristics that reduce the resistance to water loss from the leaf to the atmosphere at given water deficits.

Because of the effects mentioned above, N-fertilized cereals deplete soil water more rapidly and are subject to more severe water stress during late growth than unfertilized cereals. The vegetative growth of wheat (Brown and Campbell 1966), barley (Luebs and Laag 1967, 1969), and corn (Holt and van Doren 1961) has not infrequently been found to increase and their grain yield to decrease relative to the control when N is applied at high rates. Barley and Naidu (1964) obtained similar results for three Australian wheat cultivars, and found that early depletion of soil water caused larger reductions in the grain yield of the more freely tillering, later maturing cultivars when N fertiliser was applied at $\geq$ 180 kg ha^{-1}. On the other hand moderate levels of N fertilization seldom reduce grain yield in low rainfall areas. Viets (1965) evaluated many published data from 'dryland' experiments and found significant reductions at less than 10 per cent of the sites, and a larger number of significant yield increases than significant yield decreases. High levels of N increase grain yield per unit of water used only when there is adequate available water throughout growth (Ramig 1959, Ramig and Rhoades 1963).

(ii) Water uptake profiles

The supply of N to cereal crops often increases water use from the lower soil horizons. This may be related to the deeper root penetration observed in some studies, and partly to the lowering of the hydraulic head of water in the upper horizons which then causes increased upward flow of water through the soil pores.

Kmoch *et al.* (1957) found that although N did not affect the depth to which wheat roots penetrated on a fine sandy loam, W_p

and soil water depletion were increased below 120 cm. Olson *et al.* (1964) found that N fertilized corn and sorghum used more water than the controls from 120 to 180 cm. Viets (1962) cites studies of F.E. Koehler showing that wheat fertilized with 180 kg ha^{-1} of N used more water from 150 to 200 cm than unfertilized plants, although both treatments used similar amounts of water from the upper horizons. In contrast, Carlson *et al.* (1959) found that for irrigated corn on a loam soil, N increased the amount of water used from the top 60 cm of the profile, possibly as a result of increased E_v in the topsoil.

The results of Warder *et al.* (1963) show that soil properties influence the relative depth to which soil water is depleted on N-fertilized and unfertilized plots. On clays, N-fertilized wheat depleted the water in the subsoil more than did the controls, but on loam soils no difference was found.

2.5. Density x Nitrogen interactions

2.5.1. Influence of nitrogen on optimum density

As the nutrient status of a moist soil increases, the value of d required to give maximum yield increases. A clear example of this is given by Lang *et al.* (1956). At low N the maximum yield of corn was obtained at 4,850 ha^{-1} and at high N, a maximum yield was obtained at 8,100 ha^{-1}. As *d* increases the response to an added nutrient continues to higher levels of supply, provided water is not limiting. In wheat (Hudson 1941 a, b) and corn (Coyler and Kroth 1968), optimum *d* and rates of N have been found to vary directly with available water. Where water is limited *d* x N interactions are likely to occur.

Donald (1963) noted that at high *d* the photosynthetic capacity and growth of the individual plant was reduced, leading to reduced capacity of each plant to utilize water and minerals. As competition for light occurs at high *d*, the reduced uptake of water and minerals by each plant occurs independently of the supply of these resources and of competition for the resources themselves.

2.5.2. Grain yield

At low *d* and high N, the yield per plant is extremely high relative to that of plants at high *d* and low N. In general, total dry matter production and grain yield per plant are affected by changes in *d* more than by changes in N supply. Also, *d* and N may have different affects on the same yield component. High *d* reduces the number of grains per ear and often increases weight per grain, whereas high N tends to increase the number of grains per ear and often decreases the weight per grain.

The results of Salt (1955) provide a clear example of d x N interaction in wheat. Two cultivars were sown at 100 and 200 kg ha^{-1} of seed, d_1, and d_2, in factorial combinations with 0, 25 and 50 kg ha^{-1} of N, N_0, N_1, and N_2. For d_1 the grain yields were rated $N_0 > N_1 > N_2$ whereas for d_2 the rating was $N_0 > N_2 > N_1$. The grain yield of $d_1 > d_2$ at corresponding levels of N, and the d_2N_2 plots produced the lowest grain yield.

2.5.3. Root growth and water use

No data describing the interaction of d and N on root growth or water use are known to the author; and the topic will be considered further in discussion of the author's results.

EXPERIMENTAL PROGRAMME

3. EXPERIMENTAL PROGRAMME

3.1. Introduction

The experiments reported in this thesis are designed to study the rooting characteristics and the water use of a wheat crop grown in the field on a sandy red-brown earth. The response of the crop to variation in seeding rate and rate of applied nitrogen has been examined to complement earlier Adelaide studies on the response of the tops to these treatments. Although sufficient data were obtained on top growth to characterise the crop, emphasis has been placed throughout on the geometry of the root system and its relationship with water uptake from the soil.

3.1.1. Site

(i) Location

The experiments were carried out at the Roseworthy Agricultural College, South Australia, latitude 34.5°S, longitude 138°E. The sites were in Field E7 of area 23 ha. The field had been under wheat in 1962, oats for grazing in 1963, barley in 1964, grass-clover ley in 1965, and fallow from 1966. The areas not used for the experiments in 1967 and in 1968 were planted with wheat, *T. aestivum* L. cv. Heron at the rate of 90 kg ha^{-1} of seed on 19th July, 1967 and on the 26th July, 1968.

(ii) Climate

The locality has a climate with cool, wet winters and hot, dry summers. The mean annual rainfall (1931 to 1968) is 430 mm. The mean monthly rainfall and pan evaporation are shown in Fig. 1a, and values for 1967 and 1968 are shown in Figs. 1b and 1c; the mean maximum and minimum temperatures for each month are given in Table 10. The growing season generally extends from April to November. The long term (38 year) mean rainfall from the 1st April to 30th November is 350 mm. The rainfall during this period in 1967 was 150 mm, and in 1968 it was 510 mm.

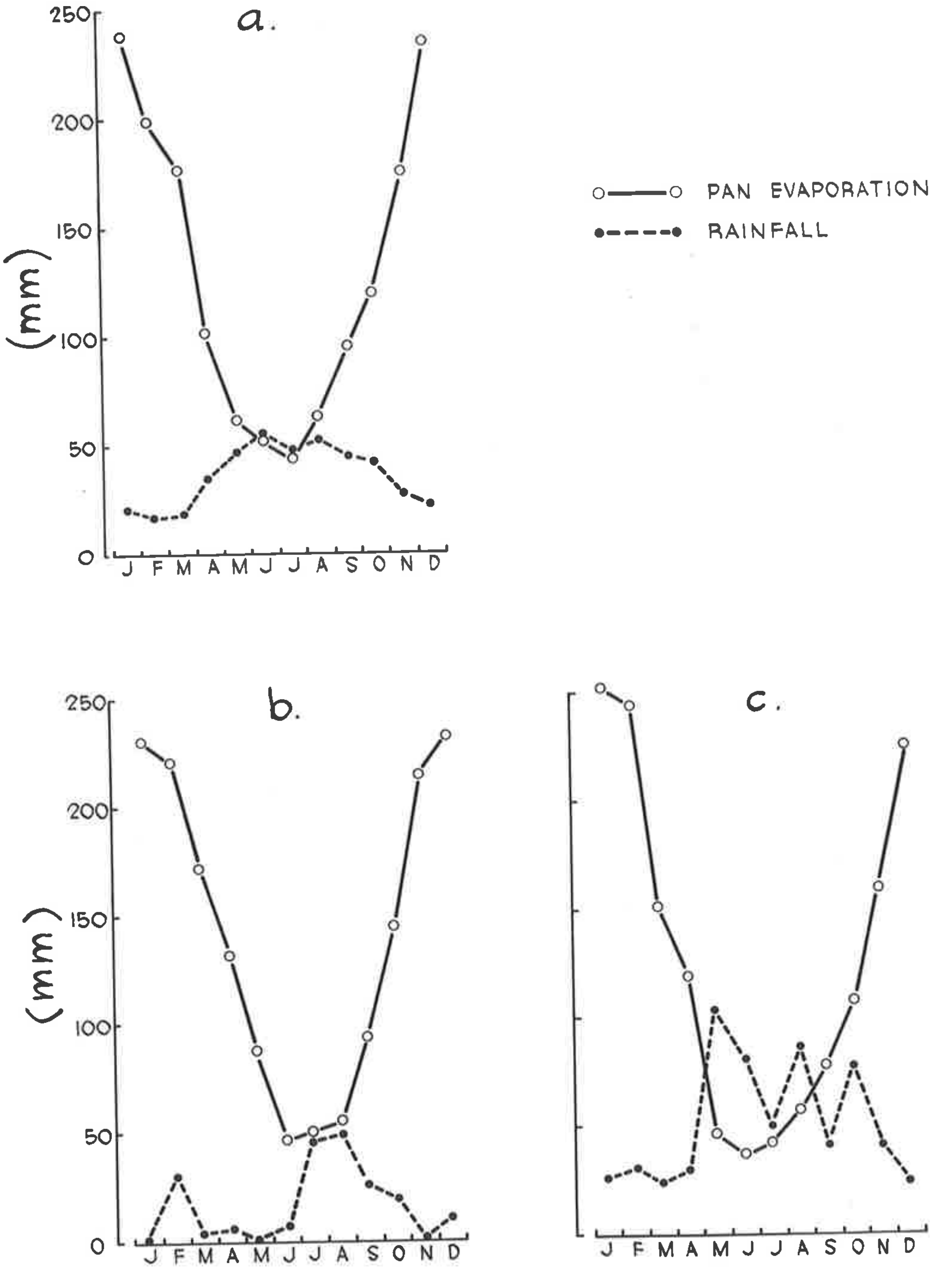


FIG. 1 Monthly rainfall and pan evaporation (Australian tank), (a) Longterm average (1931-1968). (b) 1967, (c) 1968. Data from Roseworthy Agricultural College Records.

Table 10

The mean monthly maximum and minimum air temperatures (1931 to 1968) at Roseworthy Agricultural College

Month	Temperature (°C)	
	Maximum	Minimum
January	28.2	13.9
February	28.1	14.1
March	26.2	12.5
April	21.6	10.5
May	19.7	8.6
June	15.1	6.4
July	14.2	5.5
August	15.4	5.9
September	18.2	7.0
October	25.5	8.6
November	24.4	11.2
December	26.8	13.1

(iii) General description of the soil

The soil is a sandy red-brown earth, Dr 2.33 (Northcote 1965). Red-brown earths comprise a large proportion of the wheat belt of South Australia. The thickness of the soil horizons varies considerably over distances of only a few metres and certain horizons have not been differentiated in some parts of the site.

The A_1 horizon is a weakly structured grey loamy sand of low organic matter content. The A_2 horizon is a weakly differentiated, light-brown, leached sand which changes abruptly to the B_1 horizon of red-brown medium clay with a well developed coarse prismatic structure, friable when moist and hard when dry. There is a clear change to the light brown calcareous loam of the lower B horizons, and the texture of the matrix becomes finer with depth. Carbonate concretions occur as soft patches or hard nodules in scant amounts in the B_2 and in large amounts in the B_3 horizons. The clay content increases with depth and the B_4 horizon is a light calcareous clay. This changes gradually to the C horizon which is a heavy red-brown to yellow clay with a massive blocky structure and well developed skins. The peds separate readily at medium water contents. Carbonates are present in isolated pockets and often as 'fingers' projecting downwards from the B horizon; black manganiferous concretions are often present. The depths of the horizons on the experimental site are described in Section 3.3.3.(i).

3.2. The Preliminary Experiment on rate of nitrogen

3.2.1. Objectives

This experiment was performed to test equipment for injecting radioactive solutions to specified soil depths; to develop a routine technique for measuring the total length of root in a sample; and to obtain preliminary information on the influence of rate of N supply on rooting characteristics and water use of wheat. The results were used in planning the main experiment.

3.2.2. Materials and methods

(i) Experimental design and treatments

The design was a 3 x 3 Latin square. The layout of the experiment is shown in Fig. 2. The whole field including the site of the experiment was sown with wheat, cv. Heron, in rows 18 cm apart at the rate of 90 kg ha^{-1} of seed on the 19th July, 1967. The nitrogen rates, N_0, N_1, and N_2 corresponded to 0, 55, and 170 kg ha^{-1} of N applied as $(NH_4)_2SO_4$ (21% N). The $(NH_4)_2SO_4$ was

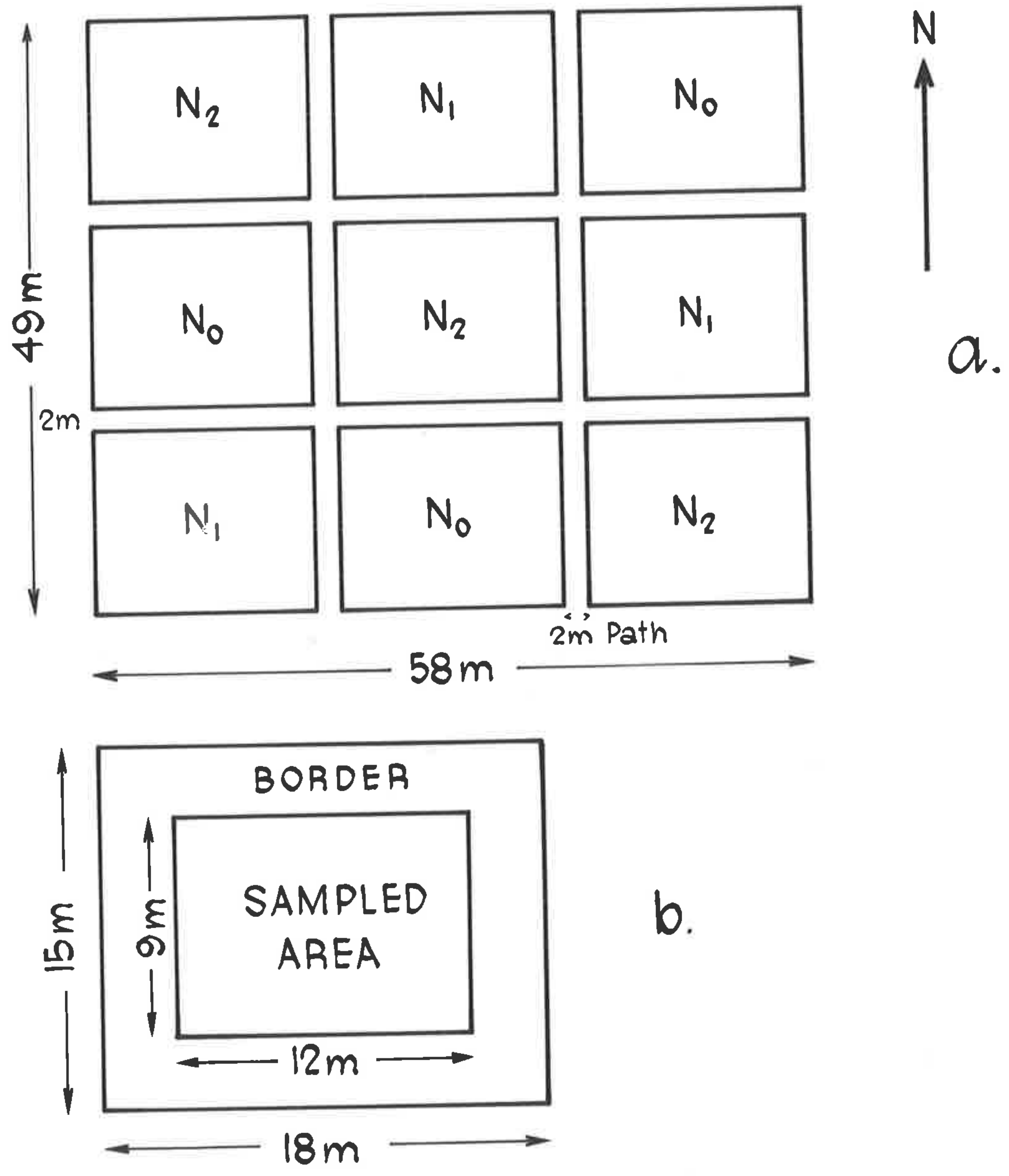


FIG. 2. (a.) Layout and randomization of the preliminary experiment. (b.) Details of individual plots.

broadcast 10 days after seedling emergence. All plots received 250 kg ha^{-1} of superphosphate containing 20 kg of P; one-half of the superphosphate having been harrowed into the top 5 cm of the soil one week before planting and the remainder being applied with the seed. The extent of crop was 10 m on the north and west and 500 m on the south and east edge of the experiment. Adjacent paddocks were sown with cereals.

(ii) Top growth

Establishment counts were made two weeks after seedling emergence along one metre lengths of row at five positions on each plot. The positions were scattered, local bias being avoided by locating exact positions with the eyes shut. The top growth on each plot was sampled at 5, 12, and 18 wk (maturity) after emergence by cutting plants at ground level from one 1 m x 1 m quadrat with one edge of the quadrat parallel to a row. The quadrats were cut at widely separated positions on each plot, local bias in placement being avoided by locating the quadrat with the eyes shut. After the number of tillers and ears in each quadrat had been counted, a subsample - approximately one-half of the sample - was separated into leaf laminae, stems and leaf sheaths, and ears. Lamina area was measured using an air-flow planimeter (Jenkins 1959). The dry weight of the tops was determined after drying in a forced draught oven at 85°C for 20 hr. Ear weight was measured at maturity. Ten ears were taken from scattered positions in the sub-samples, and, after the number of fertile spikelets per ear had been counted, the grain was separated by hand and the number and weight of grain measured.

(iii) Soil water content

Before planting, the mean water content of the soil profile at the site was measured by taking samples in 15 cm depth intervals with a 5 cm diameter sampling tube (Palm and Sykes 1962). Samples were taken to a depth of 90 cm at 20 locations scattered over the site. At six locations the depths were extended to 180 cm. At 5 and at 12 wk after emergence, three soil samples were taken on each plot within the 1 x 1 m area that had been sampled for top yield. These samples were taken from 0 to 10 cm, 10 to 25 cm and then for each 25 cm interval to a depth of 200 cm. All soil samples were weighed when wet, then dried at 105°C for 30 hr and the oven dry weights recorded. The volumetric water content θ of the soil was calculated using the equation

$$\theta = (\rho_b/\rho)W \qquad (15)$$

where ρ_b is the bulk density of the soil (determined in the main experiment), ρ is the density of water, taken as unity in c.g.s. units, and W is the gravimetric water content of the soil. The total depth of water (mm) in the ith layer of soil is given by

$$10\ \theta_i(z_{i+1} - z_i) \qquad \text{(mm)} \qquad (16)$$

where z cm is the depth (+ve downwards) to the top of the ith layer, and the depth of water in a profile of n layers is given by

$$10 \sum_{i=1}^{n} \theta_i(z_{i+1} - z_i) \qquad \text{(mm)} \qquad (17)$$

(iv) Testing of equipment and techniques

Tests were carried out to develop a non-contaminating probe, and a technique to apply solutions containing radioisotopes at specified soil depths. Two probes were tested. One consisted of a single cylinder with the ejection ports located along a 1.5 cm length of the cylinder where the diameter was 2.0 mm less than the rest of the probe. The other was a twin probe with two concentric shafts and is described in the main experiment. Each probe was connected to an automatic syringe that delivered the solution to be injected. One ml of the dye 'fast green' was injected at several positions near to the edge of a profile pit adjacent to the site of the experiment. After withdrawal of the probe, the tips were examined for contamination with the dye. The soil was then removed carefully from the side of the pit and the access holes examined for contamination with the dye along their length. The twin probe proved more satisfactory and was selected for use in the main experiment.

The line-intercept method, described by Newman (1966) and used for measuring the total length of root in a sample, was modified and evaluated. The segments of roots were spread over a plane area 5 x 5 cm on a fixed stage, and sets of pairs of numbers chosen at random were used to locate the movable head of the microscope, rather than using a permanent pattern of 'random points' marked on the plane area as described by Newman. The reliability of the intercept method was tested with a mixture of curved and straight segments of nylon thread, ranging in length from 0.3 to 1.2 cm and having a total length of either 50.0 or 100.0 cm. The diameter of the thread was 0.16 mm. Fields were viewed at a magnification of x 20 and the length of the transect was 1.1 cm. The total number of intersections between the axes of the segments of nylon thread and the line transect was recorded for each field, and the length and standard deviation calculated for increasing numbers of fields. The results are given in Table 11.

Table 11

Estimated length of 50.0 and 100.0 cm of nylon thread derived from intercept counting using equation (1) of Newman (1966)

Measured length (cm)	Number of fields viewed	Calculated length (cm)	S.D. (95% confidence limits)
50.0	10	72.4	27.0
	20	61.3	7.5
	40	51.8	12.1
	60	49.9	7.9
	80	48.8	6.0
	100	50.5	5.6
100.0	10	86.5	69.5
	20	106.6	25.5
	40	98.5	17.2
	60	101.5	13.4
	80	102.8	7.4
	100	102.5	6.8

The standard deviation decreased and more reliable estimates of the known length were obtained as the number of fields viewed was increased. For the 50.0 cm sample there was little change in the estimated length when more than 60 fields were viewed and the results were within ± 2.5% of the known length. Less reliable estimates were obtained with a total length of 100.0 cm of nylon thread on the 5 x 5 cm plane area. This was probably due to superposition of some of the segments as density of the segments was high. Nevertheless estimates within ± 2.5% of the 100.0 cm length were obtained when 40 or more fields were viewed. These results indicate that, provided the density of the root segments on the plane area being examined is within the range explored here, reliable estimates of the total length can be obtained. The details of the methods finally employed to separate the roots and to obtain estimates of root length are described in the main experiment.

Other methods followed published procedures, and references to procedures together with notes on quantities are given in Section 3.3.2.

3.2.3. Results of the Preliminary Experiment

(i) Plant growth

(a) Top growth. The seedlings emerged 9 days after planting. Germination was good and was even on all plots. However the season was extremely dry (Fig. 1b) and subsequent growth was poor. The number of grains per ear at N_1 and N_2 was significantly higher than at N_0, but the weight per grain at N_2

was significantly lower than at N_0 and N_1. There was no other significant effect of N on top growth. Five weeks after emergence lamina area index $L = 1.0$ on all plots. At anthesis, 12 wk after emergence, L had fallen to 0.5 on the N_0 and to 0.7 on the N_1 and N_2 plots. After 16 wk only the ears and stems remained green and the crop matured at 18 wk.

The total dry weight of tops and tiller density, the number of tillers per unit area, at 2, 5, 12, and 18 wk are shown in Fig. 3. The grain yield and the components of grain yield are given in Table 12. Although the grain yield was low, there were few pinched grain. The low yield was due to the small number of ears and low number of grains per ear.

Table 12

The influence of nitrogen rate on grain yield and the components of grain yield at maturity

Character	Nitrogen rate			L.S.D. (P=0.05)
	N_0	N_1	N_2	
Grain yield (g m^{-2})	96	98	110	n.s.
Number of ears (m^{-2})	257	268	287	n.s.
Weight per ear (g)	0.35	0.36	0.38	n.s.
Weight per grain (mg)	30.2	27.8	27.4	1.1
Number of grains per ear	11.6	12.9	13.9	1.3

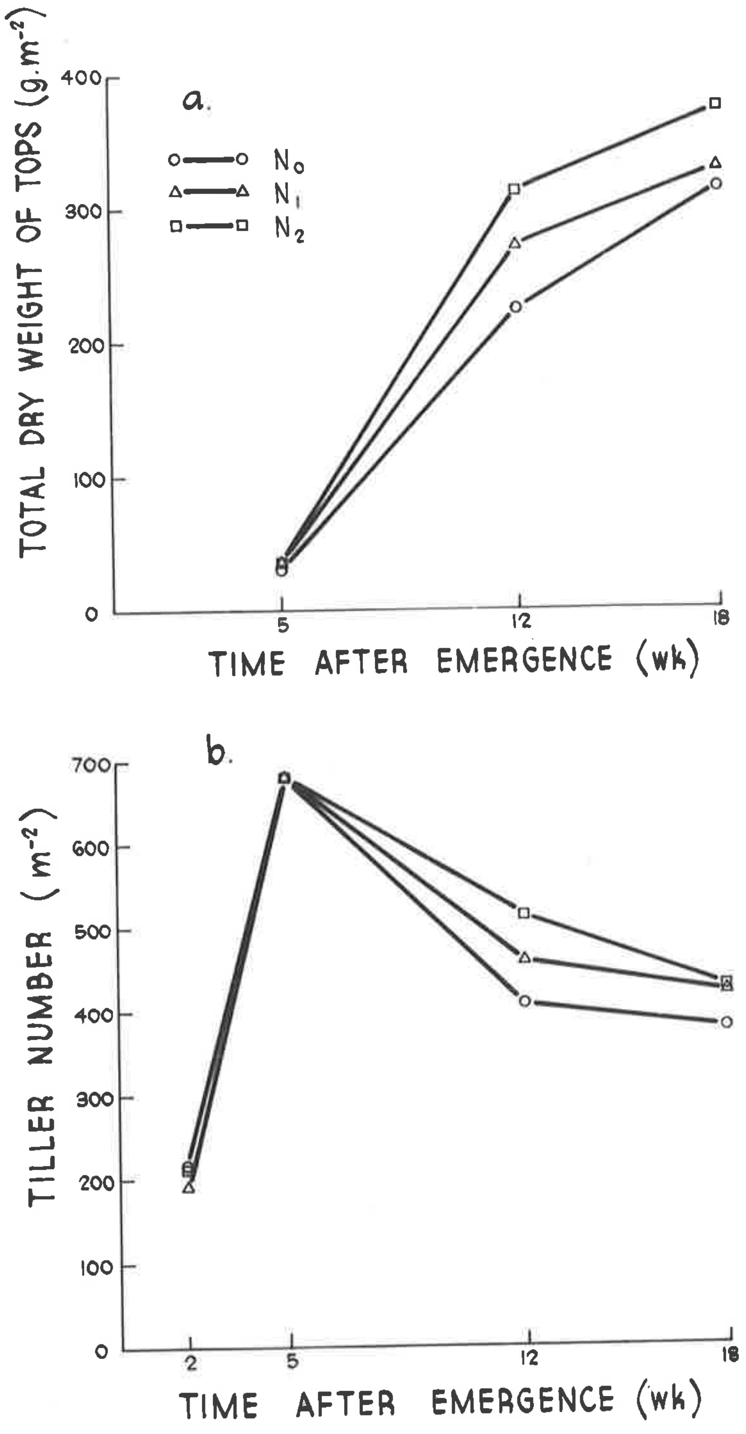


FIG. 3. The influence of nitrogen rate on (a) TOTAL DRY WEIGHT OF TOPS (b) TILLER NUMBER.

(b) Depth of rooting. Five weeks after seedling emergence roots had penetrated to between 50 and 75 cm depth, and at 12 wk to between 75 and 100 cm depth. The root samples were used to develop a procedure for the separation and measurement of root length, but statistical data were not obtained for the preliminary experiment.

(ii) Water content of the soil profile and plant water relationships

The top 150 cm of the soil profile contained 60 mm of available water (water retained at H = -300 to -15,900(1) cm of water) at planting. During the first 12 wk of the growing season total rainfall was 105 mm and the pan evaporation was 330 mm. Rainfall and pan evaporation data for the whole season are shown in Fig. 1b. Plant water stress, as shown by visible loss of turgor, occurred occasionally in the early part of the growing season, and from 7 wk after emergence the plants often wilted in the middle of the day.

The mean water content θ of each depth at the site at planting, and the mean of the N treatments at 5 and 12 wk after

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(1) The 15 atm percentage was approximated by 225 p.s.i.

emergence are shown in Fig. 4; the detailed values for each treatment and depth are included in Appendix Table 1. The N treatment did not affect θ at any time. At 12 wk the water content throughout the top 125 cm of soil profile had fallen below the values measured at planting, although the observed maximum depth of rooting was between 75 and 100 cm. At 12 wk the depth of soil occupied by the roots was as dry or drier than the arbitary wilting point, but water was retained below the root zone at suctions less than 15.8 atm.

3.3. The Main Experiment on seeding rate and rate of nitrogen

3.3.1. Objectives

This experiment was performed to assess the influence of seeding rate and the rate of N application on the extent of the root systems of individual plants, and on the rooting density and root abundance of the crop. The depths to which water was extracted by the crop were measured and the water withdrawal by the roots was determined as function of depth and time, chiefly to find whether it is necessary for the crop to root deeply in order to use water stored in the soil horizons below the root zone. Sufficient data were obtained on the tops to characterize the bulk of the crop and

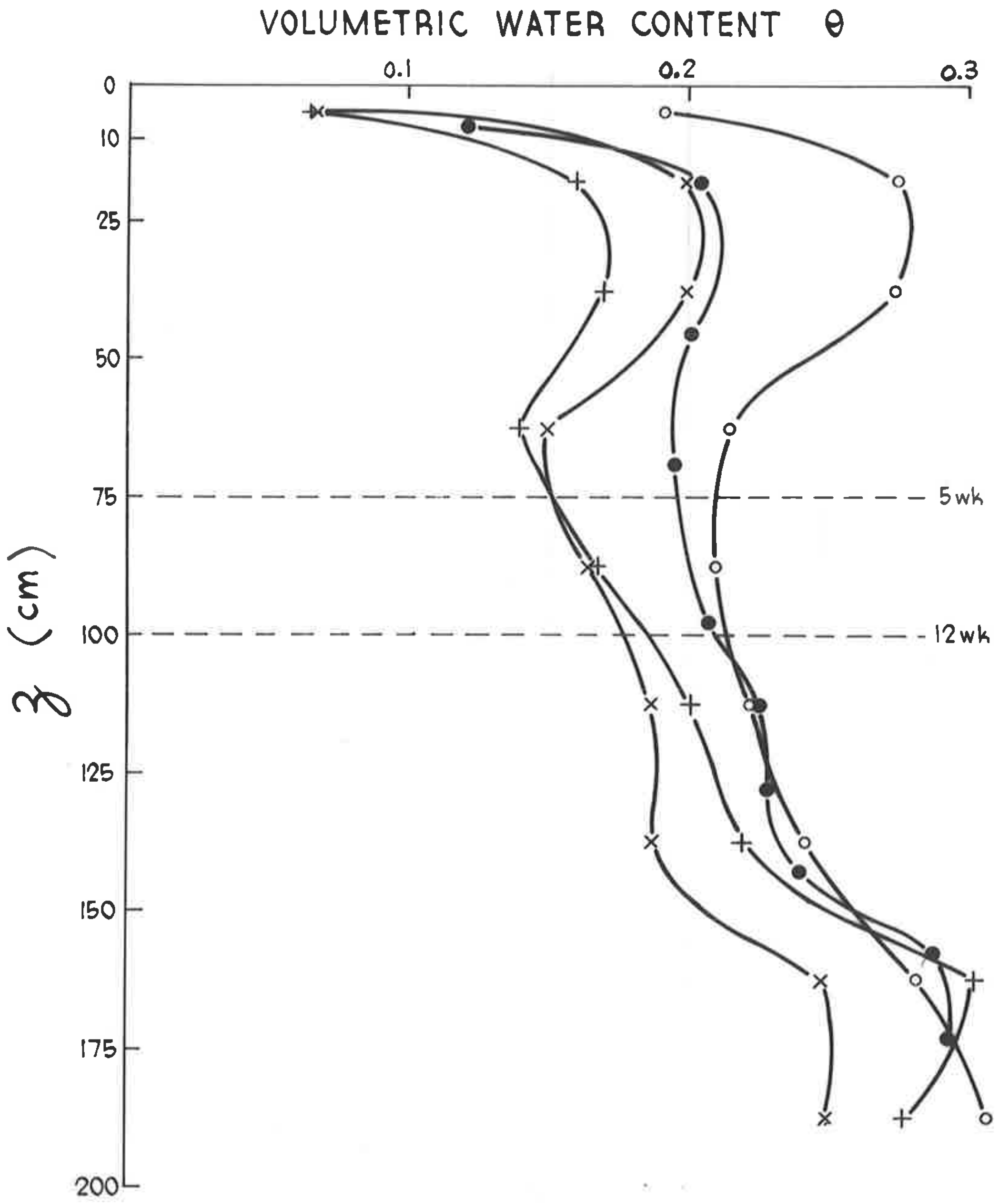

FIG. 4 Water content θ as a function of depth z
● PLANTING , ○ 5wk, + 12wk after emergence,
× the 15 atmosphere water retention.
Horizontal lines show depth of rooting at 5 and at 12 wk.

to assess the main features of the growth response of the tops. The response in top growth was not studied in detail, as it has been the subject of a number of earlier studies at Adelaide$^{(1)}$.

3.3.2. Materials and methods

(i) Experimental design and treatments

The experiment was a factorial 3 x 3 split-plot, replicated 3 times, with seeding rates as the main plots and N rates as the sub-plots. Seed of the cultivar Heron was planted on the 25th July, 1968. The three seeding rates were 10, 55, and 280 kg ha^{-1}, and are referred to later as S_1, S_2, and S_3. The seed was sown 5 cm deep in rows spaced at 18 cm intervals; S_3 was sown at the rate of 140 kg ha^{-1} of seed in each of two passes with a second set of rows at right angles to the first. The nitrogen rates, N_0, N_1, and N_2, corresponded to 0, 35, and 170 kg ha^{-1} of N applied as $NaNO_3$ (16% N). As only soil NO_3^--N was to be measured to characterize the soil, $NaNO_3$ was used in this experiment. The $NaNO_3$ was broadcast 15 days after seedling emergence. Superphosphate was applied as in the preliminary experiment.

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(1) Barley and Naidu (1964); Puckridge (1968); Puckridge and Donald (1967); Rawson (1967); Russell (1968); Donald (1963) have reviewed earlier publications.

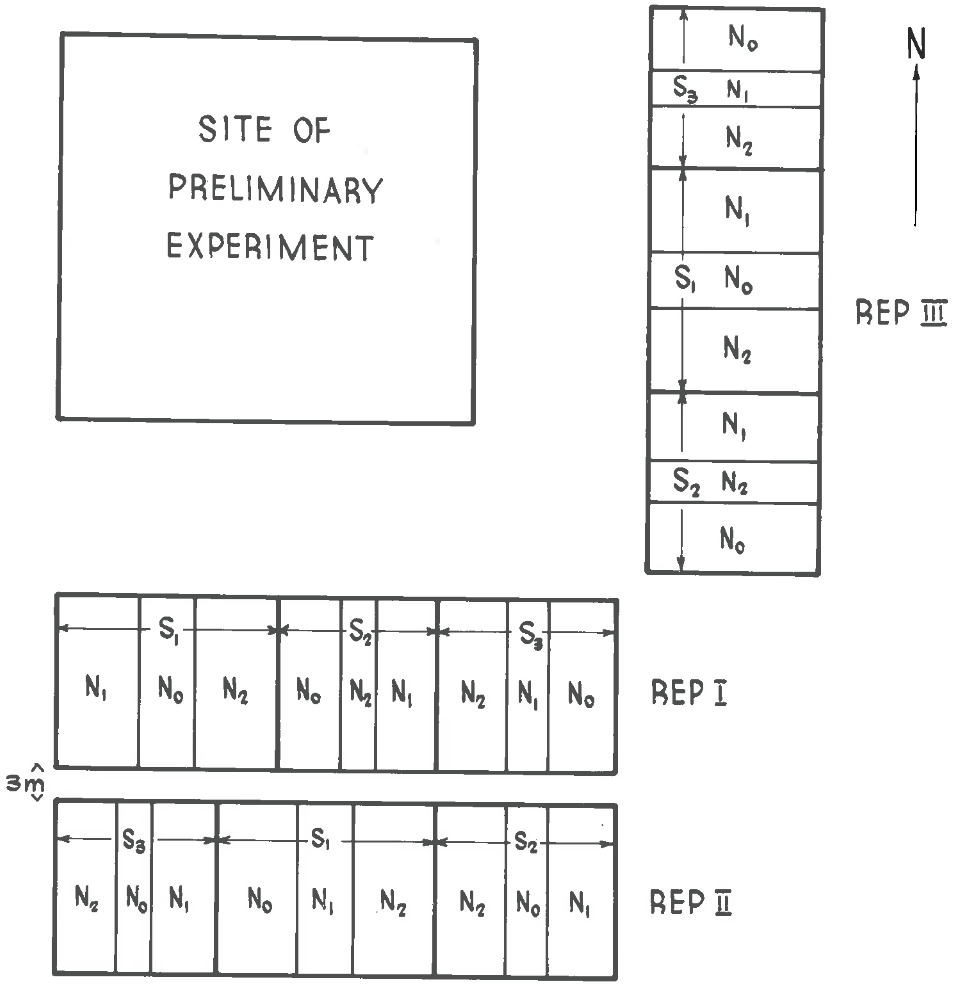
To minimize soil variability, replicates 1 and 2 were sited on the south and replicate 3 on the east of the area used for the preliminary experiment (Fig. 5). The row direction of the S_1 and S_2 plots on replicates 1 and 2 was north-south and on replicate 3 east-west. The change of row direction on replicate 3 was necessary in order to avoid turning the sowing machinery on plots that had been sown previously. A plan of the main experiment including plot sizes is shown in Fig. 5. The extent of crop was 10 m on the north and 600 m on the east of replicate 3, and 10 m on the west and 500 m on the south of replicates 2 and 3. The area used for the preliminary experiment was planted with barley. Adjacent paddocks were under cereals or naturally rejuvenating annual pasture.

(ii) Sampling schedule

A schedule of samples and measurements is shown in Table 13. The soil water characteristic, diffusivity, and capillary conductivity together with root data were obtained in the laboratory after the crop had matured and field operations had been completed.

Fig. 5. Layout and randomization of the main experiment.

The detailed layout of Rep II is shown in the lower part of the figure with the sampled areas shaded. The width of border between S rates = 5 m, and between N rates = 1 m.


SITE OF PRELIMINARY EXPERIMENT
N
N_0
S_3 N_1
N_2
N_1
S_1 N_0
N_2
N_1
S_2 N_2
N_0
REP III
S_1
S_2
S_3
N_1 N_0 N_2 N_0 N_2 N_1 N_2 N_1 N_0
REP I
3m
S_3
S_1
S_2
N_2 N_0 N_1 N_0 N_1 N_2 N_2 N_0 N_1
REP II

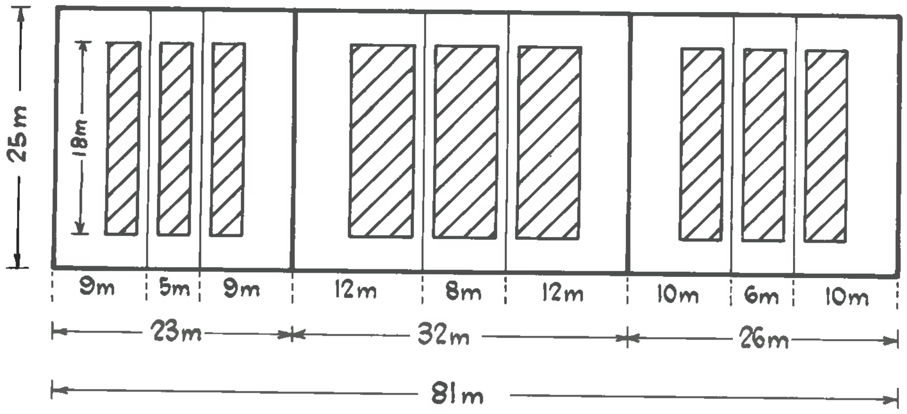

25m
18m
9m
5m
9m
12m
8m
12m
10m
6m
10m
23m
32m
26m
81m

Table 13

Sampling and measurement schedule for the main experiment

Measurement	Weeks from emergence (5.viii.68)							
	-3	+2	+8	+13	+18	+20	+22	+28
Soil:								
Depths of horizons								+
Bulk density (ρ_b)								+
Water content (θ)	+		+	+	+	+	+	
NO_3^--N	+		+		+		+	
Crop:								
Dry weight of tops			+	+	+	+	+	
Tiller density		+	+	+	+	+	+	
N content of tops			+		+		+	
Si content of tops			+		+		+	
Rooting density			+	+	+	+	+	
Root profiles					+			
Extent of root systems (with radioisotope tracers)			+	+	+			

On the occasions that radioactive solutions were injected, plant tops were sampled for radioactivity three days after injection. On the fourth, fifth and sixth days after injection, samples for measuring yield and lamina area of tops, rooting density, and soil water and nitrate contents were obtained, one replicate being sampled each day.

(iii) Characterization of the soil at the site of the main experiment

(a) Depths of the soil horizons. Two areas, each measuring approximately 150 x 100 m, located on the south and on the east of the preliminary experiment site, were surveyed by taking 5 cm diameter auger borings at 10 m centres, and the site was then chosen for the main experiment. Only 2 replicates could be accommodated on a relatively uniform site, and the third had to be located where the C horizon came closer to the surface. Nine auger borings at scattered locations along the length of each replicate, and 2 soil profile pits near the centre of each replicate, were examined to find the depths of the soil horizons.

(b) Bulk density. At the end of the growing season a profile pit was dug near the centre of each replicate, and 2 soil cores, 10.5 cm in diameter and 6.0 cm long were sampled from the middle of each soil horizon. The A and B_1 horizons were sampled by hammering metal cylinders (Coile 1936) vertically into the soil. Thin walled cans were inserted in the sampler to contain the sample and a rigid straight-edged knife used to trim the soil level with the edge of the sampler. For the lower horizons, the cylinders were pressed horizontally into the walls of the profile pits with mechanical jacks. At this time the soil profile was dry and most of the cores cracked during sampling.

Two further samples of each horizon were obtained from a second pit about 3 m distance from the first one on each replicate. Before these samples were taken, the profile had been wet to a depth of 2 m by ponding water on the surface and allowing infiltration for 2 days and drainage for a further 5 to 6 days. The moist profiles were sampled by pushing the cylinders into levelled horizontal surfaces at appropriate depths. Those samples were used for ρ_b and k measurements. After completion of these measurements the soil contained in each sample was dried to a constant weight at 105°C; ρ_b was obtained from the weight of the oven-dried soil and the volume $\pi r^2 l$, where r is the internal radius of the cutting edge of the Coile sampler and l is the internal depth of the can that served as a liner.

(c) Soil water characteristic. Desorption data were obtained for samples taken from each soil horizon on each of the three replicates.

'Undisturbed' soil cores 2.8 cm in diameter and 1.0 cm long were used to determine θ at suction heads $\leqslant$ 1035 cm of water. These samples were obtained by pushing a thin walled (1.5 mm) metal tube fitted with inner liners, 3.8 cm in diameter and 7.5 cm long, vertically into the horizontal surfaces from which moist bulk density samples were obtained. After sampling, the ends of the inner liner were sealed with polythene and water-proof tape and then stored at a constant temperature of 20 ± 1°C. Later, the soil was extruded and sectioned into 1.0 cm lengths, one section being used to determine θ at each of the specified suction heads. These sections were wet at a suction head of 10 cm of water for 12 hr. At suction heads of 10 and 100 cm of water, saturated ceramic plates were used with a bubble-tower to control suction; at 340, 680, and 1035 cm of water pressure plate apparatus was used as described by Richards and Weaver (1944).

Composite fine earth samples from each replicate were used to determine θ at suction heads $\geqslant$ 2110 cm of water. Similar quantities of soil were sampled from each of the four walls of the two pits on each replicate from which bulk density samples were obtained and bulked to give one composite sample for each horizon. After air-drying, the samples were crushed in a 'Star Two Roll Crusher' mill to pass through a 2.0 mm aperture sieve. Triplicate samples of approximately 20 g each were then used to determine θ at suction heads of 2,100, 5,280, 10,600 and 15,900 cm of water, following the pressure membrane procedure outlined by Richards (1965). The samples were allowed to absorb water off the membranes for 12 hr. Separate samples were used for each suction. All measurements were made in a constant temperature room at 20 ± 1°C. After desorption equilibrium had been reached at each suction, the samples were removed and weighed wet, dried to constant weight at 105°C, and their volumetric water contents calculated from $W_{,105^\circ C}$ and the appropriate values of ρ_b shown in Table 14 using Eq. (15).

(d) Soil water diffusivity and capillary conductivity. D and k were obtained from pressure plate outflow data at mean suction heads of 205 and 1500 cm of water. Outflow was measured from 2 samples of each horizon on each of the three replicates, except for the B_3 horizon present on replicates 1 and 2. This contained numerous calcareous concretions and could not be trimmed without excessive disturbance.

Materials. The outflow measurements were made in a constant temperature room at 20 ± 1°C using 'undisturbed' soil cores obtained from the moist profile [see Section 3.3.2.(iii)(b)]. The cores were 10.5 cm in diameter and were trimmed to 1.8 cm in height.

__Apparatus.__ Use was made of conventional volumetric pressure plate extractors manufactured by the Soilmoisture Equipment Company, Santa Barbara, California, and shown in Fig. 6. Air entered the ceramic plates at $h_p = -2000$ cm of water. Pressure heads $\leqslant 230$ cm of water were measured with a mercury manometer and heads $\geqslant 1250$ cm with a recently calibrated National Instrument Company gauge. The open end of the manometer and that of the horizontal capillary used to measure outflow were connected to gastight Winchester bottles of volume 2.5 l., the bottles serving as 'pressure dampers' to reduce pressure fluctuations in the systems when changes occurred in atmospheric pressure.

__Procedure.__ The porous ceramic plates of the extractor cells were saturated under vacuum with de-aired water before the apparatus was assembled. After being placed on the ceramic plates, the soil samples were wet at a suction of 10 cm of water for 20 hr and the initial head (180 cm of water) applied. When outflow ceased, the apparatus was flushed free of air, a first pressure increment of 50 cm was applied by raising the pressure head to 230 cm. Outflow was collected in a horizontal capillary (0.01 ml graduation) and was recorded at intervals of 15 min for a period of 6 hr.

Fig. 6. Apparatus used in the measurement of soil water diffusivity.

A = to manometer

B = to air supply and pressure regulator

C = National Instrument Company gauge

D = volumetric pressure place extractor

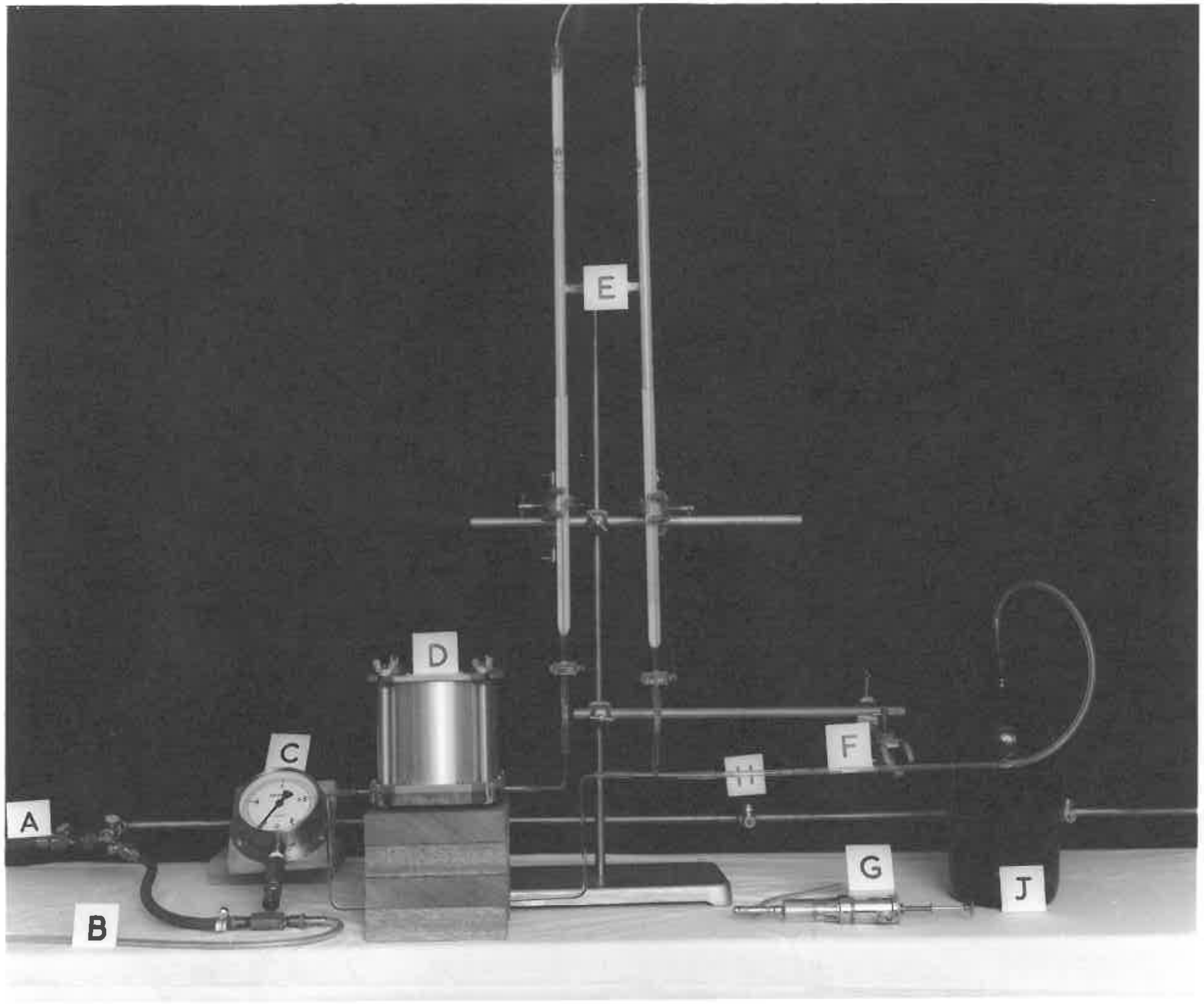
E = burettes for storage of outflow and water for flushing

F = horizontal capillary for measuring outflow

G = syringe used as aspirator for flushing

H = connection for next volumetric pressure plate extractor

J = Winchester bottle serving as a 'pressure damper'


E
D
C
F
H
A
G
J
B

The pressure head was then increased to 1,250 cm of water. After outflow had ceased, the apparatus was flushed free of air again, and a pressure increment of 500 cm was applied by raising the head to 1,750 cm. Outflow was again recorded at the times stated above. The samples were then removed and weighed wet, dried to constant weight at 105°C and weighed again.

D was derived from the outflow data by the curve matching procedure described by Peck (1966). Matching was confined to less than 0.2 l^2/D units of outflow time, where l is the length of the core. For this period the outflow is equal to that which would occur from a core of semi-infinite length (Sine and Bentz 1963). Curve matching was performed to find the approximate value of 0.2 l^2/D and then repeated in time $< 0.2\ l^2/D$. Where 0.2 l^2/D $\leq$ 60 min the value of D was checked with reference to Eq. (1) of Doering (1965). The values of D obtained by these two methods were in good agreement and the values of D used in all calculations were derived from the curve matching procedure. After D was obtained, k was calculated from

$$k = D\Delta\theta/\Delta H \qquad (\text{cm min}^{-1}) \qquad (19)$$

the value of $\Delta\theta$, the change in the equilibrium values of θ produced by the step ΔH, was obtained from the soil water characteristic curve.

For comparison with the values obtained as described above, *k* was calculated independently from the soil water characteristic curve using Eq. (7) of Marshall (1958). A porosity class interval of 0.02, and a numerical constant of 1.6 x 10^3 was substituted into Marshall's Eq. (7) to yield *k* in units of cm per min. A listing of the computer programme used for this calculation is included in Appendix 10.

(iv) Effects of the treatments on soil properties and crop growth

(a) Soil water and nitrate. Soil samples were taken with a 5 cm diameter auger from 0 to 10 cm, 10 to 25 cm, and then for each 25 cm interval to a depth of 200 cm. Before planting nine soil cores were taken at points scattered along the length of each replicate to measure the initial content of water and NO_3^--N. Within the 1 x 1 m quadrat cut for top growth on each sub-plot on each sampling occasion the soil was sampled at three points designated 1, 2, and 3. The soil from each depth interval for sample 1 was sub-sampled into three equal parts (20 - 70 g) and labelled 1a, 1b, and 1c. The soil samples were then treated as follows:

Sub-sample 1a - frozen in the field with liquid CO_2 immediately after coring and stored at

-4°C pending nitrate determination.

Sub-sample 1b - weighed wet, dried at 85°C and weighed, then dried at 105°C and reweighed to determine $W,_{85^\circ C}$ and $W,_{105^\circ C}$.

Sub-sample 1c, and samples 2 and 3 - weighed wet, dried at 85°C and weighed again to determine individual $W,_{85^\circ C}$. These samples were used later to measure root length.

For sub-sample 1b and samples 2 and 3, $W,_{105^\circ C}$ was calculated from the relation

$$(W,_{105^\circ C}) = (W,_{105^\circ C}/W,_{85^\circ C})_{1b} \cdot (W,_{85^\circ C})_{1c,\,2,\,3} \qquad (18)$$

Values of θ were calculated from $W,_{105^\circ C}$ and the appropriate value of ρ_b shown in Table 14 using Eq. (15). The NO_3^--N content of freshly thawed 0.5 g lots of sub-sample 1a were determined, without preliminary drying, by the chromotropic acid method of Clarke and Jennings (1965). One 10 g lot of the sub-sample, also taken after thawing, was dried at 105°C to determine $W,_{105^\circ C}$. The NO_3^--N contents were expressed volumetrically using the ρ_b data in Table 14.

(b) Top growth. Two weeks after emergence establishment counts were made along five 1 m lengths of row at scattered locations on the S_1 and S_2 plots, and within five 20 x 20 cm quadrats at scattered locations on the S_3 plots. Top growth was sampled at the following times:

Sampling Date	Time after emergence (wk)	Growth stage
2- 3. ix.68	8	spike initiation
8-10. x.68	13	boot stage
11-13. xi.68	18	one week after anthesis
25-27. xi.68	20	late dough stage
11-13.xii.68	22	maturity

The sampling procedure during the growth of the crop was determined primarily by the radioisotope requirements and by operational convenience. The sub-plots on replicates 1 and 2 were sampled from the northern end and those on replicate 3 from the eastern end. The area available at each sampling occasion was 3 m long and extended across the width of the sub-plot. Areas used for radioisotope work were avoided when taking soil samples, and plant samples to measure top growth. At 8 wk local bias in choosing particular plants was avoided by locating the quadrat centre by tossing pegs onto the area with the eyes shut. At later harvests the pegs could not be seen readily between the plants and the quadrat was located with the eyes shut. As in the preliminary experiment, one edge of the quadrat was set parallel to a row. Tiller density, lamina area, grain yield, and the components of grain yield were measured using the same procedures as in the preliminary experiment.

(c) **Nitrogen and silicon content of the plant tops – sampling procedure.** 25 g sub-samples of the dried plant tops were coarsely ground in a 'Wiley' mill, mixed, and further sub-sampled to measure the N and Si content of the plant tops. At 8 and at 18 wk sub-samples of whole tops were analysed. At maturity separate N determinations were made for the leaves and stems and for the grain,(1) and separate Si determinations were made for the leaves and stems, the lemmae and paleas, and for the grain.

Analytical procedures – Nitrogen. The N content of 0.5 g sub-samples was determined with a 'Technicon' Autoanalyser using the method of Williams and Twine (1967).

Silicon. 2 g sub-samples of the coarsely ground plant material were subjected to further grinding for 2 min in the 100 cc

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(1) The N content of the lemmae, paleas, awns, and rachis was not determined at maturity.

vial of a 'Seibtecknik' mill; 0.5 g sub-samples of the finely ground material were then formed into 3.1 cm diameter discs backed with boric acid. The discs were formed by applying a pressure of 2.1×10^3 kg cm^{-2} to the material with a 'Blackhawk' hydraulic ram. The Si content was then determined by x-ray fluorescence spectrography⁽¹⁾.

(d) Root growth, rooting density, and root distribution - Root length. The three soil samples from each sub-plot referred to in Section 3.3.1.(iii)(c) were bulked, fragmented in a 'Berry's Junior' mincing mill and sub-sampled to measure rooting density. The fragmentation cut the roots into short (< 2 cm) lengths and allowed more efficient sub-sampling and root separation. Because of the relatively high rooting densities in the topsoil, 50 g sub-samples of soil were used to measure root length in the top 10 cm of the soil profile at 8 wk, in the top 25 cm at 13 wk, and in the top 50 cm at 18, 20 and 22 wk; 100 g sub-samples were used for the lower depths at each harvest. Samples obtained from the lower horizons at each harvest were put through the elutriation procedure to ensure that the deepest roots were included in the measurements.

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(1) The Si measurements were made by J.T. Hutton, C.S.I.R.O., Division of Soils, Glen Osmond, South Australia. The method of analysis is described in C.S.I.R.O., Division of Soils, Tech. Memo., 47/1969.

The roots were separated from the soil by dispersion of the soil followed by elutriation, and were retained on a 0.25 mm aperture sieve (Barley 1955). The root separate was then floated in a 5 x 5 cm dish and the larger macroscopic fragments of soil organic matter were removed with tweezers. In order to avoid clumping and superposition of roots in the dish, the root separates from the 50 g topsoil (0 to 10 cm) samples were divided into two parts for measurement.

The length of root in each sample was obtained by intercept counting. For each root separate, 60 fields were viewed at a magnification of x 20, and a count was made of the intercepts formed by the axes of segments of root on randomly distributed line transects. A travelling microscope with graduated x - y axes was used to locate each field according to pairs of random numbers. Sets of 60 pairs of numbers chosen at random within the range of the scales on the x - y axes had been generated previously with a computer program which also arranged one number of each pair in ascending order. The program is listed in Appendix 11. The arrangement of the numbers saved time when selecting positions on the x - y axes. A hair line in one eyepiece of the microscope formed the line transect. The eyepiece was spun to obtain a new orientation of the transect for each of the successive 60 fields.

intercepts formed by axes of root segments with root hairs and those without root hairs were recorded separately on a two-channel counter (Fig. 7). Following Newman (1966), the total length of root R per separate was given by

$$R = \pi NA/2nl \qquad (\text{cm}) \qquad (20)$$

where N is the number of intercepts between root and transect, A (cm^2) is the plane area on which the root sections and transects were distributed, n is the number of transects and l (cm) is the length of the transect.

The root length per unit volume of soil or 'root abundance' (strictly the volumetric abundance of roots) in the sample layer, R_{v_i} was given by

$$R_{v_i} = R_i \, \rho_{b_i} \qquad (\text{cm}^{-2}) \qquad (21)$$

where R_i is the root length per g dry weight of soil. The mean root length per unit volume of soil for the entire root zone, $\overline{R}_v$ was given by

$$\overline{R}_v = \frac{\sum\limits_{i=1}^{n}[R_{v_i}(z_{i+1} - z_i)]}{\sum\limits_{i=1}^{n}(z_{i+1} - z_i)} = \frac{R_a}{Z} \qquad (\text{cm}^{-2}) \qquad (22)$$

where z (cm) is the depth to the top of each layer, Z is the depth

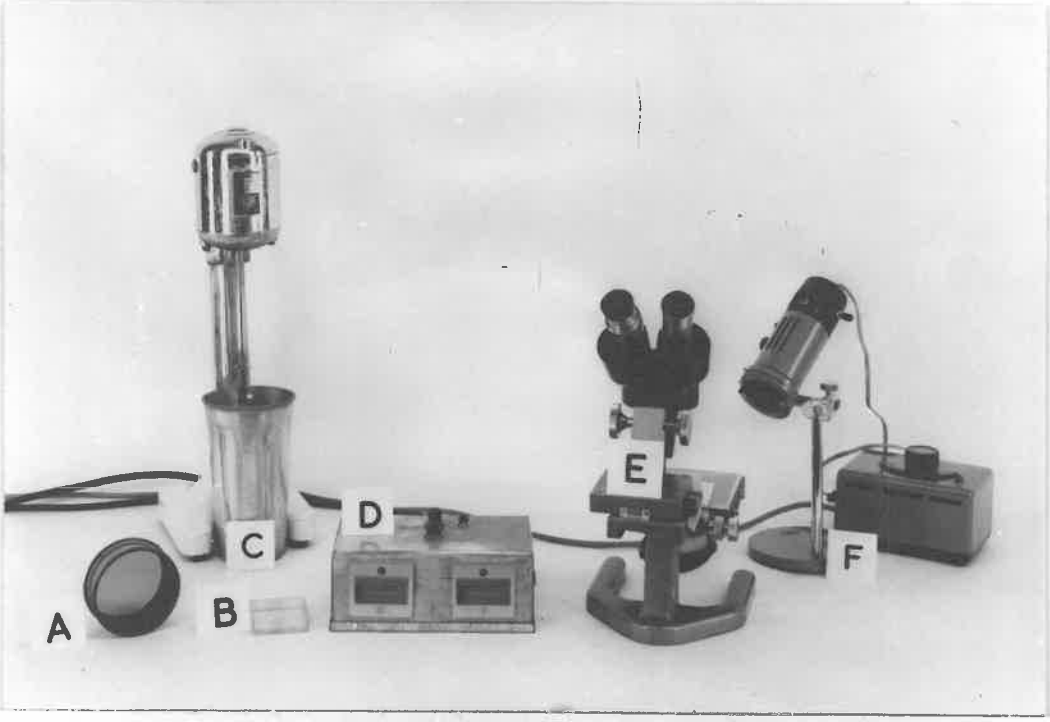


FIG. 7. Equipment used for root separation and intercept counting.

A. Sieve.
B. Dish.
C. High-speed disperser.
D. 2-Channel counter.
E. Binocular microscope with X-Y head.
F. Microscope lamp.

of the root zone, and R_a is the root length per unit area of ground surface or 'rooting density' (by analogy with plant density).

The mean root length per tiller R_T was derived from

$$R_T = R_a \times 10^4/x \quad \text{(cm)} \qquad (23)$$

where x is the number of tillers per sq. m.

The mean daily rates of change of the quantities were calculated from the changes between successive dates of sampling.

Form of the root profile. Two weeks after anthesis pin-boards were used to obtain one soil block from each sub-plot on replicate 2. The boards, 60 cm wide x 110 cm deep, were lined with black polythene and had pins 8 cm long at 5 cm centres. They were placed vertically and jacked into the walls of profile pits in a direction normal to the plant rows, and then removed together with a block of soil 10 cm thick. Soil blocks were also taken from 100 to 150 cm depth on sub-plots S_1N_0, S_1N_2, S_3N_0 and S_3N_2 using pin-boards 60 cm wide and 50 cm deep. After air-drying, the soil blocks were soaked in a solution of 0.1% sodium hexametaphosphate for 25 to 50 hr. The soil was then washed away with a non-adjustable fine spray of water delivered from a 'rose'. Finally the polythene backing sheet and the root profiles were lifted from the pinboard and photographed.

Delineation of individual plant root systems. The extent of individual plant root systems was estimated by the detection of radioactivity in the plant tops absorbed from sources placed in the soil at 5, 17, 37, 62, 87, 112 and 137 cm depths directly beneath a reference plant (Fig. 8a). There was one reference plant per sub-plot per sampling occasion for each depth and one injection was made beneath each reference plant. The injection depths were randomized. The first reference plant on each sub-plot was located on the third row of the sampled area shown in Fig. 5. The distances between reference plants on the same or on adjacent plots were set at more than twice the estimated spread of the roots and other reference plants were located by measurement (see Fig. 8a). Each injection consisted of 1 ml of a mixture of ^{32}P as orthophosphate and ^{35}S as $Na_2\,^{35}SO_4$ in aqueous solution. The injection program and the radioactivities of the solutions used on each occasion are as follows:

Time after emergence (wk)	8	13	18
Deepest injection (cm)	112	137	137
Radioactivity of solution (µC per ml)			
^{32}P	30	30	30
^{35}S	20	20	40

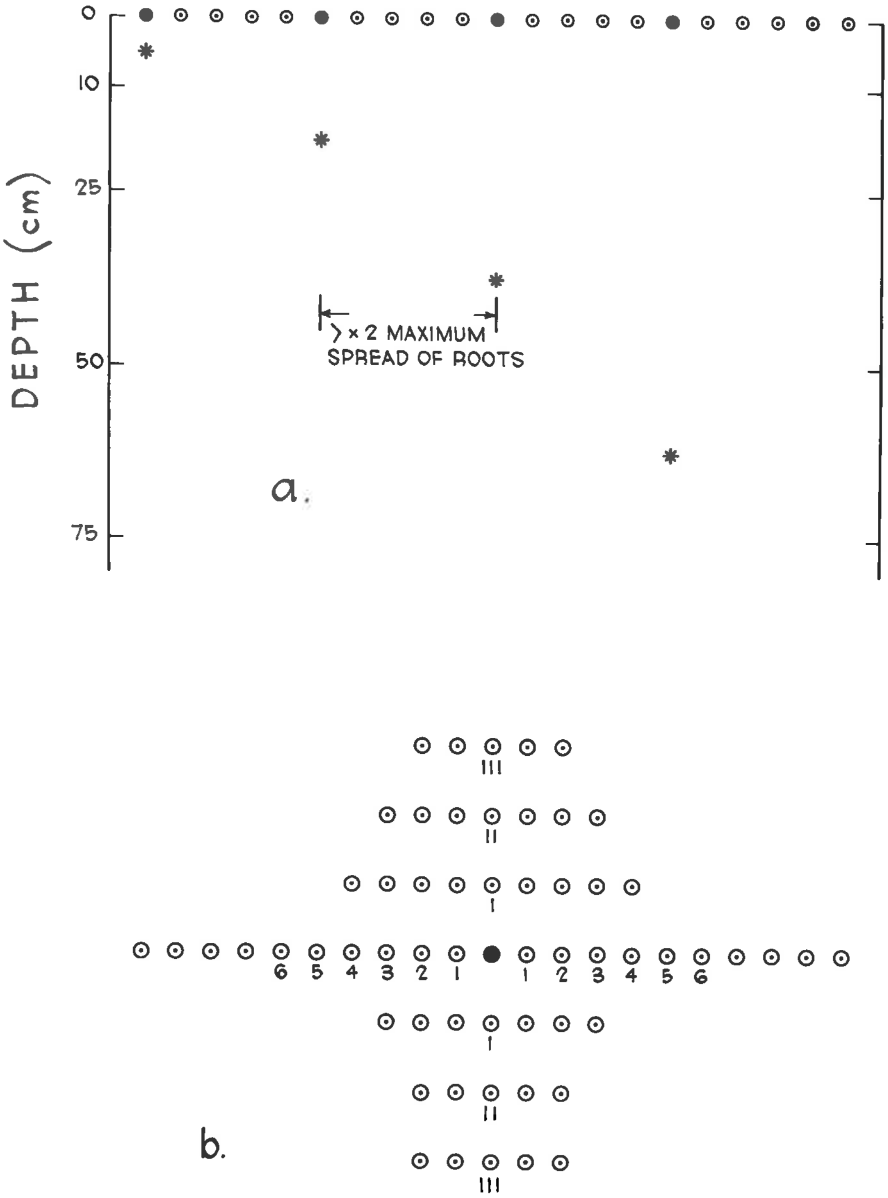


FIG. 8 (a.) Section through the soil profile showing relative location of injection points at each depth
(b.) Plants sampled for radioactive assay :
I... III = Plants sampled across rows, 1...6 = Plants sampled within rows, corresponding numbers were bulked (Not drawn to scale).
● = Reference plant, ○ = Other plants, ✱ = Injection point.

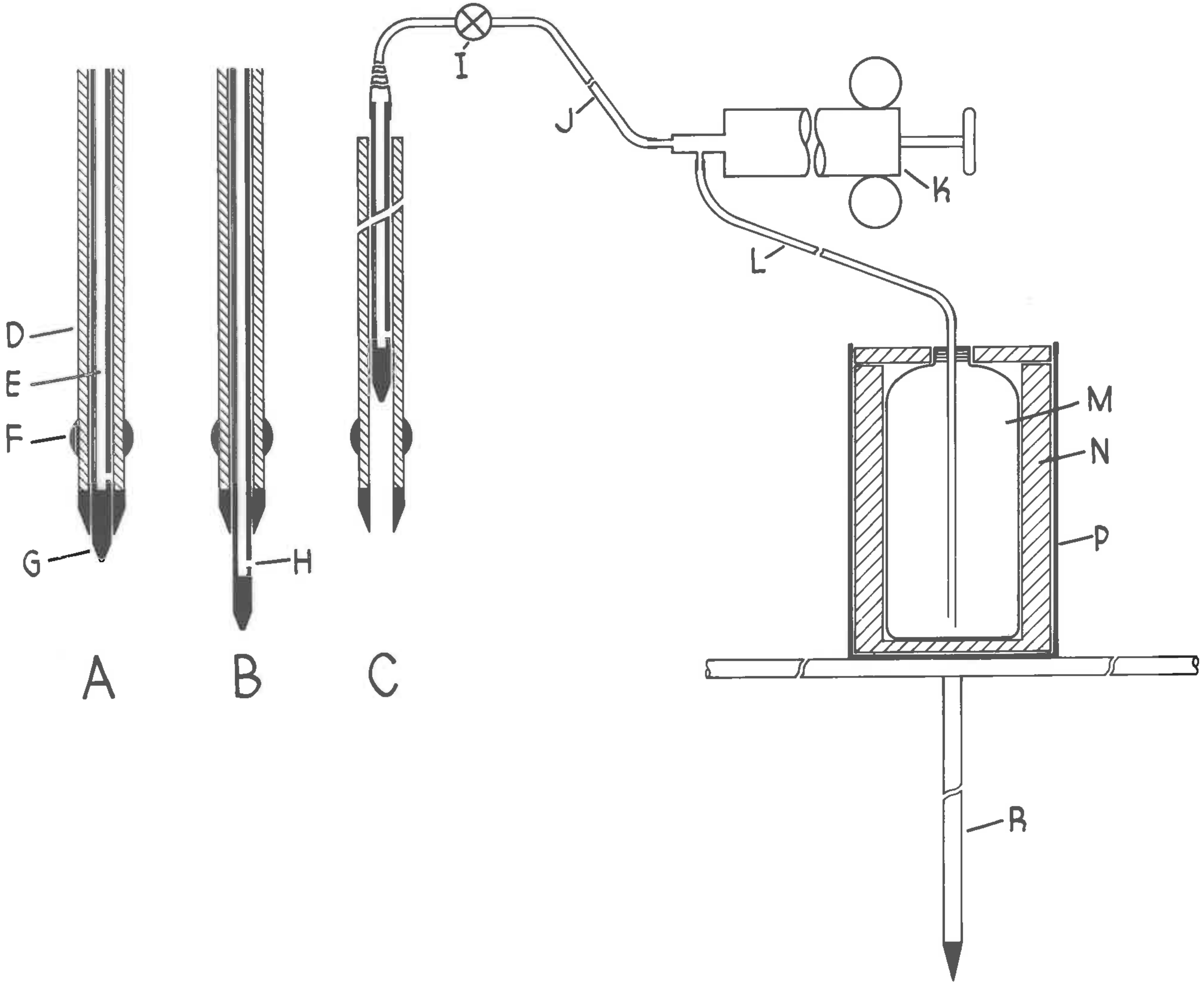
An access hole was made at each injection site by pushing a steel rod of 8.0 mm diameter to a depth 2 cm greater than the depth at which the radioactive solution was to be injected with the probe shown in Fig. 9. At the start of each series of injections, the inner cylinder, (E) - see Fig. 9 -, the syringe (K), and the connecting tubes (J), (L), were flushed free of air and filled with the radioactive solution. The tips of the inner and outer cylinders were set at position (A), the injector inserted into the access hole to the required depth, and the inner cylinder then set at position (B). One operator plunged the syringe (K) to inject the radioactive solution, while a second operator opened the control tap (I) at the beginning and closed it at the end of the downstroke of the syringe plunger. After injection of the solution the inner cylinder was retracted to position (C) and the injector was then withdrawn from the access hole. After withdrawal the tips of the inner and outer probes were cleaned of any particles of soil and reset at position (A) in readiness for the next injection.

Three days after injection the whole reference plant, and other plants at approximately 5 cm intervals on either side of the reference plant within the row, were cut off at ground level. On the S_1 and S_2 plots which had been sown in one direction only, plants were sampled on either side of the reference plant on three adjacent rows. On the S_3 plots which had been sown in two directions,

Fig. 9. The injection equipment.

Positions of the outer and inner cylindrical shafts are shown at

A – insertion, B – injection, C – withdrawal
D = outer cylinder (6.5 mm o.d., 4.5 mm i.d.)
E = inner cylinder (2.5 mm o.d., 1.5 mm i.d.)
F = welded bead, maximum diameter of probe (7.5 mm)
G = welded tip of inner cylinder
H = ejection port (0.5 mm diameter)
I = control tap
J = polyethylene connection from inner cylinder to
K = automatic syringe
L = polyethylene connection from K to M
M = polyethylene bottle (250 cc) – reservoir for radioactive solution
N = lead shield (8 mm)
P = metal container for M and N
R = stand to which P is attached


D
E
F
G
H
A
B
C
I
J
K
L
M
N
P
R

samples were taken at 5 cm intervals in the other set of rows at an angle of 90°. Plants equidistant from the reference plant - plants having the same number on Fig. 8b - were bulked for radioactive assay.

Samples of whole plant tops were dried at 85°C, ground in a 'Wiley' mill, and digests of 0.5 g sub-samples were prepared using nitric-perchloric acid digestion (Johnson and Ulrich 1959). All extracts were made up to 100 ml with distilled water and a 0.5 ml aliquot placed in 10 ml of scintillation fluid [100 g naphthalene, 7.0 g 2,5 diphenyloxazole and 0.5 g 1:4 - di(2-(5 phenyloxazolyl)) benzene in one litre dioxan] and assayed for radioactivity on a 'Packard Tri-carb' liquid scintillation spectrometer, Model 3375, fitted with automatic external standardization. ^{35}S was counted in the ^{14}C channel set at 15 to 450, and ^{32}P was counted above ^{14}C. Counts were terminated at a preset level of 5000 or 10 min, whichever came first.

At 18 wk after emergence, the injector used to apply radiotracer at depths ≥62 cm broke after injecting replicate 1; a replacement could not be obtained in time to complete the series of injections on this occasion, and the radiotracer injections were discontinued. (At 18 wk the water content of the top metre of the soil was low and the uptake of radiotracer could seldom be detected for injection points < 1 m deep.)

(a) Water withdrawal by roots and vertical flux of water through the soil. These two quantities were calculated using a computer program based on the analysis outlined by Rose *et al.* (1965) and Rose and Stern (1967). The program is listed in Appendix 12 with comments. The volumetric water content θ for each depth was plotted as a function of time after emergence, a separate graph being constructed for each sub-plot. Estimates of θ at 3 days on either side of the plotted values at 13 and at 20 wk were found by interpolation on the lines joining the points for 8, 13, and 18 wk and for 18, 20, and 22 wk. For each value of θ obtained in this manner, a corresponding value of unloaded suction was read off the soil water characteristic curve for the appropriate replicate and depth. The overburden pressure B was found from the ρ_b values in Table 14, and the increment in head due to overburden was obtained using an arbitary pore pressure coefficient $a = 0.1$. The capillary conductivity k in the vertical direction was obtained for each depth and sampling time by finding the value corresponding to θ according to the procedure outlined below Table 15. The smallest depth at which withdrawal and vertical flux were calculated was 5 cm.

3.3.3. Results and Discussion of the Main Experiment on seeding rate and rate of nitrogen

(i) Characterization of the soil at the site of the main experiment

(a) Depths of the soil horizons. The mean depths of the soil horizons on each replicate are shown in Fig. 10 and a photograph of the soil profile on each replicate is shown in Fig. 11. The development of the horizons was similar on replicates 1 and 2, but replicate 3 had fewer horizons clearly differentiated and the C horizon came nearer to the surface.

(b) Bulk density. The mean ρ_b values for the several horizons sampled at dry and moist states are given in Table 14. The ρ_b of the A_1 horizon samples taken from replicates 1 and 2 when the soil was moist, was higher than that of samples taken when the soil was dry. This difference is attributed to compaction during sampling. There were no other significant differences between the moist and dry states, or differences between replicates, and the mean values shown in Table 14 have been used in all calculations involving ρ_b in the thesis.

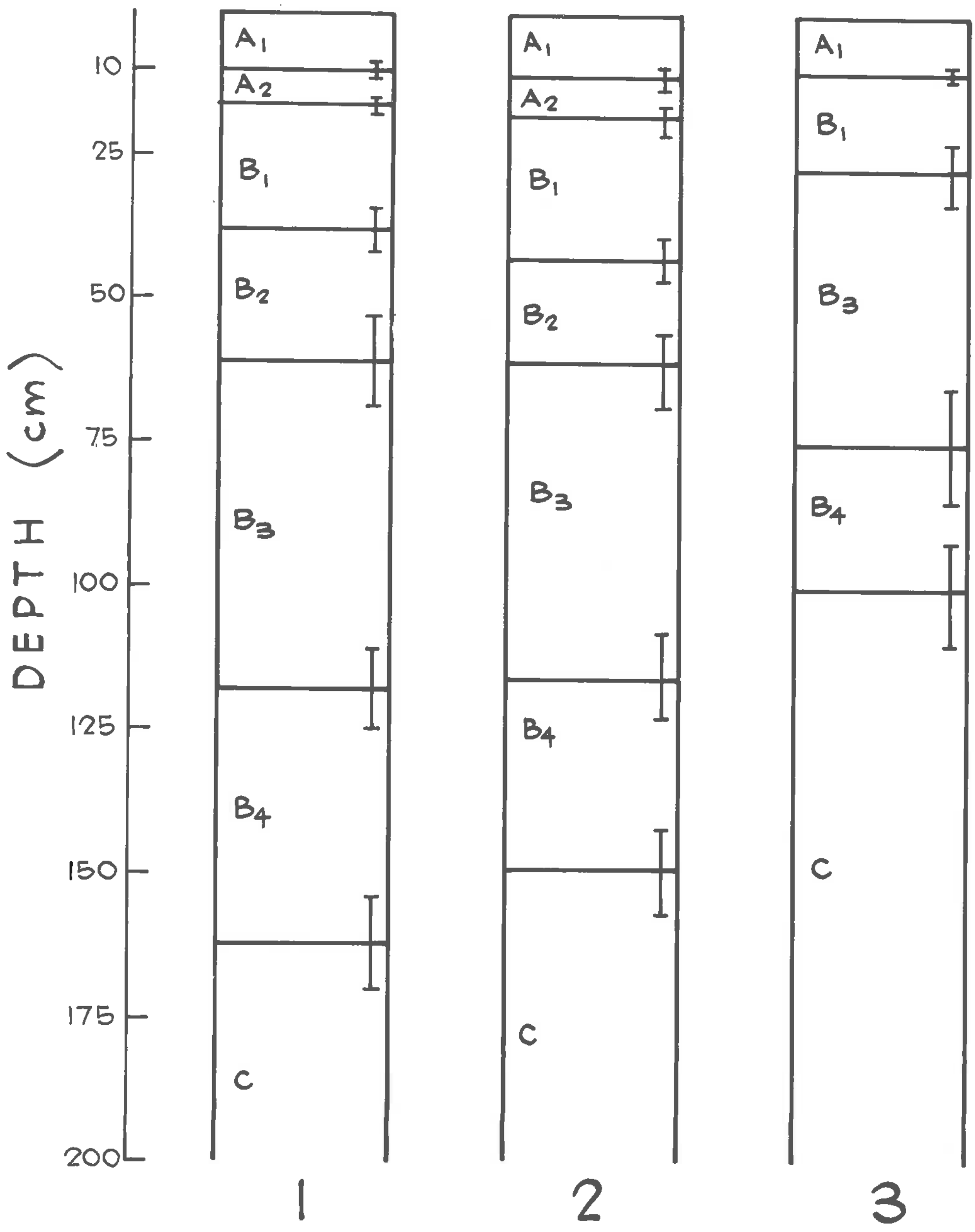


FIG. 10 Mean depths of the soil horizons on replicates 1, 2, and 3; the vertical lines represent the standard deviations from the means.

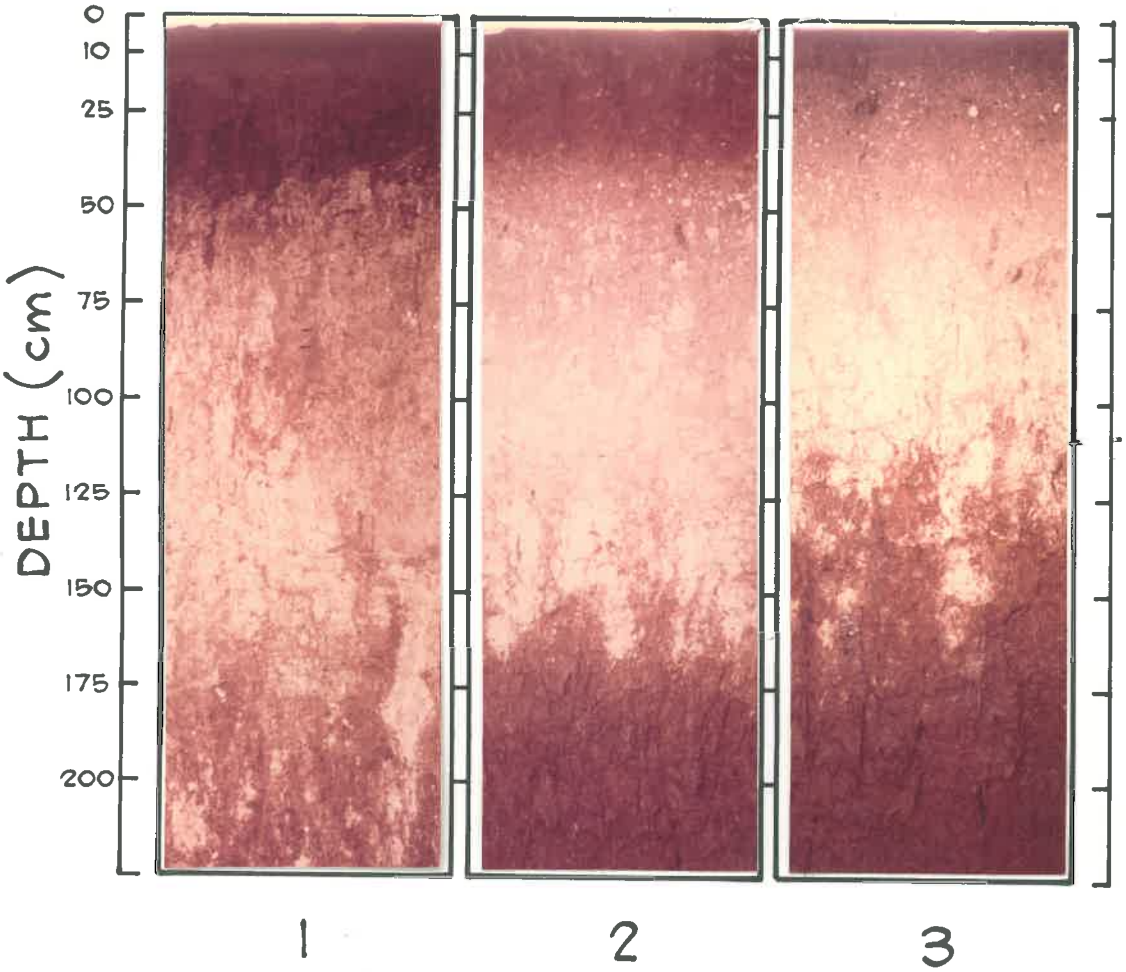


FIG. 11. Representative soil profiles on replicates 1, 2 and 3.

Table 14

The bulk density ρ_b of the soil horizons.

Values are the means of the three replicates

Soil horizon	ρ_b (g per cc) Dry	Moist	L.S.D. (P=0.05)	Mean ρ_b (g per cc)
A_1	1.53	1.59	0.06	1.56
A_2	1.70	1.72	n.d.	1.71
B_1	1.49	1.53	0.14	1.51
B_2	1.35	1.41	n.d.	1.38
B_3	1.30	1.43	0.27	1.36
B_4	1.33	1.41	0.11	1.37
C	1.54	1.57	0.22	1.56

n.d. = not determined; horizon present on replicates 1 and 2 only.

(c) Soil water characteristic. The soil water characteristic for each horizon on the 3 replicates - liquid desorption measurements for unloaded suctions - is shown in Fig. 12. Results for each horizon on each replicate were used in subsequent calculations and are included in Appendix Table 2. The curves in Fig. 12 show that most of the 'available' water in each soil horizon was retained at $h_m \geqslant -1550$ cm of water. The water content θ of the B_1

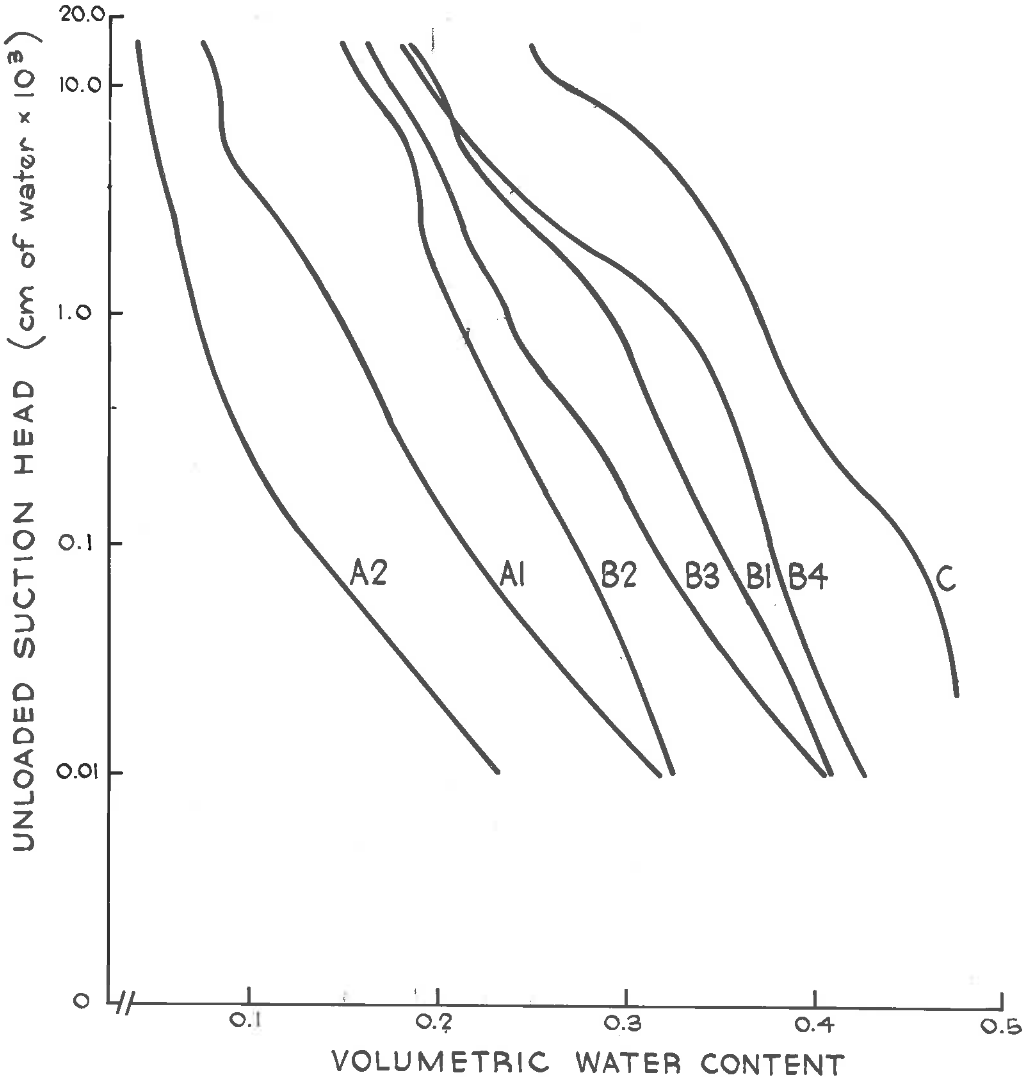


FIG. 12 Soil water characteristic (desorption) for each soil horizon at the site of the main experiment, mean of three replicates.

horizon remained high for a given value of h_m when compared with θ in the adjacent A_2 and B_2 horizons. At a given value of h_m, θ of $A_1 >> A_2$ due to the higher organic matter content of the A_1 horizon and θ of $B_1 > B_2 > A_2$ due to differences in clay content. Otherwise, θ at a given value of h_m increased with depth in the soil profile.

(d) Hydraulic conductivity - Measured values. Except for the B_1 horizons, the variation between the values of k for duplicate samples from the same replicate was of the same order as the variation between samples from different replicates (see Appendix Table 3). Mean values of k for the three replicates have been used for all horizons except B_1; for this horizon, one value has been used for replicates 1 and 2, and another for replicate 3 (Table 15). Texturing the samples from each horizon showed that for B_1, the clay content of replicate 1 = 2 >> 3. The structure of the B_1 horizon on replicates 1 and 2 was coarsely prismatic when dry but that on replicate 3 was medium granular. Other horizons were grouped as shown in Table 15 because of similar values of k and similar morphology.

Table 15

Hydraulic conductivity *k* of the soil horizons (cm per min.)

Horizon	Mean suction head (cm of water)	
	205	1500
A_1, A_2	$2.3 \cdot 10^{-6}$	$3.7 \cdot 10^{-8}$
B_1 (Reps. 1,2)	$1.7 \cdot 10^{-7}$	$1.3 \cdot 10^{-8}$
B_1 (Rep. 3)	$1.1 \cdot 10^{-5}$	$1.9 \cdot 10^{-7}$
B_2, B_3	$2.1 \cdot 10^{-6}$	$3.4 \cdot 10^{-8}$
B_4	$1.5 \cdot 10^{-6}$	$6.0 \cdot 10^{-8}$
C	$3.7 \cdot 10^{-7}$	$2.0 \cdot 10^{-8}$

The two measured values of *k* for each horizon were plotted as functions of θ on double log paper and values of *k* at water contents other than at the measured values were obtained by linear interpolation and extrapolation on the log-log scale (Gardner 1956). Reference to Fig. 12 shows that the θ range covered by *measured* values of *k* represents most of the range in the content of available water.

Calculated values. Marshall's (1958) Eq. (7) predicts *k* values of the order of 10^2 times greater than the measured values for the various horizons. The estimates given by Marshall's equation will be compared with further values of *k* for topsoils in Section 4 below.

(e) Soil NO_3^--N. Data on soil NO_3^--N are included here as, although affected by N treatment, they were obtained primarily to characterise the site and the NO_3^--N levels during the growth of the crop. Relatively high concentrations of soil NO_3^--N were measured at depths of 50 to 75 cm at planting and at depths of 75 to 100 cm throughout the growing season (Fig. 13). The high NO_3^--N concentration at depth is attributed to leaching from the topsoil partly during previous seasons and partly during the early part of the 1968 season. At sowing time the wetting front of the early winter rains had reached 50 to 75 cm depth and it was here that high concentrations of NO_3^--N were measured. Eight weeks after seedling emergence the concentration of NO_3^--N in the top 25 cm was significantly higher at N_2 than at N_0 or N_1. One hundred mm of rain fell during the second month after emergence and considerable amounts of NO_3^--N were found as deep as 75 to 100 cm depth at 8 wk. The NO_3^--N in the top 75 cm at 18 wk and throughout the top metre at 22 wk was significantly higher at N_2 than at N_0 or N_1 (Fig. 13).

During the period 8 to 18 wk the concentration of NO_3^--N in the top 50 cm at N_0 and N_1 was depleted below the levels measured at planting; after 18 wk it increased in the top 50 cm on all

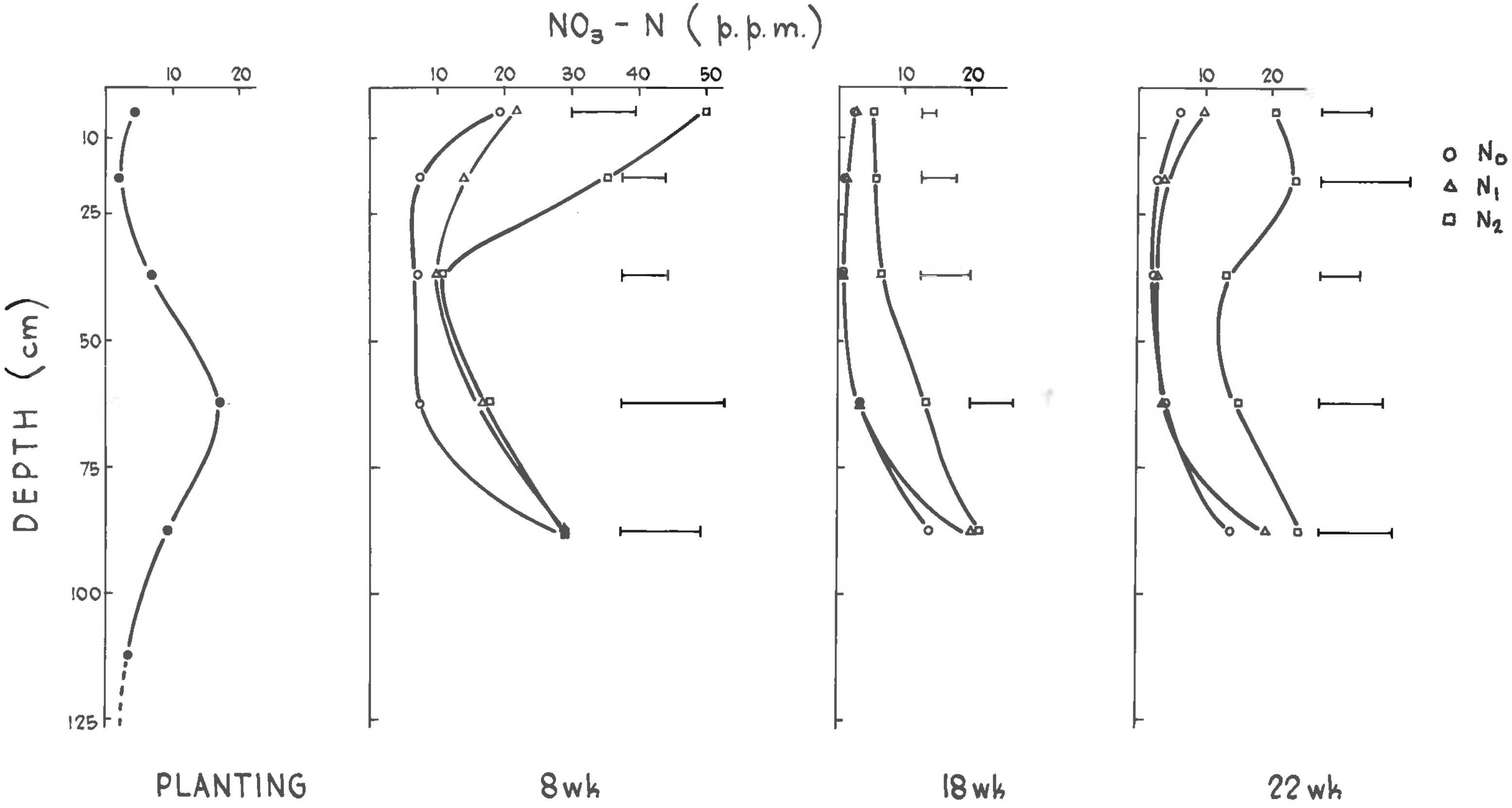


FIG. 13. The influence of N treatment on NO_3^--N content of the soil at planting and at 3 times after emergence. The horizontal lines indicate LSD (P = 0·05).

plots presumably due to mineralization, but the levels remained lower than the peak values measured at 8 wk. The decrease in the topsoil before 18 wk is attributed to uptake by the crop, leaching to the lower horizons, and possibly also to volatilization from the soil, especially at S_1 where the soil was incompletely explored by roots. The measured concentrations of soil NO_3^--N were not affected significantly by the differences in seeding rate; however the variability of the measured values prevented a precise comparison and small differences may have existed between rates.

(ii) Top growth

(a) Establishment and weed control. The seedlings emerged 2 wk after planting. Except for a patch approximately 1.5 m^2 on sub-plot S_3N_0 of replicate 2, where the soil had been compacted by machinery at planting, germination was good and even. Establishment counts made 2 wk after emergence are shown in Table 16. At that time the number of plants per sq. m. was related directly to the rate of seeding.

Table 16

Number of plants per sq. m. at establishment

Seeding rate	Nitrogen rate N_0	N_1	N_2	Mean
S_1	22	22	20	21
S_2	87	101	87	92
S_3	450	465	507	474
Mean	186	196	205	

L.S.D. (P=0.05): S=51; N=12; S x N=22

A number of weeds, mainly *Emex australis* Steinh; *Fumaria officinalis* L.; *H. leporinum* Link, and *A. fatua* L. appeared during early growth, mostly in patches on the S_1 and S_2 plots. The weeds were controlled by spraying all plots with 'Bucktril M.A.' (20% w/v 3,5-dibromo-4-hydroxybenzonitrile + 20% w/v 2-methyl-4-chlorophenoxyacetic acid as the iso-octyl ester) at the rate of 2 *l.* in 300 *l.* of water per hectare at 3 wk after emergence. In addition the more weedy patches on the S_1 and S_2 plots were hand weeded at 2 and at 4 wk.

(b) Total dry weight and nitrogen content of tops. The main effects of the S and N treatments on the total dry weight of tops per unit area are shown in Figs. 14a and 14b. (In the thesis L.S.D's are shown on figures only when the 'F' test is significant at < the 5% level of probability.) The total dry weight of the tops per unit area was consistently lower at S_1 than at S_2 or S_3. At 8 wk the dry weight of tops per unit area was related directly to the seeding rate, and the differences between the seeding rates were highly significant. If we assume that there was negligible plant mortality between 2 wk after emergence when establishment counts were made, and at 8 wk, the mean dry weight of tops per plant would have been $S_1 = 0.9$, $S_2 = 0.3$, and $S_3 = 0.2$ g at 8 wk. This indicates that, as early as 8 wk after seedling emergence, plant competition had severely restricted dry matter production per plant at S_2 and S_3. Note that at 8 wk there was little difference between the mean weight per plant at S_2 and S_3. At 13 wk the dry weight of the tops per unit area at S_3 was significantly higher than at S_1. From 13 until 20 wk the rate of dry matter production per unit area was higher at S_1 and S_2 than at S_3. At each harvest after 13 wk the dry weight of the tops at S_3 was intermediate to S_1 and S_2, and on each occasion the difference between S_1 and S_2 was significant. There was no change in the total dry weight of the tops at S_1 after 20 wk, but there were decreases at S_2 and S_3 due to more rapid senescence and greater loss of leaf material in

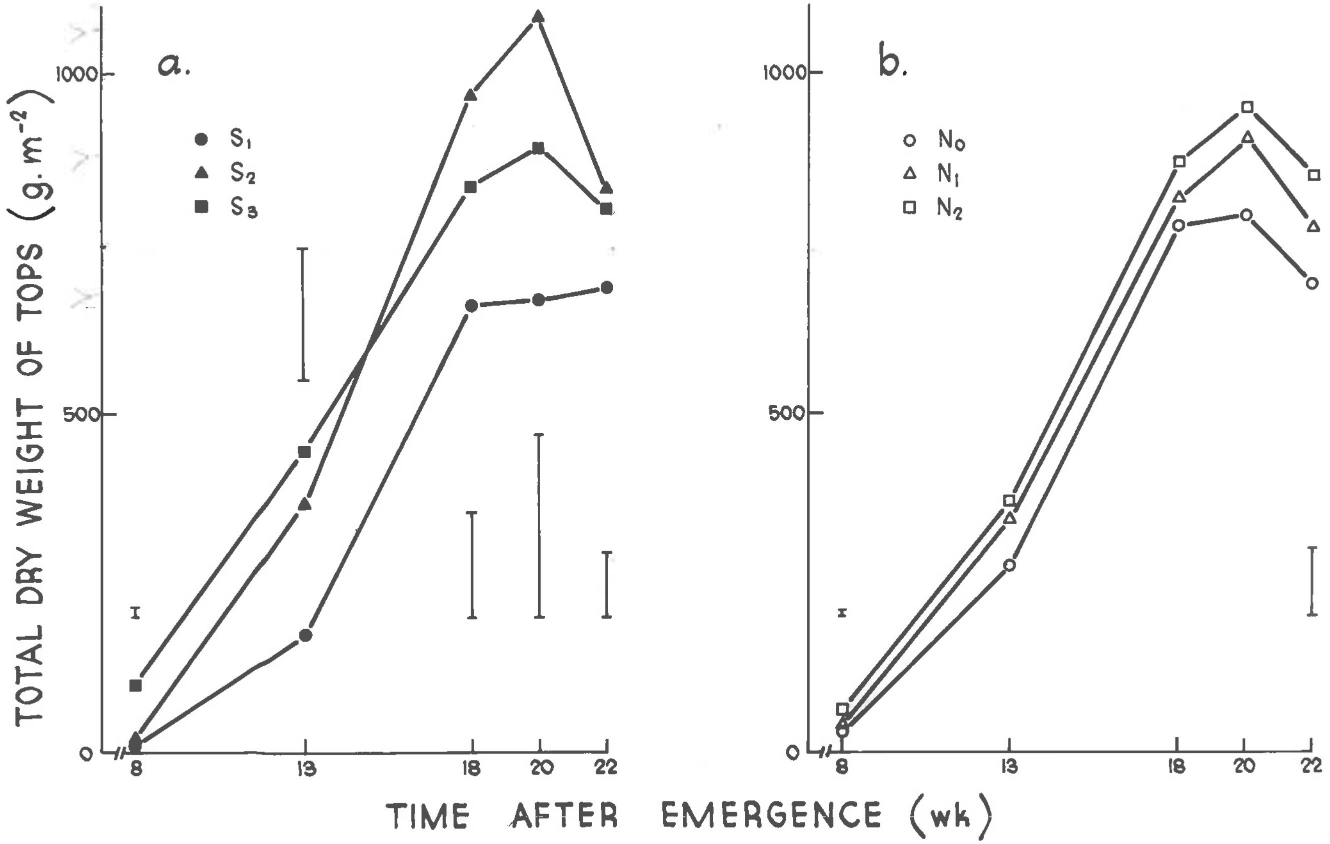


FIG. 14. The influence of (a.) SEEDING RATE and (b.) NITROGEN RATE on the total dry weight of tops (g.m^{-2}). The vertical lines indicate LSD (P = 0·05).

the field at the higher seeding rates.

The differences in the yield of tops per unit area between the S treatments during early growth are attributed to both the effects of inter-plant competition on yield per plant and to the plant density multiplier. The production of dry matter per unit area was highest at S_2 during mid- and late-season growth. Severe inter-plant competition greatly reduced yield per plant at S_3, and at S_1 the plant density was so low that, although the yield per plant was high, it was not high enough to compensate for the low density.

The influence of N on the dry weight of tops was small. N_0 consistently yielded less than N_1 and N_2 but the differences were statistically significant only between N_0 and N_2 at 8 and at 22 wk (Fig. 14b). The response to N during the first eight weeks of growth occurred at S_3 only, where the dry weight of tops increased from 79 g m^{-2} at N_0 and N_1 to 141 g m^{-2} at N_2, the difference being highly significant. At this time the foliage was darker green in colour at the higher rates of N. Presumably plant demand for N per unit area of ground surface increased with seeding rate, and scarcity of available N at N_0 and N_1 may have curtailed dry matter production at S_3. No significant interactions of main and sub-treatments were obtained at harvests later than 8 wk.

Although the per cent N content of the plant tops was consistently higher at S_1 and S_2 than at S_3, the differences were significant at the 5% level of probability only at 22 wk (Table 17). The total N content of the plant tops per unit area at 8 wk was significantly higher at S_3 than at S_1 and S_2, but at 18 and 22 wk the yield of N was significantly higher at S_2 than at S_1 and S_3. The yield of N increased to maturity at S_1 but it decreased after 18 wk at S_2 and S_3 probably due to the loss of dead leaves.

Treatment differences in N uptake was largest during early growth; most of the applied N and the bulk of the roots were in the topsoil at that time. Deep leaching, mineralization, and volatilization would have tended to reduce the differences in the supply of available N during later growth. However reference to Fig. 13 shows that, for most of the growing season, the NO_3^--N content of the soil remained significantly higher at N_2 than at N_0 or N_1.

The per cent and total N content of the plant tops was consistently higher at N_2 than at N_0 or N_1; the differences were largest during early growth and became less as the plants matured, however the values at N_2 were significantly higher than N_0 at all times. At 8 wk the yield of N differed significantly between the N rates at S_3; N_0 = 2.2, N_1 = 3.1, and N_2 = 5.8 g m^{-2}. The yields of N at S_1 and S_2 were $\leq$ 1.1 g m^{-2} and did not differ significantly between the sub-treatments. This result also suggests that the supply of N at S_3N_0 and S_3N_1 may have been below the

Table 17

Per cent nitrogen and total nitrogen content of the plant tops (g per sq. m.) at 8, 18, and 22 wk

Time after emergence (wk)	Seeding rate			L.S.D. (P=0.05)	Nitrogen rate			L.S.D. (P=0.05)
	S_1	S_2	S_3		N_0	N_1	N_2	
				NITROGEN (%)				
8	3.85	3.99	3.57	0.64	3.45	3.83	4.12	0.37
18	1.28	1.20	1.08	0.26	1.12	1.20	1.24	0.11
22	1.33	1.35	1.17	0.15	1.16	1.28	1.31	0.12
				TOTAL NITROGEN (g per sq. m.)				
8	0.33	0.84	3.68	0.70	1.00	1.46	2.39	0.36
18	8.49	12.96	9.61	3.10	8.80	10.57	11.71	2.91
22	9.18	11.16	9.40	1.40	8.74	9.87	11.13	1.53

requirements of the dense plant populations.

(c) Tiller production. Two weeks after seedling emergence the plant density was related directly to the seeding rate. Establishment counts made at this time are shown in Table 16. Tillering commenced during the third week after emergence. At all harvests the tiller density, that is, the number of tillers per unit ground area, was related positively to seeding rate and rate of nitrogen. After tillering commenced the tiller density increased sharply at S_2 and S_3, and maximum densities at S_2 and S_3 were measured at 8 wk; the densities at these two seeding rates declined sharply between 8 and 13 wk, and then slowly until the plants reached maturity. In contrast the tiller density at S_1 increased until 18 wk and had decreased only slightly at maturity (Fig. 15b). Because of these contrasting trends in tiller production and mortality, differences in tiller density between S rates were largest during early growth; nevertheless the difference between S_1 and S_3 was significant at all harvests. If we assume that there was negligible plant mortality between two weeks after emergence, when establishment counts were made, and the times at which maximum tiller densities were recorded, the mean maximum number of tillers per plant would have been $S_1 = 21.3$, $S_2 = 16.8$, and $S_3 = 3.2$.

Tiller density at N_0 was consistently lower than at N_1 or N_2. At 8 wk the differences between the three N rates were significant,

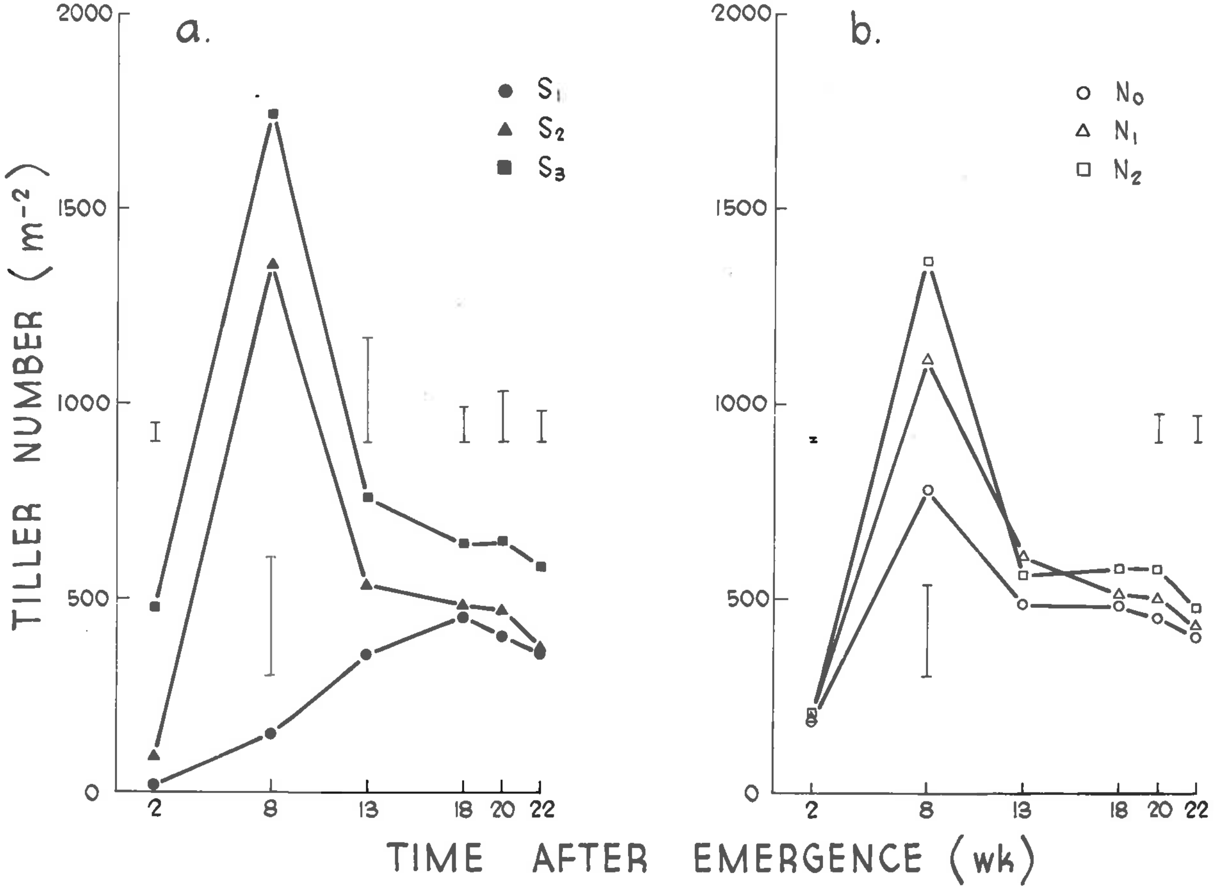


FIG. 15. The influence of (a) SEEDING RATE (b) NITROGEN RATE on tiller number (m^{-2}). The vertical lines indicate LSD (P=0·05)

but at later harvests the only significant differences were between N_0 and N_2 at 20 and 22 wk. The time trends of tiller production and mortality were similar at the three rates of N (Fig. 15b). After tillering commenced the densities increased rapidly and maximum values were measured at 8 wk at each rate of N. Tiller density decreased sharply during the 8 to 13 wk interval, the magnitude of the decrease being in the order $N_2 > N_1 > N_0$. After 13 wk there was a further but slow decline at N_1; there was no change at N_0 from 13 to 18 wk or at N_2 from 13 to 20 wk but after these times the tiller density decreased slightly.

The high tiller mortality during the 8 to 13 wk interval may have been due to inter-plant competition at the higher rates of S and to intra-plant competition at the higher rates of N. The decline in tiller density toward maturity was probably caused by the dessication of late tillers that were unable to survive the dry conditions at that time. During the first eight weeks tillering increased with N rate at S_2 and S_3 but not at S_1. At 8 wk the tiller densities (per sq. m.) were:

	N_0	N_1	N_2
S_1	124	172	153
S_2	993	1399	1674
S_3	1192	1762	2264

L.S.D.(P=0.05) = 362

After 8 wk the tiller density at each seeding rate was related positively to the rate of nitrogen, and no significant interactions were detected.

(d) Lamina area. Lamina area index *L* was related positively to S and to N during the first 13 wk of growth (Table 18). Treatment effects on *L* were most pronounced during early- and mid-season growth; by 20 wk the leaves had senesced and only the stems and ears remained green.

Table 18

The influence of seeding rate S and nitrogen rate N on lamina area index *L* at 8, 13, and 18 wk

Time after emergence (wk)	S_1	S_2	S_3	L.S.D. (P=0.05)
8	0.14	0.43	1.90	0.33
13	1.08	2.63	2.99	1.64
✓18	1.30	1.33	1.01	0.22
	N_0	N_1	N_2	
8	0.53	0.84	1.11	0.24
13	1.76	2.25	2.71	0.69
18	1.13	1.22	1.29	0.50

L_{max} was measured at 13 wk at S_2 and S_3 and at 18 wk at S_1. The increases in L that resulted from the application of N were smaller than those caused by higher seeding rates. L_{max} at each of the three N rates was measured at 13 wk, and the subsequent decline in L was greater at the higher rates of N. At 8 wk L at S_3 was increased significantly with each increment of nitrogen; N_0 = 1.19, N_1 = 1.85, and N_2 = 2.66; the increases at the lower seeding rates were not significant. Again no significant interactions were found after 8 wk.

(e) Grain yield and grain nitrogen. The grain yield, the components of the grain yield, and the per cent N content of the grain at maturity are shown in Table 19. Grain yield at the three S rates differed significantly; S_2 produced the highest yield and S_1 the lowest. The number of ears per sq. m. was related positively to S. The number of fertile spikelets per ear, the number of grains per spikelet, and the number of grains per ear were lowest at S_3, but the weight per grain was significantly higher at S_3 than at S_1 or S_2. The largest weight of grain per ear was produced at S_2.

The grain yield at S_1 was low partly because of the small number of ears, a direct result of low seeding rate. More importantly, the large number of tillers per plant at S_1 may have led to appreciable intra-plant competition, and this may explain the big reduction in

Table 19

The influence of seeding rate S, and nitrogen rate N, on grain yield the components of grain yield, and the per cent N content of the grain at maturity

Treatment	Number of ears per sq. m.	Number of fertile spikelets per ear	Number of grains per spikelet	Weight per grain (mg)	Grain yield (g per sq. m.)	N content of grain (%)
S_1	345	13.2	2.35	26.8	282	1.96
S_2	380	14.2	2.26	34.7	415	1.86
S_3	515	10.4	1.87	37.6	367	1.90
L.S.D. (P=0.05)	115	1.13	0.10	2.32	41	0.17
N_0	368	11.9	2.26	34.6	358	1.83
N_1	425	12.6	2.14	32.9	363	1.83
N_2	445	13.3	2.05	31.8	343	2.06
L.S.D. (P=0.05)	64	0.79	0.11	3.31	61	0.16

weight per grain at S_1. Perhaps the ears formed on the late tillers at S_1 did not fill their grain due to shortage of water late in the season. Yield at S_3 was lower than at S_2 because of the smaller number of grains per ear at S_3, caused presumably by high levels of inter-plant competition.

The number of ears per sq. m. increased with N rate, but the number of grains per spikelet decreased (Table 19). There was also a (non-significant) tendency for weight per grain to be related negatively to rate of N. Because of the compensating effects of these changes in the different components of grain yield, the grain yield itself did not differ significantly between the N treatments.

The per cent N content of the grain was not affected by variation in seeding rate. The yield of N in the grain increased with S and was related directly to grain yield. At maturity the yield of N in the grain at S_1 was significantly less than at S_2 and S_3 (5.5 compared with 7.4 g m^{-2}). The per cent N content of the grain increased at N_2 but not sufficiently to give significant differences in total yield of grain N.

(iii) <u>Growth and development of the root system</u>

In general variation in seeding rate had greater effects on root growth than did variation in N rate. After the cereal plant has tillered, each tiller develops its own set of adventitious (nodal) roots. As noted earlier [Section 2.3.2.(i)(b)] the number of main nodal roots per tiller is influenced less by variation in plant density than is tiller number or number of nodal roots per plant. Because the tiller becomes the effective growing unit, and also because plant number was not determined after establishment, results on root length are expressed as length per tiller when considering the effects of treatments on *development* of the root system.

(a) Extent (depth and lateral spread) of the root systems of individual plants. Results are based on the total radioactivity (^{32}P + ^{35}S counts) in the plant tops at 8, 13, and 18 wk after emergence. Because of many 'missing plots', statistical analysis of the data was not attempted.

During the first 18 wk of growth the spread of the root systems of individual plants along the row was related negatively to S. The mean extent of the root systems (mean maximum lateral distance within the row, and mean maximum depth from which tracers were absorbed) are shown in Table 20 for three sampling times. The extent of rooting at each depth on the three sampling occasions is shown in Appendix Fig. 1.

Table 20

The influence of seeding rate S on the extent of root systems of individual plants

Time after emergence (wk)	Mean maximum extent (cm)	S_1	S_2	S_3
8	Depth	62	62	62
	Lateral spread within row*	25	25	20
13	Depth	112	112	87
	Lateral spread within row*	30	30	25
18	Depth	112	137	112
	Lateral spread within row*	50	40	30

* Spread in one direction at S_1 and S_2, in two directions within the rows planted at right angles at S_3.

The results in Table 20 suggest that at 13 wk the roots had penetrated less deeply at S_3 than at S_1 or S_2. Differences in the depth of rooting were not detected when quantitative measurements of R_v were made at this time. As the radioisotope was placed at the mid-point of the layers sampled for determination of R_v [Section 3.3.2.(v)(c)], and as the depth of soil labelled was only about 3 cm, the isotope method had a higher resolution than the root length measurements. Root separation indicated extreme rooting depths of 75 to 100 cm at 8 and at 13 wk and 100 to 125 cm at 18 wk.

The lateral spread of the root systems within rows tended to increase at each depth with time - see Appendix Fig. 1. Eight weeks after seedling emergence, isotope uptake took place across two rows at S_1 and S_2, over a lateral distance of 35 cm. Uptake was not detected across three rows at any time. The application of N increased the lateral spread of roots within rows on the S_3 plots from 20 cm at N_0 to 25 cm at N_1 and N_2 at 8 wk, and from 25 cm at N_0 to 30 cm at N_1 and N_2 at 13 and 18 wk. No effects of N application on the depth of the individual root systems was detected.

The frequency of uptake (proportion of sites from which uptake occurred) of the radioisotopes was highest from sources placed in the top 50 cm of the soil and lowest from sources placed below 87 cm. This is probably because the rooting density decreased as the depth of rooting increased (Figs. 22 and 23). The photographs of intact root systems shown in Fig. 19 show that the distances between neighbouring roots in the deeper layers were often large (> 5 cm).

(b) <u>Mean root length per tiller, R_T.</u> The main effects of the S and N treatments on R_T at each time of sampling are shown in Fig. 16a and Fig. 16b. At 8 wk R_T was significantly greater at S_1 than at S_2 or S_3. Although the rooting density R_a (Fig. 18) and the tiller density (Fig. 15) at 8 wk had both increased with seeding rate, the increase in tiller density was relatively greater.

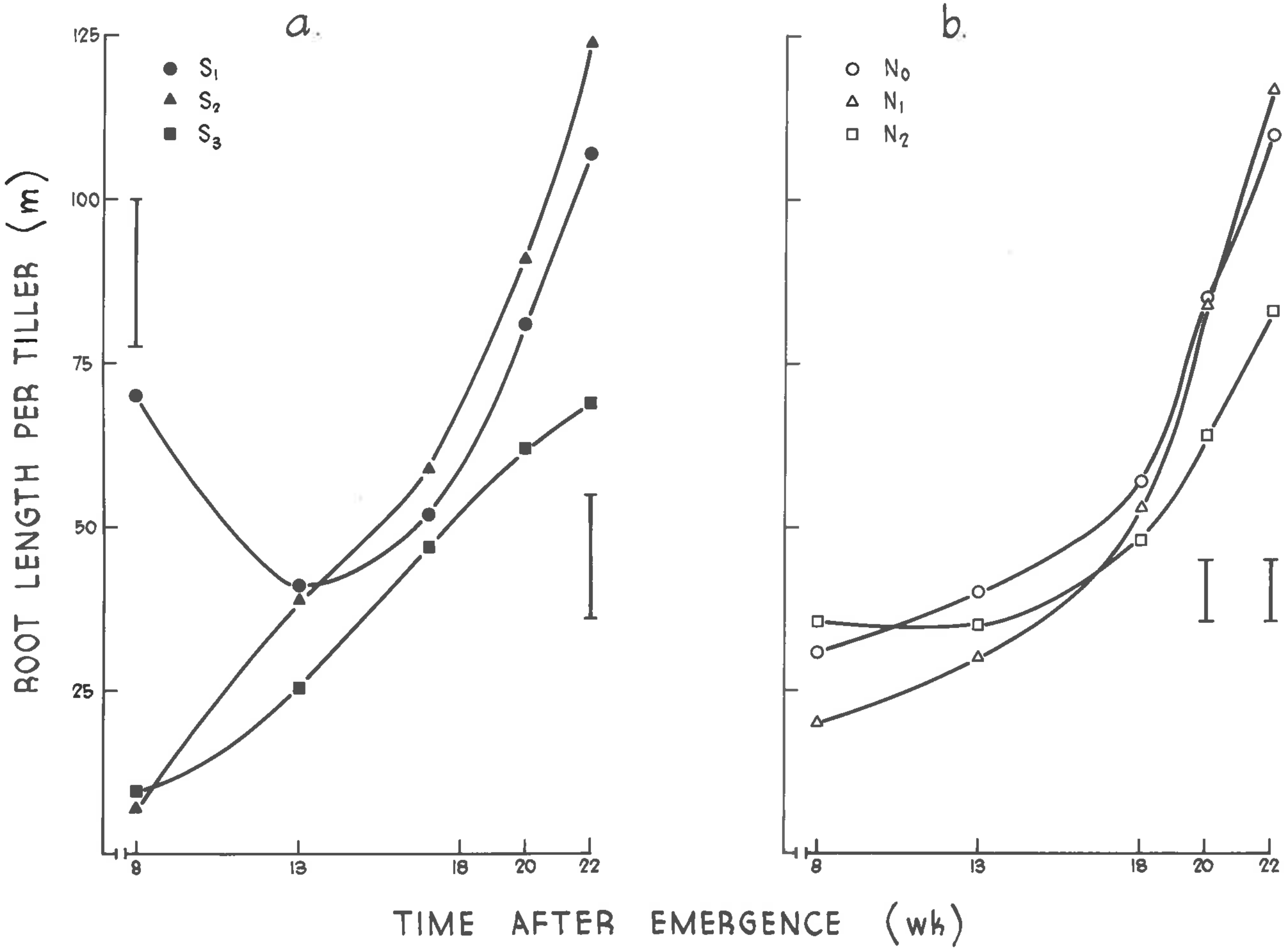


FIG. 16 The influence of (a) SEEDING RATE, S, and (b.) NITROGEN RATE N on root length per tiller (m). Vertical lines indicate LSD ($P = 0{\cdot}05$).

As the mean dry weight of tops per plant at S_2 and S_3 was considerably lower than at S_1 (p. 125), the assimilates available for root growth could have been lower at S_2 and S_3 than at S_1. In addition the apparent value of R_T at S_1 at 8 wk could have been inflated by the presence of weed roots.

During the period 8 to 13 wk each plant at S_1 produced large numbers of tillers and the mean R_T at S_1 was lower at 13 than at 18 wk. At this stage the seminal roots would have formed the major part of the total root length per plant and the large increase in the number of tillers per plant would tend to reduce the mean R_T. Otherwise R_T increased with time and tended to be lower at S_3 than at S_1 or S_2. At maturity R_T at S_3 was significantly lower than at S_1 or S_2; this difference is attributed to high levels of inter-plant competition at S_3, particularly for light, having reduced the growth of roots per tiller.

The N rates affected R_T less than did the S rates, and the only significant differences between the N rates were at 20 and 22 wk when R_T at N_2 was less than at N_0 and N_1. This difference was possibly due to the late initiation of a large number of tillers at N_2; the later tillers are unlikely to have developed extensive nodal root systems.

Significant S x N interactions were detected at 8 and at 22 wk. At 8 wk, when the rooting density at N_0 and N_1 was similar and lower than at N_2, the values of R_T on the S_1 plots at N_0, N_1, and N_2 were 70, 45, and 94 m per tiller [L.S.D.(P=0.05) = 43]. At 8 wk the values of R_T were relatively small at S_2 and S_3 and the differences between N treatments at these seeding rates were not significant. However at 22 wk R_T at N_2 was lower than at N_0 on the S_1 and S_2 plots. Again there was no significant difference between N rates at S_3, as shown by the results (m per tiller) in the following 3 x 3 table:

	N_0	N_1	N_2
S_1	140	94	89
S_2	131	146	93
S_3	59	80	67

L.S.D.(P=0.05) = 32

The significant differences in R_T at 8 wk are attributed to variation in tiller number per plant as affected by both seeding rate and rate of nitrogen. At 22 wk the lower mean R_T at high rates of N at S_1 and S_2 was probably caused by the production of tillers during late growth; this would be unlikely to occur at S_3 due to high levels of inter-plant competition.

(c) Mean rate of root growth per tiller, $\delta R_T/\delta t$. The mean of all treatments for each interval between samplings is shown in Fig. 17. The values for individual treatments were highly variable and Fig. 17 was constructed to show the general time trends of changes in $\delta R_T/\delta t$. The time trends in the number of tillers per plant and the nodal root development varied considerably between plants both within and between treatments. During the first 8 wk of growth $\delta R_T/\delta t$ at S_1 was significantly higher than at S_2 or S_3 but from 8 to 13 wk this relationship was reversed. Negative values were obtained for $\delta R_T/\delta t$ at S_1 for the period 8 to 13 wk. These values were significantly lower than those at S_2 and S_3, which not only remained positive but were also higher than during the first 8 wk. Very large numbers of tillers were produced at S_1 during the 8 to 13 wk interval, and it is probable that many of the new tillers had not developed nodal roots or had only short nodal roots when measurements were made at 13 wk. There were no significant differences between $\delta R_T/\delta t$ at the three S rates after 13 wk. Maximum values of $\delta R_T/\delta t$ for all treatments were measured during the 18 to 20 wk period. Although a small decrease occurred after 20 wk $\delta R_T/\delta t$ remained appreciable, particularly at S_1 and S_2. There were no significant differences between $\delta R_T/\delta t$ at the three N rates as the variability was high. The values were lowest during the period 8 to 13 wk, followed by a moderate increase at 13 to 18 wk and then by a big increase at 18 to 20 wk; although $\delta R_T/\delta t$ declined after

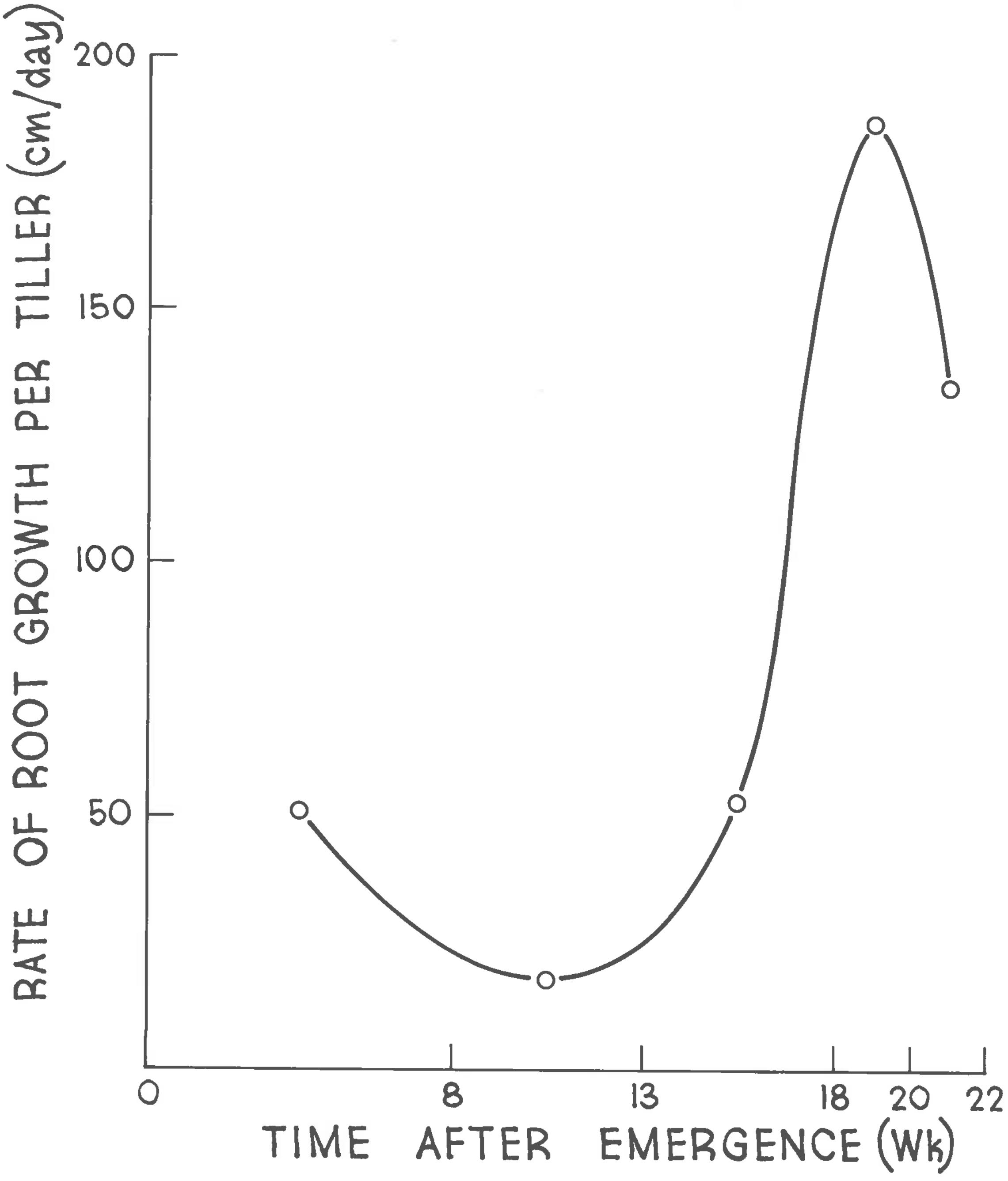


FIG. 17 The mean rate of root growth per tiller $\delta R_T/\delta t$.

20 wk it remained appreciable ($\geq$ 100 cm per tiller per day) at each rate of nitrogen.

Significant S x N interactions with respect to $\delta R_T/\delta t$ were found for the periods from emergence to 8 wk and from 8 to 13 wk. As from emergence to 8 wk $\delta R_T/\delta t = 0.018 \cdot R_T$, interactions were the same as noted for R_T at 8 wk. From 8 to 13 wk the values of $\delta R_T/\delta t$ (cm per tiller per day) were as follows:

	N_0	N_1	N_2
S_1	-43	-36	-154
S_2	91	78	91
S_3	40	38	60

L.S.D.(P=0.05) = 72

These interactions resulted chiefly from differences in the tillering response to nitrogen at the different S rates as noted previously for R_T.

In addition to the influence of the availability of assimilates for root growth, the two plant attributes that would have had the greatest influence on the time trend of $\delta R_T/\delta t$ are the number of tillers per plant during early growth, and the number of actively growing root axes during late growth. Previous mention has been made of the tendency for $\delta R_T/\delta t$ to be reduced at the growth stage when there would have been large numbers of tillers developing with a short length of root per tiller. $\delta R_T/\delta t$ was highest during late growth as the number of root axes per tiller would have been highest at this time, and, even though the rate of growth per axis may have been small, the increase in the length of root per tiller was relatively large.

(d) Percentage of the total root length with root hairs. There was no consistent effect of treatments on the percentage of the total root length with root hairs at any time of sampling, the values for individual treatments having varied between replicates considerably. Table 21 shows the mean percentage of the total length of root bearing root hairs at each depth and time.

Table 21

The percentage of the total root length with root hairs at each depth at different times of sampling

Depth (cm)	Time after emergence (wk) 8	13	18	20	22
0 - 10	16	18	11	12	6
10 - 25	15	17	14	19	14
25 - 50	19	19	19	23	16
50 - 75	32	27	20	31	22
75 - 100	56	35	25	31	25
100 - 125	-	-	25	37	17
125 - 150	-	-	-	-	36

In general hairs were present along one tenth to one third of the total root length. The percentage of the total length of root with hairs increased with depth of rooting. In the topsoil the percentage of the length with hairs decreased as the plants matured. The trend in depth was probably associated with the downward growth of the rooting front, and the higher proportion of young roots in depth. Also, the soils remained relatively moist in the deeper part of the rooting zone until later in the season. The decrease in the root length with hairs as the plants matured may be due partly to suberization of the cortex and sloughing off of hairs due to dessication.

(iv) Net effects of (iii) on

(a) Rooting density, R_a. The main effects of seeding rate on R_a are shown in Fig. 18a and the main effects of rate of nitrogen are shown in Fig. 18b. R_a increased throughout growth. During the first 18 wk there was a tendency for R_a to be related positively to S, but after 18 wk S_2 tended to be higher than S_3. At 8 wk R_a at S_3 was significantly higher than at S_1 or S_2; the difference is attributed to increase in the density of seminal root axes as a direct result of higher rates of seeding. From 8 to 20 wk the increase in R_a ranked in the order $S_2 > S_3 > S_1$, and at 13 and 18 wk S_2 was significantly higher than S_1. After 18 wk R_a

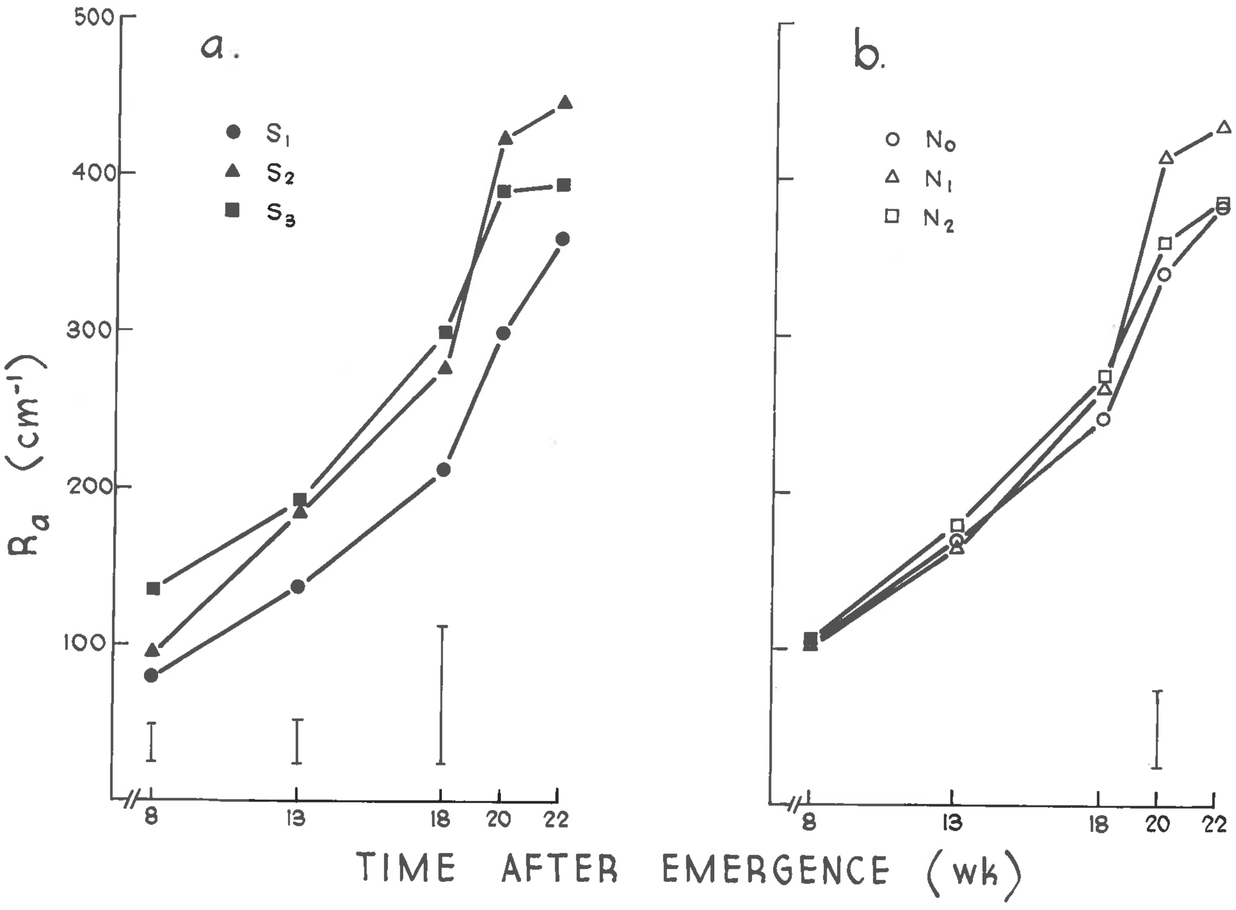


FIG. 18 The influence of (a) SEEDING RATE and (b) NITROGEN RATE on root length per unit ground area R_a (cm^{-1}). The vertical lines indicate LSD ($P = 0{\cdot}05$).

did not differ significantly between seeding rates. From 20 to 22 wk there was a substantial increase in R_a at S_1 and a small increase at S_2, but there was no change at S_3 (Fig. 18a). The trend for a higher rooting density at S_2 than at S_3 after 18 wk may have been due to differences in the growth of nodal roots. Tillering was much higher at S_1 and S_2 than at S_3 and, as the initiation of nodal roots is related positively to tillering, growth of the nodal roots after 18 wk would tend to increase rooting density at S_1 and S_2 relatively more than at S_3. However tiller density at S_1 was relatively low and R_a at S_1 was always below the values at S_2 and S_3.

Significant effects of N rate on R_a were found at 20 and 22 wk only (Fig. 18b) and there were significant S x N interactions with respect to R_a at these harvests. High rates of root growth at S_2N_1 during the 18 to 20 wk period caused R_a at N_1 to be significantly higher than at N_0 or N_2. Values of R_a (cm^{-1}) at 20 and at 22 wk were as follows:

Time after emergence (wk)		N_0	N_1	N_2	L.S.D. (P=0.05)
20	S_1	289	276	329	
	S_2	425	482	362	N means = 81 S means = 132
	S_3	303	483	389	
22	S_1	365	346	369	
	S_2	454	511	377	N means = 81 S means = 132
	S_3	328	446	409	

(b) Vertical distribution and $\delta R_p/\delta t$.

Photographs of root profiles. Fig. 19 shows root profiles for the S_1N_2, S_2N_2, and S_3N_2 treatments at 18 wk after emergence. The roots were washed from blocks of soil 110 x 60 x 10 cm. Only a few roots were recovered from soil blocks or on pit faces at depths greater than 1 m.

The positive relationship of rooting density to S, the increased rooting density at depths greater than 25 cm as S was increased, and the location of the bulk of the roots in the top metre of the soil profile are shown clearly in Fig. 19. A spreading pattern of root growth at S_1 in contrast to the more vertically downward growth of the roots at S_3, can be seen in Fig. 19 and is shown more clearly in Fig. 20. The low rooting density at 15 to 20 cm depth (Fig. 19) is attributed partly to loss of roots when washing away the clayey B_1 horizon, there is also the probability that, on replicates 1 and 2, root growth in this horizon was reduced as the clay content was high. The root profiles from the N sub-plots at S_3 are shown in Fig. 21. There is qualitative agreement with the R_p data at 18 wk: at N_2 the roots were concentrated in the top 50 cm and the rooting density below 50 cm was low when compared with N_0 and N_1. However certain anomalies occur when the rooting distribution deduced from root profiles are compared with that obtained from quantitative measurements. Fig. 21 appears to indicate that the application of

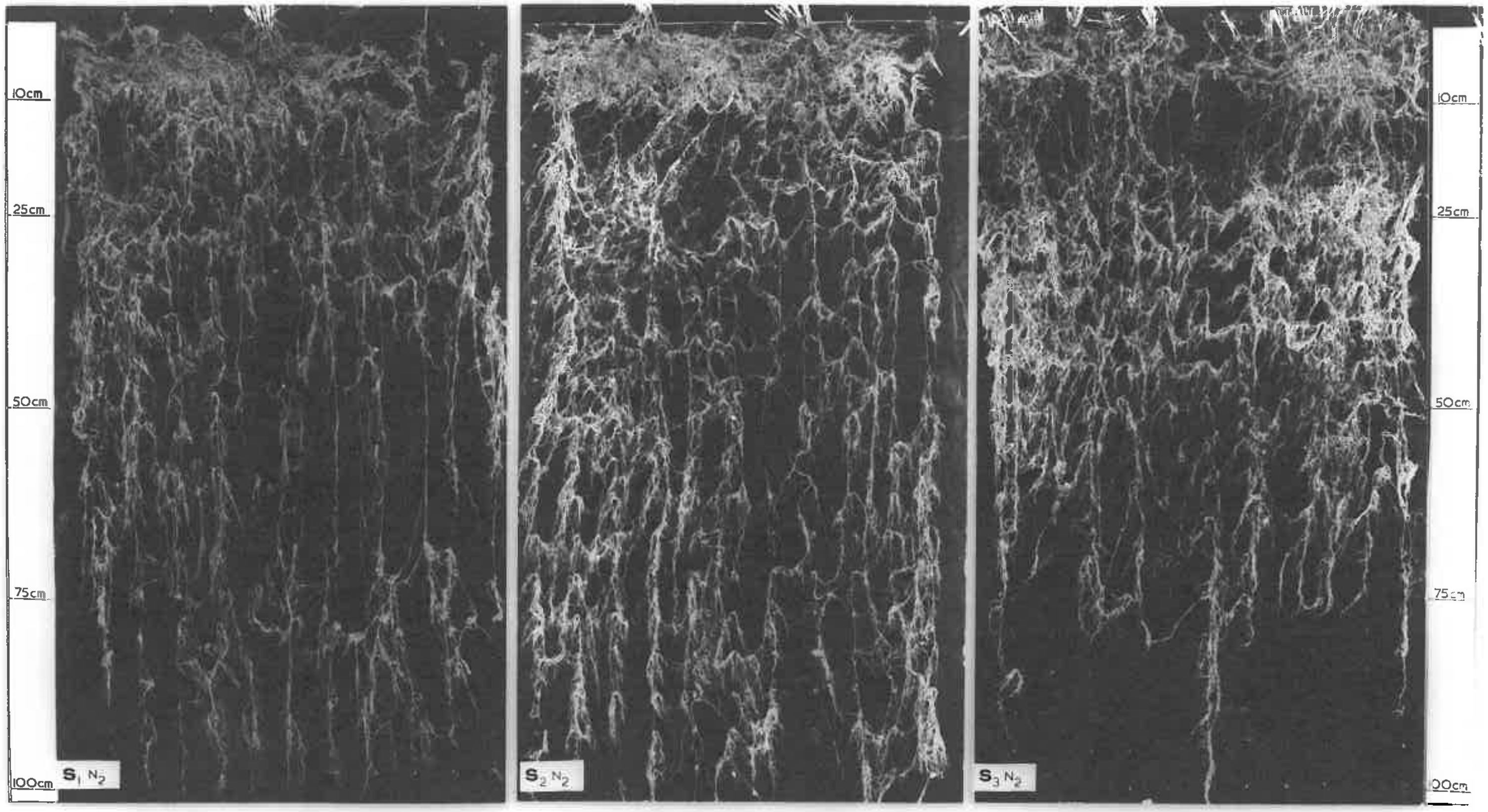


FIG. 19. Root development on the S_1N_2, S_2N_2 and S_3N_2 plots 18wk after emergence.

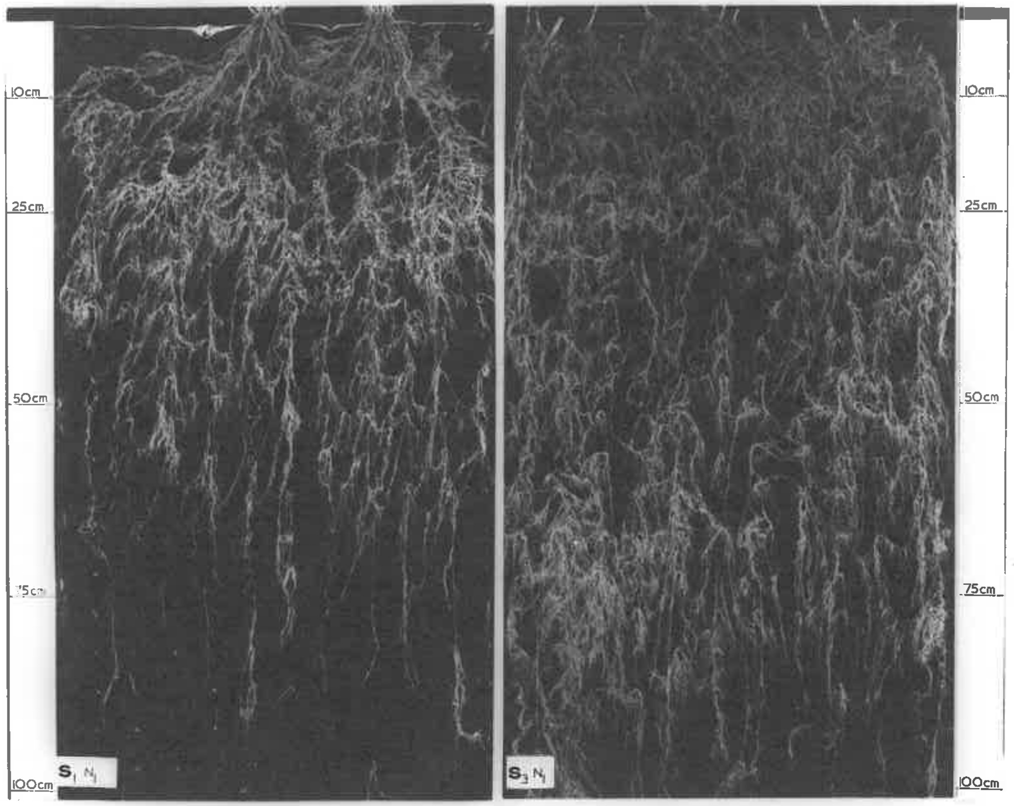


FIG. 20. Root development on the S_1N_1 and S_3N_1 plots 18wk after emergence.

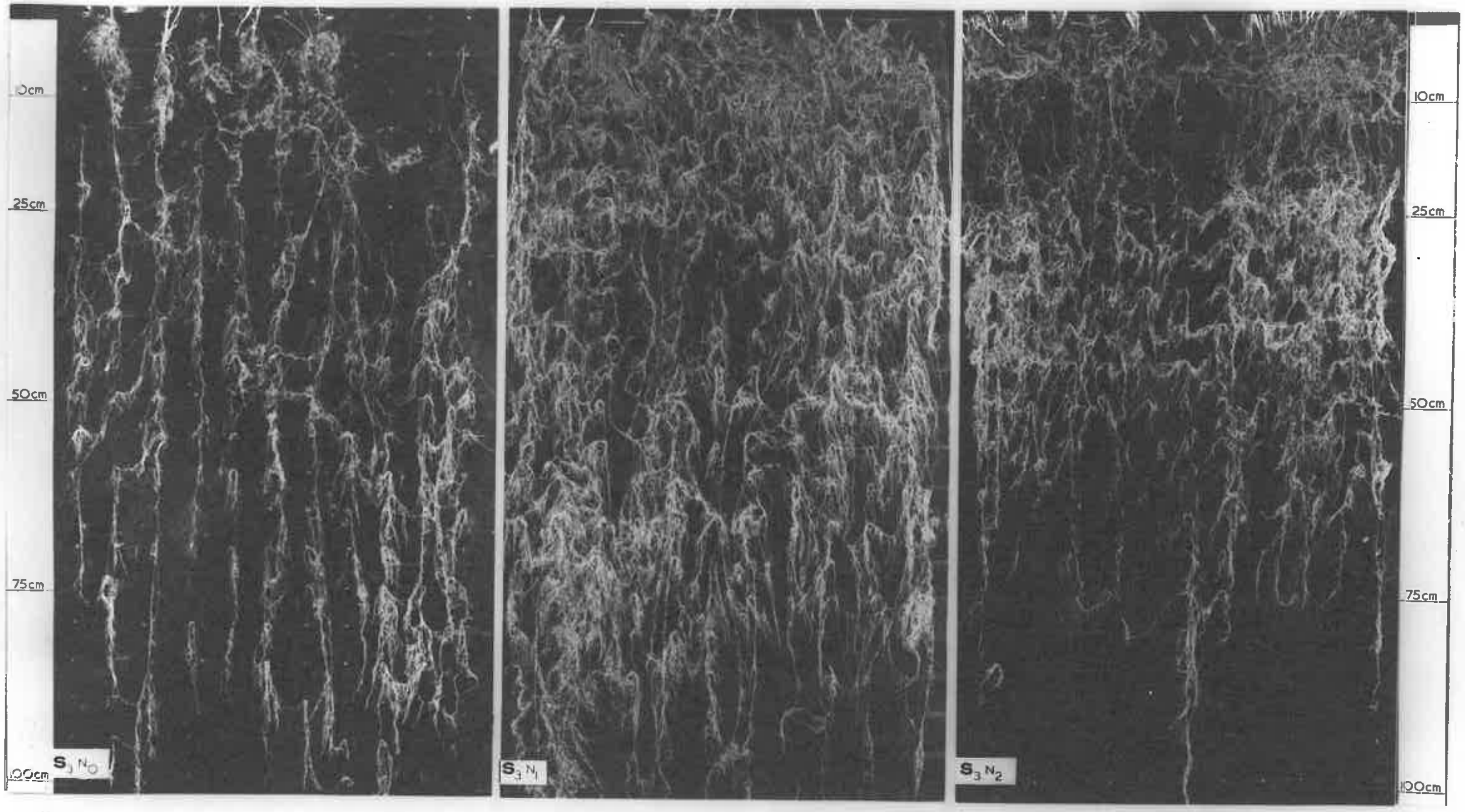


FIG 21. Root development on the S_3 sub-plots 18 wk after development.

N causes substantial increases in rooting density throughout the root zone, but this is not as shown by the quantitative R_v data. Further, Fig. 19 appears to indicate that, in the lower part of the root zone, the rooting density at S_3 was less than at S_1 or S_2, but the R_v data (Fig. 22) and also the root profiles in Fig. 20 show that the rooting density at S_3 was greater than at S_1 at all depths - note that N_2 rates are compared in Fig. 19 and N_1 rates in Fig. 20 21. These anomalies point to the inadequacy of the soil block method for the comparison of treatment effects on root development, and to the hazards present in drawing conclusions from poorly replicated massive samples.

R_v at different depths. In general, at any particular depth R_v tended to increase with S and with time but there was a decline in R_v in the top 10 cm on the S_2 and S_3 plots during the interval 20 to 22 wk. The increases in R_v at some depths, and the increases in $\overline{R}_v$ that resulted from increasing S were significant (P=0.05) during early- and mid-season but not during late season growth. The main effects of S on the z,R_v relationships at 8, 18 and 22 wk are shown in Fig. 22. Results from all five harvests are included in Appendix Table 7. Eight weeks after emergence the bulk of the roots were located in the top 50 cm and it was in this region that variation in S affected R_v significantly: in the top 10 cm R_v was higher at S_2 and S_3 than at S_1; R_v at 10 to 50 cm, and $\overline{R}_v$ were

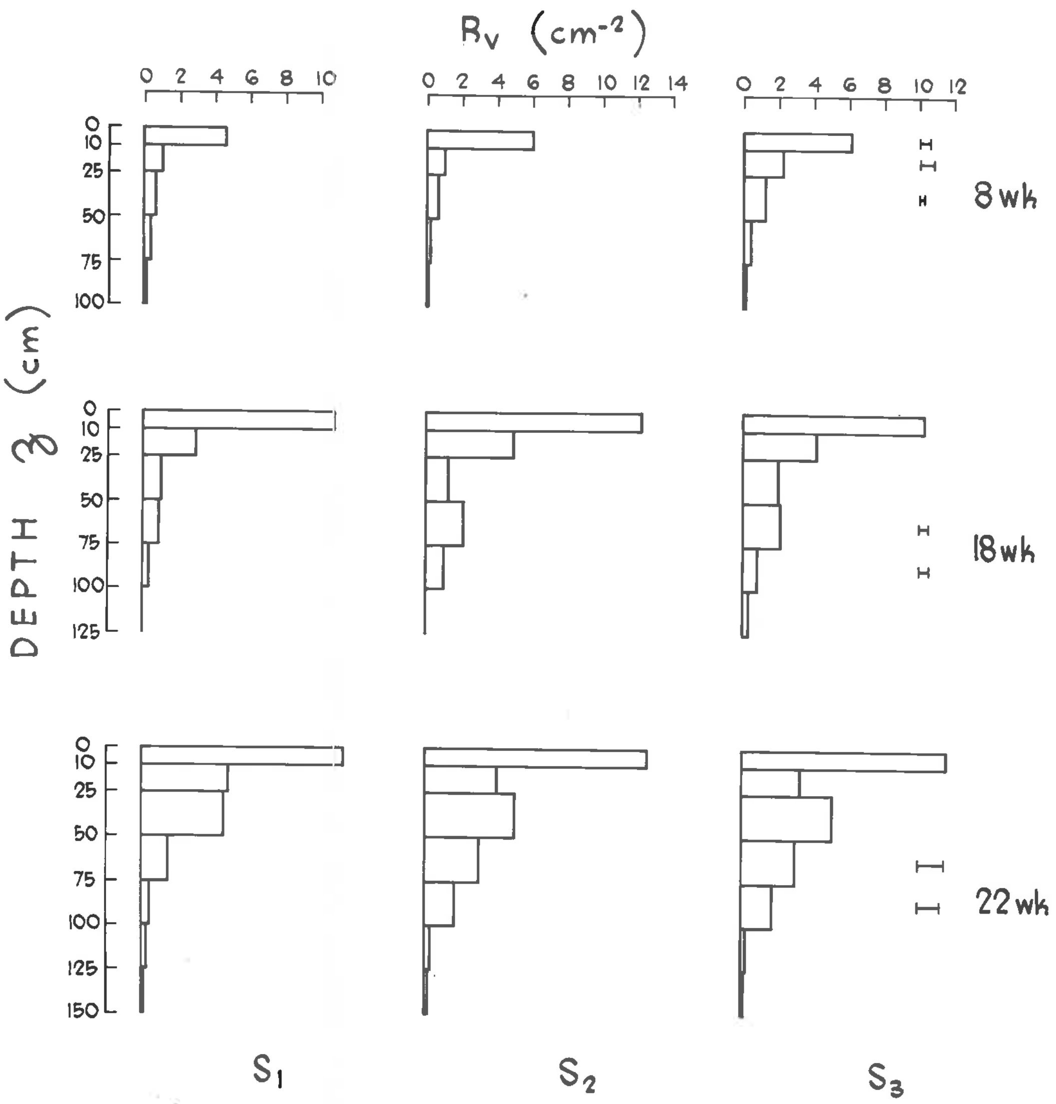


FIG. 22. z, R_v relationship for the 3 SEEDING RATES at 8, 18 and 22 wk after emergence. Horizontal lines indicate LSD ($P = 0{\cdot}05$).

higher at S_3 than at S_2 and S_1. From 8 to 13 wk R_v increased substantially throughout the root zone on all plots. At 13 wk and at all later harvests R_v in the top 10 cm tended to be ranked in the order $S_2 > S_3 > S_1$ but differences were not significant. Although R_v at deeper depths was usually related positively to S, measurements made later than 13 wk did not show any significant differences between treatments; the variation at all depths was large.

The z,R_v relationships for the three N rates at 8, 18, and 22 wk are shown in Fig. 23; the results of all harvests are included in Appendix Table 7. Application of nitrogen increased R_v in the top 10 cm of the soil during the first 18 wk of growth: at 8 wk the differences between N_2 and the lower N rates were highly significant, the differences were significant at 13 and 18 wk but not at later harvests. At 18 wk R_v at 10 to 25 cm was significantly higher at N_2 than at N_0 and N_1 but at all other times, N either did not have a significant effect or it reduced R_v at depths greater than 10 cm (Fig. 22 and Appendix Table 7). Significant decreases in R_v at N_2 were measured at successively deeper depths as the plants matured.

No differences between treatments were detected in the maximum depth of rooting when samples were taken for measuring R_v; at depths greater than 25 cm all samples were taken in 25 cm layers.

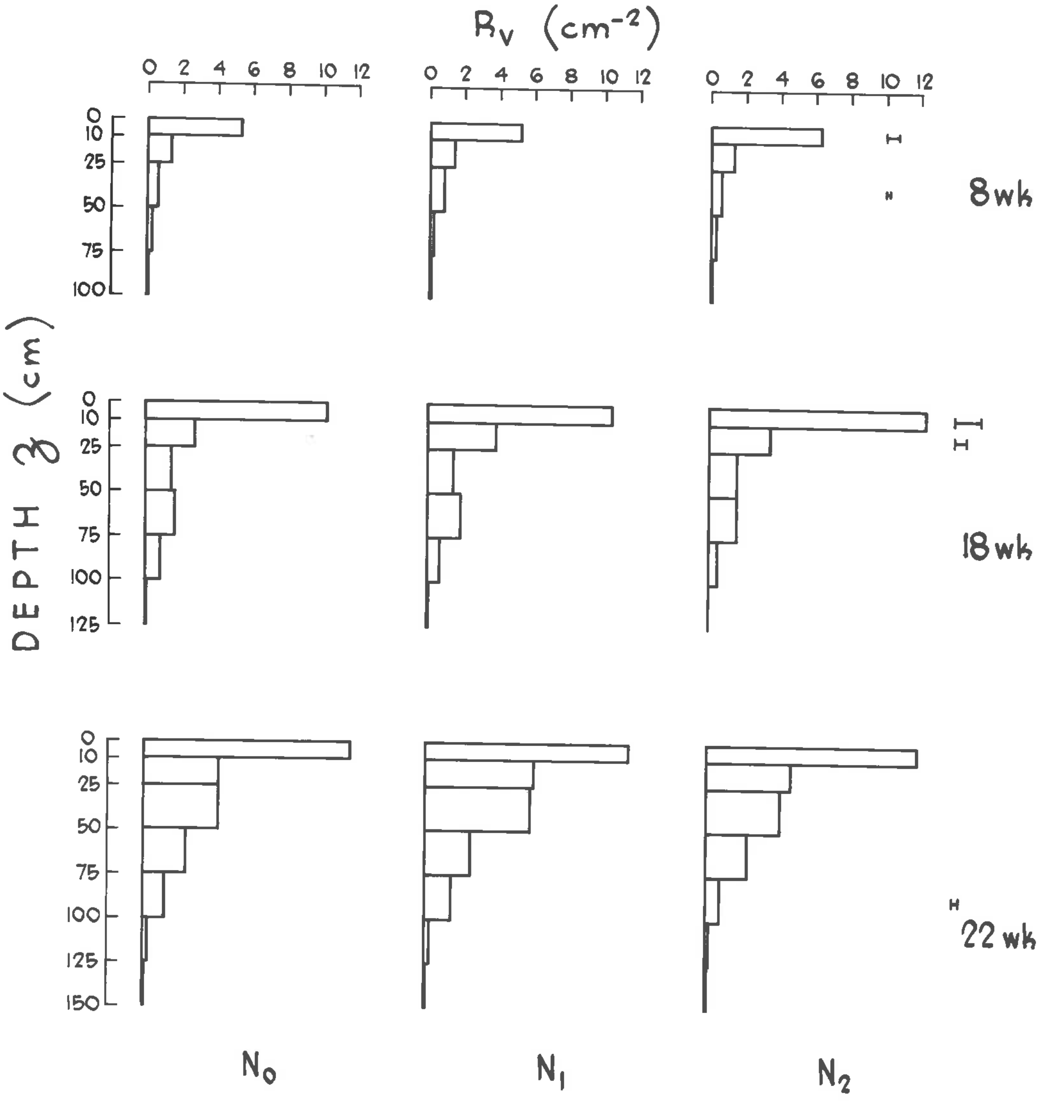


FIG. 23. z, R_v relationship for the 3 levels of NITROGEN RATE at 8, 18 and 22 wk after emergence. Horizontal lines indicate LSD ($P = 0{\cdot}05$).

At 8 wk the roots had penetrated to depths of 75 to 100 cm; no change was detected at 13 wk. At 18 and 20 wk the deepest roots were at 100 to 125 cm and 22 wk, at 125 to 150 cm.

Root abundance always decreased with increasing depth. At maturity the order of magnitude of R_v (cm^{-2}) ranged from 12 at 5 cm through 5 at 50 cm, 1 at 100 cm, and 0.1 at 150 cm. Values of R_v at each depth varied at different stages of growth and were affected by both seeding rate and rate of nitrogen.

Increasing S resulted in higher R_v in the topsoil during early growth and in the lower horizons during mid-season and late growth. The changes in R_v at each sampled depth at 8, 18, and 22 weeks that resulted from increasing S are shown in Fig. 24. The values shown are ($S_2 - S_1$), ($S_3 - S_2$), and ($S_3 - S_1$) and significant differences are indicated. Although the larger proportion of the total root length was always in the top 50 cm of the soil, the proportion below 50 cm was higher at S_2 and S_3 than at S_1, resulting in a more even distribution of roots throughout the rooting zone as S was increased. The variation in root distribution at different S rates is attributed to the tendency for most of the roots at high S to grow vertically downwards and for roots at low S to spread and branch profusely in the topsoil (see Figs. 19 and 20). The absence of significant effects of S on R_v in the top 50 cm at maturity is due to the higher rates of root growth in that part of the root zone at S_1 and S_2 than

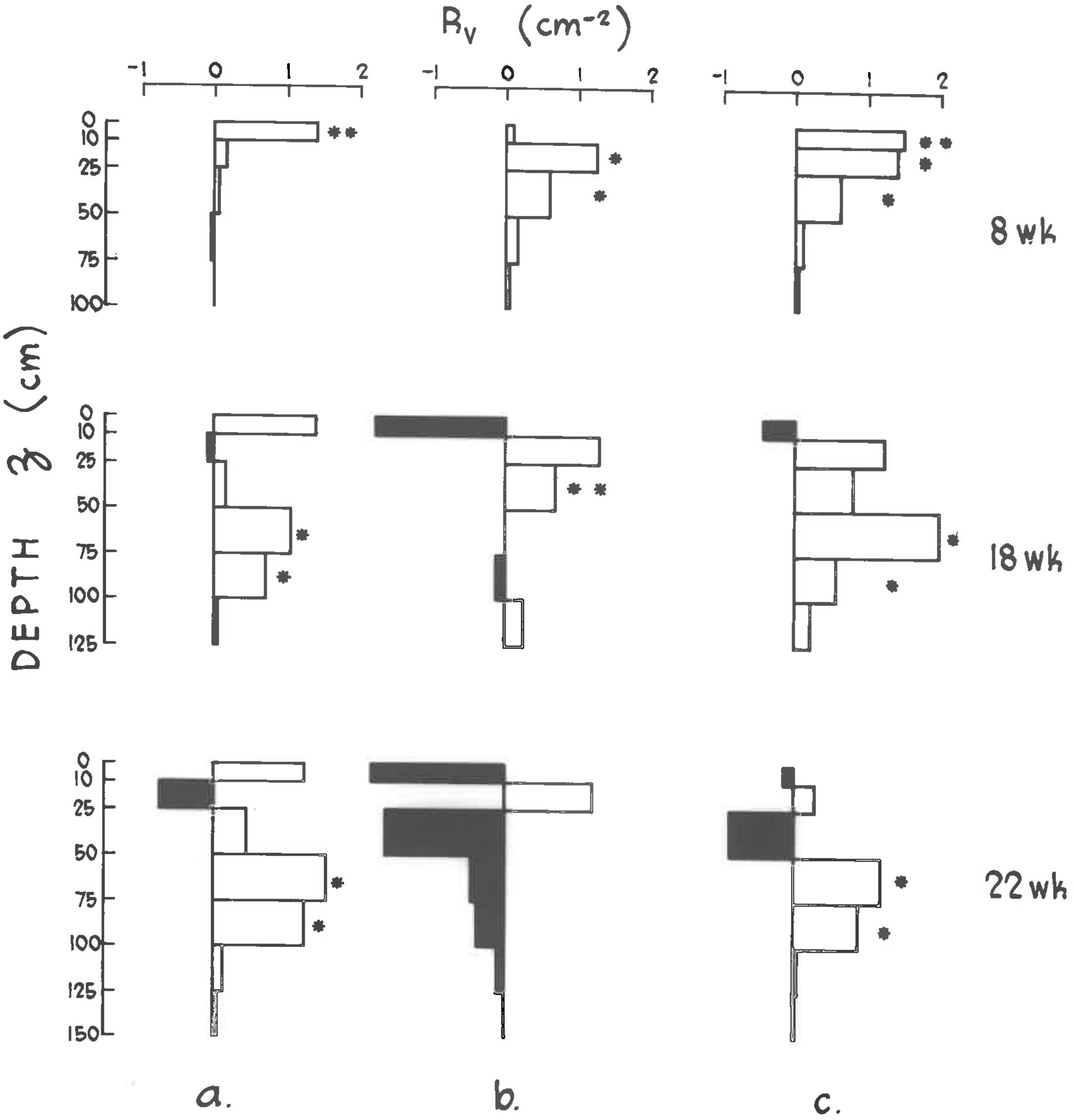


FIG. 24 Change in R_v (cm^{-2}) at each sampled depth with increase in SEEDING RATE
$a. = (S_2 - S_1)$, $b. = (S_3 - S_2)$, $c. = (S_3 - S_1)$
$*$ = Significant difference ($P \leq 0.05$), $**$ = ($P \leq 0.01$).

at S_3 after 18 wk (see Fig. 26).

The application of N increased the *proportion* of the total root length in the topsoil and decreased the *proportion* in the lower horizons. The changes in R_v for each sampled depth that resulted from the application of N are shown in Fig. 25; the values are $(N_1 - N_0)$, $(N_2 - N_1)$, and $(N_2 - N_0)$. The application of N tended to increase R_v in the topsoil during early- and mid-season growth and to decrease R_v in the lower horizons during late growth.

$\delta R_v/\delta t$ at different depths. The mean rate of root growth per unit volume of soil, $\delta R_v/\delta t$ for the 0 to 10, 25 to 50, and 75 to 100 cm depth intervals are shown in Fig. 26 for the three S rates; the results for all depths are included in Appendix Table 9. During the first thirteen weeks of growth $\delta R_v/\delta t$ was highest in the topsoil but after 13 wk it decreased in the topsoil and increased in the lower horizons. Four phases can be distinguished during which $\delta R_v/\delta t$ changed in different parts of the soil profile:

(1) Emergence to 13 wk: root growth occurred mainly in the top 25 cm of the soil. On the S_1 plots, maximum values of $\delta R_v/\delta t$ in the top 10 cm occurred during the period 8 to 13 wk, at S_2 a steady rate of root growth was maintained in the periods 0 to 8 and 8 to 13 wk, but at S_3 $\delta R_v/\delta t$ declined in the period 8 to 13 wk.

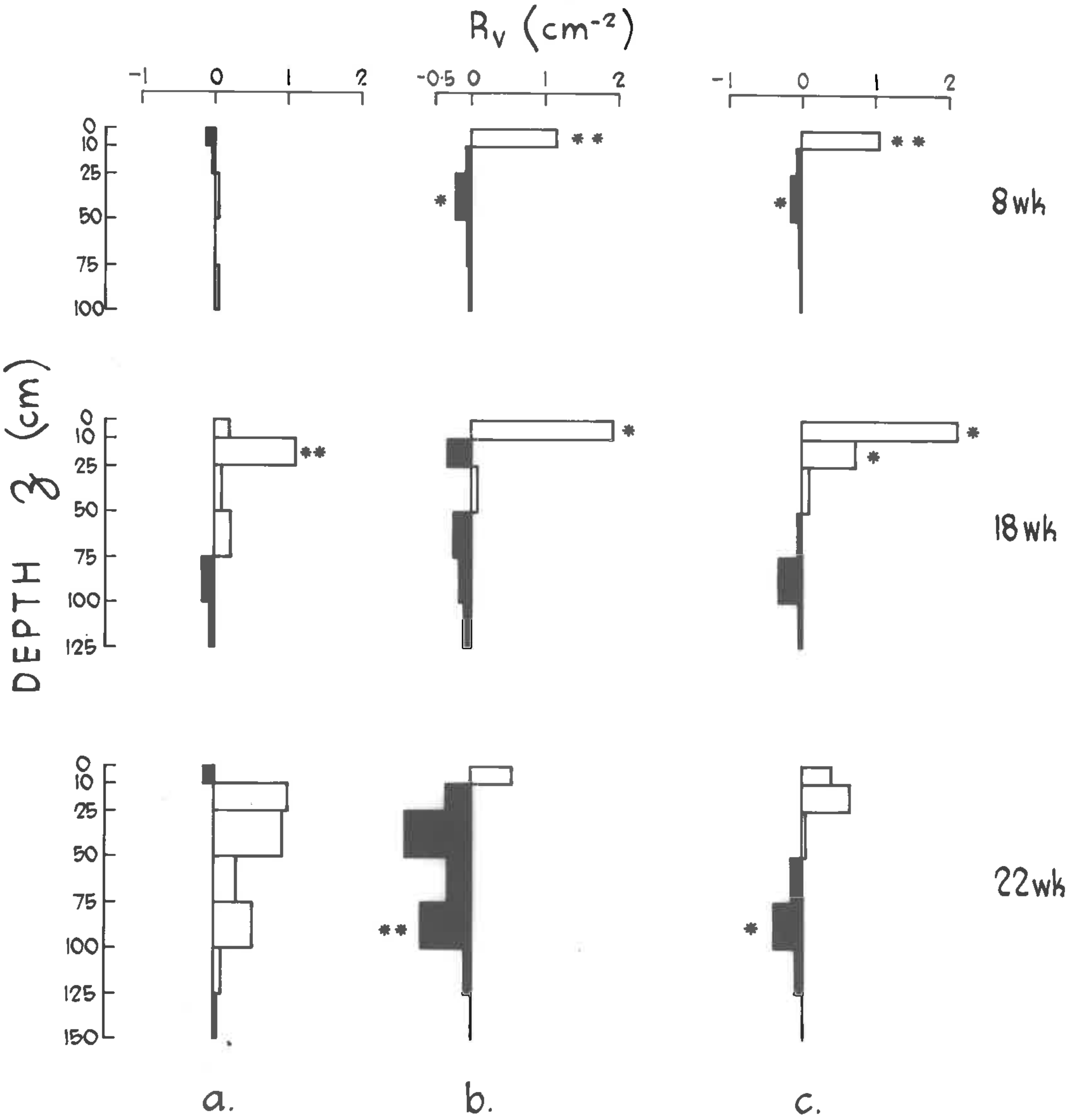


FIG. 25 Change in R_v (cm^{-2}) at each sampled depth with increase in the level of NITROGEN RATE
a. = (N_1-N_0), b = (N_2-N_1), c. = (N_2-N_0)
* = Significant difference ($P \leq 0{\cdot}05$), ** = ($P \leq 0{\cdot}01$).

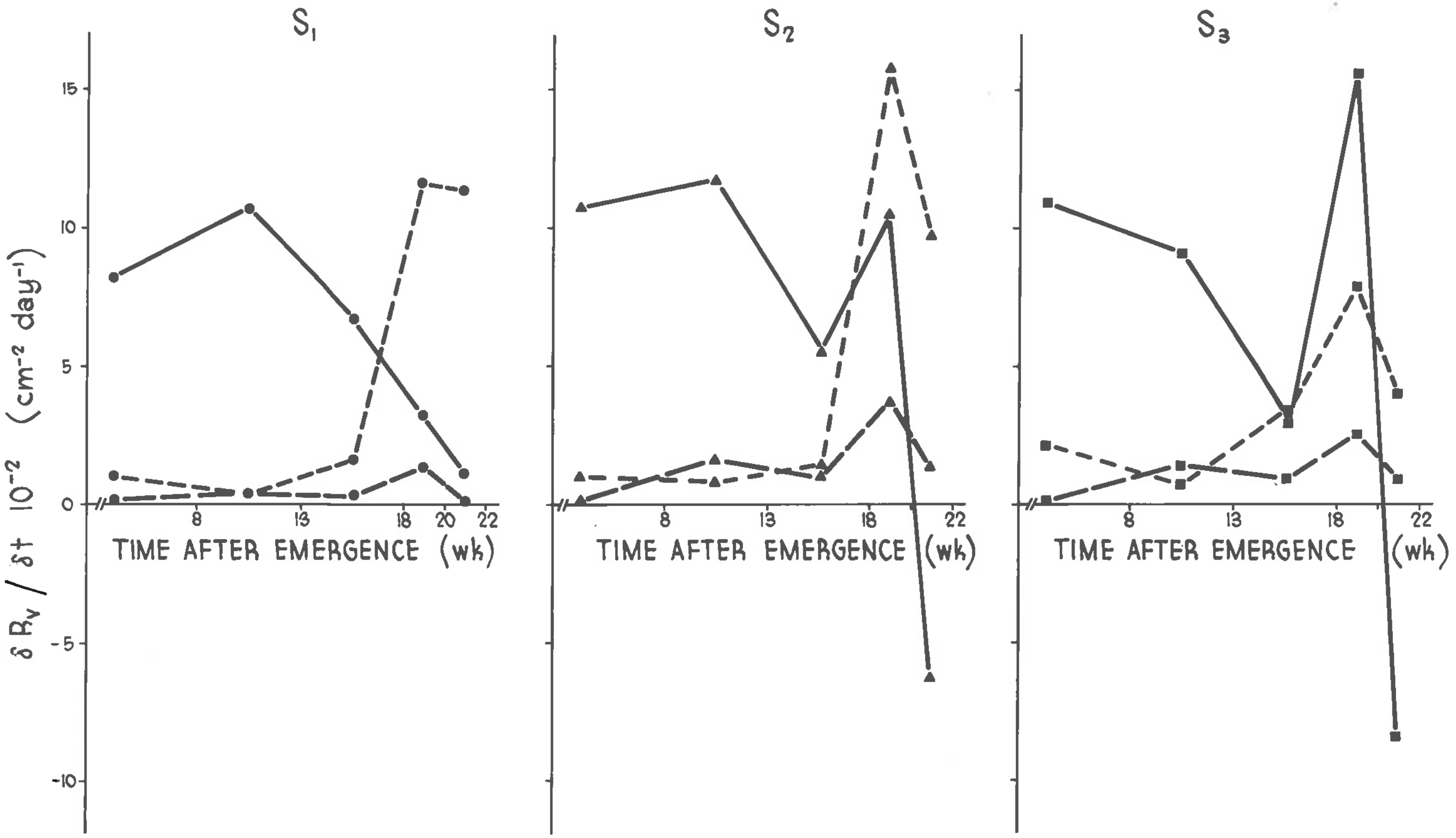


FIG. 26. The influence of SEEDING RATE, S, on $\delta R_v / \delta t$ (cm^{-2} day^{-1}) at 0 to 10, 25 to 50 and 75 to 100 cm depth.

(2) 13 to 18 wk: $\delta R_v/\delta t$ decreased in the top 10 cm and increased in the 10 to 75 cm depth interval on all plots - see Appendix Table 9 for results for depths not included in Fig. 26.

(3) 18 to 20 wk: $\delta R_v/\delta t$ increased in the 25 to 100 cm depth interval on all plots and also in the top 10 cm at S_2 and S_3. The previously observed decline in the top 10 cm continued on the S_1 plots. The increase in $\delta R_v/\delta t$ in the topsoil at S_2 and S_3 may have been due to increased availability of soil water that resulted from rain (30 mm) which fell during the seventeenth week and to increased mineralization of soil NO_3^--N in the spring.

(4) 20 to 22 wk: $\delta R_v/\delta t$ in the top 25 cm decreased sharply at all S rates and at S_2 and S_3 there was a net loss of root length in the top 10 cm. High values of $\delta R_v/\delta t$ were maintained at 75 to 100 cm on all plots with a tendency for ranking in the order $S_1 > S_2 > S_3$. During this period the roots penetrated into the 125 to 150 cm layer.

$\delta R_v/\delta t$ at 0 to 10 cm, 25 to 50 cm, and 75 to 100 cm depth intervals at the three rates of N are shown in Fig. 27 and values for all depths are given in Appendix Table 9. Four phases can similarly be distinguished for the mean rates of change $\delta R_v/\delta t$ for the N treatments, but differences between N treatments are apparent only in the last of these:

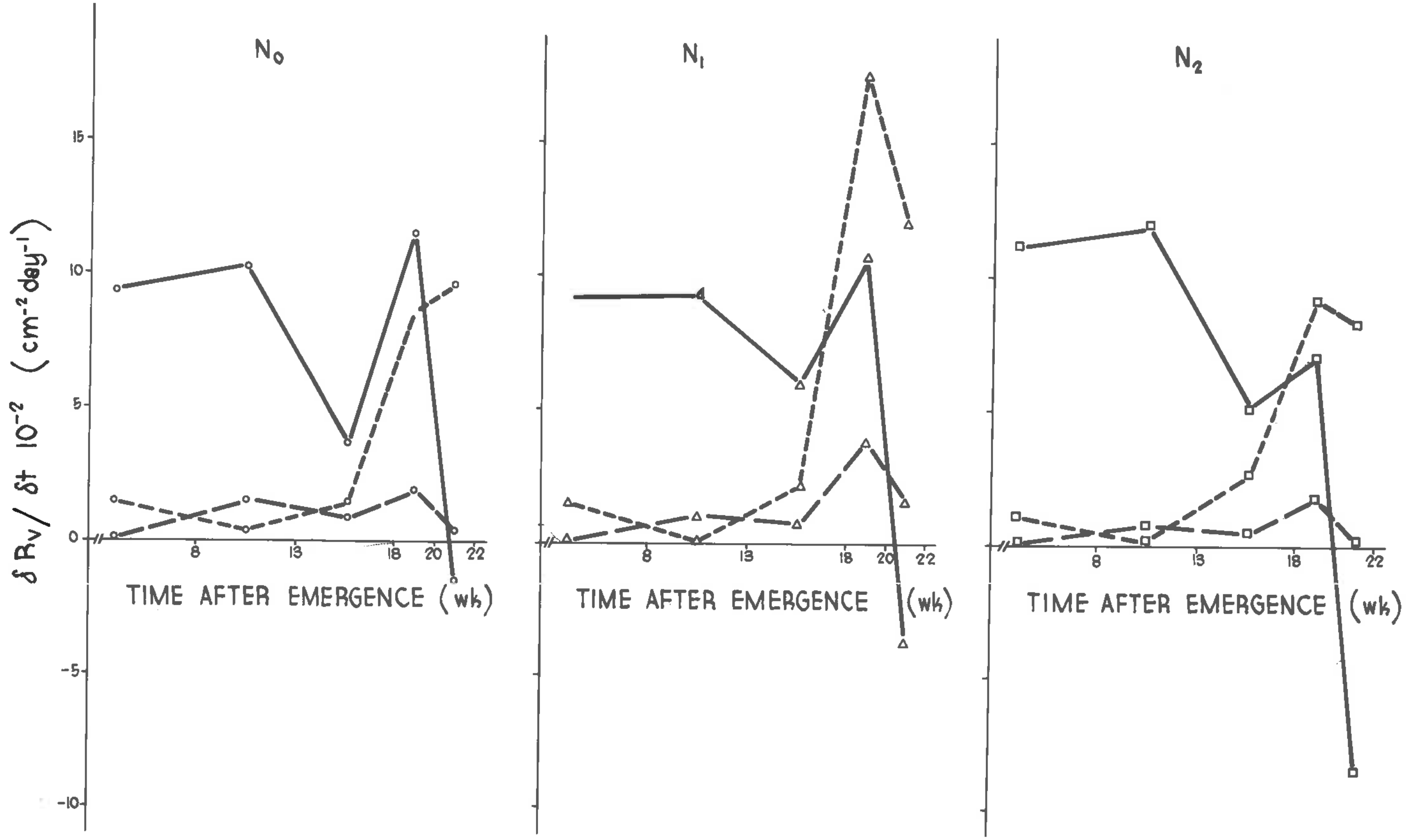


FIG. 27. The influence of NITROGEN RATE, N, on $\delta R_v / \delta t$ ($cm^{-2} day^{-1}$) at 0 to 10, 25 to 50, and 75 to 100 cm depth.

——— 0 to 10 cm — — — 25 to 50 cm - - - - - 75 to 100 cm

(1) Emergence to 13 wk: there were high values of $\delta R_v/\delta t$ in the top 10 cm and low values below 10 cm on all plots.

(2) 13 to 18 wk: $\delta R_v/\delta t$ increased at 10 to 50 cm, there was little change at depths greater than 50 cm but there was a sharp decrease in the top 10 cm on all plots.

(3) 18 to 20 wk: $\delta R_v/\delta t$ increased in the top 75 cm, the increase being most pronounced in the top 50 cm.

(4) 20 to 22 wk: high values of $\delta R_v/\delta t$ ($\geqslant 7 \cdot 10^{-2}$ cm^{-2}) were maintained at 75 to 100 cm depth on all plots. There was a net loss of length in the top 10 cm, the loss being in the order $N_0 < N_1 < N_2$.

The time sequences of $\delta R_v/\delta t$ at each sampled depth were affected partly by plant density, which influenced the orientation of the main axes of the roots (Figs. 19 and 20) and partly by the available water and the NO_3^--N concentration of the soil layer. Readily available water and NO_3^--N in the topsoil provided favourable conditions for high rates of root growth in that part of the profile for the first thirteen weeks after emergence. The subsequent reduction of $\delta R_v/\delta t$ in the topsoil and the increase in the lower horizons are attributed to reduced water and NO_3^--N in the topsoil. Also, it is probable that a large number of actively growing root apices had been produced at depth after 13 wk and most of the assimilate translocated from the shoot may have been diverted to the younger and deeper portion of the root system.

(v) Water use

(a) Water content of the soil profiles at given times. The θ,z relation at 8, 18, and 22 wk is shown in Fig. 28 for the three seeding rates and in Fig. 29 for the three nitrogen rates. Values of θ for each depth at the five times of sampling are given in Appendix Table 4.

θ tended to be lower at the higher rates of S and N. The differences between treatments were greatest at 10 to 100 cm. This was more evident for measurements made at 13 and 18 wk than at other times, and the differences between rates were more pronounced for the S than for the N treatments - see Appendix Table 4 for values of θ for those measurements not included in Figs. 28 and 29. Analyses of variance for θ at each sampled depth showed significant differences between treatments mainly during the middle of the growing season (Fig. 28, Fig. 29, and Appendix Table 4). At 18 wk θ at 10 to 25 cm and 50 to 75 cm depths was higher at S_1 than at S_3 and the differences corresponded to 26 and 60% of the available water(1) in those layers. With respect to the N rates, at 18 wk θ

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(1) $(\theta, h_m = -340 \text{ cm}) - (\theta, h_m = -15{,}900 \text{ cm})$

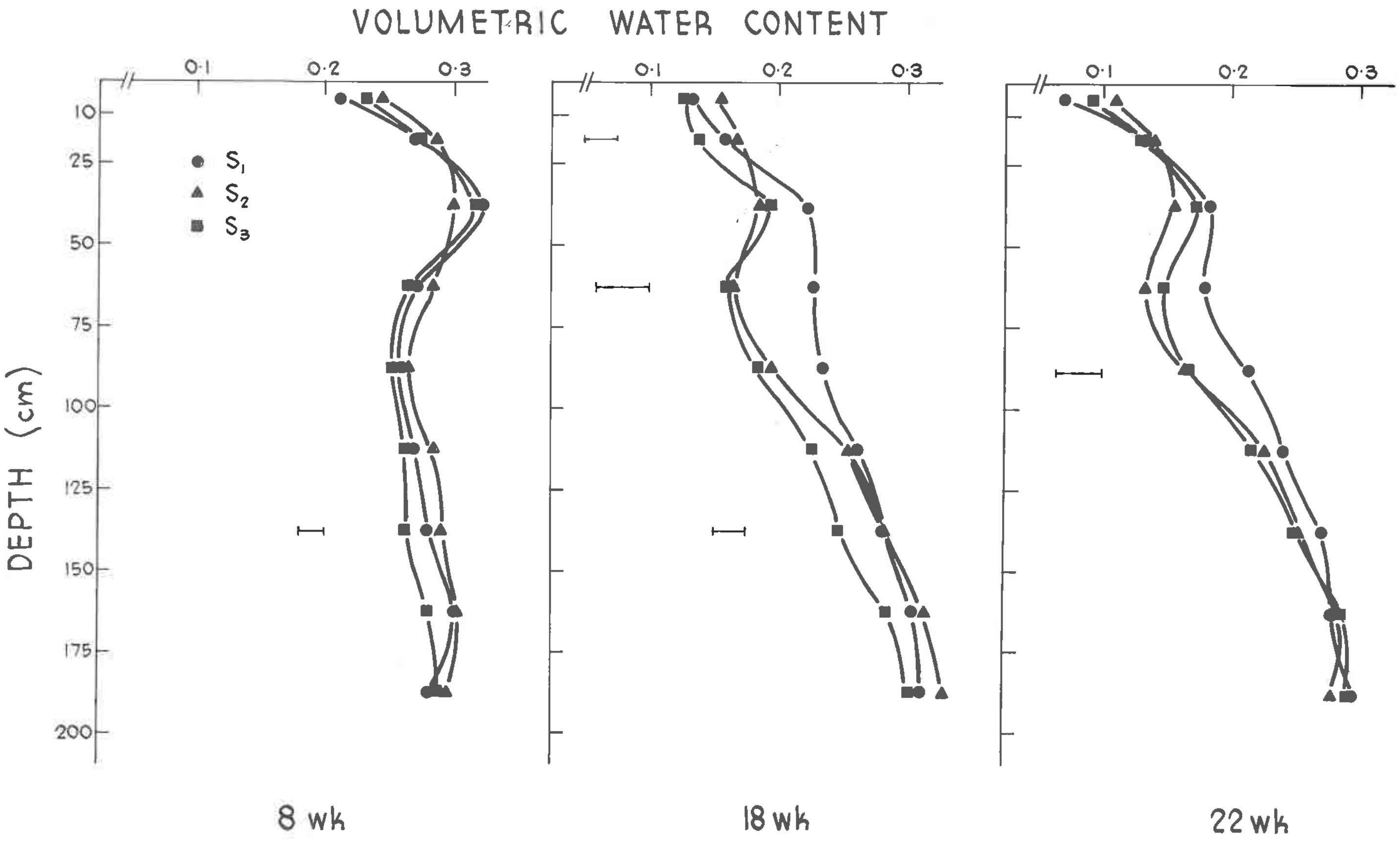

FIG. 28 The influence of SEEDING RATE, S, on the volumetric water content of each sampled depth at 8, 18, and 22 wk. Horizontal lines indicate LSD ($P = 0·05$).

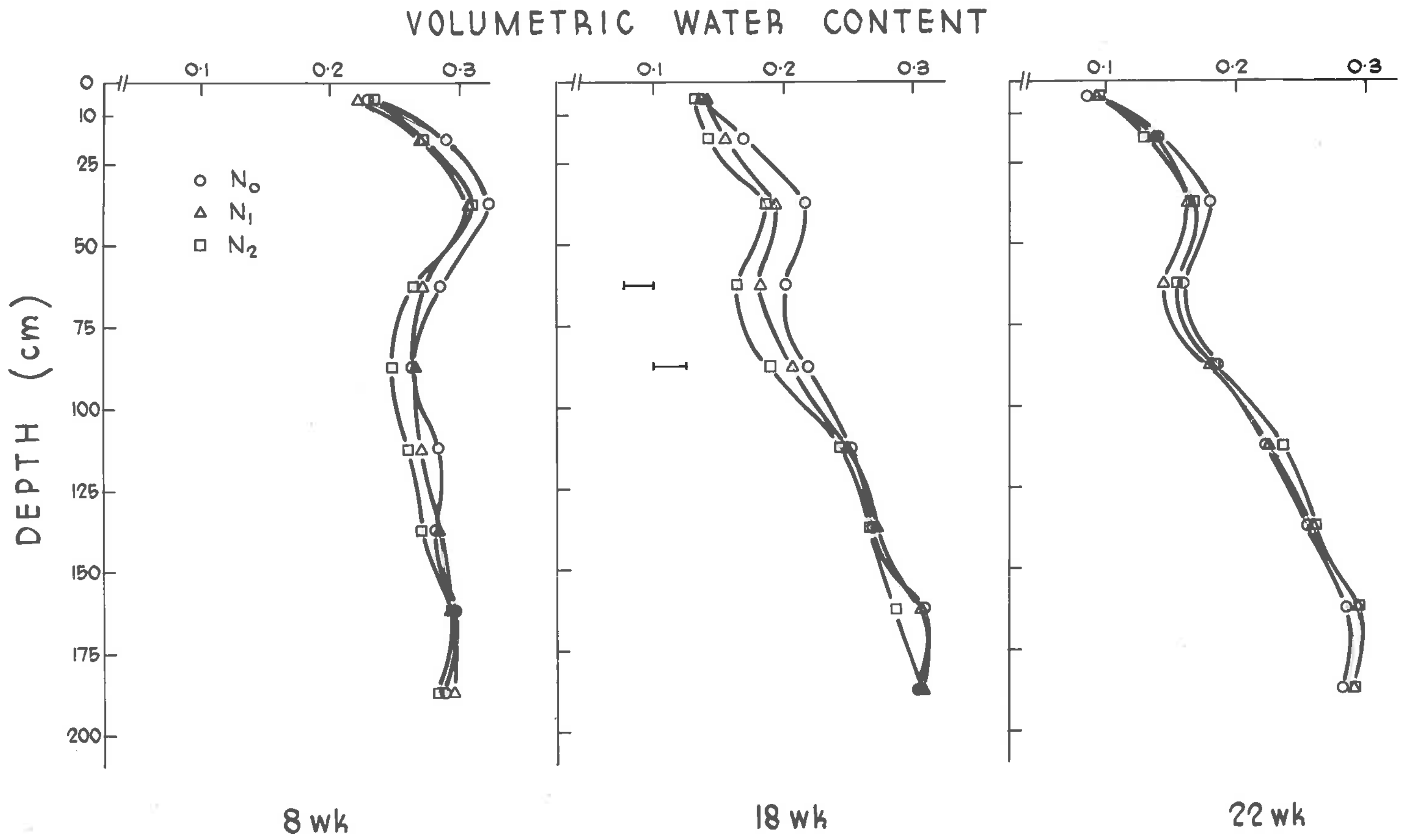

FIG. 29 The influence of NITROGEN RATE on the volumetric water content of each sampled depth at 8, 18 and 22 wk. Horizontal lines indicate LSD ($P = 0{\cdot}05$).

at 50 to 75 cm and 75 to 100 cm depths was significantly higher at N_0 than at N_2, the differences corresponding to 37 and 22% of the available water. In each comparison the lower water content was associated with a high root abundance. At 18 wk R_v (10 to 25 cm) at S_1 = 3.01 cm^{-2} and at S_3 = 4.24 cm^{-2}, at the 50 to 75 cm depth R_v at S_1 = 0.90 cm^{-2} and at S_3 = 2.11 cm^{-2}. With respect to the N rates R_v (50 to 75 cm) at N_0 and N_2 = 1.65 cm^{-2} and R_v (75 to 100 cm) at N_0 = 0.87 and N_2 = 0.53 cm^{-2}, but R_v (0 to 50 cm) was significantly lower at N_0 than at N_2 (3.62 cf. 4.35 cm^{-2}). At maturity (22 wk) h_m in the top 50 cm of the soil at S_1 and N_0, and in the top 75 cm at S_2, S_3, N_1, and N_2 was < -15,900 cm of water; below these depths water was retained at h_m > -15,900 cm.

(b) Changes in soil water content with time. The total water content of the top 2 m of soil increased on all plots from planting until 8 wk after emergence, the increase occurring almost entirely above 150 cm depth. At 13 wk and at all later times, θ throughout the top metre on all plots was below the values measured at planting. By the time the crop had matured, θ between 100 and 175 cm depth had returned to similar values to those found at planting. During the growing season there was little change in θ at 175 to 200 cm, the mean values for the experiment ranged between 0.28 and 0.31.

Time trend analyses of θ for each sampled depth for the period 8 to 22 wk after emergence show significant linear trends ($P=0.001$) throughout the top metre on all sub-plots. The variance ratios for the linear trend coefficients of the θ,t relation at each sampled depth below 75 cm are of more interest in relation to the flow across the lower boundary of the root zone, and are shown in Table 22 for the S and N treatments. The linear trend coefficient in θ below 75 to 100 cm at S_1 was not significantly different from zero, but significant trends were detected at intervals as deep as 125 to 150 at S_2, and 100 to 125 cm at S_3. On the N treatments the linear trend was significant as deeply as 125 to 150 cm at N_0, 100 to 125 cm at N_1 and 75 to 100 cm at N_2.

(c) <u>Evapotranspiration, E.</u> The derived maximum vertical flux of water at 200 cm depth (+ve downwards), was $3 \cdot 10^{-6}$ day^{-1} at 13 wk and $2 \cdot 10^{-6}$ at 20 wk. As these values of $U_{,z=200}$ are negligible, and if we further assume that no lateral movement of water occurred on a macroscopic scale, it follows from Eq. (8) that $E = I - \Delta\theta_{,0 \text{ to } 200 \text{ cm}}$. The value of N at 175 to 200 cm depth remained low throughout the season, suggesting that the wetting front had not reached that depth. Also, although lack of change in θ in a certain layer of soil does not necessarily indicate the absence of water flow through that layer, the lack of change in θ at 175 to 200 cm and at 150 to 175 cm (Table 22) is consistent with the assumption of negligible vertical flux

Table 22

The coefficient and the variance ratio of the linear time trend coefficient of θ (75 to 200 cm depth at 25 cm intervals) for the period 8 to 22 wk after emergence

Treatment	Attribute	Depth (cm) 75 to 100	100 to 125	125 to 150	150 to 175	175 to 200
S_1	Coefficient (day^{-1})	$-5.51 \cdot 10^{-4}$	$-2.74 \cdot 10^{-4}$	$-3.70 \cdot 10^{-5}$	$2.90 \cdot 10^{-5}$	$8.60 \cdot 10^{-5}$
	Variance ratio	15.66***	2.68	$9.09 \cdot 10^{-2}$	$5.94 \cdot 10^{-2}$	$5.95 \cdot 10^{-1}$
S_2	Coefficient (day^{-1})	$-1.03 \cdot 10^{-3}$	$-5.21 \cdot 10^{-4}$	$-2.84 \cdot 10^{-4}$	$-1.11 \cdot 10^{-4}$	$-1.11 \cdot 10^{-4}$
	Variance ratio	97.61***	17.98***	5.18*	1.16	1.29
S_3	Coefficient (day^{-1})	$-9.48 \cdot 10^{-4}$	$-5.36 \cdot 10^{-4}$	$-3.70 \cdot 10^{-4}$	$1.0 \cdot 10^{-5}$	$1.02 \cdot 10^{-4}$
	Variance ratio	58.83***	9.85**	2.91	$6.27 \cdot 10^{-5}$	$7.25 \cdot 10^{-1}$
N_0	Coefficient (day^{-1})	$-8.04 \cdot 10^{-4}$	$-5.55 \cdot 10^{-4}$	$-2.86 \cdot 10^{-4}$	$-1.01 \cdot 10^{-4}$	$-2.10 \cdot 10^{-5}$
	Variance ratio	28.44***	13.02***	4.51*	$7.96 \cdot 10^{-1}$	$3.41 \cdot 10^{-2}$
N_1	Coefficient (day^{-1})	$-9.65 \cdot 10^{-4}$	$-8.42 \cdot 10^{-4}$	$-2.22 \cdot 10^{-4}$	$2.20 \cdot 10^{-5}$	$4.00 \cdot 10^{-6}$
	Variance ratio	85.34***	17.90***	2.96	$3.70 \cdot 10^{-2}$	$1.20 \cdot 10^{-3}$
N_2	Coefficient (day^{-1})	$-7.63 \cdot 10^{-4}$	$-2.95 \cdot 10^{-4}$	$-1.83 \cdot 10^{-4}$	$6.00 \cdot 10^{-6}$	$9.20 \cdot 10^{-5}$
	Variance ratio	23.28***	2.22	$6.79 \cdot 10^{-1}$	$2.25 \cdot 10^{-3}$	$7.27 \cdot 10^{-1}$

* $P = 0.05$ ** $P = 0.01$ *** $P = 0.001$

across the lower boundary of the profile examined. Values of E during each sampling interval are given in Table 23 for the S and N treatments. E was related positively to seeding rate; during the period 8 to 13 wk, and over the entire growing season water use at S_2 and S_3 was significantly higher than at S_1. There was no significant effect of N rate on water use during any sampling interval.

(d) <u>Water withdrawal by roots and vertical flux of water within the profile.</u> The derived rate of withdrawal of water by the roots at each sampled depth $\dot{\lambda}$ (day^{-1}) and the integral rate of withdrawal $\int_0^z \dot{\lambda}\,dz$ (mm day^{-1}) for the three S rates centred at 13 and at 20 wk are shown in Figs. 30 and 31. In evaluating the integral to find the total withdrawal an arbitary value of $z = 200$ cm has been chosen, this being in excess of the maximum depth of rooting at all times. The curves in Figs. 30 and 31 were constructed from the means of the values of $\dot{\lambda}$ and $\int_0^z \dot{\lambda}\,dz$ derived from the mean values of θ and dependent variables for each of the three replicates. Results are not given for different N rates as this would have involved taking averages of derived values across S rates between which large differences in the measured values of θ are known to exist. The alternative would be to present estimates of $\dot{\lambda}$ and $\int_0^z \dot{\lambda}\,dz$ for each sub-treatment but the limited replication available for the primary

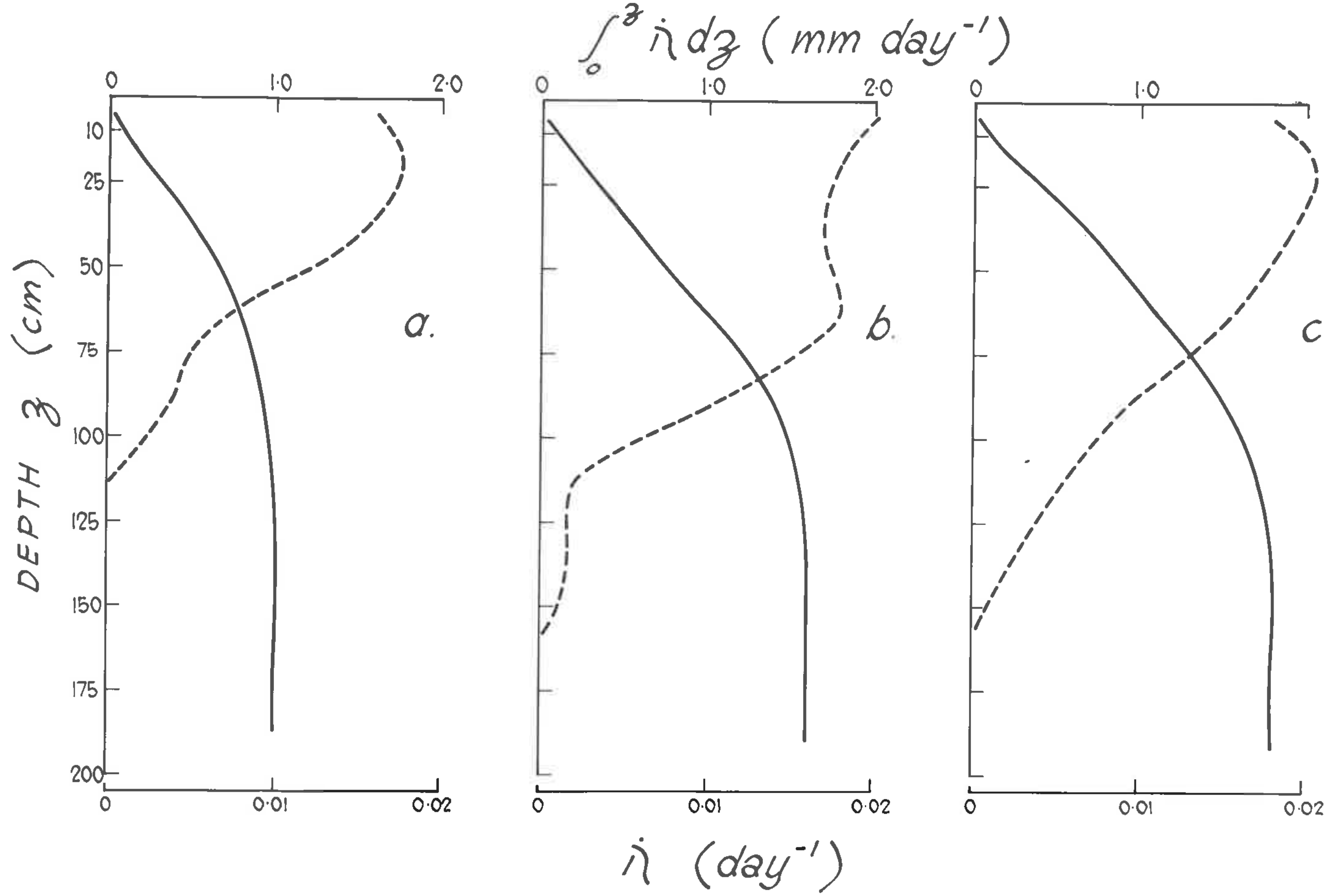

FIG. 30 Water withdrawal by roots at 13wk. $a = s_1$, $b = s_2$, $c = s_3$

---- = $\dot{\lambda}$, —— = $\int_0^z \dot{\lambda}\, dz$

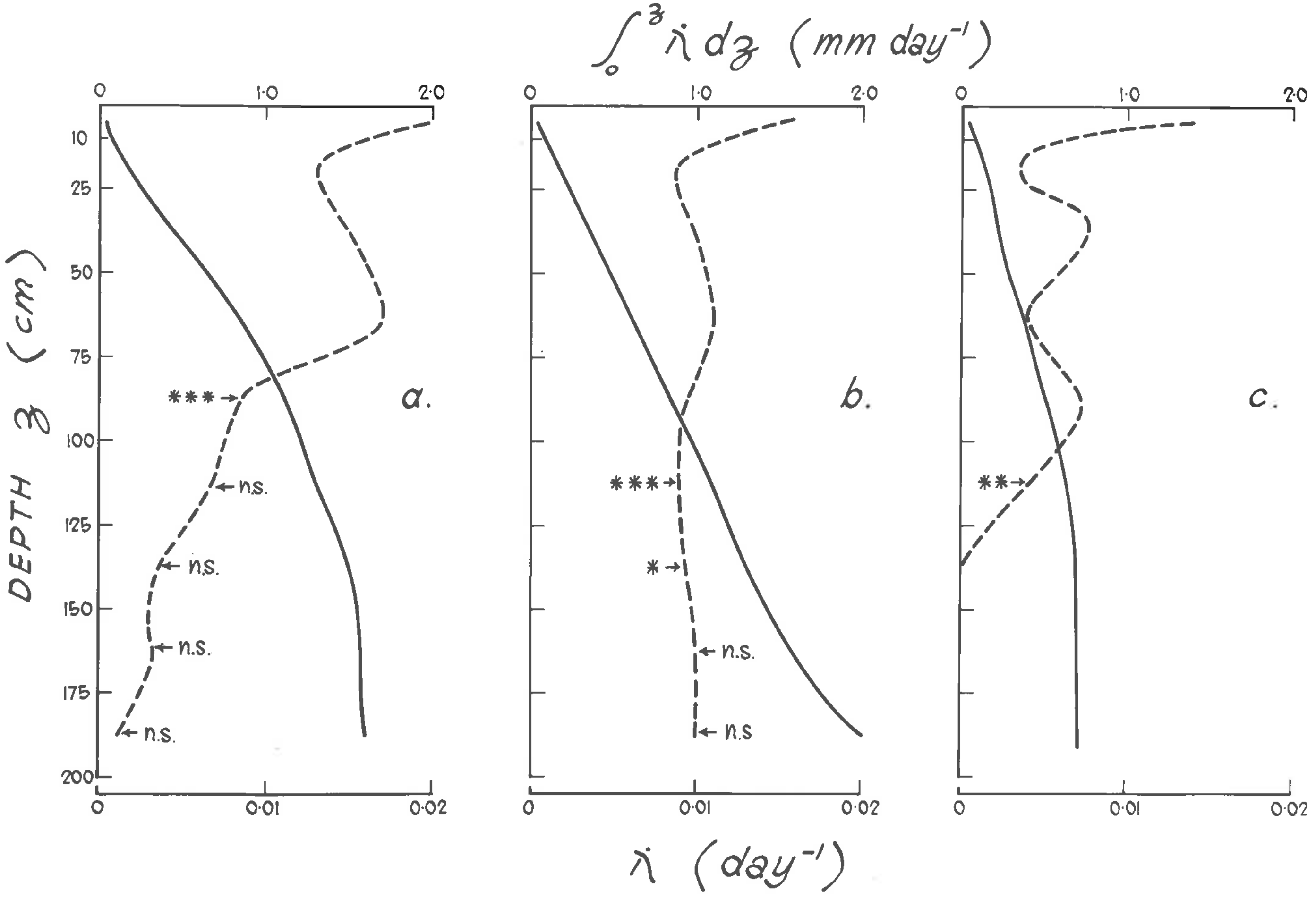

FIG. 31. Water withdrawal by roots at 20 wk. $a = S_1$, $b = S_2$, $c = S_3$, - - - - - λ, ——— $\int_0^z \lambda \, dz$. The significance of the linear time trend coefficient for θ (8 to 22 wk) is shown as * = ($P = 0{\cdot}05$), ** = ($P = 0{\cdot}01$), *** = ($P = 0{\cdot}001$) n.s. = not significant.

Table 23

Evapotranspiration* for different time intervals after emergence (cm)

Time after emergence (wk)	Treatment			L.S.D. (P=0.05)
	S_1	S_2	S_3	
0 to 8	8.2	6.7	9.3	n.s.
8 to 13	7.8	13.2	11.8	3.3
13 to 18	12.7	12.0	15.2	n.s.
18 to 20	5.4	4.6	4.1	n.s.
20 to 22	2.0	3.8	2.1	n.s.
0 to 22	36.1	40.2	42.1	5.8
	N_0	N_1	N_2	
0 to 8	6.8	8.0	9.4	n.s.
8 to 13	11.2	10.9	10.7	n.s.
13 to 18	12.2	13.4	14.3	n.s.
18 to 20	5.7	4.5	3.9	n.s.
20 to 22	2.8	2.6	2.4	n.s.
0 to 22	38.7	39.4	40.3	n.s.

* $E = I - \Delta\theta,_{0 \text{ to } 200 \text{ cm}}$

data obtained for each sub-treatment makes it hazardous to calculate derived values, as the latter are sensitive to small changes in θ. It should be noted that the estimates are based on measurements made at relatively long periods of time, and that the nominal referral of the derived fluxes to the mid-point of the time interval examined does *not* imply that the derived value operated instantaneously at that time.

At 13 wk water withdrawal by the roots was mainly from the top 75 cm, with a little additional withdrawal from 75 to 100 cm depth. $\dot{\lambda}$ at 50 to 75 cm tended to be higher at S_2 and S_3 than at S_1. At this time the bulk of the roots were in the top 50 cm of the profile, the deepest roots had penetrated to 75 to 100 cm, and R_v (50 to 75 cm) was higher at S_2 and S_3 than at S_1. The total withdrawal (mm day^{-1}) at S_1 = 1.0, S_2 = 1.6, and S_3 = 1.8. In contrast, at 20 wk, $\dot{\lambda}$ in the top metre was related negatively to S (Fig. 31). At S_2 $\dot{\lambda}$ was relatively uniform at all depths within the root zone being approximately 1.10^{-2} day^{-1}. At 20 wk, θ increased but R_v decreased with depth (see Appendix Tables 4 and 7). Since, as noted in Section 2.2.2, water withdrawal by roots from an element of soil is related positively to θ and to R_v, it is likely that at S_2 the effects of the decrease in R_v with depth were balanced by those of the increase in θ. There is an anomaly at depths greater than 150 cm at S_1 and S_2 as $\dot{\lambda}$ is estimated to have a small positive value but no roots were observed below 150 cm even at 22 wk. The linear time trend coefficients of θ were not significant at depths greater than 150 cm and the anomaly probably arises from sampling errors.

At 20 wk the total withdrawal at S_1 and S_2 = 1.5 and S_3 = 0.7 mm day^{-1}. This reversal of the effects of seeding rate noted at 13 wk is attributed to more water being available at S_1 than at S_3 at 20 wk. In the period from 0 to 18 wk at S_1, S_2, and S_3, R (cm) = 28.7, 31.8, and 37.9. The z,θ values (Appendix Table 4) also show that more water was available in the soil at S_1 than at S_3 at 20 wk.

The highest rates of water withdrawal occurred from those parts of the soil profile with large values of both R_v and θ. It appears that during early growth while θ is still high, $\dot{\lambda}$ is influenced chiefly by R_v, but towards maturity, when the root system is well developed and when θ is low, $\dot{\lambda}$ is influenced more by θ than by R_v.

The vertical flux of water through the soil pores at 200 cm depth was negligible both at 13 and 20 wk: $\dot{U}_{,z=200\ \text{cm}}$ ranged from $-2 \cdot 10^{-7}$ to $3 \cdot 10^{-6}$ mm day^{-1} at 13 wk and from $-7 \cdot 10^{-7}$ to $3 \cdot 10^{-6}$ mm day^{-1} at 20 wk. The maximum downward flux in the profile at 13 wk occurred at 24 cm, the value being $4 \cdot 10^{-1}$ mm day^{-1}. At 20 wk, the maximum downward flux again occurred at 24 cm and was $3 \cdot 10^{-2}$

mm day^{-1}. The maximum upward flux through the soil at 13 wk was $-1 \cdot 10^{-2}$ mm day^{-1} at 52 cm, and, at 20 wk it was $-2 \cdot 10^{-4}$ mm day^{-1} at 15 cm. At 13 wk the downward flux through the soil pores exceeded $\dot{\lambda}$ only in the 10 to 25 cm layer; at 20 wk the vertical flux at each depth was $< 0.1\ \dot{\lambda}$. The negligibly small values of $\dot{\lambda}$ below the maximum depth of rooting indicate that the vertical flux of water across the lower boundary of the root zone was negligible at 13 and at 20 wk. The suction head of water at 175 to 200 cm depth remained high throughout the season, suggesting that the wetting front did not reach this depth.

As noted in Section 3.3.2.(iv)(e), the values of θ used in the calculation of water withdrawal were obtained after linear interpolation between the measured values of θ; ideally, a polynomial function should have been fitted to the θ,t curve but, noting that the time intervals between samplings on either side of the 13 and 20 wk samples were equal, the arithmetic means of the slopes connecting the 8, 13, and 18 wk and the 18, 20, and 22 wk samples were taken to simplify the calculations.

More accurate estimates of $\dot{\lambda}$ could be obtained by carrying out experiments at a site with less variable soils, and by measuring the water content of the soil profile at shorter intervals of time. Nevertheless, the results are compatible with the z,H_p and the z,θ data, and serve to show that, given the θ,H and the θ,k

relationships, vertical flux of soil water into and out of the root zone, and the pattern of water withdrawal by roots can be estimated with sufficient accuracy to help interpret the results of field experiments on water use by crops.

(e) <u>The Silicon content of the plant tops as related to water use.</u> Most of the Si taken up by cereal plants is deposited in the epidermal cells and the cell walls of transpiring organs (Smithson 1958). Richardson, Trumble and Shapter (1931), Jones and Handreck (1965), and Handreck and Jones (1968) have found a high positive correlation between the uptake of Si and the amount of water transpired by oat and wheat plants grown in pots of soil. Such correlations are difficult to obtain in field experiments as a large part of the leaf lamina, which contains high concentrations of Si (Jones *et al.* 1963, Handreck and Jones 1968), is often lost in the field toward maturity. Approximately 40% of the total Si was in the husks(1) of the plants examined by Jones and Handreck (1965) and Handreck and Jones (1968). Hutton and Norrish(2) suggest that analysis of the husks offers a means of estimating the total water transpired by wheat crops in South Australia. As the only data

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(1) Lemmae, paleae, and awns.

(2) Pers. Comm. with reference to a paper 'Silicon content of wheat husks in relation to water used', presented to the Australian Cereal Agronomy Conference, Wagga Wagga, New South Wales, Australia. 1970.

available to Hutton and Norrish were rainfall and water contents of the soil at sampling and at maturity, their estimates of E_c are somewhat arbitary. No data on runoff were available, and evaporation from the soil and flow across the lower boundary of the sampled layer were not measured.

The percentage Si in the husks may be useful as an index of E_c if transpiration from the husks is a consistent fraction of E_c and if the evapotranspiration in the period after the ears have emerged is a consistent fraction of that occurring in the whole season. In the present study, at one week before ear emergence, more water remained in the soil at the lower seeding rates, and E 13 to 22 wk at S_1, S_2, and S_3 = 20.1, 20.4, and 21.4 cm representing 0.56, 0.51, and 0.51 of E_{total}. It seems likely therefore that the regression of E_c on percentage Si in the husks would be affected by seeding rate. More generally, there is no reason why E_c before ear emergence should be related closely to E_c after ear emergence, as the relation would be affected by seasonal conditions and sowing date. At maturity the *per cent* Si in the tops and husks at the three rates of N was

	N_0	N_1	N_2	L.S.D. (P=0.05)
% Si in the tops	3.0	2.6	2.1	0.48
% Si in the husks	5.3	5.1	3.9	0.92

The application of N significantly increased the lamina area index and tended to increase the dry weight of the tops; once the canopy had closed any further increase in the crop surface would have resulted in a decline in the rate of transpiration per unit of surface area and presumably per unit of dry weight also. Reduction in the per cent Si content of cereals has been noted in previous studies (see Jones and Handreck 1967). Data on the dry weight of the husks were not obtained, but volumetric dilution may have explained the effect of N.

GENERAL DISCUSSION AND CONCLUSIONS

4. GENERAL DISCUSSION AND CONCLUSIONS

Comment on the reasons for particular treatment effects has been made in the course of the thesis. Here we turn to a number of matters of more general interest. The study was conducted in an environment where water supply generally limits grain yield. The main objectives were to further understanding of the growth and development of the wheat root system in the field, and to describe the relationship of root growth and the pattern of water withdrawal from the soil. Top growth was measured also, but only to the extent needed to characterize the crop. Although the results are limited to one site in two seasons, information of general significance and interest has emerged.

The influence of rate of seeding (S) and of the rate of N application (N) on top growth confirm the results of previous studies conducted in South Australia [Wassermann 1964 (N and S), Barley and Naidu 1964 (N rates only), Puckridge and Donald 1967 (S rates only)]. In the present study and in that conducted by Wassermann, variation in S rates had a greater effect on yield of dry matter per plant and per unit area of ground area than did variation in N rate, and in each of the studies referred to, the general influence of the treatments on vegetative growth was more pronounced during the early part of the growing season.

As early as 8 wk after seedling emergence inter-plant competition had restricted dry matter production per plant significantly at S_2 and S_3. As the mean length of root per tiller was related negatively to S at 8 wk, it is likely that there was already a shortage of assimilates for root growth at this time. As noted previously by Donald (1963) and Puckridge and Donald (1967) the maximum tiller density and L_{max} were attained earlier and declined more rapidly at the higher levels of S and N. Total dry weight of tops per unit of ground area increased at the higher rates of S and N; however the tops dried off earlier at these rates, and the treatment effects on grain yield were relatively small and also differed in relation to one another compared with the effects on vegetative growth:- grain yield per unit area differed significantly between the three S rates, with S_2 producing the highest yield. There was no difference in grain yield between the N rates. As noted by Colwell (1963), Fischer (1963), and by Barley and Naidu (1964), in dry years the application of N usually either has no effect on grain yield or tends to reduce it. The present study showed that the root system became more superficial at high rates of N supply (see Fig. 25), and this, together with greater drying of the top metre of the root zone during mid-season (see Fig. 29), may explain why the crop lost turgor earlier. Given plant densities similar to S_2 and a tillering response similar to that noted in this study, it is likely that, if water had not been limiting, the application of N would have increased grain yield. In this study the lack of a grain yield response to N can be attributed to the shortage of water during the latter half of the growing season, when water supply became the main limiting factor.

There is little published data with which to compare the measured values of R_a and R_v. The values of R_a reported by Pavlychenko (1937) and Pavlychenko and Harrington (1934, 1935) in their experiments in Saskatchewan, Canada range from 1000 to 4000 cm^{-1}. These values are considerably higher than those obtained in the present study ($\leq$ 500 cm^{-1}). The reasons for this are not clear. Although Pavlychenko and Harrington reported a growing period of only 80 days after seedling emergence, the day length would have been relatively long. If radiation levels were high, net daily photosynthesis may have provided a large surplus of assimilate for translocation to the roots. Furthermore, water may not have been limiting in the Canadian work as no mention is made of water stress in the papers concerned. The rooting densities of different species of cereals grown in the same environment are known to differ markedly (Pavlychenko 1937, Pavlychenko and Harrington 1935), and it may well be that the rooting characteristics of different cultivars differ as much as those of different species. Possibly the cultivars studied in the Canadian work produced higher orders of laterals than the cultivar of wheat used in the present experiment. A difference of one order of branching could have a large effect on R_a.

It is interesting to find that root growth in length continued until maturity. It is generally reported in the literature (Kamel 1959, Welbank and Williams 1968, Schuurman 1959) that root weight declines as cereals mature. The reduction in root weight may result from net translocation of carbohydrates to the tops, from losses due to root respiration following reduced translocation from the tops, and from sloughing of the cortex from older proximal zones of roots. Continued downward growth of the roots late in the season has been noted previously (Weaver 1926), and the value of continued root extension late in the season as a varietal attribute influencing grain yield has been noted by McClure and Harvey (1962). However the author is not aware of any previous statistical study of the growth in length of the root system of a wheat crop. In earlier studies, failure to sample the whole rooting depth, and the use of weight data, have both led to excessive emphasis being placed on the abundance of roots in topsoils. Although root weight per unit volume of soil decreases rapidly with increasing depth, the specific length of roots tends to increase with depth (Derera *et al.* 1969). Moreover in climates similar to that at Roseworthy, the deeper roots are generally the most important for water uptake during the latter part of the growing season when grain yield is largely determined.

During the period 8 to 18 wk after emergence the mean rates $\dot{E}$ and $\dot{E}_c$ tended to increase with S rates – $\dot{E}$: $S_1 = 2.9$, $S_2 = 3.6$, $S_3 = 3.9$ mm day^{-1}; $\dot{E}_c$: $S_1 = 1.0$, $S_2 = 1.6$, $S_3 = 1.8$ mm day^{-1}. From 18 to 22 wk the ranking altered – $\dot{E}$: $S_1 = 2.5$, $S_2 = 2.8$, $S_3 = 2.1$ mm day^{-1}; $\dot{E}_c$: $S_1 = S_2 = 1.5$, $S_3 = 0.7$ mm day^{-1}. In comparison $\dot{E}_o$ increased from 4.3 mm day^{-1} during the 8 to 18 wk period to 7.6 mm day^{-1} during the 18 to 22 wk period. Differences between the N dates were less than those between the S rates. Reduction in $\dot{E}$ and $\dot{E}_c$ late in the season when $\dot{E}_o$ is increasing is due to reduced availability of soil water (Fig. 28). Kirby (1970) has found similarly that $\dot{E}$ for a barley crop was related positively to S rates during the early part of the season but negatively during later growth.

Although the total evapotranspiration was significantly higher at S_3 than at S_1, no significant differences were detected between N levels. Nevertheless the soils dried more rapidly between 50 and 100 cm during mid-season at the higher rates of N. Although differences in water use are often interpreted in terms of canopy development only, there are two possibilities: firstly, increased leaf area intercepting more radiant energy, and secondly, greater root abundance reducing the resistance to water flow from the soil into the root network. The relative importance of canopy and root system development in relation to water uptake in the present study is not altogether clear, but there is a strong indication that the latter was influential as, for a given depth of soil, R_v was related positively to soil water depletion (see pp. 158–159).

Although soil conditions do not appear to have restricted root growth in the lower horizons, available water remained below 100 cm depth at maturity. The proportion of available water used was greatest in the top soil and became progressively less with increasing depth. As the plants lost turgor before the end of the season, greater root development at depth would presumably have increased water uptake from the lower horizons. This applies particularly to the high S and high N rates at which the plants showed diurnal wilting as early as the seventeenth week. By maturity, where $R_v \geq 2.5$ cm^{-2} θ had been reduced to or below the wilting point, but where $R_v \leq 1.5$ cm^{-2} θ remained above the wilting point. This result agrees surprisingly well with a prediction of Philip (1957), who suggested on theoretical grounds that, for roots of mean radius 0.07 cm, an abundance of 1.1 cm^{-2} would be needed to dry the soil to wilting point.

The measured values of *k* are low when compared with published data for disturbed loams and sands, but compare with limited published data for undisturbed loams (Rose *et al.* 1965, Butijin and Wesseling 1954). When Marshall's (1958) equation (7) is used in conjunction with the appropriate moisture characteristics to estimate *k*, it sometimes predicts values 10^2 times greater than values of the vertical conductivity measured for undisturbed loams, as shown in the following table:

Source of data		(cm)	Marshall (cm min^{-1})	Measured (cm min^{-1})
Rose *et al.* (1965)	0.2	200	$2 \cdot 10^{-3}$	$3 \cdot 10^{-5}$
Present study	0.2	200	$4 \cdot 10^{-4}$	$2 \cdot 10^{-6}$

Many field soils with a history of eluviation or consolidation may be grossly anisotropic, when Marshall's equation would not apply. Talsma (1960) has shown that in soils with distinctly developed horizons and in which eluviation has occurred, *k* in the vertical direction is less than that in the horizontal and is also highly variable. The soil used in the present study shows considerable eluviation of both clay and carbonates, and the downward transfer of fine material may have tended to block the 'horizontal' aspect of the pores. The outflow data obtained are considered to be reliable, as they fit Peck's (1966) ideal curve (see p. 104), and the calculations themselves have been checked using Eq. (1) of Doering (1965). It is difficult to obtain statistical data on *k*; however, as the *k* values measured were always low, the relatively small number of samples taken for this determination matters little in the present experiment, where it is clear that, except in the topsoil, the rate of (macroscopic) upward flow of water through the soil was small compared with the rate of withdrawal by the roots.

At 13 wk the mean values of water withdrawal per unit length of root, *q*, (cm^2 day^{-1}) ranged from $7 \cdot 10^{-4}$ at S_1 to $1 \cdot 10^{-3}$ at S_2 and S_3. At 20 wk the values ranged from $2 \cdot 10^{-4}$ at S_3 to $5 \cdot 10^{-4}$ at S_1 and S_2. Maximum values of $1 \cdot 10^{-3}$ cm^2 day^{-1} were found in the lower soil horizons at 13 wk, and minimum values of $1 \cdot 10^{-5}$ cm^2 day^{-1} were found in the top 10 cm at 20 wk. Generally, *q* was of the order of $1 \cdot 10^{-4}$ or $1 \cdot 10^{-3}$ cm^2 day^{-1}. This is one or two orders of magnitude less than the values assumed by Gardner (1964) in his theoretical studies. Barley (1970) suggests, however, that there is little uptake of water from drying soils except by root zones with root hairs, as the axial parts of roots are too large to occupy those voids that remain filled with water at field capacity. When calculated per unit length of hair bearing zone the rate of water uptake is increased to $1 \cdot 10^{-3}$ to $1 \cdot 10^{-2}$ cm^2 day^{-1}. Peak values for the root hair zone occurred at lower depths late in the season, being of the order $1 \cdot 10^{-1}$ cm^2 day^{-1}. This happens to coincide with a value assumed by Gardner for the whole length of root in his 1960 study. Newman's (1969) conclusion that *generally* $A_r >> A_s$ (see p. 38) may apply, but only to topsoils under established crops or pastures. When, as in the present experiment, towards the end of the season most of the uptake of water is performed by relatively sparse deeper roots and $\dot{E}_o$ is large, A_s is likely to far exceed A_p.

In general a more intensive and less arbitary pattern of sampling would have been preferred, but the methods adopted were necessitated by the lack of time and labour. Further experimentation along the lines of the present experiment, aimed to cover the environment of the cereal growing areas of South Australia, will clearly require a team approach rather than that of the single investigator.

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Appendix Table 1

The Preliminary Experiment

The volumetric water content θ of the soil profile
at planting, and at 5 and 12 wk after emergence[+]

Planting		Time after emergence (wk)								
Depth (cm)	θ	Depth (cm)	5				12			
			N_0	N_1	N_2	Mean[++]	N_0	N_1	N_2	Mean[++]
0 - 15	.12	0 - 10	.20	.18	.20	.19	.05	.06	.08	.06
15 - 30	.20	10 - 25	.23	.27	.27	.26	.14	.16	.18	.16
30 - 60	.20	25 - 50	.27	.27	.27	.27	.18	.17	.16	.17
60 - 90	.20	50 - 75	.20	.22	.23	.22	.14	.14	.14	.14
90 - 105	.22	75 - 100	.20	.22	.21	.21	.16	.17	.17	.17
105 - 120	.22	100 - 125	.19	.24	.22	.22	.20	.21	.18	.20
120 - 135	.23	125 - 150	.21	.27	.25	.24	.23	.24	.19	.22
135 - 150	.24	150 - 175	.27	.30	.27	.28	.29	.29	.33	.30
150 - 165	.24	175 - 200	.29	.31	.31	.30	.30	.29	.24	.28
165 - 180	.29									

[+] Means of three determinations

[++] No significant differences between N treatments

Appendix Table 2

The Main Experiment

The volumetric water content θ at specified suction heads and for the different replicates and horizons (the soil water characteristic)

		Suction head	(cm of water)							
Rep.	Horizon	10	100	340	680	1,035	2,110	5,280	10,570	15,900
1	A1	.31	.19	.17	.16	.13	.11	.06	.06	.05
	A2	.24	.13	.09	.08	.07	.07	.05	.05	.04
	B1	.43	.38	.36	.34	.33	.29	.24	.22	.20
	B2	.33	.26	.23	.21	.21	.19	.19	.16	.15
	B3	.37	.31	.28	.22	.21	.20	.19	.18	.17
	B4	.43	.39	.37	.35	.34	.30	.20	.17	.17
	C	.45	.41	.40	.38	.37	.36	.33	.26	.25
2	A1	.30	.20	.16	.14	.13	.10	.08	.08	.07
	A2	.23	.14	.09	.08	.07	.06	.05	.04	.04
	B1	.42	.39	.34	.34	.32	.27	.23	.21	.20
	B2	.32	.29	.24	.23	.21	.19	.19	.16	.15
	B3	.41	.32	.29	.27	.26	.24	.20	.17	.16
	B4	.41	.26	.34	.32	.31	.26	.22	.20	.18
	C	.43	.41	.38	.36	.35	.32	.31	.26	.25
3	A1	.35	.26	.19	.19	.18	.16	.12	.11	.11
	B1	.38	.28	.25	.23	.22	.21	.17	.16	.16
	B3	.45	.32	.27	.25	.23	.20	.20	.17	.16
	B4	.44	.39	.36	.35	.32	.25	.24	.22	.20
	C	.56	.53	.42	.41	.39	.36	.31	.27	.25

Appendix Table 3

The Main Experiment

The hydraulic conductivity (cm per min) of the different replicates and horizons

Rep.	Horizon	Mean suction head (cm of water)			
		205		1500	
		Sample 1	Sample 2	Sample 1	Sample 2
1	A1	2.4×10^{-6}	2.9×10^{-6}	3.7×10^{-8}	6.7×10^{-8}
	A2	9.2×10^{-7}	n.d.	3.9×10^{-8}	n.d.
	B1	3.1×10^{-7}	1.6×10^{-7}	1.4×10^{-8}	1.7×10^{-8}
	B2	8.6×10^{-7}	1.3×10^{-6}	3.8×10^{-8}	3.9×10^{-8}
	B3	n.d.	n.d.	n.d.	n.d.
	B4	1.8×10^{-6}	1.7×10^{-6}	7.9×10^{-8}	5.6×10^{-8}
	C	7.1×10^{-7}	6.7×10^{-7}	1.2×10^{-8}	2.9×10^{-8}
2	A1	3.2×10^{-6}	4.9×10^{-6}	2.3×10^{-8}	3.3×10^{-8}
	A2	5.6×10^{-7}	n.d.	2.6×10^{-8}	n.d.
	B1	9.7×10^{-8}	1.0×10^{-7}	5.7×10^{-9}	5.2×10^{-9}
	B2	1.4×10^{-6}	2.4×10^{-6}	2.3×10^{-8}	2.6×10^{-8}
	B3	n.d.	n.d.	n.d.	n.d.
	B4	1.9×10^{-6}	1.8×10^{-6}	7.6×10^{-8}	5.4×10^{-8}
	C	3.2×10^{-7}	3.2×10^{-7}	1.8×10^{-8}	6.9×10^{-9}
3^{+}	A1-2	1.0×10^{-6}	n.d.	3.3×10^{-8}	n.d.
	B1	1.1×10^{-5}	n.d.	1.9×10^{-7}	n.d.
	B3	3.5×10^{-6}	3.5×10^{-6}	5.1×10^{-8}	2.8×10^{-8}
	B4	9.5×10^{-7}	1.1×10^{-6}	2.7×10^{-8}	6.5×10^{-8}
	C	7.6×10^{-8}	7.7×10^{-8}	2.1×10^{-8}	2.2×10^{-8}

n.d. = not determined

+ B2 present only in thin, discontinuous layer

Appendix Table 4

The Main Experiment

The volumetric water content θ of the soil at different times and at different depths

AT PLANTING+

Depth (cm)	0-10	10-25	25-50	50-75	75-100	100-125	125-150	150-175	175-200
θ	.22	.27	.29	.26	.22	.21	.24	.28	.30

+ Mean of 9 cores

AFTER EMERGENCE

Depth (cm)	Seeding Rate S_1	S_2	S_3	L.S.D. (P=0.05)	Nitrogen Rate N_0	N_1	N_2	L.S.D. (P=0.05)	S x N+ Interaction
					8 wk				
	x 340	x 340	x 340						
0 - 10	.21 71.5	.24 81.6	.23 78.3	.04	.23	.22	.24	.03	
10 - 25	.27 92	.29 98.6	.27 92	.03	.29	.27	.27	.04	
25 - 50	.32 109	.30 102	.32 109	.05	.32	.31	.31	.02	
50 - 75	.27 92	.28 95.3	.26 88.5	.03	.29	.27	.26	.02	*
75 - 100	.26 83.5	.26 88.5	.25 85	.03	.26	.26	.25	.02	
100 - 125	.27 92	.28 95.3	.26 88.5	.03	.28	.27	.26	.02	
125 - 150	.28 95.3	.29 98.6	.26 88.5	.02 6.8	.28	.28	.27	.02	
150 - 175	.30 102	.30 102	.28 95.3	.03	.30	.29	.29	.02	
175 - 200	.28 95.3	.30 102	.29 98.6	.04	.29	.30	.28	.03	Continued..

Appendix Table 4 (continued)

The volumetric water content θ of the soil at different times and at different depths

---

13 wk

0 - 10	.23 783	.23 783	.24 816	.03	.23	.23	.24	.02
10 - 25	.28 953	.26 885	.28 953	.04	.28	.28	.26	.03
25 - 50	.31 107	.27 92	.27 92	.04	.31	.28	.26	.04
50 - 75	.26 885	.23 783	.21 715	.03	.25	.24	.22	.03
75 - 100	.26 885	.23 783	.23 783	.02	.24	.25	.24	.03
100 - 125	.27 92	.26 885	.27 92	.04	.26	.27	.27	.03
125 - 150	.29 986	.28 953	.28 953	.05	.28	.28	.29	.03
150 - 175	.32 109	.30 103	.30 103	.02	.31	.31	.31	.03
175 - 200	.31 107	.30 101	.30 103	.02	.30	.31	.31	.03

18 wk

0 - 10	.13	.15	.13	.03	.14	.14	.14	.01
10 - 25	.16	.17	.14	.02	.17	.16	.14	.02
25 - 50	.22	.19	.19	.05	.22	.20	.19	.03
50 - 75	.23	.16	.16	.04	.20	.18	.16	.03
75 - 100	.24	.19	.19	.06	.22	.21	.19	.02
100 - 125	.26	.26	.23	.03	.25	.25	.23	.02
125 - 150	.28	.28	.25	.02	.27	.27	.27	.02
150 - 175	.31	.31	.29	.04	.31	.31	.29	.04
175 - 200	.31	.31	.30	.03	.31	.31	.31	.02

Continued..

Appendix Table 4 (continued)

The volumetric water content θ of the soil at different times and at different depths

	S1	S2	S3					
				20 wk				
0 - 10	.09	.12	.09	.02	.10	.10	.10	.01
10 - 25	.13	.15	.13	.03	.15	.14	.13	.03
25 - 50	.19	.17	.18	.06	.19	.18	.17	.03
50 - 75	.19	.14	.15	.05	.17	.15	.15	.01
75 - 100	.21	.16	.17	.06	.19	.18	.17	.03
100 - 125	.25	.24	.22	.03	.23	.24	.24	.03
125 - 150	.27	.27	.23	.05	.26	.27	.25	.05
150 - 175	.31	.31	.28	.04	.29	.30	.30	.03
175 - 200	.30	.30	.29	.03	.29	.30	.30	.04
				22 wk				
0 - 10	.07 23.4	.11 37.4	.09 30.6	.04	.09	.09	.09	.01
10 - 25	.13 44.3	.14 47.6	.13 44.3	.04	.14	.14	.13	.02
25 - 50	.18 61.2	.15 50.4	.17 57.9	.05	.18	.16	.17	.02
50 - 75	.18 61.2	.13 44.3	.15 50.4	.04	.16	.15	.15	.02
75 - 100	.21 71.5	.17 57.9	.17 57.9	.04 13.6	.19	.18	.18	.03
100 - 125	.24 81.6	.23 78.3	.22 75	.02	.22	.22	.24	.04
125 - 150	.27 92	.25 85	.25 85	.03 — 10.2	.26	.26	.26	.03
150 - 175	.30 102	.29 98.6	.29 98.6	.02	.29	.29	.30	.03
175 - 200	.30 102	.28 95.3	.29 98.6	.03	.28	.29	.29	.03

+ Where important interactions occur 3 x 3 tables are given in the text.

Appendix Table 5

Analysis of variance format

Source of variation	d.f.
Rep stratum	2
Rep*Main plot stratum	
Seedrate	2
Residual (a)	4
Total	6
Rep*Main plot*Sub-plot stratum	
N	2
Seedrate*N	4
Residual (b)	12
Total	18

This format has been used for all Analyses of Variance relating to the Main Experiment.

Appendix Table 6

The Main Experiment

Analysis of variance table for $\theta_{s,0-200}$ cm

at each time of measurement after emergence (wk)

Source of Variation	8 wk		13 wk		18 wk		20 wk		22 wk	
	M.S.	F	M.S.	F	M.S.	F	M.S.	F	M.S.	F
Rep	74.6	11.47	33.5	1.86	18.1	2.50	48.5	3.53	38.8	2.43
Rep*Main plot										
Seedrate	15.4	1.65	49.7	55.78	97.3	6.28	55.1	5.09	52.2	11.9
Residual (a)	9.3	1.44	0.9	0.05	15.5	2.14	10.8	0.79	4.4	0.27
Total	11.4	1.75	17.2	0.95	42.8	5.90	25.6	1.86	20.3	1.27
Rep*Main plot*Sub-plot										
N	15.2	2.33	8.6	0.48	31.4	4.34	5.2	0.38	1.3	0.08
Seedrate*N	9.1	1.41	16.3	1.02	15.6	2.16	18.1	1.32	24.0	1.50
Residual (b)	6.5		18.0		7.2		13.7		16.0	
Total	8.1		17.0		11.8		13.8		16.1	

Appendix Table 7

The Main Experiment

Root length per unit volume of soil R_v (cm^{-2})
at different times after emergence and at different depths

Depth	Seeding Rate S_1	S_2	S_3	L.S.D. (P=0.05)	Nitrogen Rate N_0	N_1	N_2	L.S.D. (P=0.05)	S x N$^+$ Interaction (P=0.05)
					8 wk				
0 - 10	4.60	6.00	6.11	.628	5.27	5.15	6.30	.724	
10 - 25	.81	.96	2.20	.786	1.36	1.34	1.29	.617	
25 - 50	.55	.59	1.17	.311	.81	.85	.64	.148	*
50 - 75	.28	.25	.39	n.s.	.32	.32	.28	n.s.	
75 - 100	.02	.02	.06	n.s.	.02	.05	.03	n.s.	
					13 wk				
0 - 10	8.57	10.34	9.47	n.s.	9.08	8.60	10.69	1.625	
10 - 25	1.15	1.30	1.80	n.s.	1.19	1.47	1.58	n.s.	
25 - 50	.71	.88	.91	n.s.	.96	.82	.73	.153	*
50 - 75	.48	.99	1.34	.403	.89	1.01	.92	n.s.	
75 - 100	.18	.63	.56	.394	.56	.45	.35	n.s.	*

Continued..

Appendix Table 7 (continued)

Root length per unit volume of soil R_v (cm^{-2}) at different times after emergence and at different depths

				18 wk					
0 - 10	10.75	12.16	10.33	n.s.	10.31	10.50	12.42	1.477	
10 - 25	3.01	2.92	4.24	1.819	2.79	3.88	3.51	.633	*
25 - 50	1.22	1.35	2.03	n.s.	1.45	1.54	1.61	n.s.	*
50 - 75	.90	2.13	2.11	.539	1.66	1.87	1.61	n.s.	*
75 - 100	.28	.97	.85	.589	.87	.70	.53	n.s.	
100 - 125	.01	.05	.28	n.s.	.12	.06	.16	n.s.	
				20 wk					
0 - 10	11.21	13.64	12.61	n.s.	11.92	12.13	13.41	n.s.	
10 - 25	4.31	5.00	5.00	n.s.	4.09	5.47	4.75	n.s.	
25 - 50	2.85	3.57	3.14	n.s.	2.65	4.00	2.90	.931	
50 - 75	1.43	3.19	3.10	n.s.	2.39	2.98	2.35	1.045	
75 - 100	.46	1.49	1.19	n.s.	1.14	1.23	.77	.553	
100 - 125	.10	.24	.15	n.s.	.15	.21	.14	n.s.	
				22 wk					
0 - 10	11.40	12.63	11.27	n.s.	11.68	11.54	12.07	n.s.	
10 - 25	4.89	4.12	5.19	n.s.	4.21	5.19	4.84	n.s.	
25 - 50	4.66	5.13	3.78	1.694	4.20	5.12	4.25	n.s.	
50 - 75	1.51	3.06	2.69	1.461	2.41	2.59	2.26	n.s.	*
75 - 100	.45	1.71	1.32	1.231	1.21	1.48	0.80	.359	*
100 - 125	.18	.30	.21	n.s.	.20	.30	.20	n.s.	
125 - 150	.11	.14	.13	n.s.	.14	.08	.10	n.s.	

+ Where important interactions occur 3 x 3 tables are given in the text.

Appendix Table 8

The Main Experiment

Analysis of variance table for root length per unit area of ground surface

R_a (cm^{-1}) at 5 times after emergence

Source of Variation	8 wk		13 wk		18 wk		20 wk		22 wk	
	M.S.	F	M.S.	F	M.S.	F	M.S.	F	M.S.	F
Rep	518.3	4.25	2410.6	4.19	5770.0	4.50	24609.0	10.34	0.23	0.08
Rep*Main plot										
Seedrate	7209.6	21.71	8110.4	18.20	18118.0	4.07	38209.0	2.01	1.48	0.83
Residual (a)	332.1	2.72	445.7	0.78	4456.0	3.47	18975.0	8.13	1.78	0.61
Total	2624.6	21.52	3000.6	5.22	9010.0	7.02	25387.0	10.88	1.68	0.58
Rep*Main plot*Sub-plot										
N	41.2	0.34	597.5	1.04	1798.0	1.40	13505.0	5.79	7.24	2.49
Seedrate*N	246.7	2.02	1531.4	2.66	1790.0	1.39	12017.0	5.15	2.61	0.90
Residual (b)	122.0		574.7		1283.0		2334.0		2.90	
Total	140.7		289.8		1453.0		5727.0		3.32	

Appendix Table 9

The Main Experiment

The mean rate of root growth per unit volume of soil $\delta R_v / \delta t$

at different soil depths for each interval between samplings (x 10^{-3} = cm^{-2} day^{-1})

Depth (cm)	Seeding Rate				Nitrogen Rate				S x N^{+} Interaction (P=0.05)
	S_1	S_2	S_3	L.S.D. (P=0.05)	N_0	N_1	N_2	L.S.D. (P=0.05)	
				Emergence to 8 wk					
0 - 10	82.2	107.2	109.2	11.2	94.1	91.9	112.4	12.9	
10 - 25	14.5	17.1	39.3	14.0	24.2	23.9	22.8	n.s.	
25 - 50	9.8	10.5	20.9	5.54	14.6	15.3	11.4	2.64	
50 - 75	5.1	4.4	7.0	n.s.	5.8	5.7	5.0	n.s.	*
75 - 100	0.3	0.3	0.1	n.s.	0.4	0.8	0.5	n.s.	
				8 to 13 wk					
0 - 10	107.2	117.1	90.8	n.s.	103.0	93.4	118.7	n.s.	
10 - 25	9.2	9.2	-10.9	n.s.	- 4.4	3.7	8.3	n.s.	
25 - 50	4.3	7.8	- 6.9	11.9	3.8	- 1.1	2.4	n.s.	*
50 - 75	5.2	20.2	25.8	13.8	15.2	18.7	17.2	n.s.	
75 - 100	4.3	16.4	13.6	9.28	14.6	10.9	8.8	6.72	*

Continued..

Appendix Table 9 (continued)

The mean rate of root growth per unit volume of soil $\delta R_v/\delta t$ at different soil depths for each interval between samplings ($\times 10^{-3}$ = cm^{-2} day^{-1})

13 to 18 wk

0 - 10	66.6	55.2	28.9	n.s.	37.2	61.2	52.4	n.s.
10 - 25	56.1	49.1	74.2	n.s.	48.1	73.1	58.3	n.s.
25 - 50	15.6	14.3	33.9	n.s.	15.1	22.0	26.8	n.s.
50 - 75	12.7	34.5	23.2	15.3	23.4	26.0	21.0	n.s.
75 - 100	3.3	10.4	8.6	n.s.	9.4	7.7	5.2	n.s.
100 - 125	0.3	1.6	8.5	n.s.	3.6	1.8	4.9	n.s.

18 to 20 wk

0 - 10	31.8	105.6	156.1	n.s.	115.1	107.6	70.8	n.s.
10 - 25	92.8	148.1	54.3	n.s.	93.6	113.0	88.7	n.s.
25 - 50	115.9	158.6	79.1	n.s.	85.8	175.9	91.9	8.14
50 - 75	38.3	75.4	70.8	n.s.	52.3	79.3	52.8	n.s.
75 - 100	12.6	37.3	24.6	n.s.	19.0	37.8	17.6	n.s.
100 - 125	6.7	13.1	- 9.1	n.s.	1.9	10.6	- 1.8	n.s.

20 to 22 wk

0 - 10	11.4	-63.0	-83.5	n.s.	-14.8	-36.6	-83.7	n.s.
10 - 25	35.0	-51.2	11.6	n.s.	7.6	-17.5	5.4	n.s.
25 - 50	113.3	97.4	39.7	n.s.	96.3	69.8	84.2	n.s.
50 - 75	4.9	- 7.8	-25.7	n.s.	1.1	-23.9	- 5.8	n.s.
75 - 100	- 0.5	13.6	8.5	n.s.	4.4	15.5	1.6	n.s.
100 - 125	4.5	4.3	3.8	n.s.	3.3	5.5	3.8	n.s.
125 - 150	6.7	8.5	8.4	n.s.	5.3	9.0	9.3	n.s.

+ Where important interactions occur 3 x 3 tables are given in the text.

Appendix 10

```
      PROGRAM AKCALC(INPUT,OUTPUT)

C         AKMAR=HYDRAULIC CONDUCTIVITY CALCULATED ACCORDING
C         TO PRINCIPLES OUTLINED BY MARSHAL (1958)

      DIMENSION H(50),AKMAR(50),NDEPTH(50),DELTHTA(50),
     $MM(50),SUCT(50)
  100 FORMAT(16I5)
  110 FORMAT (11F7.0)
  120 FORMAT(1H1//10X,*CALCULATIONS AT DEPTH*,I5,* CMS*//10X
     $,*N*,5X,*DELTHETA*,14X,*AKMAR (CM/MIN)*,8X*SUCTION*/)
  130 FORMAT(10X,I2,5X,F6.4,5X,E16.2,13X,F10.2)
    7 READ 100,NMDEPTH,(NDEPTH(I),I=1,NMDEPTH)
C         NMDEPTH=NUMBER OF DEPTHS
C         NDEPTH=ACTUAL DEPTH AT WHICH OBSERVATIONS WERE
C         MADE
      IF (NMDEPTH.EQ.0) GO TO 999
      READ 100,(MM(J),J=1,15)
C         MM=NUMBER OF POROSITY CLASSES
      NUMRUN=0
    1 NUMRUN=NUMRUN+1
      N=M=MM(NUMRUN)
      READ 110,(H(J),J=1,M)
C         H=SUCTION VALUES
      DO 2 J=1,M
      KKK=M-J+1
    2 SUCT(KKK)=H(J)
      W=0.05
C         W=SIZE OF POROSITY CLASS INTERVAL
   20 S=0.0
      DO 30 I=1,N
   30 S=S+(2*I-1)/(H(I)*H(I))
      AKMAR(N)= 270.*S*W**2.0*60.
      AM=M
      DELTHTA(N)=N*W
      N=N-1
      IF(N.EQ.0)GOTO 50
      DO 40 I=1,N
   40 H(I)=H(I+1)
      GOTO 20
   50 PRINT120 ,NDEPTH(NUMRUN)
      PRINT 130,((N, DELTHTA(N),AKMAR(N),SUCT(N)),N=1,M)
      IF (NUMRUN.LT.NMDEPTH) GO TO 1
      GO TO 7
  999 STOP
      END
```

Appendix 11

```
      PROGRAM RANDOM (INPUT, OUTPUT)
C     RANDOMLY PAIRED NUMBERS, ONE COORDINATE ORDERED
      DIMENSION MX(10,20)
      INTEGER T
      IX = 863259885639
      DO 9 LY=1,20
      PRINT 1
    1 FORMAT (36H1ORDERED RANDOM NUMBERS FROM 0 TO 50)
      DO 3 J=1,10
      DO 4 L=1,20
      CALL RN2(IX,R)
      MX(J,L) = R*50.
    4 CONTINUE
    3 CONTINUE
      DO 12 LX = 1,20
   12 PRINT 13, (MX(J,LX), J=1,10)
   13 FORMAT (1X, 10I8)
      DO 11 J=1,10,2
      N=20
      N1 = N-1
      DO 5 I=1,N1
      VMIN = MX(J,I)
      KMIN = I
      I1 = I+1
      DO 6 K =I1,N
      IF (MX(J,K) .GE. VMIN) GO TO 6
      VMIN = MX(J,K)
      KMIN = K
    6 CONTINUE
      IF (KMIN.EQ.I) GO TO 5
      T = MX(J,I)
      MX(J,I) = MX(J,KMIN)
      MX(J,KMIN) = T
    5 CONTINUE
   11 CONTINUE
      DO 7 L = 1,20
    7 PRINT 8, (MX(J,L), J=1,10)
    8 FORMAT (/ 1X, 10I8)
    9 CONTINUE
      STOP
      END
```

Appendix 12

```
      PROGRAM UPTAKE (INPUT•OUTPUT)

C           CALCULATION OF WATER WITHDRAWAL BY ROOTS USING THE
C           METHOD OF ROSE AND STERN (1967)

      DIMENSION DEPTH(10)•TH(200•3•3)•HO(200•3,3)•
     $TH2(200,3•3)•H1(200•3•3)•H2(200•3•3),DIFF(200,3,3)
      DIMENSION X(200),RHOB(200•3),RHOBO(10•3)•P(200)
      DIMENSION BUF(612),BUF2(612),TH1(200,3,3)•A(10•3)•
     $B(10,3)
      COMMON/ABC/DEPTH•ND
      COMMON/DEF/A•B
      READ 100•ND•DAY1•DAY2•(DEPTH(I)•I=1,ND)
  100 FORMAT (I4•2F4/10F6.1)
C           ND=NO. OF DEPTHS AT WHICH MEASUREMENTS WERE MADE
C           DAY1• DAY2=TIME OF MEASUREMENTS
C           DEPTH=DEPTH AT WHICH MEASUREMENT WAS MADE
      READ 19•((RHOBO(I•J),J=1,3),I=1•ND)
   19 FORMAT (8X,3F8.4)
C           RHOBO=OBSERVED VALUES OF BULK DENSITY
      DO 1 I=1,196
    1 X(I)=I+4
C           X=DEPTH FROM SOIL SURFACE (ONE CM INTERVALS)
      DO 20 J=1•3
      DO 20 I=1•183
      RHOB(I•J)=ALNTERP(X(I)•RHOBO(1•J))
   20 CONTINUE
C           RHOB=LINEARLY INTERPOLATED VALUES OF BULK DENSITY
      READ 101•(((TH(I•J•K)•K=1•3)•J=1•3)•((HO(I•J•K)•K=1•3)
     $•J=1,3)•I=1•ND)
  101 FORMAT (8X•9F8.3/8X•9F8.0)
C           TH=OBSERVED VALUES OF THETA
C           HO=OBSERVED VALUES OF UNLOADED SUCTION
      PRINT 103•DAY1
  103 FORMAT (1H0/•60X•15HRESULTS FOR DAY•F4)
      PRINT 104
  104 FORMAT (1H0•24X•24HOBSERVED VALUES OF THETA•43X, 3HOBS
     117HERVED VALUES OF H)
      PRINT 105
  105 FORMAT (1H0•2(14X•7HBLOCK 1,14X•7HBLOCK 2•14X,6HBLOCK
     11H3))
      PRINT 106
  106 FORMAT (2X5HDEPTH•2X6(3X•2HD1,5X•2HD2•5X•2HD3•2X))
      PRINT 107•(DEPTH(I)•((TH(I•J•K)•K=1•3)•J=1•3)•((HO(I•J
     $•K)•K=1•3)•J=1•3)•I=1•ND)
  107 FORMAT (2X•F5•2X,9F7.3,9F7)
      DO 4 J=1•3
      DO 4 K=1•3
      GREG=0.
      DO 2 I=1,183
```

```
      TH1(I,J,K)=ALNTERP(X(I),TH(1,J,K))
C           TH1=LINEARLY INTERPOLATED VALUES OF THETA
      IF(I.EQ.1) 17,18
C           APPLIED PRESSURE P DUE TO OVERBURDEN IS CALCULATED
C           BY THE METHOD OF ROSE ET AL. (1965)
   17 P(I)=RHOB(1,J)+TH1(1,J,K)
      GO TO 2
   18 GREG=GREG+0.5*(RHOB (I-1,J)-RHOB(I,J)+TH1(I-1,J,K)+TH1
     $(I,J,K))
      P(I)=GREG-.833333*(RHOB(I,J)+RHOB(I-1,J)-RHOB(2,J)+RH
     $OB(1,J)+TH1(I,J,K)-TH1(I-1,J,K)-TH1(2,J,K)+TH1(1,J,K))
    2 CONTINUE
      DO 3 I=1,183
    3 H1(I,J,K)=ALNTERP(X(I),HO(1,J,K))-0.1*P(I)
C           H1=ACTUAL VALUES OF SUCTION
    4 CONTINUE
      PRINT 108
  108 FORMAT (1H022X,28HINTERPOLATED VALUES OF THETA,39X,
     124HINTERPOLATED VALUES OF H)
      PRINT 105
      PRINT 106
      PRINT 107,(X(I),((TH1(I,J,K),K=1,3),J=1,3),((H1(I,J,K)
     $,K=1,3),J=1,3),I=1,183)
C           ABOVE CALCULATIONS ARE REPEATED FOR SECOND TIME OF
C           OBSERVATION
      READ 101,(((TH(I,J,K),K=1,3),J=1,3),((HO(I,J,K),K=1,3)
     $,J=1,3),I=1,ND)
      PRINT 103,DAY2
      PRINT 104
      PRINT 105
      PRINT 106
      PRINT 107,(DEPTH(I),((TH(I,J,K),K=1,3),J=1,3),((HO(I,J
     $,K),K=1,3),J=1,3),I=1,ND)
      DO 7 J=1,3
      DO 7 K=1,3
      SUMTH1=SUMTH2=0.
      GREG=0.
      DO 5 I=1,183
      TH2(I,J,K)=ALNTERP(X(I),TH(1,J,K))
      SUMTH1=SUMTH1+TH1(I,J,K)
      SUMTH2=SUMTH2+TH2(I,J,K)
      DIFF(I,J,K)=SUMTH1-SUMTH2
      IF(I.EQ.1) 21,22
   21 P(I)=RHOB(1,J)+TH2(1,J,K)
      GO TO 5
   22 GREG=GREG+0.5*(RHOB(I-1,J)-RHOB(I,J)+TH2(I-1,J,K)+TH2
     *(I,J,K))
      P(I)=GREG-.833333*(RHOB(I,J)+RHOB(I-1,J)-RHOB(2,J)+RH
     $OB(1,J)+TH1(I,J,K)-TH1(I-1,J,K)-TH1(2,J,K)+TH1(1,J,K))
     *-TH2(I,J,K)-TH2(I-1,J,K)-TH2(1,J,K)
```

```
    5 CONTINUE
      DO 6 I=1,183
    6 H2(I,J,K)=ALNTERP(X(I),H0(1,J,K))-0.1*P(I)
    7 CONTINUE
      PRINT 108
      PRINT 105
      PRINT 106
      PRINT 107,(X(I),((TH1(I,J,K),K=1,3),J=1,3),((H1(I,J,K)
     $,K=1,3),J=1,3),I=1,183)
      PRINT 115
  115 FORMAT (1H0/55X, 28HDIFFERENCES IN WATER CONTENT )
      PRINT 112,(X(I),((DIFF(I,J,K),K=1,3),J=1,3),I=1,184)
C          VALUES FOR LOG CONDUCTIVITY VERSUS LOG THETA
C          GRAPHS ARE INPUT
      READ  102,(((TH(I,J,K),K=1,2),J=1,3),((TH(I,J,K),K=3,4
     1),J=1,3),I=1,ND)
  102 FORMAT (8X,3(E9.1,F7.3))
C          COEFFICIENTS FOR CONDUCTIVITY ESTIMATION ARE
C          CALCULATED
      DO 25 K=1,4
      DO 25 J=1,3
      DO 26 I=1,ND
   26 TH(I,J,K)=ALOG10(TH(I,J,K))
   25 CONTINUE
      DO 9 J=1,3
      DO 8 I=1,ND
      B(I,J)=(TH(I,J,1)-TH(I,J,3))/(TH(I,J,2)-TH(I,J,4))
    8 A(I,J)=TH(I,J,1)-B(I,J)*TH(I,J,2)
    9 CONTINUE
      PRINT 118,((A(I,J),I=1,ND),(B(I,J),I=1,ND),J=1,3)
  118 FORMAT (1X,9E15.5)
      DO 15 J=1,3
      DO 14 K=1,3
      DO 13 I=1,183
      TH(I,J,K)=(TH1(I,J,K)+TH2(I,J,K))/2.
      H0(I,J,K)=(H1(I,J,K)+H2(I,J,K))/2.
      TH1(I,J,K)=CONDUC(I,J,TH(I,J,K))
      IF(I.EQ.1)10,11
   10 H3=0.
      GO TO 12
   11 H3=H0(I-1,J,K)
   12 H1(I,J,K)=(TH1(I,J,K)+TH1(I,J,K)*(H0(I,J,K)-H3))*(DAY2
     $-DAY1)
      TH2(I,J,K)=((DIFF(I,J,K)-H1(I,J,K))*10.0)/(DAY2-DAY1)
      DIFF(I,J,K)=H0(I,J,K)-H3
      IF (I.EQ.1) 13,16
   16 H2(I,J,K)=TH2(I,J,K)-TH2(I-1,J,K)
   13 CONTINUE
      H2(1,J,K)=H2(2,J,K)
   14 CONTINUE
```

```
   15 CONTINUE
C           NOW TH=MEAN VALUE OF THETA OVER TIME INTERVAL
C           NOW HO=MEAN VALUE OF ACTUAL SUCTION OVER TIME
C           INTERVAL
C           TH1=CONDUCTIVITY
C           H1=SEEPAGE
C           TH2=AMOUNT OF WATER REMOVED ABOVE DEPTH X(I)
C           H2=RATE OF WATER REMOVAL
        PRINT 109
  109 FORMAT (1H0/,26X.20HMEAN VALUES OF THETA.47X.
     116HMEAN VALUES OF H)
        PRINT 105
        PRINT 106
        PRINT 107.(X(I).((TH (I,J,K).K=1.3).J=1.3).((HO(I,J.K)
     $.K=1.3),J=1.3).I=1.183)
        PRINT 110
  110 FORMAT (1H0/60X.12HCONDUCTIVITY)
        PRINT 112.(X(I).((TH1(I,J,K),K=1.3).J=1,3).I=1.184)
  112 FORMAT (2X,F5.2X.9E14.5)
        PRINT 111
  111 FORMAT (1H0/60X,7HSEEPAGE)
        PRINT 112.(X(I).(( H1(I,J,K).K=1.3),J=1.3).I=1,184)
        PRINT 113
  113 FORMAT (1H0/60X.2HRZ)
        PRINT 112.(X(I).((TH2(I.J.K).K=1.3).J=1.3).I=1.184)
        PRINT 114
  114 FORMAT (1H0/60X.9HLITTLE RZ)
        PRINT 112.(X(I).(( H2(I,J.K).K=1,3).J=1.3).I=1,184)
C           MEANS OVER BLOCKS ARE CALCULATED
        DO 27 K=1.3
        PRINT 116.K
  116 FORMAT (1H1.40X9HDENSITY D.I1)
        DO 29 I=1.183
        TH1(I.1.K)=(TH1(I.1.K)+TH1(I.2.K)+TH1(I.3.K))/3.
         H1(I.1.K)=( H1(I.1.K)+ H1(I.2,K)+ H1(I.3,K))/3.
        TH2(I.1.K)=(TH2(I.1.K)+TH2(I.2,K)+TH2(I.3,K))/3.
         H2(I.1.K)=( H2(I.1.K)+ H2(I.2.K)+ H2(I.3.K))/3.
        PRINT 112.X(I).TH1(I.1.K).H1(I.1.K).TH2(I.1.K),H2(I.1
     $.K)
   29 CONTINUE
C           UPTAKE AND RATE OF UPTAKE ARE PLOTTED AGAINST
C           DEPTH
        CALL LP GRID(BUF.1.1)
        CALL LP GRID(BUF2.1.1)
        BUF(1)=BUF2(1)=0.
        BUF(2)=BUF2(2)=200.
        BUF(3)=0.
        BUF(4)=3.0
        BUF2(3)=-0.005
        BUF2(4)=0.02
```

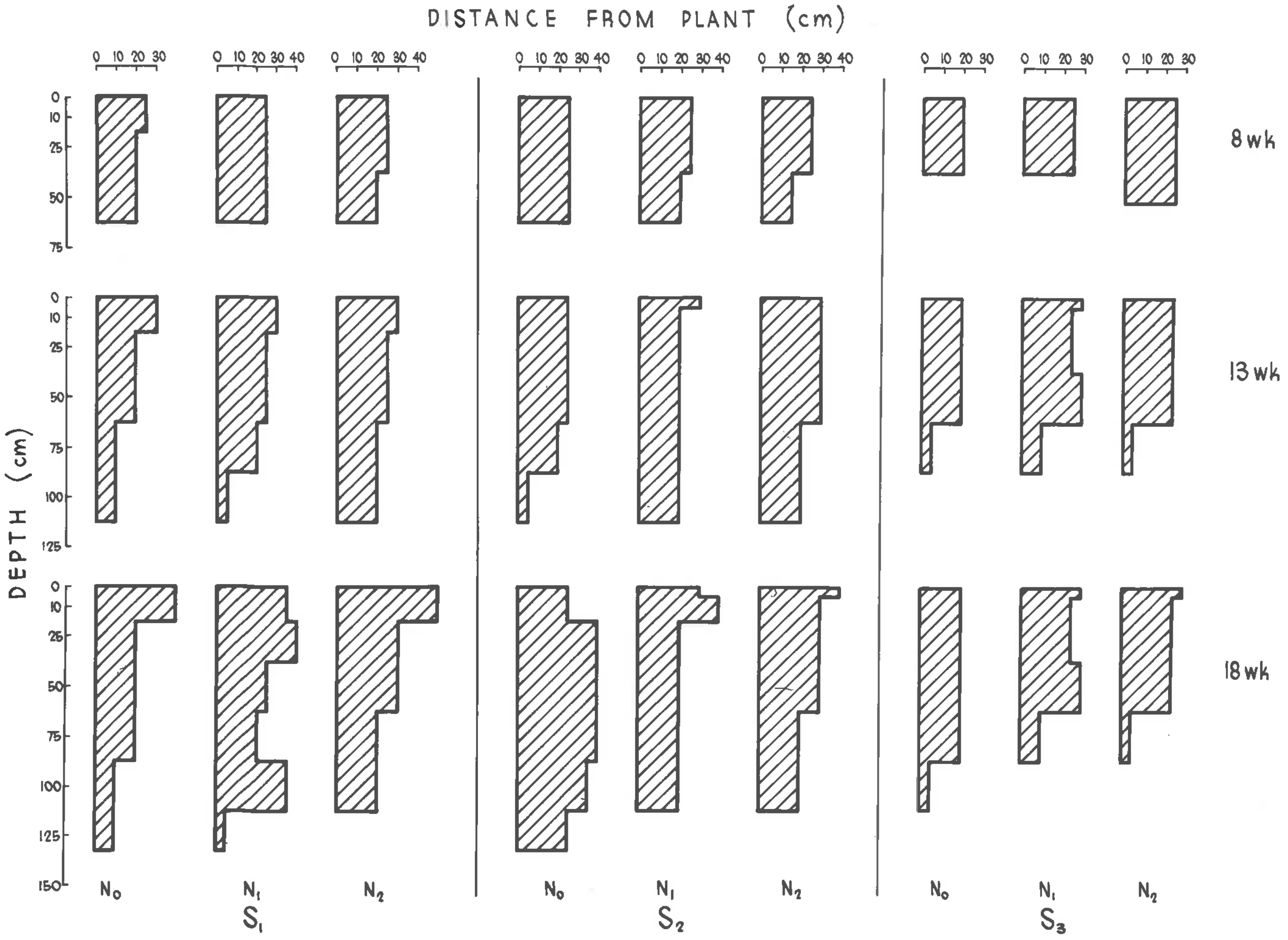
```
      BUF(5)=BUF2(5)=-10000.
      CALL LP PLOT(BUF.X,TH2(1.1.K).183.1.1H*)
      CALL LP PLOT (BUF2.X,H2(1,1.K).183.1.1H*)
      CALL LP OUT (BUF.7H*DEPTH*.4H*RZ*,0.55)
      CALL LP OUT (BUF2.7H*DEPTH*.11H*LITTLE RZ*,0.55)
   27 CONTINUE
      STOP
      END
```

```
      FUNCTION CONDUC(I.J.THETA)
      COMMON/DEF/A(10.3).B(10.3)
      K=1
      IF (I.LT.  7) GO TO 1
      K=2
      IF (I.LT. 22) GO TO 1
      K=3
      IF (I.LT. 47) GO TO 1
      K=4
      IF (I.LT. 72) GO TO 1
      K=5
      IF (I.LT. 97) GO TO 1
      K=6
      IF (I.LT.122) GO TO 1
      K=7
      IF (I.LT.147) GO TO 1
      K=8
      IF (I.LT. 172) GO TO 1
      K=9
    1 TH=ALOG10(THETA)
      EX=B(K.J)*TH+A(K.J)
      CONDUC=10.**EX
      RETURN
      END
```

```
      FUNCTION ALNTERP (X.YY)
      DIMENSION YY(200)
      COMMON/ABC/DEPTH(10).ND
      K=2
    1 IF (X.LE.DEPTH(K)) GO TO 2
      K=K+1
      IF (K.LT.ND) GO TO 1
    2 ALNTERP=(YY(K)-YY(K-1))*(X-DEPTH(K))/(DEPTH(K)-DEPTH(K
     1-1))+YY(K)
      RETURN
      END
```

Appendix Fig. 1.

The mean extent (maximum spread and depth) of the root systems of individual plants at 8, 13, and 18 wk. The values at 8 and 13 wk are the means of the 3 replicates, but the values at 18 wk are for replicate 1 only.



EXTENT OF INDIVIDUAL ROOT SYSTEMS AT 8, 13 AND 18 wk.

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