CORN ROOT GROWTH AND DISTRIBUTION AS INFLUENCED BY SOIL PHYSICAL PROPERTIES

by

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(ABSTRACT)

Mechanisms of root growth under variable field conditions were investigated by observing corn (Zea mays L.) root growth and distribution in the field and by observing the influence of soil physical stresses on corn seedling root growth in controlled environments. The field soil was Groseclose silt loam (clayey, mixed, mesic Typic Hapludult). Groseclose A horizon material was used for the growth chamber experiments where corn was grown in a range of aggregate sizes, bulk densities, low and high soil moisture levels, and temperatures. Rooting patterns in the field were altered by drought. Root length density decreased in the dry surface soil and proliferated in the moist subsurface soil. Distribution of root length densities was skewed. A few samples contained many roots and many samples contained few roots because roots were restricted to interpedal voids. In the growth chamber experiments, roots were not able to penetrate large aggregates and were restricted to interaggregate zones. This tortuous path of root growth led to transitory impedances as roots were deflected around aggregates. Corn roots were able to push small aggregates out of their path. An equation was developed to describe this impedance as a function of aggregate size, root diameter, and deflection angle. Mechanical impedance, oxygen stress, lower temperatures, and moisture stress reduced seedling root elongation to some extent, but the influence of reduced temperature was the most dramatic. At 6 days corn root length at 21°C was 20% of that at 25°C while root length at 17°C was only 5% of that at 25°C. Mechanical impedance and reduced temperatures also increased root diameter. In wet soil, oxygen stress was the most immediate factor affecting root growth, but after 4 days root elongation was stimulated suggesting other unknown factors. Two semi-empirical models were developed. One was based on the exponential growth rate of the root system and the other based on the linear growth rate of each root member. These models accounted for the reduction in root growth rate due to the soil physical stresses.

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INTRODUCTION

MASS BALANCE APPROACH

Water use by plants has been studied many ways, the two basic approaches being the mass balance approach and the Ohm's law analogy. Mass balance (water into the soil profile equals water removed from the profile plus the water stored in the profile) is the simplest and most popular. Water is added to the profile from precipitation, irrigation, and upward rise from a water table. Water is removed from the profile by evapotranspiration (ET) and drainage. The mass balance approach is often combined with models for predicting potential ET (pan evaporation, Penman's equation, etc.). This approach utilizes the concept of "available water" (amount of water stored between "field capacity" and "wilting point"). Water in some cases is assumed equally available between "field capacity" and "permanent wilting point," but more often a distinction is made between "available water" and "readily available water" (water held at tensions between "field capacity" and part way to the wilting point).

Although the concept of available water often works as a first approximation, there are some problems with this concept. The term "field capacity" implies that equilibrium is approached within a day or two after a rainfall event, but drainage may continue beyond two days or until ET reverses the direction of flow (Van Bavel and Ahmed, 1976). The whole profile has been considered to be at the same matric potential (ϕ_m) when at "field capacity," usually -0.01 or -0.033 MPa. But even if the soil profile were at equilibrium, ϕ_m would decrease to balance the gravitational potential increasing with depth. The assumption is made that plants cannot use soil water at a ϕ_m above "field capacity" because the water will rapidly drain. Since the water does not drain immediately, this moisture is available to plants unless the plants are oxygen-stressed.

Another problem is the concept of "wilting point." Plants do not immediately wilt when the average ϕ_m of the soil is -1.5 MPa, but water is progressively less "available." Conversely, plants may die long before the entire soil profile is dried to the "wilting point." On some sandy soils, plant growth may be reduced if ϕ_m falls below -0.01 MPa. Wilting point depends on plant and atmospheric conditions as well as soil properties (Van Bavel and Ahmed, 1976). In addition, ET models usually lump plant factors into an empirical crop coefficient. Dyer and Dwyer (1982) used root density measurements to develop crop coefficients which could be modified for water-stressed conditions.

"Available water" is assumed to be the water held in the soil between ϕ_m corresponding to "field capacity" and "permanent wilting point," both of which are nebulous concepts as pointed out previously. Supposedly only the water originally present in the root zone is plant available; however, Van Bavel and Ahmed (1976) have shown that water can move into the root zone from deeper in the soil profile. As much as 30% of the water lost to evapotranspiration may enter the root zone from below.

OHM'S LAW ANALOGY

An alternative approach to plant water use is to consider water uptake in the soil-plant-atmosphere continuum (SPAC) by an Ohm's law analogy as follows (Van Den Honert, 1948):

$$F = \Delta\phi / R$$

where F is the transpiration flux or uptake rate, $\Delta\phi$ is the difference in potential between two given points in the soil-plant continuum, and R is the resistance to water flow. Sometimes total plant resistance is calculated from

$$R_p = (\phi_r - \phi_e)/F$$

where ϕ_r is the water potential at the root surface and ϕ_e is the leaf water potential. Plant resistance is often divided into many components [root, stem, petiole, lamina (Black, 1979)], assuming the flow rate to be constant within a component. In SPAC models soil resistance and soil-root interface resistance would also be included.

Molz (1981) has cautioned that the Ohm's law analogy is a gross oversimplification when applied to a whole plant because steady state conditions do not exist due to changes in capacitance associated with storage in the plant (Aston and Lawlor, 1979), and plant resistances typically decrease with increasing transpiration rate (Aston and Lawlor, 1979; Black, 1979; Seaton et al., 1977; Shone and Flood, 1980). Techniques and units used for plant resistances to water flow have not been standardized (Table 1). The units for resistances depend on the units used for flow rate which may be expressed per surface area of roots or leaves, per root length, or without specifying flow rate per anything but the plant.

Two approaches are used to describe water uptake by Ohm's law analogy: the microscopic approach and the macroscopic approach. The microscopic approach assumes a steep ϕ_m gradient (hence high resistance to water flow) occurs in the soil immediately around the root (Gardner, 1960; Cowan,

Table 1. Resistances of various species, plant parts, and techniques.

Ref.	Technique	Plant	Plant Part	Resistance MPa/uptake	Uptake units	Uptake per x
(2)	Ohm's law analogy; field grown	Soybeans	root	5.5E-1 to 2.2E-8	$\frac{mm^3}{s\ mm}$	root length
		Corn	root	2.1E-6 to 8.4E-7		
(14)	Ohm's law analogy, soln. culture	Sunflower	plant	1.1E-3	$\frac{mm^3}{s\ mm}$	root length
			roots	5.5E-4		
			stem	1.3E-4		
			petiol	9.0E-5		
			lamina	2.8E-4		
(80)	Ohm's law analogy, soln culture	Sorghum	single leaf	0.3 to 4.9	$\frac{mg}{s}$	per plant
			whole roots	0.1 to 1.85		
			single roots	0.2 to 1.85		
(91)	Detopped root system rate of exudation (per length)	Broad bean	whole roots	0.8E-7	$\frac{mm^3}{s\ mm}$	root length
		Dwarf bean		1.9E-7		
		Sunflower		1.4E-7		
		Maize		4.2E-7		
		Tomato		2.3E-7		
	(per surface area)	Broad bean		0.18	$\frac{mm^3}{s\ mm^2}$	root area
		Dwarf bean		0.18		
		Sunflower		0.14		
		Maize		0.45		
		Tomato		0.16		
(109)	Ohm's law analogy, soln culture	Wheat	whole plant	0.3E-3 to 4.0E-3	$\frac{mm^3}{s}$	per plant
(113)	Ohm's law analogy, root tensiometer	Corn	nodal roots	1.39E-7 to 4.17E-7	$\frac{mm^3}{s\ mm}$	root length
(114)	Ohm's law analogy, root psychrometer	Soybeans	single roots	3.33E-6	$\frac{mm^3}{s\ mm}$	root length

1965). This approach models water uptake from a single long cylindrical root; however, since root distribution involves branching and much root-to-root competition in terms of water uptake, the potential gradient near the root is generally small (Dunham and Nye, 1976a, b). Soil resistance near the root is almost always less than plant resistance except for very sparse root systems or very dry soil (Andrews and Newman, 1969; Ehlers et al., 1981; Hansen, 1974; Lawlor, 1972; Molz, 1981; Newman, 1969a, b; Reicosky and Ritchie, 1976; and Williams, 1974). Herkelrath (1977) has shown better prediction of observed data if moisture films around the roots are taken into consideration.

Pararhizal resistance is the resistance of water movement from a horizon outside of the root zone to the root zone. This resistance may be significant in drier soils, especially at high transpiration rates (Newman, 1969a, b). Weatherley (1979) has shown that pararhizal resistance is not as significant as the resistance at the soil-root interface. This resistance may be due to decreasing moisture films at the interface (Herkelrath, 1977) and may lead to gaps at the interface that increase resistances even further (Weatherley, 1979).

The microscopic aproach is not practical on a field scale since flow to each individual root must be considered

(Motz, 1981). Alternately, the macroscopic approach is employed combining the Darcy-Richards equation (water flow equation) with a sink term representing plant water uptake. The equation is given by

$$\partial \theta / \partial t = \nabla (K_s \nabla \phi_w) - S$$

where θ is the volumetric moisture content, t is time, ∇ is the vector operator, ∇ is the divergence operator, K_s is soil hydraulic conductivity, ϕ_w is the soil water potential, and S is the water extraction function (Molz, 1981). The soil can be divided into layers with water uptake assumed uniform within a layer. Rowse et al. (1978) have tested their macroscopic model in the field for soybeans with good results and showed that an exact value for root resistance is not very critical for prediction of water uptake.

ROOT GROWTH

Of much greater concern than prediction of plant resistances is prediction of root growth. Net root growth is a balance between newly initiated roots and roots that have died (Mengel and Barber, 1974). Root distribution is not uniform but tends to decline with depth (Rowse, 1974). Even within a horizon root densities are not uniform because roots are deflected around aggregates of high strength (Dexter and Hewitt, 1978).

Many stresses affect root growth and distribution. If one part of a root system is stressed, another part of the root system may proliferate which partially compensates for the reduction (Crosett et al., 1975; Hackett, 1971). Water stress slows root elongation (Murin, 1979; Ciamporova and Luxova, 1976) and sometimes increases root diameter (Ciamporova and Luxova, 1976). Mechanical impedance slows root elongation, increases root diameter (Goss and Russell, 1980; Lachno et al., 1982; Kays et al., 1974), and sometimes induces formation of lateral roots (Goss and Russell, 1980; Kays et al., 1974). This altered root morphology may be related to hormone involvement. Indolacetic acid (IAA) is 3.5 times greater in impeded root tips than in unimpeded roots (Kays et al., 1974). Low temperature slows root elongation (Burholt and Van't Hof, 1971; Gregory, 1983; Mackay and Barber, 1984). Oxygen stress slows root elongation (Bar Yosef and Lambert, 1979; Murin, 1981) and increases ethylene production leading to hastened emergence of corn nodal roots, aerenchyma formation, and reduced root elongation (Drew et al., 1979; Drew et al., 1981; Jackson et al., 1979). In general 0.02 µL/L ethylene stimulates elongation of roots, but elongation is inhibited by ethylene concentrations 1.0 µL/L and higher (Konings and Jackson, 1979). Auxin and coumarin induce swelling of maize and wheat roots (Svensson, 1972). Since compensatory root growth can also lead to thickened roots (Crosett et al., 1975; Hackett, 1971, Troughton and Drew, 1980), perhaps hormones are involved in compensatory growth. Such physiological root responses are difficult to fit into physical models.

Modeling root growth has been approached in a variety of ways. Simple root growth models describe root distribution as an exponentially declining function of depth, extending deeper with time (Rowse, 1974). Root growth models have been developed to predict root weight of an unstressed root system (Hackett and Rose, 1972; Lambert et al., 1976; Lungley, 1973); however, water uptake is more closely related to root length than to root weight (Narda and Curry, 1981).

Narda and Curry (1981) developed a model to predict soybean root elongation of an idealized system; however, the predicted root system always develops the same ideal branching pattern which is only applicable to roots grown under nonlimiting conditions. They describe growth rates for each root member, assume 95% water in the roots, and calculate elongation rates using the average radius of each root member and the available photosynthate. Hillel and Talpaz (1976) developed a model that includes root initiation, root extention into a lower horizon, and death of roots; however, the input constants and model development were purely speculative with no supporting data. The equation used is as follows:

$$\begin{aligned} R_i^{j} &= R_i^{j-1} + R_i^{j-1} P \, \Delta t \\ &\quad - R_t^{j-1} P \, \Delta t + R_{i-1}^{j-1} E \, \Delta t \end{aligned}$$

where R_i^{j} is root length density in layer i at time j, R_i^{j-1} is root length density at the previous time (Δt time units earlier), P is the proliferation rate (as a fraction of existing roots), E is extension rate per unit time as a fraction of the number of roots present at the previous time step in the overlying layer.

Fitter (1981) developed a method for describing root systems by comparing them to branched river systems which obey Horton's Law of Branching. First the names of root branches are redefined (Fig. 1). First order laterals are the growing tips, second order laterals are the roots that first order laterals are attached to, third order laterals are attached to second order laterals, etc. One root may have sections that are first, second, third and higher order laterals. Only first order laterals actually elongate; higher order laterals increase in length as branching occurs. Horton's Law of Branching predicts that a plot of the log of the number of root branches against the root order

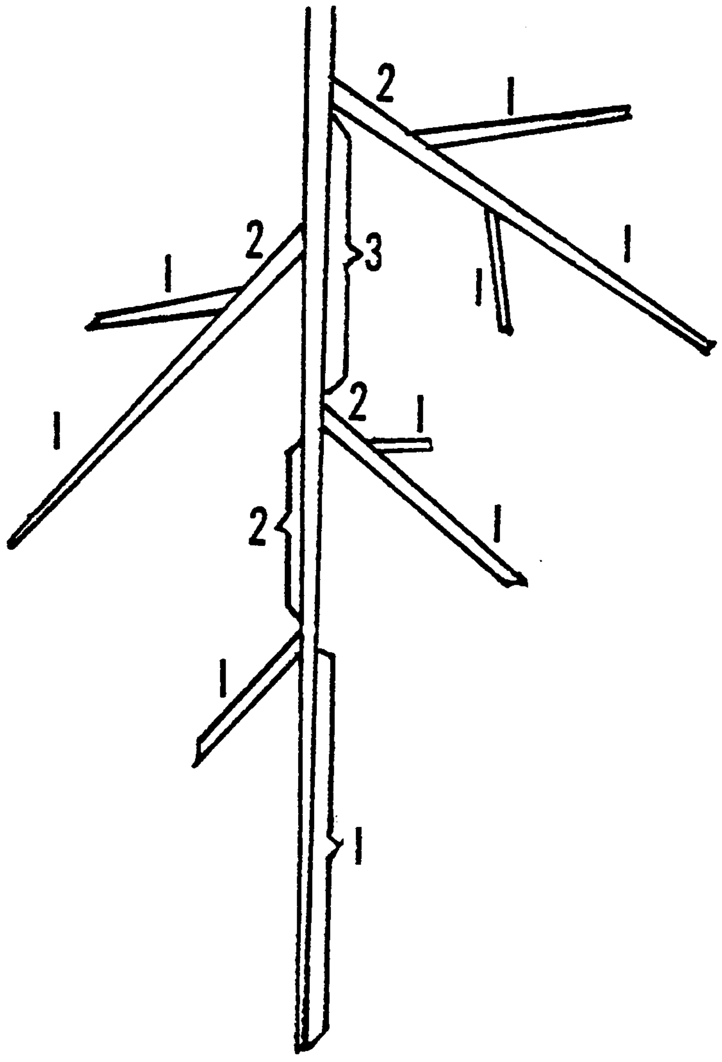

Fig. 1. Morphometric description of root branching (Fitter, 1982). 1 designates first order laterals, 2 second order laterals, and 3 third order laterals.

yields a straight line. Similar plots of mean root diameters or mean root lengths against order are also often linear. Next Fitter (1982) obtains polynomial regression equations in the form

$$\ln y = a + bt + ct^2 + dt^3$$

for y = length(L) and y = number(N) of roots of a given order, where t is time in days. These regression equations were employed to evaluate:

$$RMR = d \ln N/dt$$

$$RER = d \ln L/dt$$

$$MBL = L/N$$

$$UER = N^{-1}\ dL/dt$$

where RMR is relative multiplication rate of elements of each order, RER is relative extension rate of the elements of each order, MBL is mean branch length in each order, and UER is unit extension rate per element.

Page and Gerwitz (1974) developed another unique approach to model root growth based on diffusion equations. Roots "diffuse" from where they are more concentrated to where they are less concentrated. Fick's Second Law of Diffusion is given by:

$$\partial c/\partial t = D \nabla^2 c$$

where D is the diffusion constant, and c is the root length density as applied by Page and Gerwitz (1974). This has been solved for hemispherical growth from a point source into a semi-infinite medium (bounded by soil/air interface), radial growth from a row into a semi-infinite medium, and vertical growth into semi-infinite medium from continuous ground cover.

Dexter (1978) modeled the growth of roots in structured soil. He represented soil structure along a line by a series of 0's and 1's of 1 mm increments, where 0 represents a void and 1 an aggregate (Dexter, 1976). From measured patterns of 0's and 1's, longer strings were generated having the same statistical structure as the original patterns. Roots either grew around an aggregate or through the aggregate depending on the strength of the aggregate.

The assumptions used to develop root growth models are not usually developed from actual root data. Hillel and Talpaz (1976) admit a lack of "any proven formulation of root growth dynamics." They developed a root elongation model with the understanding that their root growth parameters were conjectural, and they indicated the need for "experimentation and analysis of real data." Lambert et al. (1976) developed an equation to describe potential root growth, but the equation is based on the exponential growth potential of young cotton (Gossypium hirsutum) bolls, due to "lack of better information." Narda and Curry (1981) mention the unavailability of qualitative root growth data necessary to check the validity of the parameters used in the model (SOYROOT). Taylor and Klepper (1978) point out that so many factors affect root growth that these models will not describe field situations. They indicate "much research is needed before we can model rooting volumes or rooting densities with satisfactory precision." Unfortunately, as Molz (1981) says, "Too many models have been called successful simply because they can be made to fit data." Macroscopic extraction models are often calibrated with soil moisture, rainfall, and transpiration data, etc; and then parameters such as root density, root permeability, and root water potential are chosen by trial and error to make the overall model fit the data (Molz, 1981).

One step in model building is data collection (Baker and Curry, 1976). Model constants, parameters, and initial values for variables are derived from data. The assumptions upon which models are based must come from available data if the models are to have any credibility. Data are also needed for verification and validation of models (Baker and Curry, 1976). Loomis et al. (1979) indicate that 50 to 80%

of their modeling work involves obtaining data where the information base is weak. As an example of the amount of data needed, Sudar et al. (1981) in calibrating a model for water stress of corn, collected data from three locations (30-60 ha each) in Iowa for 12 yrs, and from four plots (3.5 x 22 m each) in Missouri for 3 yrs. Then for model verification they collected data from a site in Missouri for 10 yrs.

Since such data collection cannot be accomplished in a short time, the emphasis of the present research will only be indirectly related to modeling. The purpose of the present research was to provide qualitative root growth data that may be used for developing more accurate assumptions upon which to base root growth models (which eventually could be used as part of water and nutrient uptake models). Although roots have been studied for some time (Bohm, 1979), many of the methods for studying roots are still in their infancy. Because of the heterogeneous distribution of roots (Reynolds, 1970), improved techniques will provide more reliable data. Although the qualitative response of roots will apply to many species, the quantitative data will be specific for corn (Zea mays L.).

Root growth and distribution are probably the most important yet least understood aspect of water uptake by plants, especially under limiting conditions. During dry conditions, root distribution is altered due to dry surface soil layers. Field studies were conducted to quantify this effect and also to study statistically the variability of field root samples. Corn roots were grown in aggregates of different sizes to study the slight impedances associated with structured soil. Many soil physical stresses affect root morphology similarly, which could simplify modeling of root growth under limiting conditions. Growth chamber experiments were conducted to describe corn root growth when stressed by low temperature, soil strength, limited moisture, or limited oxygen. The objectives of this study were to:

1. Describe root growth and distribution in the field;
2. Evaluate the effects of aggregate size, bulk density, oxygen stress, lower temperature, and water stress on root morphology.

Results from this study will provide useful information pertinent to the analysis of root growth and distribution in field soils.

Chapter II

CORN ROOT GROWTH AND DISTRIBUTION DURING A DRY SEASON

The distribution of roots is important to water uptake in the field. In a humid climate as soil moisture is depleted in the surface horizons, roots must be able to extract moisture from subsurface layers to meet transpiration demand or yield will be reduced. Rowse (1974) has described root weight distribution in soil as decreasing exponentially with depth. In contrast many other investigators have shown the pattern to be altered under drought conditions. As the surface layers of soil dry, roots proliferate in the moist soil deeper in the profile (Boyer et al., 1980; Gales, 1979: Garay and Wilhelm, 1983; Merrill and Rawlins, 1979; Rowse, 1974; and Sivakumar et al., 1977).

Unstressed corn root systems have been described by Mengel and Barber (1974) and Taylor and Klepper (1973) who recorded root length densities (L_v) with depth at several times during the growing season. Robertson et al. (1980) described corn root distribution at one sampling date for different irrigation treatments. The purpose of the present study was to observe root growth and distribution in the field over a growing season.

MATERIALS AND METHODS

A study was conducted for corn 'SS-727' grown on Groseclose silt loam (clayey, mixed, mesic, Typic Hapludult) at the Agronomy Research farm, Blacksburg, Virginia. Rye (*Secale cereale*) planted in the fall of 1982 was fertilized with 45 kg N, 67 kg P, and 67 kg K ha^{-1}. In the spring 146 kg liquid N ha^{-1} was applied. The rye was killed with herbicide and the corn was planted no-till on 10 May. The planting density was not uniform but averaged 48 000 plants ha^{-1}. Rows were generally 0.98 m apart. Tensiometers were installed at 0.1, 0.25, 0.5, 0.75, 1.0 and 1.5 m depths at two areas within the field.

On 8 June roots of six plants were extracted mechanically with a drill rig (as described below) and compared with six plants sampled by hand with a split spoon sampler. There were no differences in L_v for sampling procedures, so all subsequent samples were taken mechanically.

Roots were sampled mechanically during the growing season from two areas in the field (A and B). Soil cores (44 mm in diameter) were taken next to the corn plant to a depth of 0.75 m (or to the depth of root penetration). The core was subdivided into 0.15 m sections. Soil cores were also taken in the middle of the row down to 0.15 m depth (since below this depth L_v is not expected to differ with location--Mengel and Barber, 1974).

The soil core sections were broken into small pieces and soaked overnight in sodium hexametaphosphate. Each softened sample was diluted into a bucket and intact clods were mashed by hand. Then the dispersed sample was washed into a submerged sieve (840 µm diameter) to allow soil to pass through while the fine roots floated. The contents of the primary sieve were washed into a fine sieve and finally into plastic bags. Formaldehyde (0.37 kg kg^{-1}) was added to the wash water to preserve the roots. Root length was measured by the modified line--intersection method of Tennant (1975). Only roots living at the time of sampling (as determined by visual inspection) were measured.

RESULTS AND DISCUSSION

Measured shoot dry weight did not increase steadily as expected (Fig. 2). Perhaps this reflected insufficient drying of samples and field variablity. Area B contained less total root length than area A (Fig. 2) perhaps due to increased coarse fragments in this area that were not present in the rest of the field. Area A better represented the field. For area A the decline in root length on day 71 was probably due to moisture stress (Fig. 2). Mengel and Barber (1974) did not observe a decline in root length until after tasseling when total root length per plant was 2864 m.

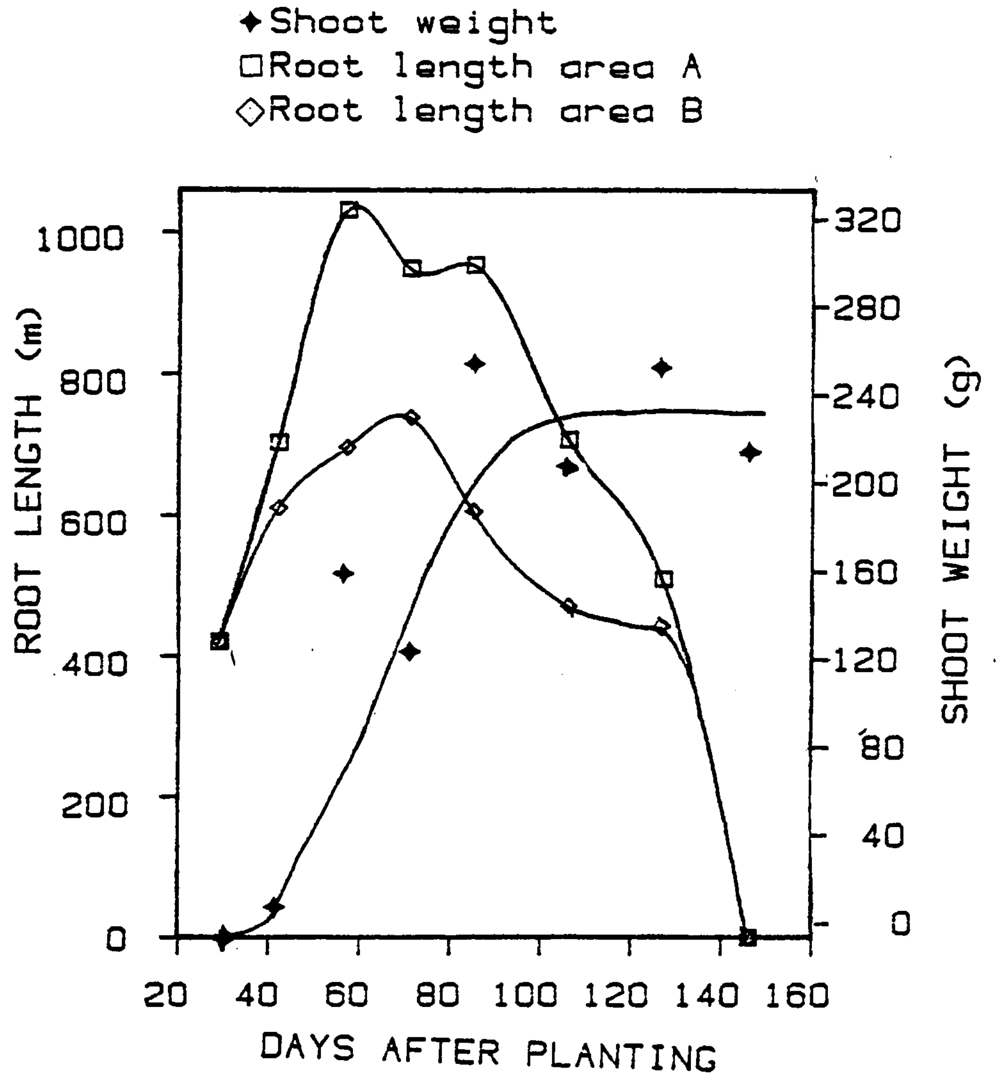

Fig. 2. Shoot dry weight and living root length per corn plant for 1983. The root length and shoot dry weight at 29 days are the means of all plants (six sampled by hand and six mechanically extracted). The shoot dry weights from days 42 to 127 are the means of six plants. The root lengths from areas A and B are the means of three plants. The shoot weight from day 146 is the mean of every third plant from four 3.05 x 0.98 areas.

Their rainfall was adequate and evenly distributed throughout the 1971 growing season resulting in a final shoot dry weight per plant about twice that observed here, and their grain yields were 37% higher (11 700 kg ha^{-1} compared to 8530 kg ha^{-1}).

Although within each soil horizon L_v generally increased, leveled off, and declined as reported by Mengel and Barber (1974), some exceptions are noted (Fig. 3). The effects of compensatory growth are evident at 71 days, since rain had not fallen for 11 days (Table 2). The surface soil layers were dry (Fig. 4), and apparently roots were dying faster than they were elongating. Clay in the 0.30 to 0.45 m depth held more moisture (-0.1 MPa) than the surface layers, and the roots proliferated which partially compensated for the decline in root length in the surface.

Similar alterations of root distribution have been described for soybeans (Glycine max) during the early days of a drought (Boyer et al., 1980; Garay and Wilhelm, 1983; and Sivakumar et al., 1977) when L_v is low in the dry soil surface layers, but higher in deeper, moist soil layers. Perennial ryegrass - Lolium perene (Gales 1979), lettuce - Lactuca sativa - (Rowse, 1974), and sorghum - Sorghum bicolor - (Merrill and Rawlins, 1979) also show this altered distribution under drought stress. Robertson et al. (1980)

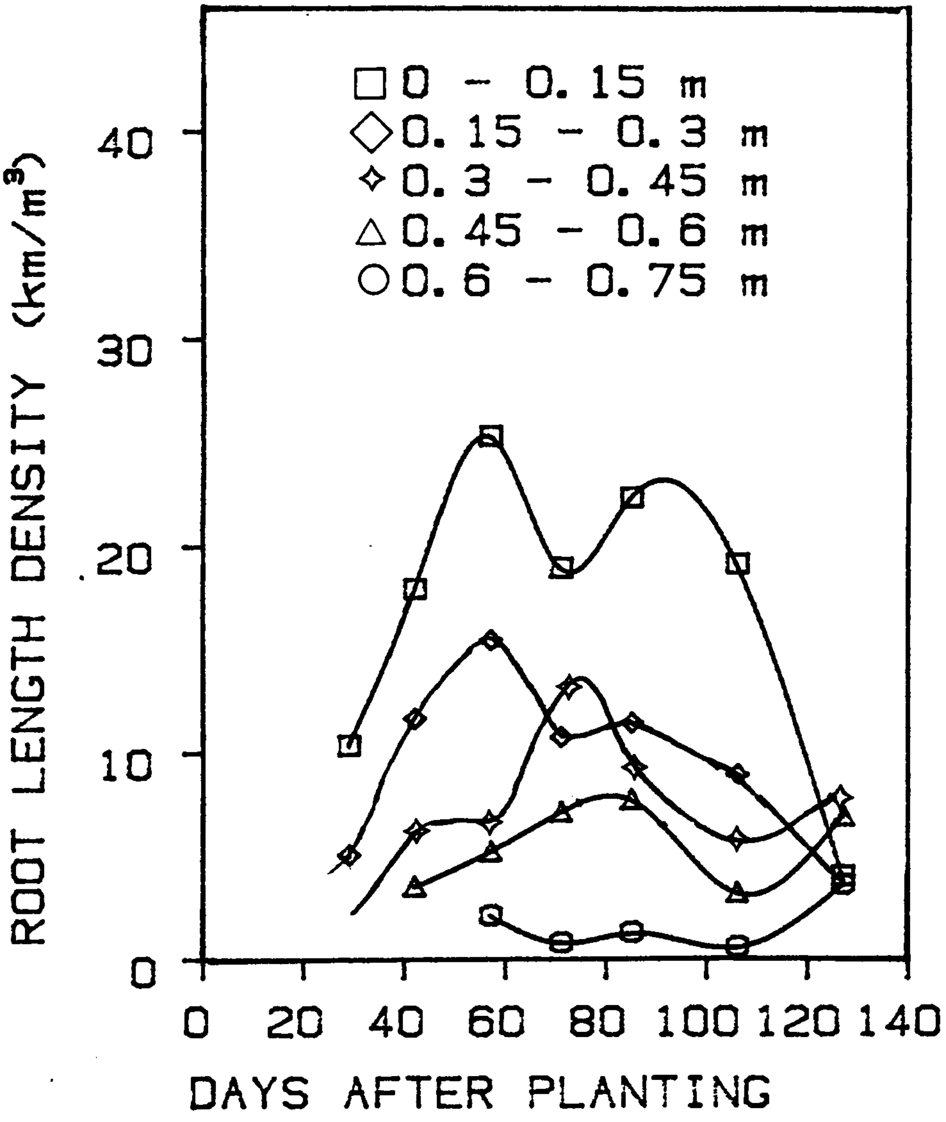

Fig. 3. Root length density for five soil depths for area A during the growing season of 1983. The surface is the mean of six samples (half taken between the rows and half taken next to the rows), and the other depths are the mean of three samples taken next to the rows.

Table 2. Rainfall distribution during the 1983 growing season and the date the rain gauge was read.

Rain-fall	Date read	Plant age	Rainfall	Date read	Plant age
mm		Days	mm		Days
1	2 June	24	32	25 July	79
17	4 June	26	4	2 August	87
9	7 June	29	14	4 August	89
1	15 June	37	1	5 August	90
12	16 June	38	11	12 August	97
1	21 June	43	4	24 August	109
2	23 June	45	2	26 August	111
6	29 June	51	1	29 August	114
6	1 July	55	11	3 Sept	119
6	4 July	58	15	13 Sept	129
12	6 July	60	11	14 Sept	130
6	22 July	76	12	22 Sept	138

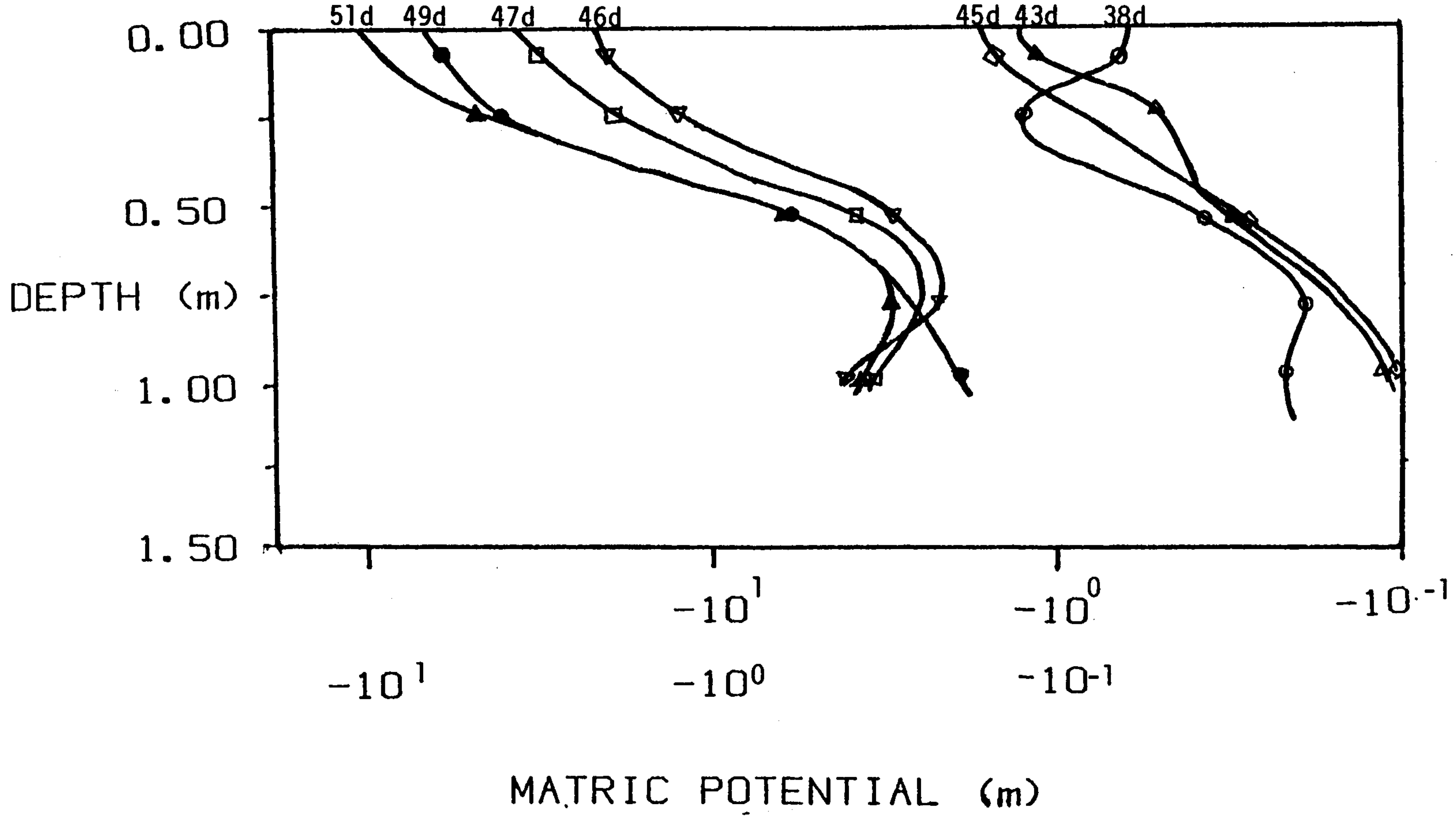

Fig. 4. Matric potential with depth at several dates during 1983. The upper x-axis units are for days 38 to 45, and the lower x axis units are for days 46 to 51.

did not observe such an altered root distribution in nonirrigated corn grown on Lakeland fine sand. This is not unexpected since sand does not retain as much water as fine textured soils even deep within the profile. Instead L_V was reduced in every horizon. Nonirrigated corn roots in Pomona fine sand did not penetrate as deeply as those of irrigated plots, due to restriction by a dry spodic horizon.

On day 79, 32.2 mm of rain fell which penetrated the surface layer of soil (Table 2, Fig. 4). Roots again proliferated in the surface 0.15 m layer but not in the 0.15 to 0.30 m depth where rain did not penetrate (Figs. 3 and 4). However, visual inspection indicated newly initiated nodal roots had only penetrated about 70 mm. Thick lateral roots had been initiated from these nodal roots but had not elongated more than 40 or 50 mm. The lateral roots lay one on top of another and only the tips were in contact with the soil. (One sample from day 106 had 67 lateral roots from a 25 mm length of nodal roots.) The short thickened roots were probably a result of mechanical impedance since mechanical impedance increases as the soil dries (Gerard et al., 1982; Mirreh and Ketcheson, 1972; Rowse, 1974; Williams and Shaykewich, 1970). The measured root length was probably not the same as the root length effective in water uptake. Mengel and Barber (1974) measured L_V's > 40 km m^{-3} in the surface, but the maximum observed here was < 30 km m^{-3}. The increase in L_V at the end of the season in the lower depths was probably due to varying solum thickness as sampling proceeded further into the field (Kathy Molten, 1983, personal communication). The solum was thicker here and allowed roots to extend deeper into the profile down planes of weakness.

Tensiometer data indicated that soil dried mostly above 0.75 m (the root zone), but some moisture was lost below this depth (Figs. 4 and 5). Nonequilibrium conditions and water loss below the root zone do not fit well in the available water concept (Van Bavel and Ahmed, 1976).

In conclusion, root distribution was altered when the surface soil layers dried. Since the subsurface soil horizons are moist, and no pan or other factor was restricting root penetration, roots proliferated deeper in the profile which partially compensated for the reduction in roots in the dry surface layer. A uniform planting density is needed for valid L_V measurements. A control (non water stressed) would be helpful to compare with the altered pattern of root growth in the water stressed plants. These results point to the need for controlled field studies with uniform planting densities and an appropriate statistical design.

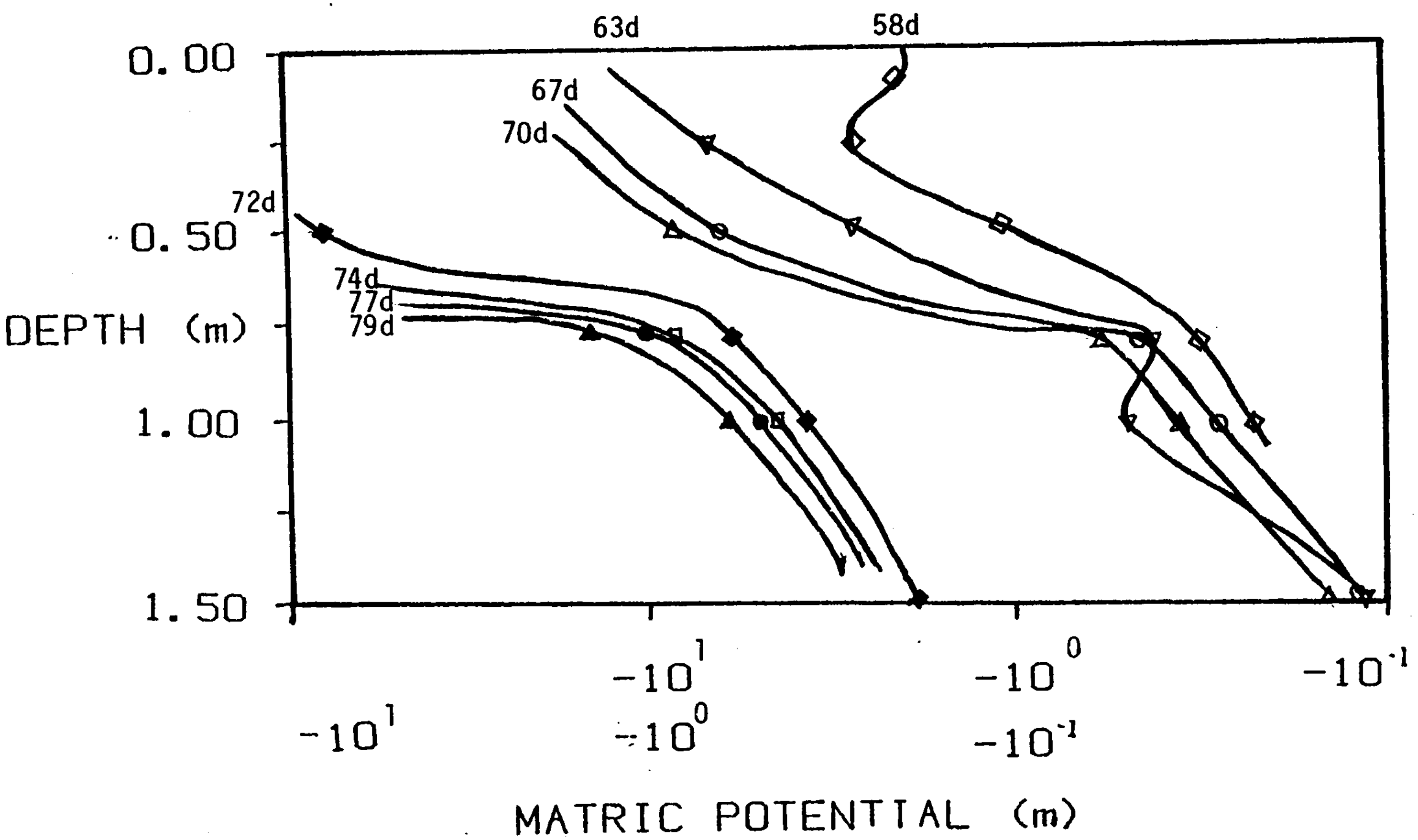

Fig. 5. Matric potential with depth at several dates during 1983 (cont.). The upper x-axis units are for days 58 to 70, and the lower x-axis units are for days 72 to 79.

Chapter III

ROOT VARIABILTY IN THE FIELD

Many methods have been developed for studying root systems in their natural setting (Bohm, 1979). The most common method in recent years is to mechanically extract soil cores and subdivide them into samples (Table 3). Since core diameters are often small (for speed in sampling), length of sample is increased to obtain a sufficient quantity of roots. None of the field researchers using core samples has attempted to assure that the sample sections had fairly homogeneous soil characteristics, nor has attention been given to horizon boundaries. Many studies report only one replicate per treatment (for each depth and date) which cannot be analyzed statistically.

The present study was conducted to statistically study corn root systems in plantings with evenly spaced rows and plants. Initially the goal of the study was to compare root growth and distribution of well-watered with non-watered corn. Under drought conditions roots may be able to proliferate in deeper, moist soil horizons thus preventing a significant reduction in grain yield, even if the surface dries during a critical growth stage such as silking.

Table 3. Root sampling techniques.

Researcher	Crop	Sample Dimensions	Sampling Method	Number of Tmts.	Depths	Dates	Loc.	Reps.
Boyer et al., 1980	Soybeans	38$^2\pi$ x 300mm^3	hydraulic coring machine	5	5 - 6	3	3	1
Garay and Wilhelm, 1983	Soybeans	38$^2\pi$ x 150mm^3	hydraulic coring machine	2	10	2	3	4 or 3
Grimes et al., 1975	Corn	20.5$^2\pi$ x 150mm^3 or x 300mm^3	hydraulic coring maching	4	?	1	2	2
Mengel and Barber, 1974	Corn '70 '71	38$^2\pi$ x 150mm^3	hydraulic coring machine	1 1	5 5	4 11	4 3	3 5
	'70 '71		total excavation	1 1	1 1	5 3	1 1	3 5
Raghaven et al., 1979	corn	50 x 50m^2	trench	1	3	1	4	1
Reynolds, 1970	fir trees	34$^2\pi$ x 150mm^3 or x 300mm^3	coring maching	1	5	4	4	4 X 10
Robertson et al., 1980	corn, soybeans, peanuts	25$^2\pi$ x 150mm^3 or x 300mm^3	Al-irrigation tubing - driven into ground	4	7	1	2 to 6	4
Rowse, 1974	lettuce '71 '72	20.5$^2\pi$	tube driven in by motorized hammer	2 2		2 6	5 1	1 x 35 3 x 4
Sivakumar et al., 1977	soybeans	0.3 x 0.07m^3 or x 0.15m^3	pinboard	1	16	5	1	1

MATERIALS AND METHODS

Corn 'Pioneer 3901' was planted 16 May 1984 evenly by hand at twice the desired density and thinned to a density of 59 300 plants ha^{-1} on a Groseclose silt loam. Phosphorus and K were applied at the rate of 28 kg ha^{-1} and N at the rate of 169 kg ha^{-1} according to soil test recommendations. Herbicides were applied as 2.3 L Bladex[1], [1] 4.7 L Lasso, and 1.2 L Aatrex ha^{-1}. The experimental design (Fig. 6) involved four blocks, two moisture treatments, three sampling dates, five depths, and two locations between rows for a total of 240 samples plus 32 initial samples. This was a split plot design with moisture treatments as the whole plot and dates and locations as the split plots, blocked by field location and order of sampling. Initially dates and depths were analyzed separately. Treatments and locations were pooled to get an estimate of root variability in the field. Coefficients of variation and sample number necessary were calculated by standard techniques (Steel and Torrie, 1980). The three deepest depths and the three sampling dates were also pooled to get an estimate of the skewed distribution of L_V data. Normality was tested by chi-square (χ^2) analysis.

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[1] Trade names included for the reader's benefit do not imply endorsement or preferential treatment by the author.

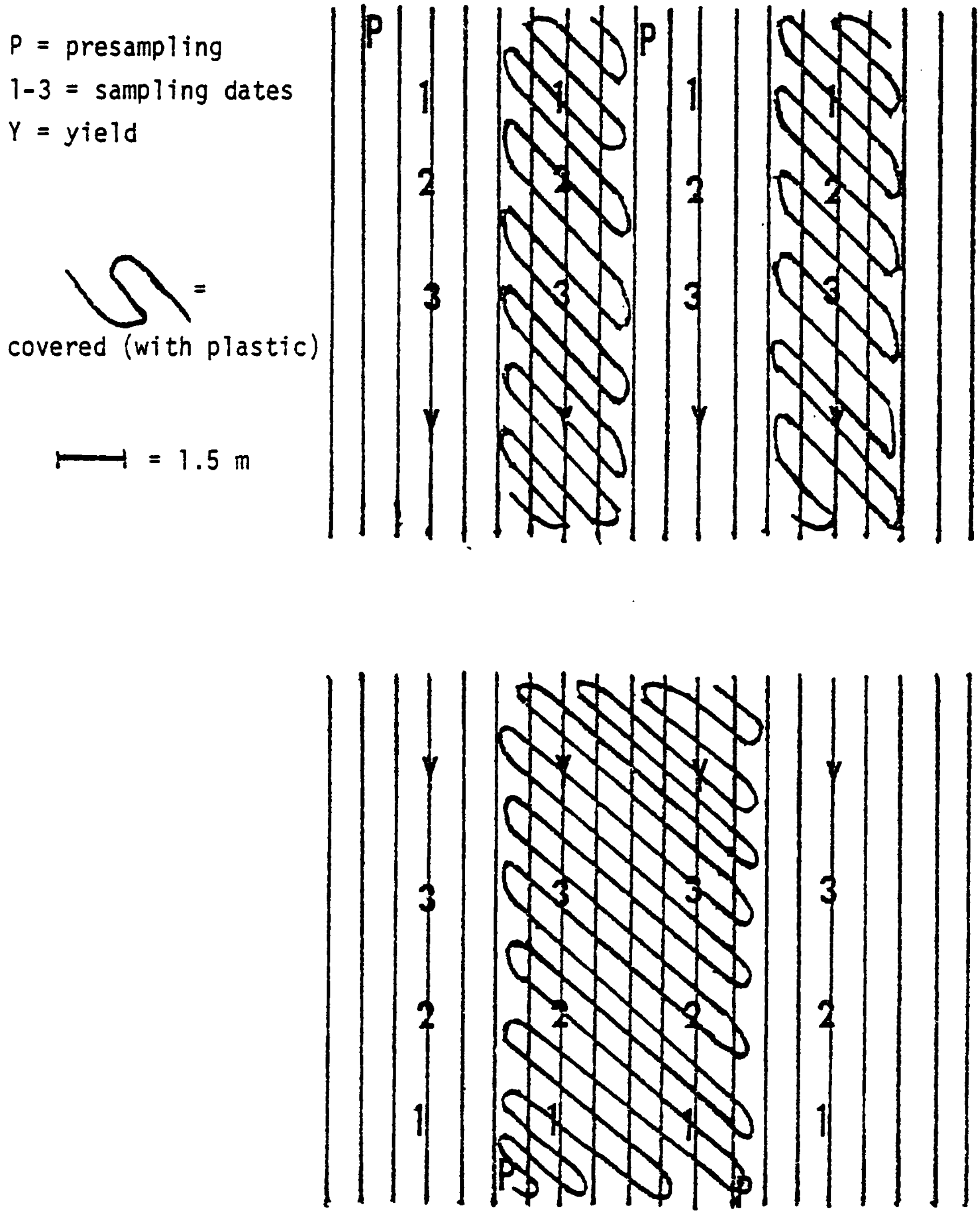

Fig. 6. Field layout and root sampling plan for the 1984 field season.

After the plants were established, trickle irrigation was set up on the watered treatments, but irrigation was only performed once when the soil surface was dry. The non-watered plots were covered with plastic to reduce infiltration from precipitation. The edges of the nonwatered plots were surrounded by aluminum flashing to prevent runon.

Roots were sampled 8 July 1984 prior to plastic placement (one plant from each block) and three times after initiating the treatments (25 July, pre silk; 2 August, at silking; 17 August, grain filling). Roots and shoots were sampled as described in Chapter II, except that soil--root samples were taken to the depth of root penetration both next to the plant and between rows. Roots were washed and then measured by the intersection method (Tennant, 1975) as described in Chapter II. Soil cores were also taken (2 August and 17 August) for measurement of bulk density and moisture content. Leaf samples were taken 20 July and 2 August. The third mature leaf from the top was used for measuring leaf water potential in a water potential sample chamber. An initial trial was conducted to establish the times: equilibration time was 15 min, cooling time was 8 s, and delay time was 20 s psychrometrically and 60 s for the dew point method. Grain yields were measured from two rows in each plot 3.05 m long and 0.76 m apart. Differences and correlations were considered to be significant at the 0.05 level or less.

RESULTS AND DISCUSSION

Leaf Water Potential

Average leaf water potential for the noncovered plots was 671 kPa by the psychrometric mode and 679 kPa by the dew point method. For the covered plots, averages were 721 kPa psychrometrically and 727 hygrometrically. The differences between covered and noncovered plots were not significant.

A chamber such as Wescor C-52 appeared to be an accurate isothermal way to measure water potential of soil, leaves, roots, solutions, etc. The relationship between the psychrometric mode and the dew point mode was almost 1:1 (Fig. 7), but the psychrometric method takes less time and is slightly less variable.

Root Variability

Because the season was not dry, no water stress developed. There were no differences between treatments for L_V (Figs. 8 and 9), volumetric moisture contents (Table 4), or leaf water potentials. Grain yields from the covered plots (10 040 kg ha^{-1}) were significantly higher than from the noncovered plots (9840 kg ha^{-1}). Except for day 79, shoot

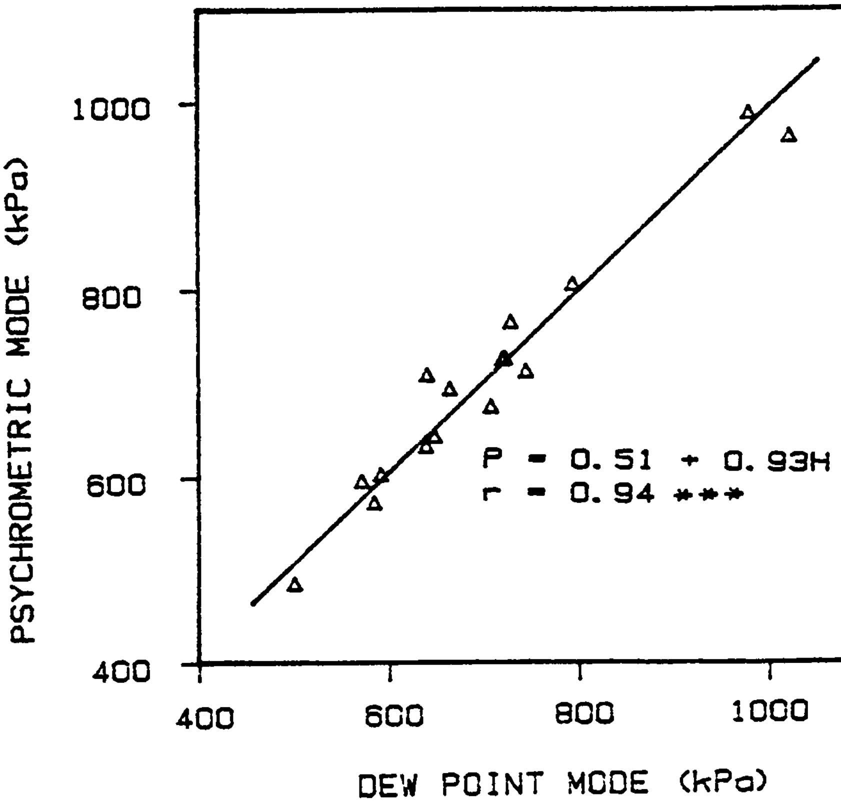

Fig. 7. Relationship between psychrometric and dew point modes for determining leaf water potentials. *** denotes significance at the 0.001 probability level.

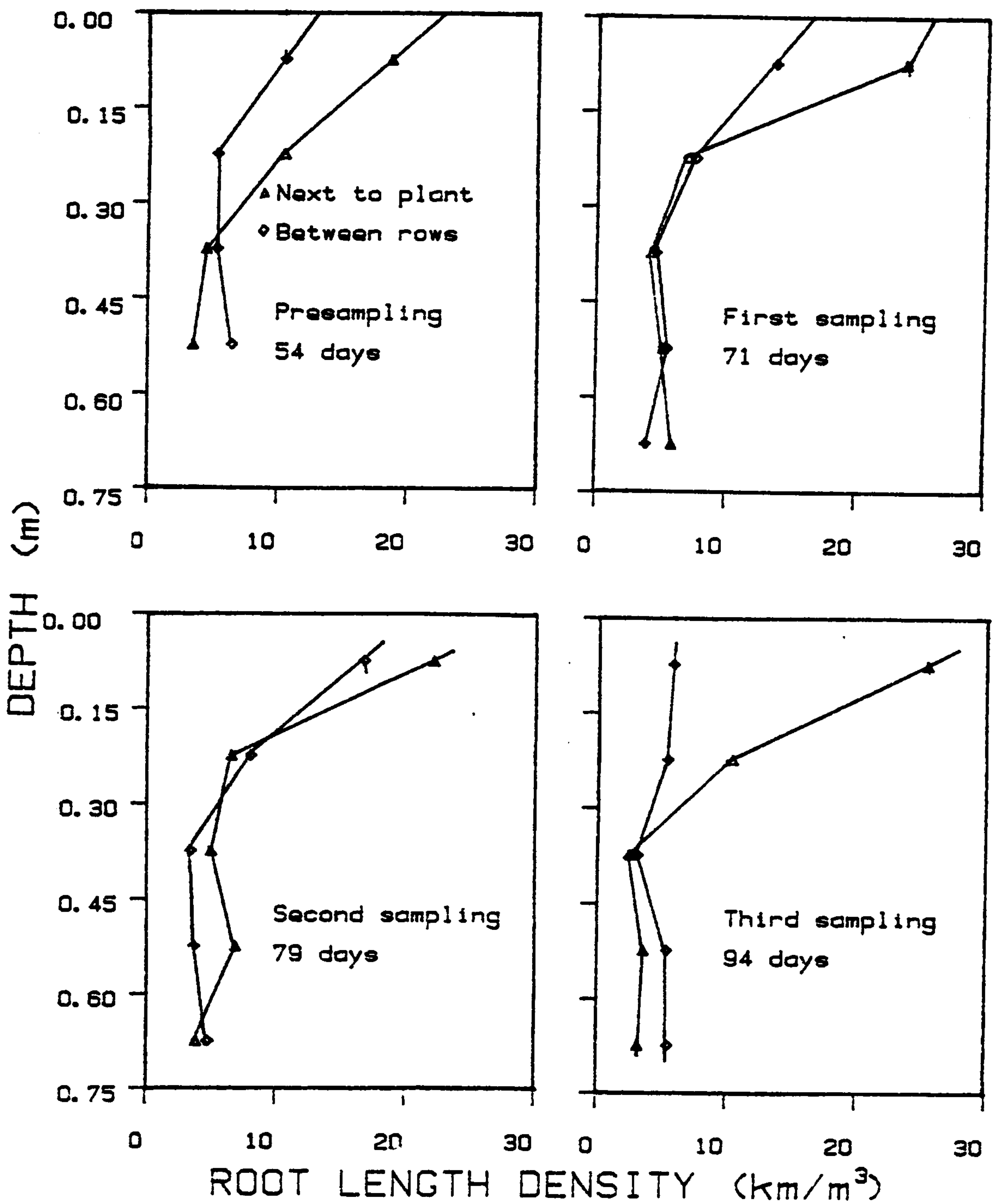

Fig. 8. Root length density with depth for covered plots in 1984.

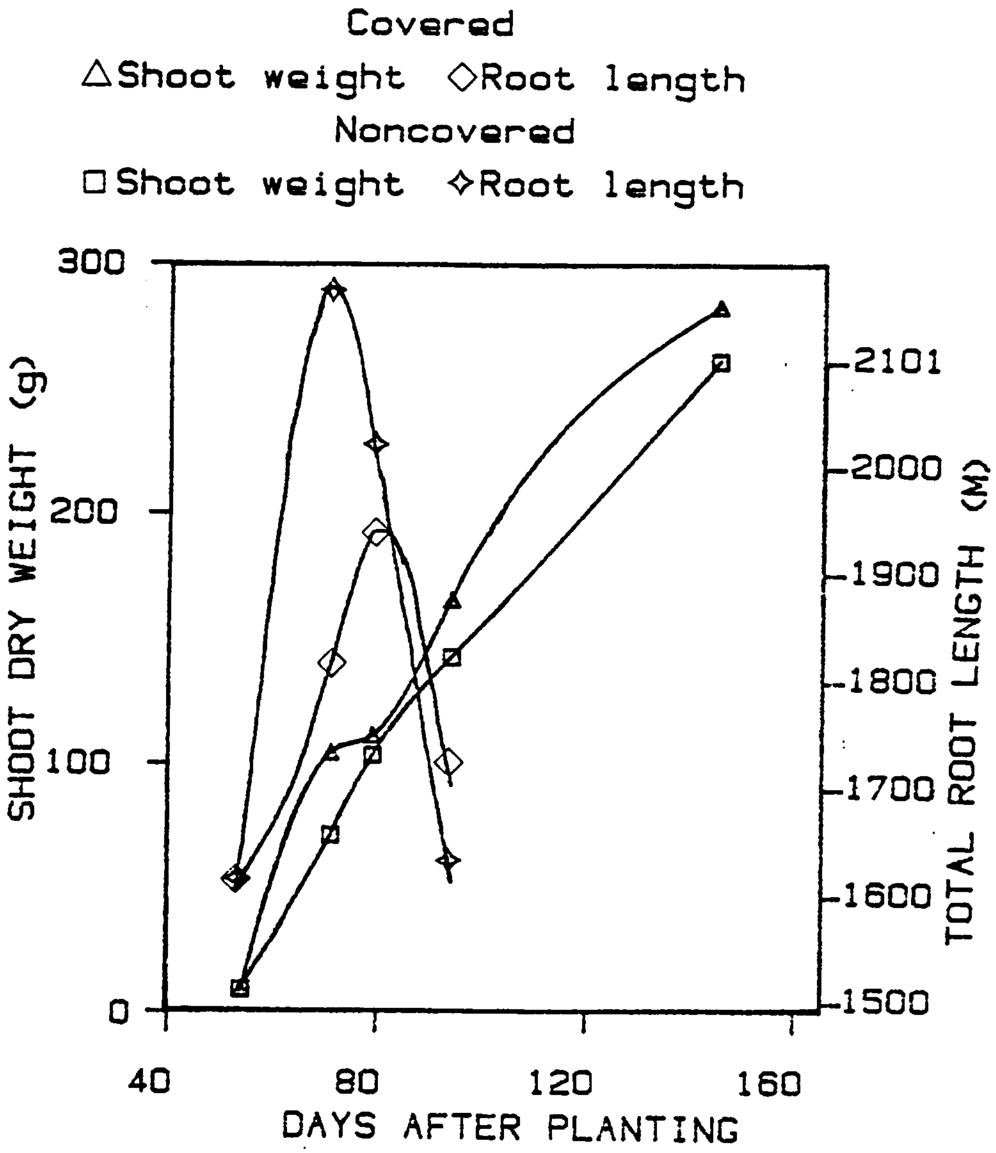

Fig. 10. Shoot dry weights and root lengths per corn plant in 1984. Except for day 145, each shoot dry weight and total root length is the mean of every four plants. The shoot dry weights from day 145 are the means of every third plant from four 3.05 x 0.76 m areas each.

Table 4. Soil volumetric moisture contents for covered and noncovered plots of Groseclose silt loam at several depths in 1984.

	Soil volumetric moisture contents*			
	August 2		August 12	
Depth	Covered[1]	Not covered	Covered	Not covered
m	$m^3\ m^{-3}$			
0.075	0.23	0.21	0.26	0.27
0.225	0.26	0.27	0.26	0.29
0.375	0.32	0.32	0.33	0.32
0.525	0.38	0.38	0.42	0.38
0.675	0.45	0.42	0.47	0.41

*Moisture contents were not significantly different at the 0.05 probability level for covered and noncovered plots.

[1] The covered plots were covered with clear plastic between the rows.

dry weights were significantly higher in the covered plots (Fig. 10). Although not statistically significant, the covered plots had slightly lower total root lengths. The plastic was a barrier to most nodal brace roots which may have allowed more photosynthate to remain in the shoot. All of these plant measurements were higher than last year (Fig. 2).

Since there were no differences between treatments or between locations for L_v, these data were pooled to get an estimate of root variability. The three deepest depths and the three sampling dates were also pooled to examine the skewed distribution of root length density data. Coefficients of variability were fairly high ranging from 28 to 82% (Table 5). This would indicate the need for approximately 100 samples in the surface layer and as many as 1000 samples in the deepest horizon in order to estimate the mean within 5% at a probability level of 0.05 (Table 5).

Rowse (1974) had difficulty detecting significant differences for 1972 root data because he only had 12 measurements per depth. In 1971 he had 35 samples for each mean, and more of the differences were significant; however, for each treatment, the samples were all taken from one plot. For comparing differences between treatments, the samples must be taken from blocks or replicates, not subsamples of

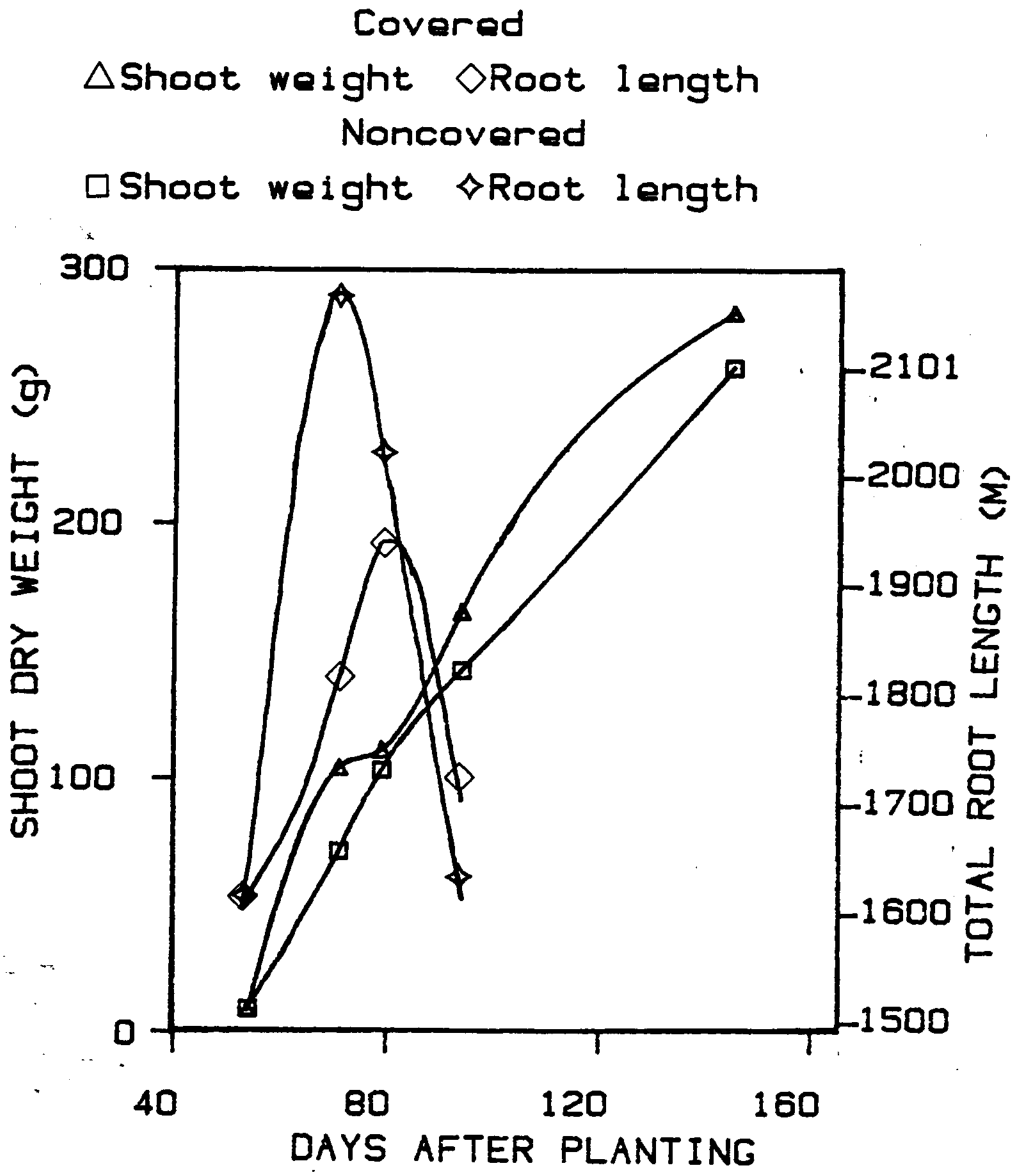

Fig. 10. Shoot dry weights and root lengths per corn plant in 1984. Except for day 145, each shoot dry weight and total root length is the mean of every four plants. The shoot dry weights from day 145 are the means of every third plant from four 3.05 x 0.76 m areas each.

Table 5. Coefficients of variation and sample numbers for field root samples in 1984.

	Coefficients of variation Date			Sample numbers[1] Date		
Depth	25 July	2 Aug	17 Aug	25 July	2 Aug	17 Aug
m		%			No.	
0.075a[2]	28.9	38.5	23.7	131	228	90
0.075b	52.9	63.1	64.6	430	612	641
0.225a	64.9	58.4	66.0	647	524	669
0.375a	59.4	53.3	54.5	565	437	456
0.525a	60.1	56.0	68.2	555	482	715
0.675a	60.7	82.1	72.0	566	1036	797

[1] The sample numbers are needed to determine the mean within 5% with a probability of 0.05.

[2] Samples taken next to the plant are designated by 'a', and samples taken between the row are designated by 'b'.

one replicate (Steel and Torrie, 1980). Reynolds (1970) also mentioned excessive variabilty of field root samples of fir trees (Pseudotsuga taxifolia). He suggested that some of the variabilty could have resulted from variations in the amount of rainfall entering the soil due to differences in interception and stemflow under the canopy. Roots proliferate where there is moisture, then deplete the moisture from this zone. As the area dries, fine roots die leaving only coarse roots. When rain again moistens the area, the coarse roots initiate new fine roots perpetuating the cycle. He could not detect significant differences in L_v even between depths or zones. Grimes et al. (1978) attributed 80% of the observed variation in alfalfa (Medicago sativa) L_v to increased soil strength in the surface. Wheel traffic and soil depth were the independent variables to predict L_v.

Distribution of L_v data was skewed (Fig. 11) significantly and non-normally distributed according to χ^2 analysis. A few samples contain many roots, and many samples contain few roots as Reynolds (1970) also pointed out. Hack (1957) discusses apparent non-normality of root lengths from two depths of tomato plants grown in a greenhouse. For one of the depths from χ^2 analysis he concluded that the calculated F values and mean squares were as good as could be expected from a normal population, but this conclusion was un-

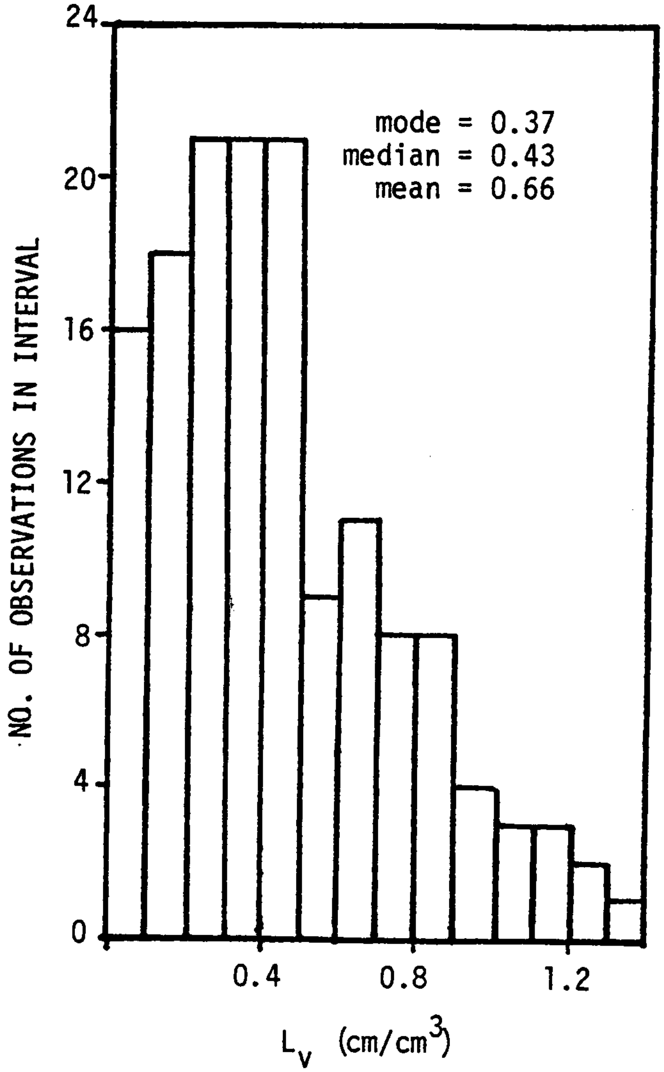

Fig 11. Pooled distribution of root length densities (L_V) in 1984. Distribution is pooling two treatments, four replicates, three depths, three sampling dates, and two locations (with respect to the row).

founded for the other depth. He was analyzing a completely randomized design and suggested that the results might be different for designs that restrict randomization. When non-normality is indicated, standard tables will underestimate the frequency of occurence of cases indicating significance.

To avoid the problem of non-normality, Rowse (1974) used a nonparametric technique (Kalmorgorov--Smirnov) to detect differences, and Schumacher and Smucker (1984) used a square root transformation. A square root transformation did not remove the skewed distribution of the data (Fig. 12) in the present study. A log transformation skewed the data tailing to the left (Fig. 13).

Modifications must be made in the sampling procedure to reduce the variability and obtain more reliable data without taking an exorbitant number of samples. Guidelines for future field root sampling include:

1. Never allow a sample to extend outside the bounds of a single soil horizon.
2. Larger samples would reduce the number of samples needed but greatly increase root sampling time. Although the samples must be taken volumetrically, the structure does not need to be preserved as for undisturbed core samples. Several small samples could be

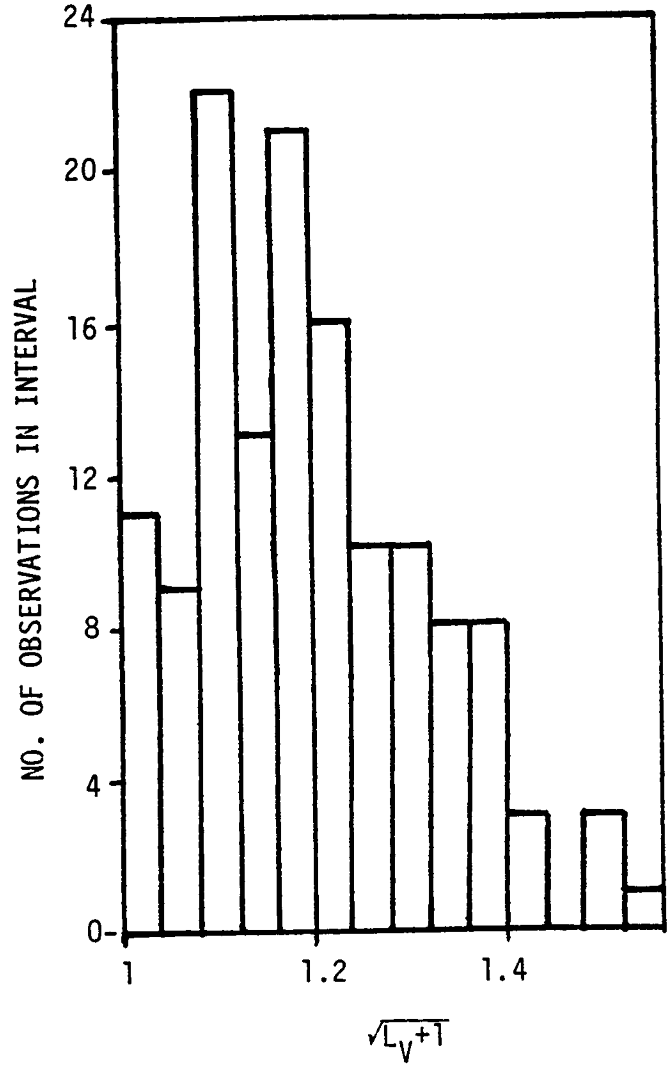

Fig. 12. Square root transformed distributions of root length density (L_V) data in 1984. Distribution is pooling two treatments, four replicates, three depths, three sampling dates, and two locations (with respect to the row).

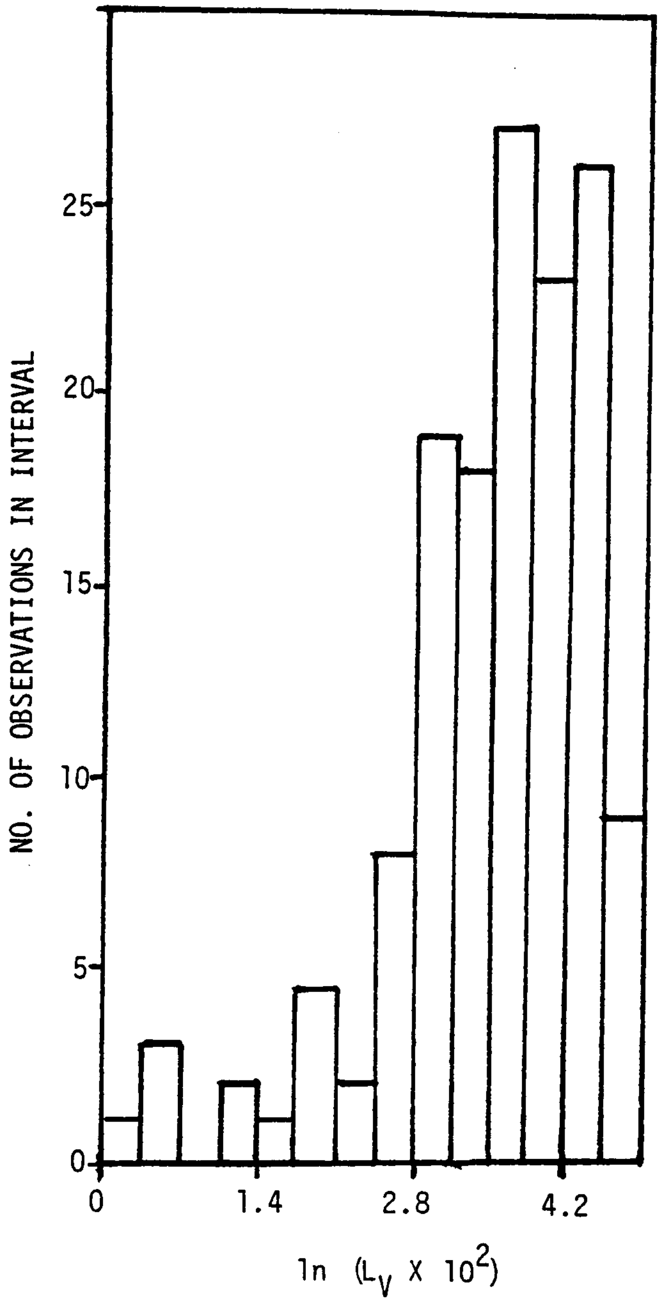

Fig. 13. Log transformed distribution of root length densities (L_V) in 1984. Distribution is pooling two treatments, four replicates, three depths, three sampling dates, and two locations (with respect to row).

pooled together to form one large sample, yet sampling time would be much less than for the large sample.

3. By pooling several small samples, the horizontal cross-sectional area of the net sample is increased. This will allow the vertical dimensions to be greatly decreased and lessen the chances of a sample crossing horizon boundaries. Long cores extracted mechanically could be subdivided into short subsamples (30 mm). If five cores are taken from one location (with respect to the row) within a plot, the five subsamples from each thin depth could be combined to form a sample large enough for analysis. At deeper depths where roots are more sparse, subsamples could be longer vertically but still should not extend beyond the horizon boundaries. Since for corn there is no difference for location with respect to the row for the deeper depths, perhaps these two locations could be pooled. By pooling these samples, the root length will be increased to a level in which measurements are more reliable.

Many researchers (Table 3) have examined root systems by taking small core samples, assuming the samples adequately represent the whole depth. Horizon boundaries and the soil structure have been ignored leading to variable results. When using other techniques such as trench (Raghaven et al.,1979), pinboard (Sivakumar et al., 1977), or rhizotron (Taylor and Klepper, 1973), the number of replications is limited due to the time involved, which eliminates statistical comparisons. The proposed sampling technique should reduce the variability and allow legitimate statistical comparisons.

In conclusion, root variability did not allow detection of significant differences between treatments, locations, dates, or even depths. This point to point variability is to be expected since root distribution depends on the heterogeneous nature and continuity of large soil pores. Sampling techniques should be altered to decrease the vertical dimension of the sample but increase the horizontal cross-sectional area.

Chapter IV

ROOT GROWTH IN STRUCTURED SOIL

Mechanical impedance has been studied in the past from the standpoint of the maximum pressure a root can encounter and still elongate, rather than the minimum pressure necessary to reduce the rate of elongation. In the field some impedance is inevitable even in well granulated soil. Evidence is accumulating that the response to mechanical impedance (reduced root elongation and increased diameter) is hormonally related (Goss, 1977; Goss and Russell, 1980; Kays et al., 1974; Lachno et al., 1982).

Increased root diameter might help the root in penetrating the soil. Abdalla et al. (1969) showed that alternating application and release of pressure on barley seedlings grown in modified triaxial cells, produced alternating thickened and normal root diameters. From this observation they developed a theoretical model of root elongation which is a form of inverse--peristalsis.

1. When elongation of roots ceases because the root cap cannot penetrate the soil, the diameter of the elongation zone of the root increases.
2. This increased diameter causes a reduction in the penetration resistance of the root cap.

3. The root then elongates until the root cap is again impeded.
4. The cycle repeats from (1).

Hettiaratchi and Ferguson (1973) concluded that this "inverse peristaltic" form of root elongation enables a root to grow through dense soils by exerting five times the pressure possible by a uniform growth mechanism.

Mechanical impedance can be induced by increasing bulk density for a given soil texture (Bar Yosef and Lambert, 1981; Camp and Lund, 1967; Phillips and Kirkham, 1962). Applying a pressure to the growth media leads to more impedance than just increasing the bulk density (Castillo et al., 1982; Goss, 1977; Goss and Russell, 1980). Even aggregate size has an effect on mechanical impedance. Wiersum (1962) showed that apple (Malus pumila) seedlings grown in soil with large clods had short, coarse roots with little branching while those grown in loose, friable soil were fine and well branched. Shoot dry mass from the first and second cuttings of ryegrass grown on four surface soils and seven subsoils, was greater for plants grown in small aggregates (1-2 mm), than in larger aggregates [(2-3, 3-5, 5-9, and >9 mm (Tabatabai and Hanway, 1968)]. Anderson and Kemper (1964) observed that intermediate aggregate stability lead to greater shoot dry mass than did high or low aggregate stabilty.

Transitory impedances in structured soil may explain some of the variability in root distribution. Grimes et al. (1978) observed that most of the variability in alfalfa root distribution was due to differences in soil strength caused by wheel traffic. Fissures in the soil due to shrinkage, worm channels, old root channels, etc. may permit root growth even in soil of higher strength. Ehlers et al. (1983) showed that the limiting penetration resistance for root growth in tilled loess soil was 3.6 MPa, but was 4.6 to 5 MPa in the untilled Ap horizon and in the subsoil, the difference being due to continuous large pores present in the no-till plots. The untilled soil had increased soil strength and bulk density in the surface, but root growth was not reduced. Whiteley et al. (1981) noticed a greater negative correlation between penetrometer resistance and root growth in remolded soil than in field clods. The densities and pore size distributions of field soils are highly variable. Dexter (1978) described the pattern of root growth as follows (see Fig. 16):

1. Roots grow geotropically until they encounter an aggregate.
2. If the strength of the aggregate is small, the root will continue to grow through the aggregate.

3. If the aggregate strength is too large, the root will be deflected around the aggregate until geotropic growth can be resumed.
4. The cycle is repeated from (1).

In this study corn seedlings were grown in aggregates of different sizes to study the effects of aggregate size on slight root impedances.

MATERIALS AND METHODS

Corn was grown in the A horizon of Groseclose silt loam in a growth chamber at 25° C with 16 h of daylight. The bottom of the growth chamber was flooded to keep humidity high, and pots were watered daily to return the soil to a volumetric moisture content (θ_V) of 0.24 m^3 m^{-3}. Soil was covered with styrofoam pieces to slow evaporation.

For the first trial, different aggregate sizes were compared as listed in Table 6. The aggregates had been moist seived into the size fractions. Corn 'Fla 82:152x151 (H93xAg32)' was grown in a completely randomized design and four replicates were sampled after 7 days. Leaf area was determined from the length and width of each leaf multiplied by a factor of 0.75 (Dale et al., 1980). Shoot dry mass was also measured. Total root length and length of main axes were measured by the modified intersection method of Tennant

(1975). Lateral root length was calculated by difference. Root diameter was calculated from the rehydrated mass assuming the fresh root density to be 1 Mg m^{-3} (Rowse, 1974).

For the second trial, different aggregate sizes were again compared (Table 7), with corn variety 'Becks 60X.' The statistical design was a a randomized complete block design. The experiment was blocked by placement in the growth chamber, seed size, and order of sampling. Seven replications for each treatment were sampled after 6 days with shoot and root measurements the same as before. Shoot dry mass was not measured because the plants were still small.

The third trial was as the second trial except that four replicates of each treatment were sampled after 4 days. Lateral roots had not begun to elongate so they were not measured. Lengths of main axes were measured with a ruler, and root diameter was calculated from the fresh mass of roots. Shoots had barely emerged so they were not measured. After air drying the roots overnight, the rehydrated mass of roots was measured to develop an equation relating rehydrated mass to fresh mass. Root lengths were again measured both by a ruler and by the intersection method (Tennant, 1975).

For all statistical tests, the 0.05 probability level or less was considered to be significantly different.

RESULTS AND DISCUSSION

Aggregate size had an effect on root morphology. Larger aggregates (>3 mm) tended to reduce elongation of main axes and lateral roots, but this reduction was not always significant (Tables 6, 7, and 8). Effects of aggregate size on germination were not separated from the effects on root growth. Lateral roots were more impeded than main axes. This was also shown by Barley et al. (1965) for plants grown in both confined and unconfined cores. Root diameters were generally significantly increased when grown in soil with larger aggregates (Tables 7 and 8).

Root diameters (Table 6) at 4 days were much larger than diameters at 6 days (Table 7). This is because the diameters were averages, and 4-day-old roots did not yet have the smaller diameter lateral roots. Also rehydrated masses were only about half of fresh root masses (Fig. 14) yielding smaller calculated diameters. The regression equation comparing rehydrated mass with fresh mass (Fig. 14) was used to calculate fresh mass (and hence fresh diameter) for trial two. Root length was slightly but not significantly reduced by air drying and rehydration (Fig. 15). The slope of the regression equation was not significantly different from one, and the intercept was not significantly different from zero.

Table 6. Root growth of 4-day-old corn seedlings 'Becks 60X' as influenced by different aggregate sizes.

Aggregate size	Bulk density	Root length	Avg. fresh root diam.
mm	Mg m^{-3}	--------- mm	---------
<1	1.30	460NS[1]	0.88NS
1-2	1.25	437	0.92
2-3	1.25	367	0.93
3-6	1.25	372	0.97

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[1] NS designates not significant at the 0.05 level.

Table 7. Root and shoot growth of 6-day-old corn seedlings 'Becks 60X' as influenced by different aggregate sizes.

Aggregate size	Bulk density	Leaf area	Root length			Avg. root diam.	
			Total	Axes	Laterals	Rehyd.	Fresh[1]
mm	Mg m^{-3}	mm^2	--------- m --------			---- mm ---	
<1	1.30	1580NS	2.66NS	0.64NS	2.02NS	0.32a*	0.45
1-2	1.25	1730	3.77	0.76	3.01	0.31a	0.44
2-3	1.25	2840	2.84	0.62	2.22	0.32a	0.45
3-6	1.25	2440	2.44	0.66	1.78	0.40b	0.57

*Means followed by the same letter are not significantly different at the 0.05 level by Duncan's multiple range test. NS designates not significant.

[1] Fresh diameters were calculated from the regression equation relating rehydrated mass to fresh mass.

Table 8. Root and shoot growth of 7-day-old corn seedlings 'Fla 82:152x151' as influenced by different aggregate sizes.

Aggregate size	Bulk density	Leaf area	Root length Total	Axes	Laterals	Avg. root diam. rehyd.
mm	Mg m^{-3}	mm^2	--------	m	---------	mm
<1	1.35	2800NS	7.50a*	1.16NS	6.34NS	0.27a*
1-2	1.25	2970	7.35a	1.11	6.25	0.30ab
2-3	1.25	2090	4.62ab	0.97	3.65	0.34bc
3-6	1.20	2080	3.99b	0.80	3.19	0.36c

*Treatments followed by the same letter are not significantly different at the 0.05 level by Duncan's multiple range test. NS designates not significant.

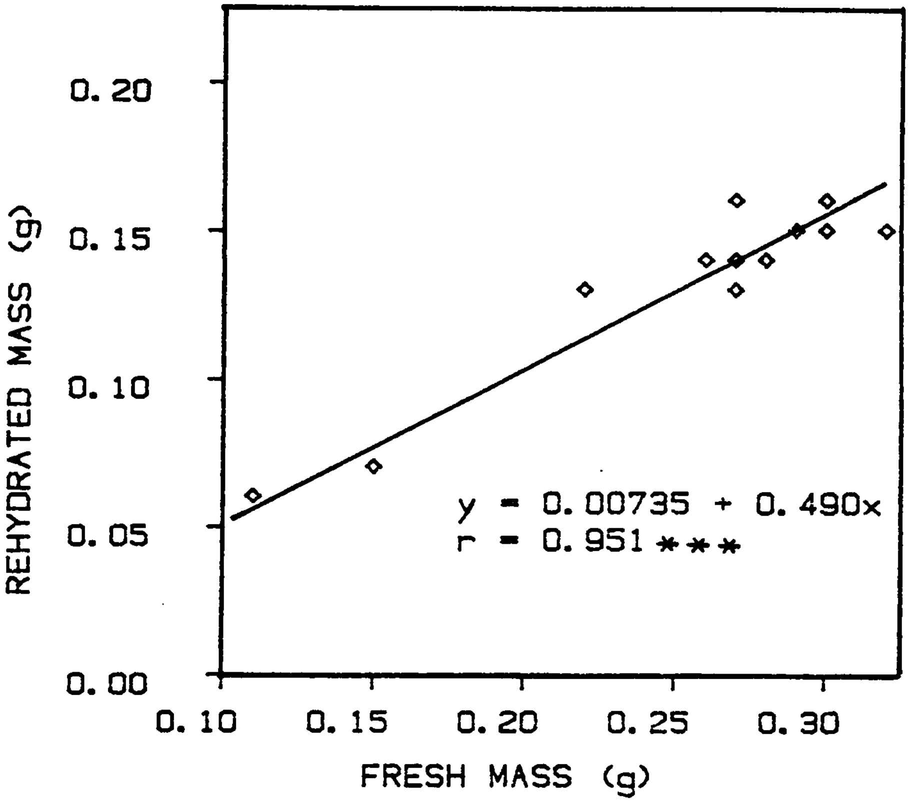


Fig. 14. Rehydrated corn root mass compared with fresh root mass. *** denotes significance at the 0.001 level. Roots were air-dried overnight.

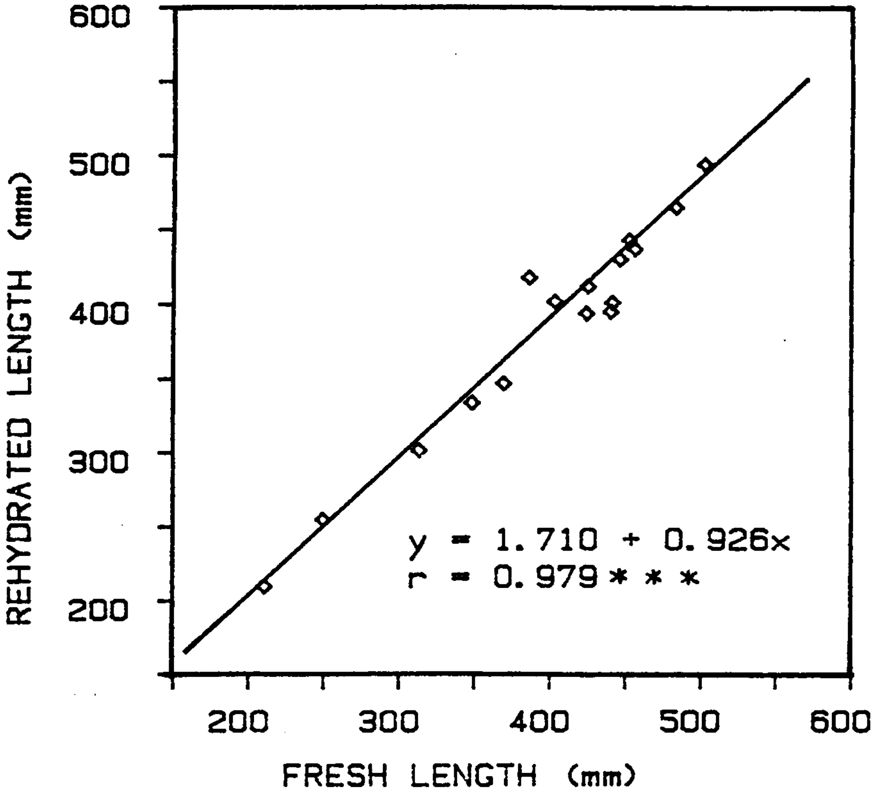
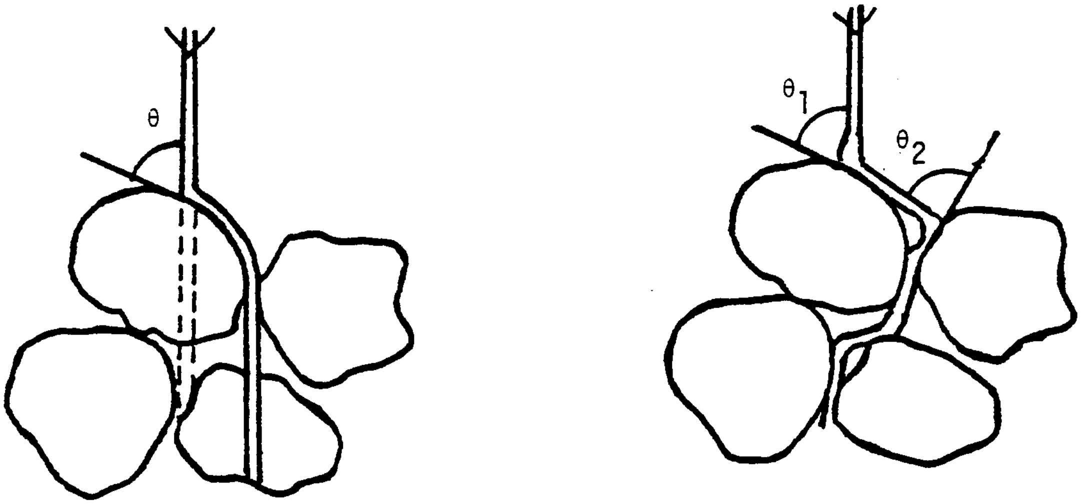


Fig. 15. Rehydrated corn root length compared with fresh root length. *** denotes significance at the 0.001 level. Roots were air-dried overnight.

Some researchers have shown large aggregates to impede root growth (Anderson and Kemper, 1964; Tabatabai and Hanway, 1968; Wiersum, 1962). Conversely, Goss (1977) showed no difference in barley (Hordeum vulgare) root elongation when grown in glass beads of different sizes (100 to 1000 µm) unless confining pressures were applied. Under applied pressure, roots could only elongate in pores of equal or larger diameter than themselves. Even when no pressure was applied, the roots in all of his root studies were severely impeded. As an example with no applied pressure, the root length of 7-day-old corn was approximately 50 to 190 mm (about two orders of magnitude lower than those reported here). Perhaps the underlying impedance in Goss's experiments was due to the small size of his growth container (12.5 x 1.2 x 20 mm). Phillips and Kirkham (1962) have shown increasing impedance in glass tubes of decreasing diameter due to the volume of root material causing pressure on other roots. Schneider and Gupta (1985) showed that large (geometric mean diameter or GMD = 11.1 mm) or small (GMD = 0.5 mm) aggregate sizes led to delayed emergence of corn. They concluded that large aggregates had less seed-soil contact. Since they started with dry soil, the smallest aggregates consolidated upon wetting causing increased penetrometer resistance. Nash and Baliger (1974) obtained soybean emergence 4 days earlier from pots with 2 to 4 and 1 to 2 mm aggregates than with larger or smaller aggregates. The 4 to 6 mm aggregates had poor seed-soil contact perhaps leading to poor water relations, and the 0 to 0.5 mm aggregates perhaps led to poor aeration conditions.

In the present study the roots grown in soil with larger aggregates appeared to have zones of thicker and thinner diameter in the curved and twisted roots indicating transitory impedances as roots were deflected around aggregates. This would tend to support the "inverse peristalsis" hypothesis of Abdalla et al. (1969). Roots grown in fine aggregates were smooth and straight, readily pushing the small aggregates out of their path.

Dexter's (1978) pathway of root growth (Fig. 16) could be modified for corn grown in aggregates of high strength. Corn radicles do not grow totally geotropically unless seeds are placed vertically, and then only if the soil is warm enough (Hawkins, 1963). Even seminal roots from these vertically placed seeds grew at an angle from horizontal. Instead of a root curving around an aggregate, a corn root will continue to grow in the direction of its deflection until deflected again (Fig. 16). Roots were not observed to grow "through" aggregates in this study. Roots grew around larger aggregates and pushed smaller aggregates out of their



Dexter, 1978

Proposed

Fig. 16. Representations of possible paths of a root axis through aggregates.

path. Nash and Baliger (1974) observed that soybean roots can push silt particles out of their way. Perhaps some larger aggregates could have been broken by root pressure allowing roots to grow in a straight path (Barley et al., 1965).

Dexter (1978) and Hewitt and Dexter (1979) modeled the growth of roots in structured soil. They represented soil structure along a line by a series of 0's and 1's of 1 mm increments where 0 represents a void, and 1 an aggregate (Dexter, 1976). From measured patterns of 0's and 1's, longer strings were generated having the same statistical structure as the original pattern. Roots were assumed to follow the path displayed in Fig. 16, either growing around an aggregate or through it depending on the strength of the aggregate. They describe the proportion of roots penetrating an aggregate (c) by a Boltzmann-type expression (Dexter, 1978):

$$c = \exp[-F(\theta)S/(S_{max} - S)] \qquad [1]$$

where $F(\theta)$ is determined from Table 9, S is the soil strength, and S_{max} is the maximum pressure beyond which a root will not penetrate. The maximum pressure is either the strength in which a root will no longer elongate (S_e), or the strength causing "buckling" of a root (S_b). Dexter and

Table 9. Values used for the function F in equation [1].

angle	F(θ)
°	
0-15	100.00
15-30	10.55
30-45	1.82
45-60	0.50
60-75	0.23
75-90	0.13

Hewitt (1978) calculated buckling strength from the following equation:

$$S_b = 80.8\ EI/\pi d_r^2\ y^2 \qquad [2]$$

where d_r is root diameter, E is Young's modulus of the root, I is inertia, and y is the length of the void through which a root has grown. Young's modulus of root was determined from the deflection of roots after applying loads, assuming roots behave as elastic columns with circular cross-section. Young's modulus can be calculated from the following equation (Dexter and Hewitt, 1978):

$$E = fx^3\ 64/3\delta I \qquad [3]$$

where x is the length of root involved (see Fig. 17), and δ is the deflection distance. From Fig. 17 we see that

$$\delta = 2x \sin(\theta/2) \qquad [4]$$

where θ is the deflection angle.

Three possible problems arise from this analogy. Roots are not of uniform diameter but taper somewhat toward the end. Roots are not really elastic. If a load is applied to the tips of horizontal roots, they will deflect by slightly larger increments for each additional increment of load. Roots are not homogeneous but contain many different kinds of tissues (Dexter and Hewitt, 1978).

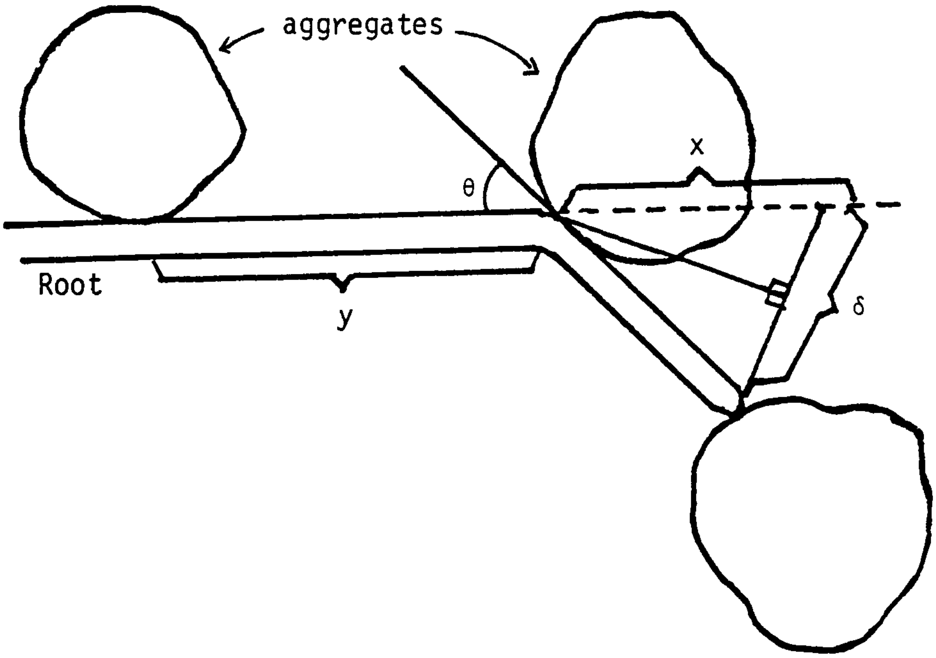


Fig. 17. Representation of the deflection of a root.

Dexter and Hewitt (1978) give representative values for their measured Young's Modulus for different species, ranging from 17 to 97 MPa. This gives buckling strengths around 200 kPa. As a comparison, Goss (1977) has shown that the minimum applied pressure impeding corn and barley roots is as small as 25 kPa.

Dexter (1978) does not take into account the impedance caused by the size of larger impenetrable aggregates. Assuming a spherical aggregate with an aggregate density of 1.75 Mg m^{-3}, an overall θ_v of 0.24 m^3 m^{-3}, and no moisture between aggregates; the aggregate's dry mass, volumetric moisture content, and moist mass can be calculated (Table 10). Obviously, the mass of an aggregate is directly proportional to the cube of its diameter. So

$$f = mg \qquad [5]$$

where f is force, m is mass of an aggregate, and g is acceleration due to gravity. If the aggregate weight is assumed to be the load acting on the root, then equations [2], [3], [4], and [5] can be combined to the following equation:

$$S_b = 80.8\ mgx^2/[\pi\ d_r^2\ 6\ \sin(\theta/2)y^2] \qquad [6]$$

which if x equals y, simplifies to:

$$S_b = 4.29\ mg/[d_r^2\ \sin(\theta/2)] \qquad [7]$$

Table 10. Aggregate properties used for calculation of aggregate moist mass[1].

Average aggregate diameter	Aggregate volume	Aggregate mass	
		dry	moist
mm	mm^3	mg	
0.5	0.0491	0.0859	0.1148
1.5	1.325	2.32	3.10
2.5	6.14	10.7	14.3
4.5	35.8	62.6	83.6
7.5	166.	290.	387.
10.5	455.	796.	1 063.

[1] Calculations of moist mass of a spherical aggregate with an aggregate density of 1.75 Mg m^{-3}, interaggregate porosity of 0.286 m^3 m^{-3}, and aggregate volumetric moisture content of 0.336 m^3 m^{-3}.

Equation [7] describes root pressure in terms of aggregate mass, root diameter, and deflection angle. As aggregate size increases, the root pressure necessary to avoid deflection increases. Smaller roots require more root pressure to avoid deflection. Roots encountering the edge of an aggregate have a greater tendency to be deflected. Whiteley et al. (1981) mention the possibility of a size dependence of root tips for pressures required to penetrate soil.

This model may be compared to the data presented. Using axis, lateral, and total root lengths, and average fresh diameters of 6 day old corn seedlings (Table 8), diameter of laterals can be calculated using the following equation:

$$L_a\ d_a + L_l\ d_l = L_t\ d_t$$

where L_a, L_l, and L_t are axis, lateral, and total root length, respectively; and d_a, d_l, and d_t are diameters of the same. This gives lateral diameters of 0.31, 0.32, 0.32, and 0.42 mm for the <1, 1 to 2, 2 to 3, and 3 to 6 mm aggregate size treatments, repectively. Equation [7] was used to calculate root pressure to avoid deflection (Table 11), and equation [1] was used to calculate the percentage of roots penetrating the soil without being deflected (Table 12), assuming the maximum pressure restricting corn root penetration to be 1 MPa (Whiteley, et al., 1981), and the angle of

Table 11. Prediction of corn root pressures necessary to avoid deflection.

Aggregate size	Root pressure[1] Laterals	Axes
mm	------- kPa	-------
0.5	0.131	0.0163
1.5	3.33	0.401
2.5	15.3	1.81
4.5	52.0	9.75
7.5	170.	42.4
10.5	476.	117.

[1] For the aggregate sizes 0.5 to 4.5 mm, root diameters were measured. For the aggregate sizes 7.5 and 0.5 mm, root diameters were assumed to be 0.5 and 1.0 mm, respectively, for laterals and axes. Angle of incidence was assumed to be 45°.

Table 12. Predicted percentage of aggregates a corn root penetrates without deflection.[1]

Aggregate size	Roots	
	Laterals	Axes
mm	------ %	-------
0.5	99.9	99.9
1.5	99.6	99.9
2.5	98.2	99.8
4.5	93.8	98.9
7.5	78.9	95.0
10.5	36.2	85.8

[1] For the aggregate sizes 0.5 to 4.5 mm, root diameters were measured. For the aggregate sizes 7.5 and 10.5 mm, root diameters were assumed to be 0.5 and 1.0 mm, respectively, for axes and lateral roots. Angle of incidence was assumed to be 45°. The maximum pressure beyond which a root will not elongate is assumed to be 1 MPa.

incidence to be 45°. Hewitt and Dexter (1979) later used equation [1] to describe the path of a single root, in terms of the percentage of aggregates a root encounters without deflection.

If the maximum pressure restricting corn root penetration is 1 MPa, we would expect no roots to be severly impeded by aggregates <6 mm diameter (Table 11). In terms of slight impedance (pressures >25 kPa: Goss, 1977), we would expect lateral roots in the 3 to 6 mm aggregate size range to be slightly impeded. Root lengths were not significantly reduced, but diameters did significantly increase (Tables 6, 7, and 8). From Table 12 we see that aggregates would need to be larger than 9 mm to cause much root deflection. Goss and Russell (1980) have shown that when a corn root tip makes contact with a ballotini, elongation is slowed by 70% for about 10 min. If contact with an impenetrable aggregate, and subsequent deflection of roots lead to impedance, large aggregates could impede root growth slightly. Further study is needed to test this model with seedlings grown in larger aggregate sizes where impedance is expected to be more significant.

The discussion thus far does not include overburden pressure. If the fraction of aggregates making contact with other aggregates at a horizontal plane is 0.05, and assuming a depth of 75 mm (center of pot), then the contribution of overburden pressure is 21.9 kPa. If this pressure is added to the root pressures in Table 11, then for 10.5 mm aggregates and lateral roots, the percent of roots penetrating the soil without deflection is 31.6%, and for 7.5 mm aggregates is 75.9%. Only a slight increase in root deflection is indicated. If the fraction of contact of aggregates is 0.02, then the additional pressure is 54.8 kPa. For 10.5 mm aggregates and lateral roots, percent of roots penetrating the soil undeflected is 28.5%, and for 7.5 mm aggregates is 72.9%, again only a slight increase in deflection. However if extended to a depth of 0.75 m, the additional pressure is 548 kPa, which alone would only allow 24.5% of the roots to grow undeflected. For lateral roots in 10.5 mm aggregates, none would grow undeflected.

The effect of overburden would be small in the surface soil. At greater depths overburden pressure is the major resistance to root penetration of peds. Also soil peds are generally larger at lower depths. Roots are then restricted to large pores such as cracks, worm holes, etc. If the macrostructure of the soil is not very tortuous, roots could still grow relatively undeflected.

Dexter's (1976, 1978) system of describing soil structure seems to be an adequate method for describing root contact with soil along a line. Eight to 10 m of generated root growth is needed to adequately characterize the system because of variability (Dexter, 1978). This sounds incredibly long for a single root, but is feasible for a branched root system. His method has not yet been refined to include branching.

The purpose of the models (Dexter, 1978; Hewitt and Dexter, 1979) was to calculate the "effective" surface area of a root in contact with the soil in conjunction with nutrient uptake. Possibly the same idea could be applied to water uptake. Perhaps these models could be improved by using a more accurate method to calculate root buckling strength (which includes aggregate size and root diameter), the correct pattern of root growth (Fig. 16), and allow for root branching. Some questions remain to be answered. If a root is impeded by an aggregate and deflected, is the elongation rate reduced (if only temporarily)? How does impedance affect branching in a nonrigid system? Understanding the slight impedances encountered in every field situation and the pattern of root growth in structured soil could help to provide a basis for a physical explanation of root growth and distribution in the field.

Chapter V

SOIL PHYSICAL EFFECTS ON ROOT MORPHOLOGY

Soil physical stresses often have similar effects on root morphology -- shortening and thickening of roots. The effects of mechanical impedance have been linked to plant hormones (Goss, 1977; Goss and Russell, 1980; Kays et al, 1974; Lachno et al., 1982). Conceivably, the effects of other physical stresses may also be related to plant hormones. Altered root morphology under oxygen stress (hastened emergence of nodal roots, aerenchyma formation, and reduced root elongation) has been linked to ethylene (Drew et al., 1979; Drew et al., 1981; Jackson et al., 1979). Lower temperatures slow root elongation (Burholt, and Van't Hof, 1971; Gregory, 1983; Hawkins, 1963; Mackay and Barber, 1984). Water stress induced by polyethylene glycol (PEG) slows root elongation (Bar Yosef and Lambert, 1979; Ciamporova and Luxova, 1976; Lawlor, 1973; Murin, 1979) and increases root diameter (Ciamporova and Luxova, 1976), but the results of low soil moisture are variable. Portas and Taylor (1976) have indicated that corn and tomato (*Lycopersicon esculentum*) roots are able to elongate (however slowly) even in a soil with matric potentials (ϕ_m) as low as -900 MPa. Malik et al. (1979) have shown cotton root growth can actually increase under mild water stress when impedance is not a problem. Merrill and Rawlins (1979) did not observe a statistically significant decline in sorghum L_v at ϕ_m of -500 and -1000 kPa. Gales (1979) suggests that increased root length under water stress may be due to P deficiency induced by the low soil moisture content. Decreased root growth in dry soil is often due to increased mechanical impedance (Camp and Lund, 1968; Ehlers et al., 1983; Gerard et al., 1982; Merrill and Rawlins, 1979; Mirreh and Ketcheson, 1972; Rowse, 1974; Williams and Sheykewich, 1970).

Most of these studies involve the response of roots to only one factor. Murin (1981) observed the isolated effects of temperature, osmotic potential (ϕ_s), and oxygen levels, on the mitotic cycle of *Vicia faba* root members. Bar-Yosef and Lambert (1981) studied the isolated effects of bulk density and ϕ_m on corn and cotton root growth. Schumacher and Smucker (1981) examined the interaction of mechanical impedance and low oxygen on drybean (*Phaseolus vulgaris*) root morphology. Schneider and Gupta (1985) measured the interaction effects of soil temperature, ψ_m, and aggregate size distribution on the emergence of corn. The purpose of this study was to separate the effects of mechanical impedance, lower temperature, oxygen stress, and water stress on corn root morphology. Stress was assumed to be any factor that reduced corn growth from that under ideal conditions.

MATERIALS AND METHODS

Corn 'Becks 60X' was grown in A horizon material of Groseclose loam. The soil was moist sieved through a 2 mm sieve since larger aggregates can induce slight impedances (see Chapter IV). The 2.75 L pots were placed in a growth chamber and received 16 h of daylight during each 24 hour period. The bottom of the chamber was flooded to maintain high humidity. The soil was covered with styrofoam pieces to slow evaporation. All seeds were planted horizontally - one per pot - with the embryos facing up. In each trial except for low temperature, the statistical set up was a randomized complete block design. Experiments were blocked by placement in the growth chamber, seed size, and order of sampling. Seedlings were sampled after 4 days (four replicates) and after 6 days (six replicates). Shoot and root morphology was measured as described in Chapter IV using fresh root mass to calculate root diameters. Plant height was also measured in selected trials.

To induce mechanical impedance moist soil was packed into pots at different bulk densities (1.10, 1.22, 1.35, and 1.47 Mg m^{-3}) in 0.25 L increments. After each addition of soil, the surface was scratched before the next addition to prevent formation of a smeared layer. The growth chamber temperature was set for 25°C, and the pots were watered daily to bring to a θ_v of 0.24 $m^3\ m^{-3}$.

To induce oxygen stress, soil was brought to different θ_v (0.24, 0.27, 0.30, and 0.33 $m^3\ m^{-3}$) at a uniform bulk density (1.22 Mg m^{-3}) and temperature (25°C). This is adequate to produce oxygen stress since other stresses associated with flooding take much longer to develop (Trought and Drew, 1980). Oxygen diffusion rate (ODR) was measured with a platinum microelectrode (Lemon and Erickson, 1952), five electrodes per pot.

To examine lower temperature stress, corn was grown at different soil temperatures (approximately 17, 21, and 25°C) with the same bulk density (1.22 Mg m^{-3}) and θ_v (0.24 $m^3\ m^{-3}$). Table 13 shows actual soil and air temperatures in the growth chamber. The soil temperatures were measured with thermocouples at the center of each pot, and air temperatures were measured with a thermometer. Temperature was a fixed effect. Root angles were measured with a protractor.

In the first water stress trial, soil was brought to different θ_v (0.24, 0.22, 0.20, 0.18 $m^3\ m^{-3}$) at a constant bulk density (1.22 Mg m^{-3}) and temperature (25°C). Seeds were pregerminated overnight in moist paper towel. Corn

Table 13. Soil and air temperatures in the growth chamber during dark and light periods

Placement	Temperature		
	Low	Middle	High
	°C		
Soil[1]			
Dark	15.1	20.1	24.2
Light	17.9	22.4	25.2
Air			
Dark	15.0	19.9	24.5
Light	18.3	22.3	26.7

[1] The soil temperatures were the average of 10 replications determined by thermocouples at the center of each pot.

plants were sampled after 3.5 (four replicates) and 6.5 days (six replicates). A water potential sample chamber was used (in the psychrometric mode) to determine soil ϕ_m from small subsamples taken just below the seed. Equilibration time was 20 min, cooling time 8 s, and delay time 20 s.

For the main water stress trial, soil was brought to different θ_v (0.24, 0.21, 0.18, and 0.15 $m^3\ m^{-3}$) at a uniform bulk density (1.22 Mg m^{-3}) and temperature (25°C). Again soil ϕ_m were determined from small subsamples.

Treatment sums of squares were partitioned into linear, quadratic, and cubic components each with one degree of freedom. An F test with the pooled mean square error was used to test the significance of each component (Steel and Torrie, 1980). The 0.05 probability level or less was considered to be statistically significant.

RESULTS AND DISCUSSION

Mechanical Impedance

Four-day-old corn seedlings had significantly shorter, thicker roots when grown at a bulk density of 1.47 Mg m^{-3} than at lower bulk densities (Table 14). As bulk density increased, root length decreased linearly (Fig. 18). Six-day-old seedlings grown at higher bulk densities had signi-

Table 14. Root growth of 4-day-old corn seedlings as influenced by bulk density.

Bulk density	Root length	Root diameter[1]
Mg m^{-3}	-------- mm	---------
1.10	425b*	0.92a*
1.22	379b	0.90a
1.35	352b	0.90a
1.47	215a	1.11b

*Means followed by the same letter are not significantly different at the 0.05 level by Duncan's multiple range test.

[1] Root diameters are averaged per root system.

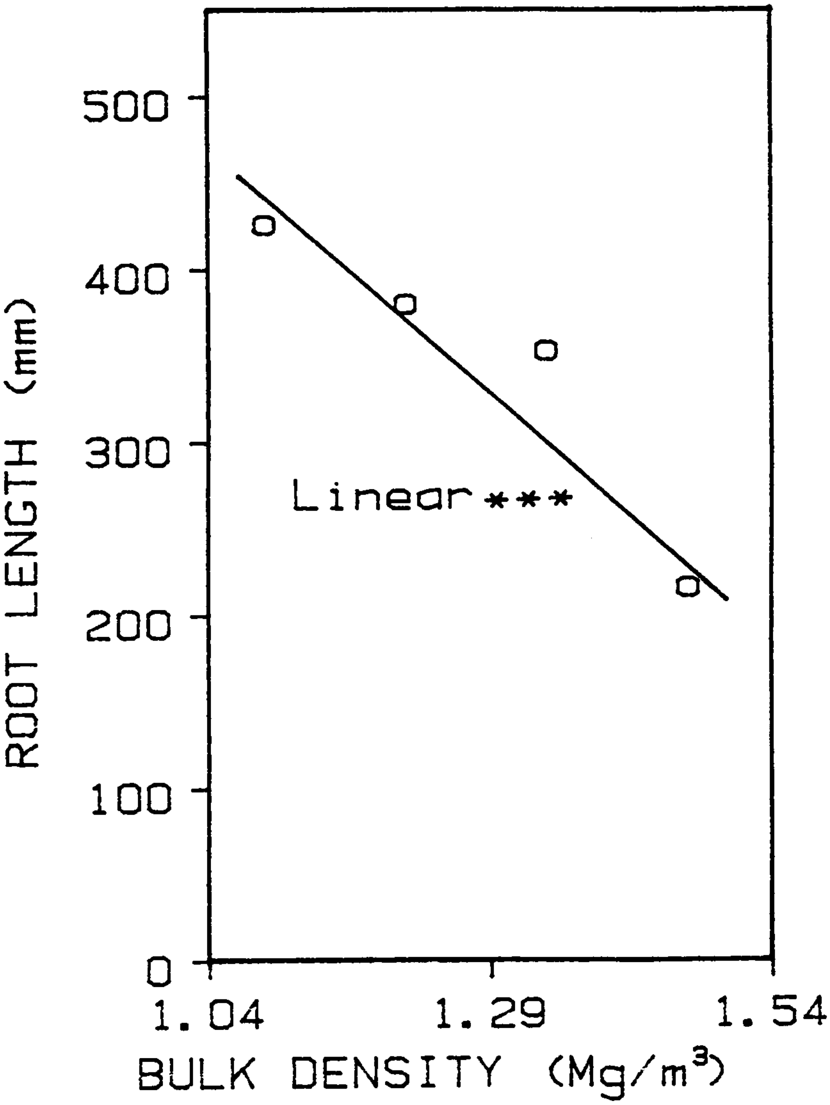


Fig. 18. Root length of 4-day-old corn seedlings as influenced by bulk density. *** denotes significance at the 0.001 probability level.

ficantly shorter roots (both main axes and laterals) with increased root diameter, although there were no significant differences in leaf area (Table 15). Again as bulk density increased, root length decreased, and root diameter increased with a linear component (Fig. 19). Often sample variability prevented detection of significant quadratic components. Increased root diameter was partially due to greater impedance of lateral roots (smaller diameter) than main axes (larger diameter). Individual root members also were thicker because root diameter was significantly increased even in 4 day old impeded roots before lateral roots had developed. Others have reported that mechanical impedance produces short, thick roots (Abdalla et al., 1969; Castillo et al., 1982; Goss and Russell, 1980; Lachno et al., 1982). Barley et al. (1965) also reported pea lateral roots being more impeded than the radicle.

Phillips and Kirkham (1962) induced mechanical impedance of corn seedlings in Colo clay by increasing the bulk density from 0.94 to 1.1 or 1.3 Mg m^{-3} which decreased root growth to approximately half and a fourth of that at 0.94 Mg m^{-3}, respectively. Camp and Lund (1968) noticed increased impedance of cotton roots grown in Norfolk fine sandy loam as the bulk density was increased from 1.4 to 1.7 Mg m^{-3}, and in Magnolia sandy loam and Greenville loam as the bulk

Table 15. Root and shoot growth of 6-day-old corn seedlings as influenced by bulk density.

Bulk density	Leaf area	Root length			Root diameter[1]
		Total	Axes	Laterals	
Mg m^{-3}	mm^2	--------	m	--------	mm
1.10	1610NS	2.95b*	0.79b*	2.16c*	0.50a*
1.22	1700	2.52b	0.64b	1.88bc	0.54a
1.35	1640	1.69b	0.61ab	1.08ab	0.59a
1.47	1280	0.75a	0.40a	0.35a	0.75b

*Means followed by the same letter are not significantly different at the 0.05 level by Duncan's multiple range test. NS designates not significant.

[1] Root diameters are averaged per root system.

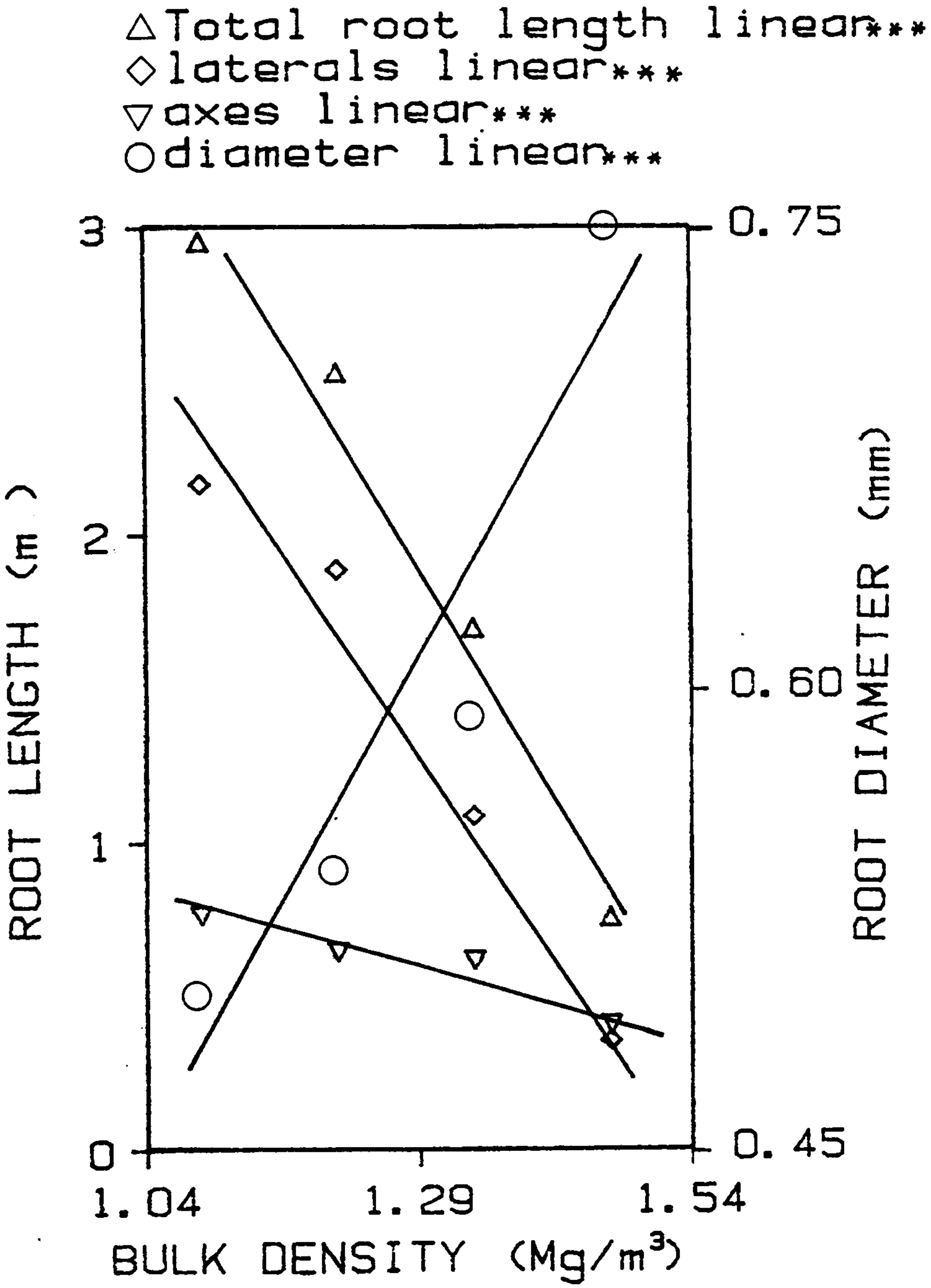


Fig. 19. Root length and diameter of 6-day-old corn seedlings as influenced by bulk density. *** denotes significance at the 0.001 probability level.

density was increased from 1.3 to 1.6 Mg m^{-3}. Wiersum (1957) observed that the critical bulk density restricting root penetration is around 1.75 for sand and 1.4 to 1.63 Mg m^{-3} for clay. Campbell et al. (1974) showed that a bulk density of 1.65 Mg m^{-3} in the E horizon of Paleudults restricted root penetration. Edwards et al. (1964) showed that for a clay pan in the B horizon, the ped density restricting corn root penetration is around 1.8 Mg m^{-3}.

Varying bulk density is an adequate method of obtaining mechanical impedance as long as soil structure is uniform and moisture and aeration are sufficient (Bar Yosef and Lambert, 1981; Gerard et al., 1982). Large aggregates of high strength can be a slight impedance to roots (Anderson and Kemper, 1964; Tabatabai and Hanway, 1968; Wiersum, 1962). As soil of high strength dries, impedance increases (Gerard et al., 1982; Merrill and Rawlins, 1979; Mirreh and Ketcheson, 1972). If aeration is limited, mechanical impedance compounds the problem of poor aeration (Bertrand and Kohnke, 1957; Grable and Siemer, 1968; Schumacher and Smucker, 1981).

Oxygen Stress

In spite of θ_V as high as 0.33 m^3 m^{-3} (soil saturated at bottom of pot), the lowest average ODR's were only in the moderately critical range (3.33 to 6.67 mg m^{-2} s^{-1} - Erickson and Van Doren, 1960), and θ_V was at the border between critical and noncritical (Table 16). Five of the pots at a θ_V of 0.33 m^3 m^{-3} and one pot at a θ_V of 0.30 m^3 m^{-3} were in the severely critical range. All the pots at θ_V's of 0.27 and 0.24 m^3 m^{-3} were within the noncritical range. The slight decrease in ODR in soil at a θ_V of 0.24 m^3 m^{-3} was probably due to decreasing moisture films on the electrode (Lemon and Erickson, 1955).

Low ODR was associated with significantly lower root length at 4 days but not at 6 days (Tables 16 and 17). As moisture content increased, root length of 4 day old corn seedlings generally decreased with a linear component. Seedlings grown at θ_V of 0.24 m^3 m^{-3} had shorter roots, perhaps due to slight impedance. Root diameter and shoot growth were not affected. Individual plants were stressed, but the stressed plants were not always from the pots with the lowest ODR readings, and ODR readings in the severely critical range did not always produce stressed plants. After 4 days root elongation rate was increased for the two wettest treatments. At 6 days the increased root length in soil at

Table 16. Root growth of four day old corn seedlings as influenced by high-soil-moisture-induced oxygen stress.

θ_V[1]	ODR[2]	Root length	Root diameter[3]
m^3m^{-3}	$mg\ m^{-2}s^{-1}$	--------- mm	---------
0.33	5.05	118ab*	0.96NS
0.30	6.82	267bc	1.02
0.27	11.05	399c	0.93
0.24	10.40	326c	1.00

*Means followed by the same letter are not significantly different at the 0.05 level by Duncan's multiple range test. NS designates not significant.

[1] θ_V is soil volumetric moisture content.

[2] ODR is oxygen diffusion rate.

[3] Root diameters are averaged per root system.

Table 17. Root and shoot growth of 6-day-old corn seedlings as influenced by high-soil-moisture-induced oxygen stress.

			Root length			
θ_v[1]	Leaf area	Plant height	Total	Axes	Laterals	Root diam.[2]
m^{3}m^{-3}	mm^2	mm	-------	m	--------	mm
0.33	1460NS	119NS	1.70a*	0.56NS	1.14a*	0.57NS
0.30	1640	133	3.61b	0.72	2.90b	0.47
0.27	1610	124	2.82ab	0.73	1.92ab	0.49
0.24	1440	98	2.80ab	0.66	1.81ab	0.53

*Means followed by the same letter are not significantly different at the 0.05 level by Duncan's multiple range test. NS designates not significant.

[1] θ_v is soil volumetric moisture content.

[2] Root diameters are averaged per plant.

a θ_v of 0.30 $m^3\ m^{-3}$ contributed to a quadratic component (Fig. 20).

Several possible explanations are given for the limited response of corn to low ODR. Corn has a higher tolerance to poor aeration than many other species (Erickson and Van Doren, 1960). Purvis and Williamson (1972) have shown that corn root weight after 4 days at 1% oxygen was not significantly reduced from the control (21% oxygen) unless carbon dioxide was also increased. Konings and Jackson (1979) observed that small amounts of ethylene (<0.02 µL L^{-1}) actually stimulated root elongation whereas larger amounts (<1.0 µL) inhibited root elongation. Perhaps small amounts of ethylene had accumulated in pots at a θ_v of 0.30 $m^3\ m^{-3}$, especially during the last days of the study. Roots from this treatment were longer than any of the controls for the other trials (see Tables 17, 15, and 19).

Wengel (1966) reported that corn emergence decreased dramatically as ODR values dropped below 2.33 mg $m^{-2}\ s^{-1}$ with 3.33 to 4.17 mg $m^{-2}\ s^{-1}$ being the critical limit. Malik et al.(1979) reported thickening of cotton roots when oxygen stressed. Grable and Siemer (1968) observed that the elongation rate of corn roots dropped off dramatically as air porosity decreased, the critical air porosity depending on aggregate size and bulk density.

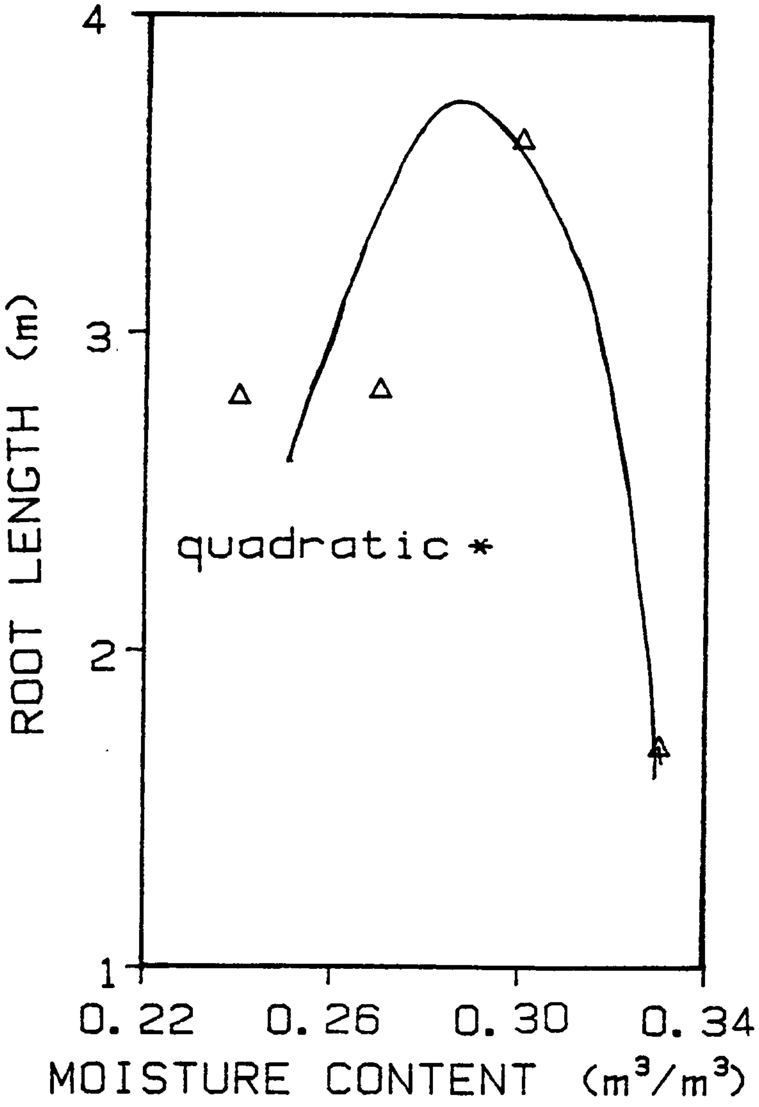


Fig. 20. Root length of 6-day-old corn seedlings as influenced by high soil moisture induced oxygen stress. * denotes significance at the 0.05 probability level.

The variability of ODR readings within each pot could help explain the variable results. Roots may have proliferated in the better aerated portions of the pots (especially along the edges). Schumacher and Smucker (1984) have shown that if anoxia is localized, dry bean roots will proliferate in the better aerated zones to partially, but not totally, compensate for the decline in root growth in poorly aerated zones. The difficulty of correlating root growth directly to ODR values suggests that after 4 days factors besides poor aeration were affecting root growth.

Low Temperature Stress

Lower temperature had the most dramatic effect on germination and root elongation (Tables 18 and 19). Plant growth as a whole was slowed. Length of roots at 4 days and axes at 6 days increased linearly as temperature increased (Figs. 21 and 22); however, total root length at 6 days increased exponentially with temperature (Fig. 23). Much of the linear effects could be due to influences on germination rather than root growth. This is due to the exponential increase in root number. At 6 days as temperature was increased, root diameter decreased and plant height increased (Table 19). The differences in root diameter were mainly

Table 18. Root growth and angle of root members of 4-day-old corn seedlings as influenced by lower temperatures.

Temper-ture	Average angle of root growth			Root length	Root diam.[2]
	Radicle	2 seminals	1 seminal		
°C	-- ° from horizontal ---			----- mm ----	
17	12 ↓[1]	7 ↓	43 ↑	14	1.40
21	50 ↓	9 ↓	49 ↑	149	0.90
25	43 ↓	33 ↓	25 ↑	327	0.93

[1] Directions are indicated by ↓ for downward and ↑ for upward.

[2] Root diameters are averaged per root system.

Table 19. Root and shoot growth of 6-day-old corn seedlings as influenced by lower temperatures.

Temper-ture	Leaf area	Plant height	Root length			Root diameter[1]
			Total	Axes	Laterals	
° C	mm^2	mm	------- m --------			mm
17	0	0	0.14	0.14	0.00	1.04
21	0	56	0.50	0.45	0.05	0.99
25	1330	89	2.46	0.71	1.75	0.52

[1] Root diameters are averaged per root system.

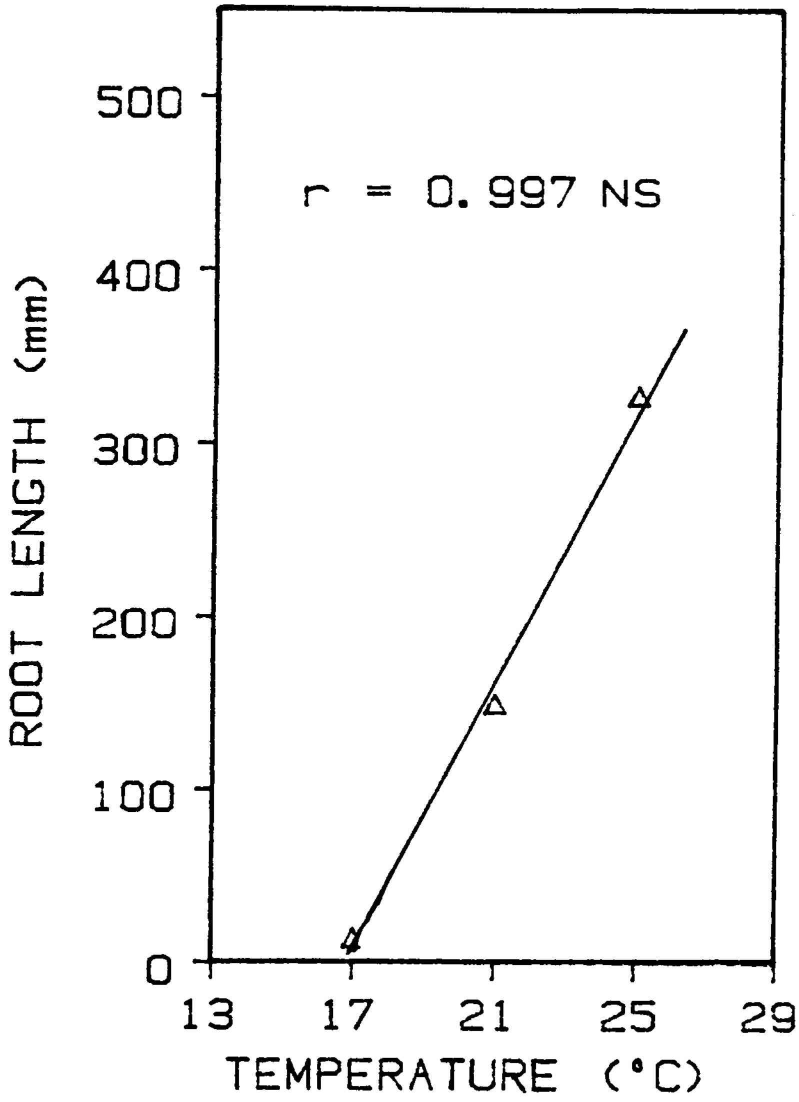


Fig. 21. Root length of 4-day-old corn seedlings as influenced by lower temperatures.

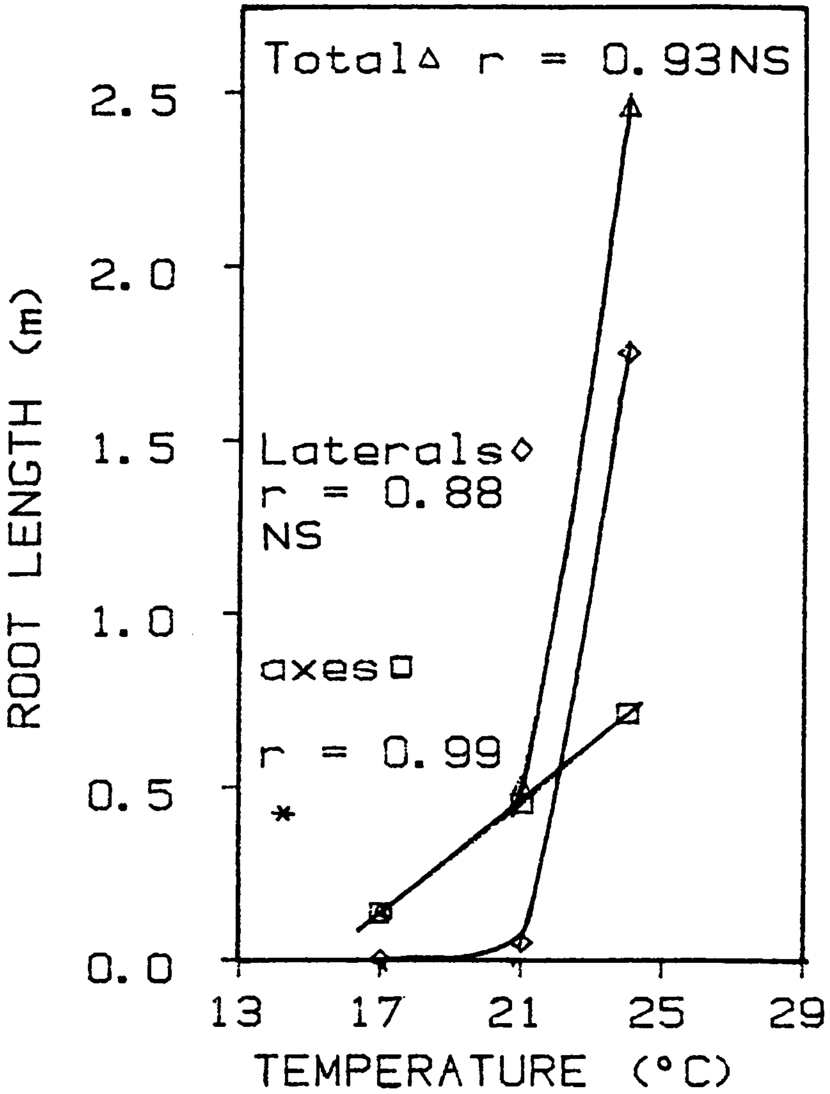


Fig. 22. Root length of 6-day-old corn seedlings as influenced by lower temperatures. The correlation coefficients are each for three means. * denotes significance at the 0.05 probability level.

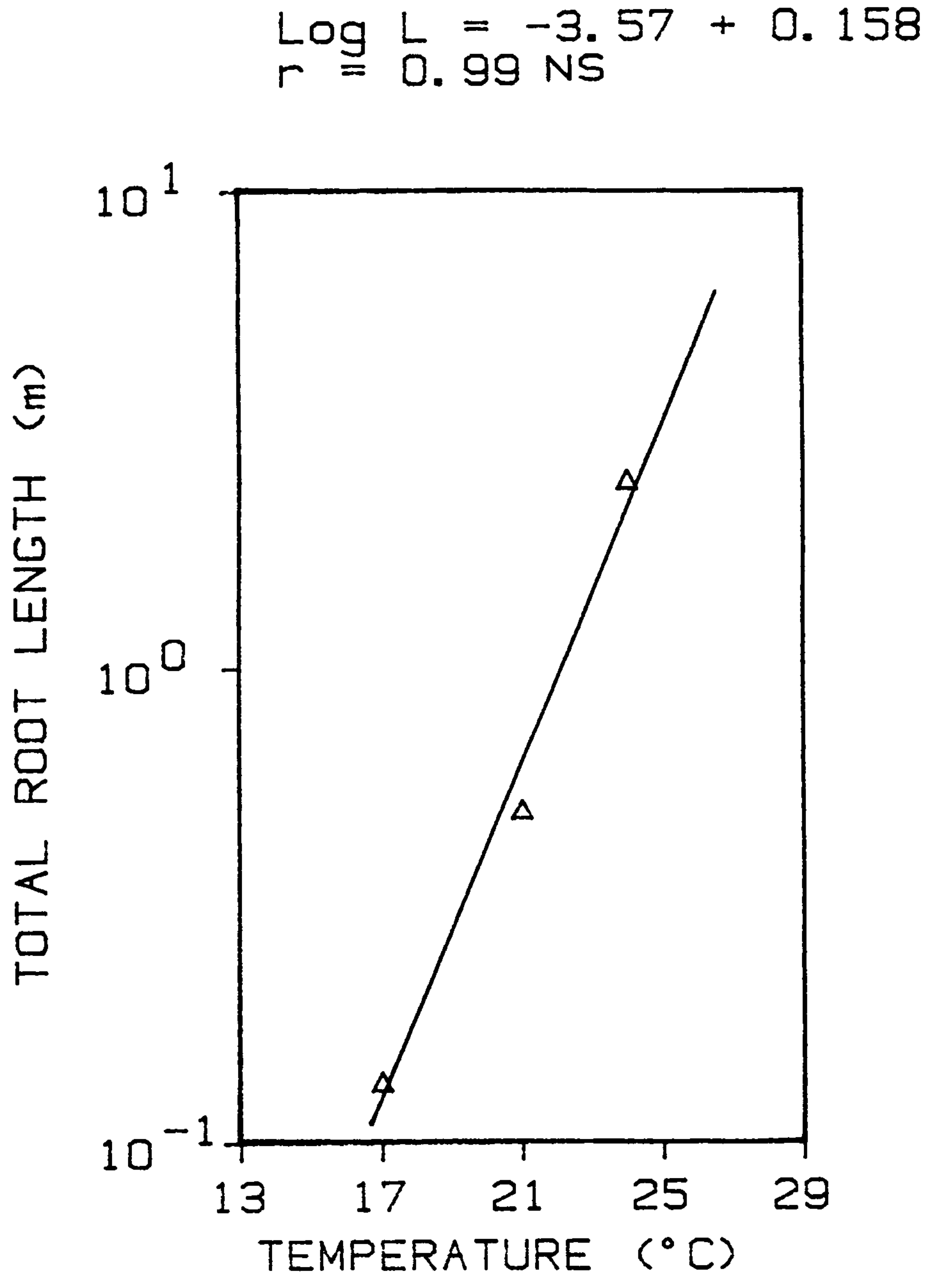


Fig. 23. Exponential increase in root length with temperature. The correlation coefficient for the log of three means was not significant.

due to different proportions of various root members. At 4 days seedlings at the lowest temperature only had the radicle, hence a large diameter. The seedlings from the higher temperatures also had seminal roots, which have slightly smaller diameters. The 6-day-old seedlings at the lower temperature also had seminal roots (Table 19). The 6-day-old seedlings at 21°C had emerging lateral roots that were just beginning to elongate. The diameters of the main axes at 17 and 21°C were somewhat larger than expected, and perhaps individual root members were somewhat thickened.

Others have indicated slow seedling development at low temperatures. As soil temperature increased from 12.5 to 17.5°C, days to emergence for corn decreased from 16 to 9 (Beauchamp and Lathwell, 1967). Although development was slowed, at a given stage of development both shoots and roots had greater mass in the low temperature treatment. This greater mass could indicate thickening of roots. Corn roots grown at 15°C were shorter and more branched than roots grown at 25°C (at the four and six leaf stage of development--Beauchamp and Lathwell, 1967). The effect of temperature on days to emergence for corn is a curvilinear response (Warrington and Kanemasu, 1983). At 18°C, emergence took 7 days, 5 days at 23°C, 4 days at 25°C, and 3 days at 30°C.

Lower temperature affected corn root orientation (Tables 18 and 20). Although corn roots are not very geotropic (Mosher and Miller, 1972) especially when planted horizontally (Hawkins, 1963); as temperature decreased, roots grew more horizontally than at higher temperatures. One seminal root on each seedling even grew up at an angle. The reorientation of corn roots by low temperature has been shown by others (Mosher and Miller, 1972). Hawkins (1963) showed a more horizontal orientation in fine textured soils. When pots were covered with plastic and incubated before planting seeds, the corn roots grew horizontally (Hawkins, 1963). The horizontal root growth was not caused by a temperature gradient or by a carbon dioxide gradient (although both low temperature and high carbon dioxide slowed root elongation).

Water Stress

The first study conducted on water stress using pregerminated seeds, showed no significant differences in root length or diameter at either 3.75 or 6.5 days (Tables 21 and 22). The lowest ϕ_m obtained was only around -400 kPa which was not low enough to reduce root growth of pregerminated seeds. Collis-George and Hector (1966) showed that presoaking seeds greatly increases germination rates even when sub-

Table 20. Angles of root memebers of 6-day-old corn seedlings as influenced by lower temperatures.

Temperture	Radicle		2 seminals		1 seminal	
	Avg.	Range	Avg.	Range	Avg.	Range
°C	° from horizontal					
17	11↓[1]	54↓-55↑	13↓	52↓-67↑	46↑	0-85↑
21	37↓	10-54↓	28↓	0-54↓	27↑	25↓-76↑
25	22↓	0-40↓	59↓	10-90↓	12↑	90↓-70↑

[1] Directions are indicated by ↓ for downward and ↑ for upward.

Table 21. Root growth of 3.75-day-old corn seedlings as influenced by slight moisture stress.

Moisture content	Matric tension	Root length	Root diameter[1]
$m^3\ m^{-3}$	kPa	------ mm	-------
0.24	<100	276NS[2]	0.89NS
0.22	<100	277	0.83
0.20	220	252	0.86
0.18	390	283	0.76

[1] Root diameters are averaged per root system.

[2] NS designates not significant at the 0.05 level.

Table 22. Root and shoot growth of 6.5-day-old corn seedlings as influenced by slight water stress. slight water stress.

Matric tension	Leaf area	Root length			Root diameter[1]
		Total	Axes	Laterals	
kPa	mm^2	--------	m	--------	mm
<100	2060b*	4.34NS	0.87NS	3.47NS	0.45NS
<100	1790ab	3.53	0.74	2.79	0.49
220	1450a	2.52	0.61	1.91	0.48
390	1350a	3.79	0.64	3.15	0.45

*Means followed by the same letter are not significantly different at the 0.05 level by Duncan's multiple range test. NS designates not significant.

[1] Root diameters are averaged per root system.

sequently placed in dry soil. In this trial the soil was packed loosely to prevent mechanical impedance. The soil in the dry treatments remained loose and did not consolidate as did the moist treatments. The only exception was a crust at the surface due to slaking when watered. In some cases the crust delayed emergence. Although root growth was not affected by water potentials to -400 kPa, shoot growth was significantly reduced (Table 22). As soil moisture decreased, shoot growth decreased linearly (Fig. 24).

Four-day-old corn root length decreased with a linear component as θ_v decreased (Table 23, Fig. 25). Although θ_v was the incremental factor used for the analysis, linearity was improved by comparing root length with ψ_m rather than θ_v (Fig. 26). For a large pot, ψ_m at the dry end would be more difficult to regulate than would θ_v. Water needed for elongation moves into the root according to a ϕ_w gradient, which helps explain why root elongation appeared to be more closely related to ψ_m than to θ_v. Again the increased diameter at -1090 kPa was partly due to the radicle being the main part of the root system (Table 23).

At day six root length was significantly reduced for roots in soil at -1090 kPa compared to moister treatments (Table 24). Root diameter was significantly increased partly due to less lateral root growth; however, not to the ex-

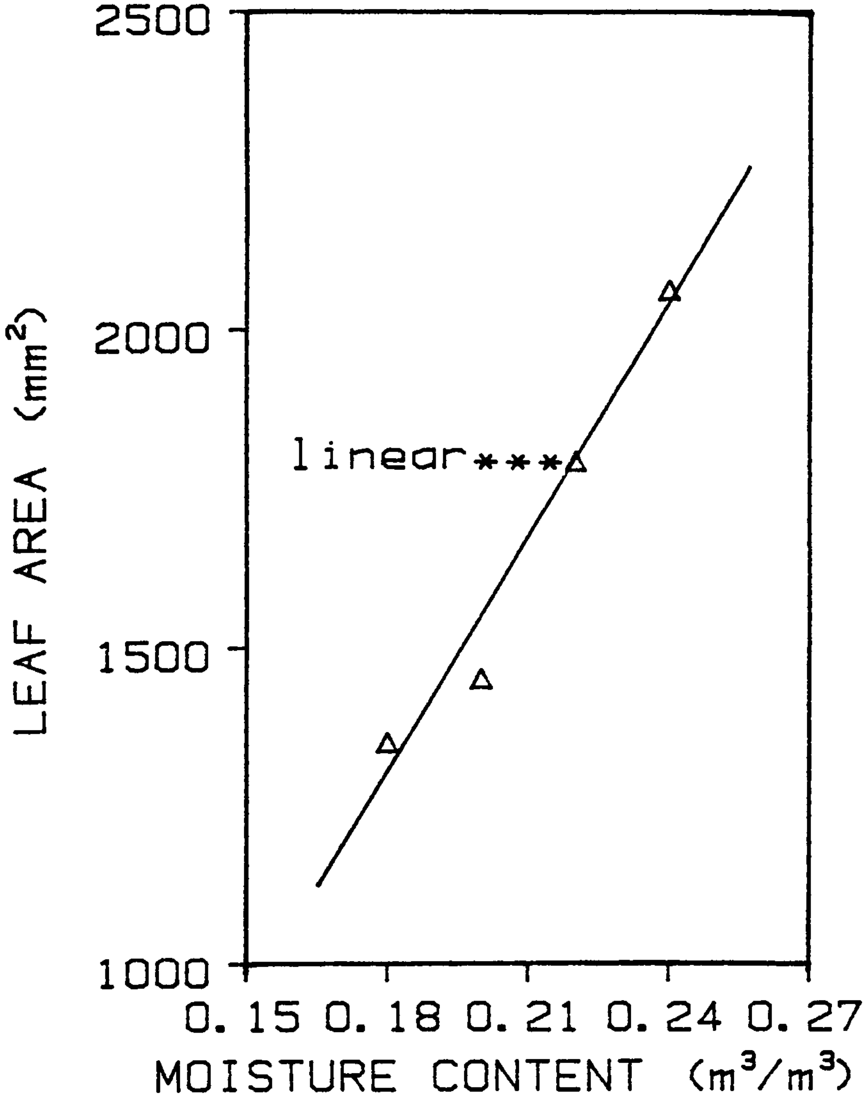


Fig. 24. Leaf area of 6.5-day-old corn seedlings as influenced by slight moisture stress. *** denotes significance at the 0.001 probability level.

Table 23. Root growth of 4-day-old corn seedlings as influenced by moisture stress.

Moisture content	Matric tension	Root length	Root diameter[1]
$m^3\ m^{-3}$	kPa	------- mm ------	
0.24	200	327NS	0.93NS[2]
0.21	240	316	0.94
0.18	330	295	0.91
0.15	1090	157	1.21

[1] Root diameters are averaged per root system.

[2] NS designates not significant at the 0.05 level.

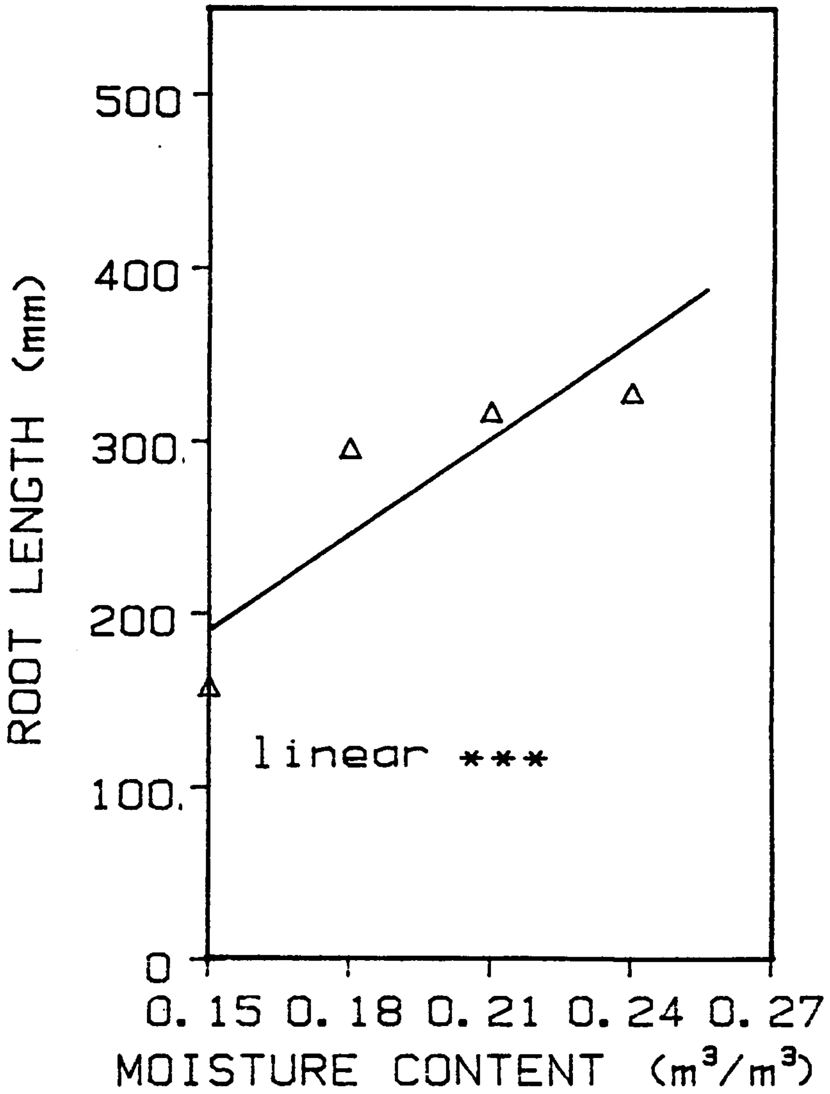


Fig. 25. Root length of 4-day-old corn seedlings as influenced by moisture stress. *** denotes significance at the 0.001 probability level.

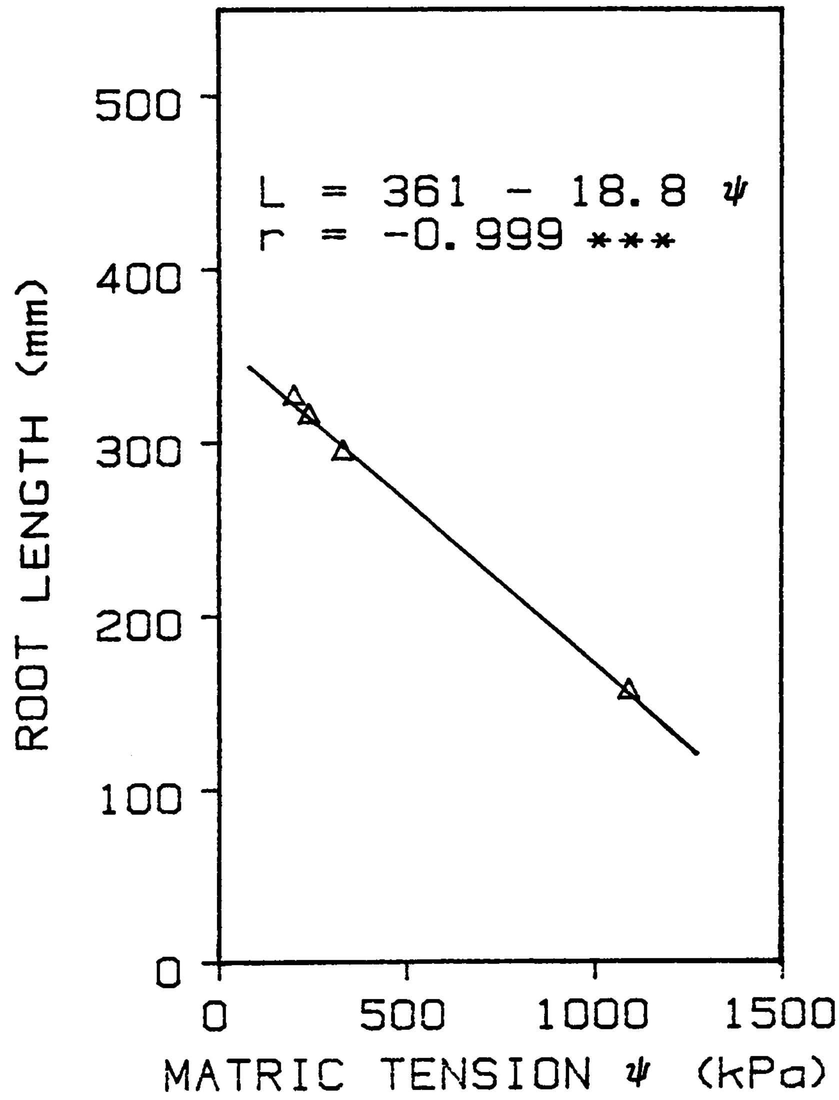


Fig. 26. Root length of 4-day-old corn seedlings as influenced by soil water tension. *** denotes significance at the 0.001 probability level.

Table 24. Root and shoot growth of 6-day-old corn seedlings as influenced by moisture stress.

Matric tension	Leaf area	Plant ht.	Root length			Root diameter[1]
			Total	Axes	Laterals	
kPa	mm^2	mm	--------	m	--------	mm
200	1360c*	95b*	2.46b*	0.71b*	1.75b*	0.52a*
240	1180c	96b	3.06b	0.70b	2.36b	0.51a
330	690b	69b	2.52b	0.53b	1.99b	0.48a
1090	90a	32a	0.54a	0.29a	0.25a	0.67b

*Means followed by the same letter are not significantly different at the 0.05 level by Duncan's multiple range test.

[1] Root diameters are averaged per root system.

tent that low temperature slowed lateral root development (Tables 19 and 24). Plant height and leaf area were also reduced, but again not as much as the reduction caused by low temperature. As θ_v was decreased, plant height decreased with a linear component (Fig. 27). Total root length, lateral root length, and root diameter also had a quadratic component with θ_v (Fig. 28) which may just be variability since this observation was not supported by the previous water stress trial. Perhaps the plants in soil at a θ_v of 0.24 $m^3\ m^{-3}$ were slightly impeded due to clumping of the aggregates. Prebble (1970) has shown that ψ_m lower than 10 kPa greatly restricts root penetration into smeared soil. This is much wetter than the lowest ψ_m in this study.

Notice the proportion of the root system that are laterals (Table 24--water stress, 1090 kPa, 6 days) compared to the proportion that are laterals at lower temperatures (6 days, 21°C). The total root length is similar, but the water stressed roots had shorter main axes and more lateral root development compared with plants stressed by lower temperature. Water stress did not delay initiation of new root members but reduced elongation, whereas lower temperature retarded initiation and elongation of roots. The effects of these stresses on the whole plant are difficult to separate from the effects on the whole root system. Some of

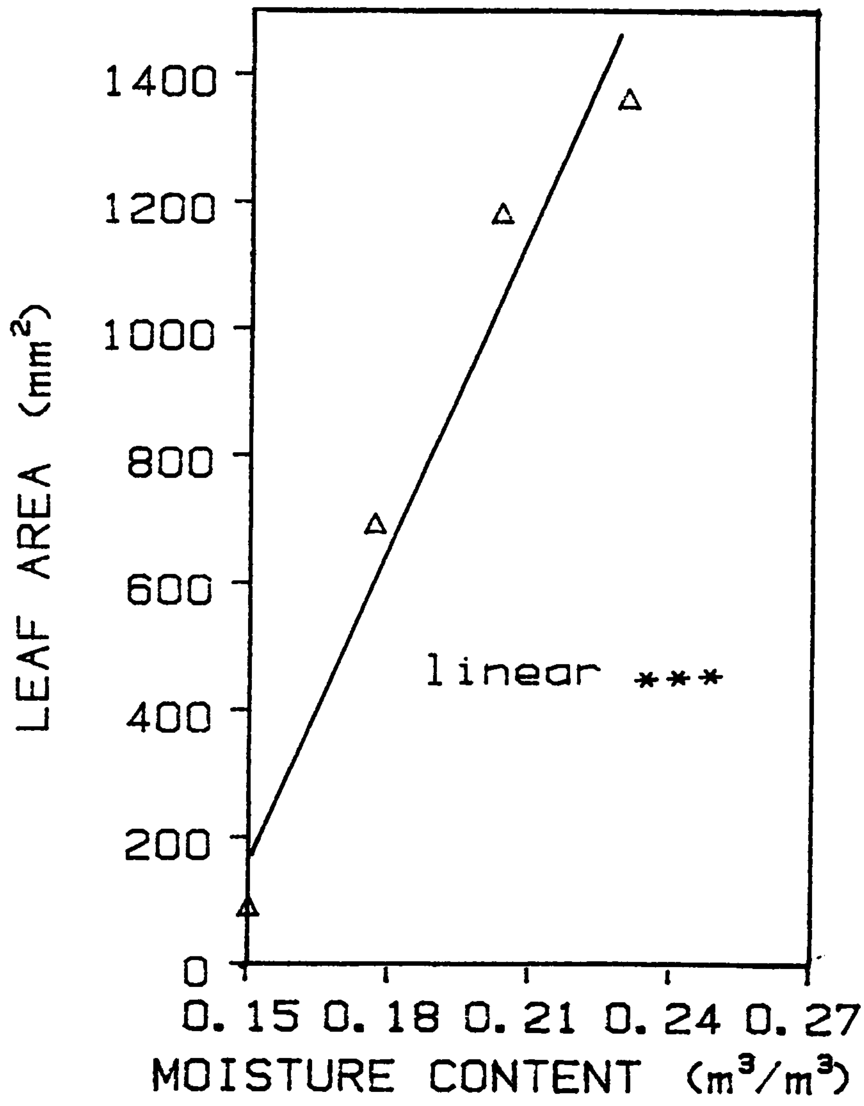


Fig. 27. Leaf area of 6-day-old corn seedlings as influenced by moisture stress. *** denotes significance at the 0.001 probability level.

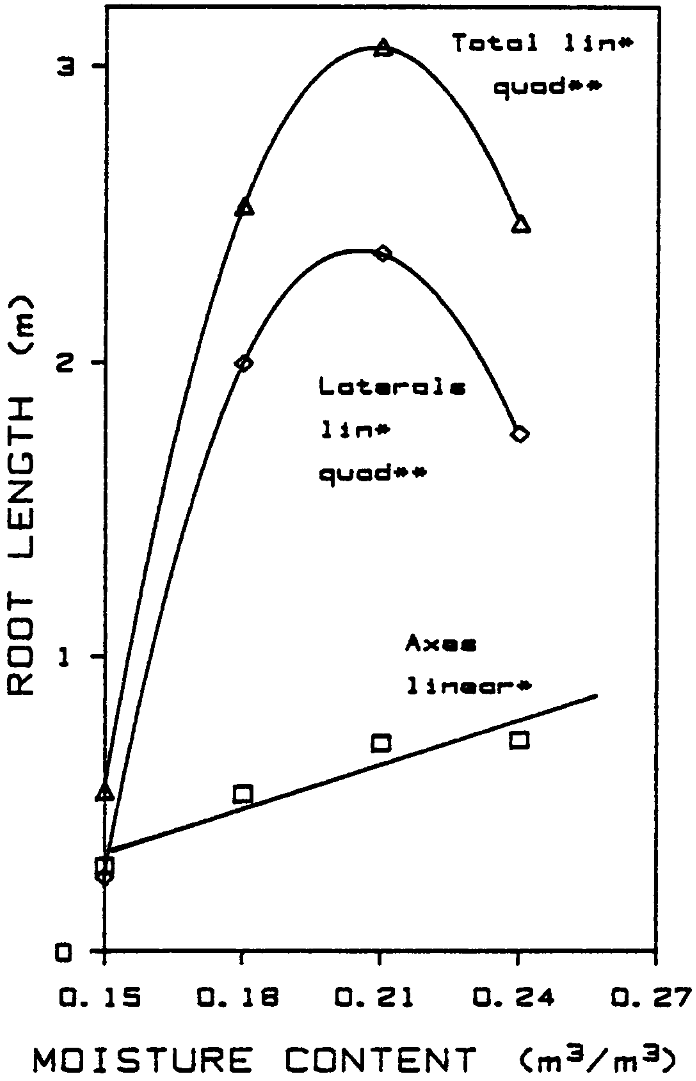


Fig. 28. Root length of 6-day-old corn seedlings as influenced by moisture stress. * denotes significance at the 0.05 probability level. ** denotes significance at the 0.01 probability level.

the reduction in root length may have been due to delayed germination since in this trial seeds were not pregerminated.

Bar-Yosef and Lambert (1981) observed that corn elongated fastest at -7 kPa (in Norfolk sandy loam packed to a bulk density of 1.45 Mg m^{-3}). Elongation decreased at ϕ_m lower than -620 kPa. Mechanical impedance may have been a factor. Ciamporova and Luxova (1976) showed that for the radicle of corn seedlings, elongation was slowed from 40 mm a day at -12.2 kPa osmotic potential (ϕ_s) to 2 mm a day at -1266 kPa. If grown for 4 days at -1266 kPa, there was no recovery for corn root elongation even if subsequently brought to -12.2 kPa. Portas and Taylor (1976) observed that the visible corn root length (in a rhizotron) decreased from 3211 mm at a ϕ_m of -600 kPa to 19 mm at -90 000 kPa. These were individual roots, not the whole root system. Elongation decreased most rapidly below -1090 kPa. Schneider and Gupia (1985) showed that lower temperature (from a range of 10 to 25°C) had a more dramatic effect on days to emergence than did low ϕ_m (from a range of -10 to -500 kPa).

In each of these experiments except for the first water stress trial, seeds were not pregerminated. The influence of these factors on germination was not separated from their effects on root and shoot growth.

Modeling Corn Root Growth

Two semi-empirical models of corn root growth were developed and calibrated from the data. For the first model, the length of the pregerminated radicle was measured to be approximately 2 mm. Using this as initial root length and assuming exponential growth during the study period, regression equations were developed for root length (L in mm) at each bulk density (ρ_b in Mg m^{-3}), as a function of time (in days):

$$\ln L = 0.799 + 1.234\ t \qquad (\rho_b = 1.10)$$

$$\ln L = 0.797 + 1.207\ t \qquad (\rho_b = 1.22)$$

$$\ln L = 0.838 + 1.147\ t \qquad (\rho_b = 1.35)$$

$$\ln L = 0.849 + 1.014\ t \qquad (\rho_b = 1.47)$$

A regression equation was developed describing the exponential growth rate LGR = d ln L/dt as a function of bulk density.

$$LGR = 1.896 - 0.580\ \rho_b \qquad r = -0.948NS$$

This relation assumes all other conditions to be optimal. Likewise for temperature stress:

$$\ln L = 0.498 + 0.691\ t \qquad (T = 17.0°C)$$

$$\ln L = 0.828 + 0.943\ t \qquad (T = 21.6°C)$$

$$\ln L = 0.769 + 1.198\ t \qquad (T = 25.9°\mathrm{C})$$

The range in intercepts indicate differences of 1.65 to 2.21 mm for actual root length. The exponential growth rate as a function of temperature is as follows:

$$LGR = -0.433 - 0.649\ T \qquad r = 0.996\mathrm{NS}$$

For water stress (in terms of ψ):

$$\ln L = 0.769 + 1.198\ t \qquad (\psi = 200\ \mathrm{kPa})$$

$$\ln L = 0.730 + 1.228\ t \qquad (\psi = 240\ \mathrm{kPa})$$

$$\ln L = 0.743 + 1.198\ t \qquad (\psi = 330\ \mathrm{kPa})$$

$$\ln L = 0.828 + 0.956\ t \qquad (\psi = 1090\ \mathrm{kPa})$$

and the exponential growth rate as a function of ψ_m is:

$$LGR = 1.284 - 2.983\times10^{-4}\ \psi \qquad r = -0.989\mathrm{NS}$$

For oxygen stress (in terms of ODR or θ):

$$\ln L = 0.750 + 1.217\ t \qquad (\theta = 0.24,\ \mathrm{ODR} = 10.40)$$

$$\ln L = 0.792 + 1.225\ t \qquad (\theta = 0.27,\ \mathrm{ODR} = 11.40)$$

$$\ln L = 0.671 + 1.246\ t \qquad (\theta = 0.30,\ \mathrm{ODR} = 6.85)$$

$$\ln L = 0.603 + 1.109\ t \qquad (\theta = 0.33,\ \mathrm{ODR} = 5.05)$$

The exponential growth rate does not have a high linear correlation with ODR or moisture content:

$$LGR = 1.087 + 0.0134\ ODR \qquad r = -0.628NS$$

$$LGR = 1.487 - 1.01\ \theta \qquad r = -0.637NS$$

These equations only consider isolated affects, not interactions. They only describe seedling root elongation when growth is still exponential. Perhaps oxygen stress should be eliminated as a factor due to the stimulation of root growth at a moisture content of 0.30 $m^3\ m^{-3}$. An initial root length must be known to use these equations.

When comparing predicted to actual corn seedling root length (Fig. 29), the equations for bulk density and water stress tend to underpredict root length at 4 days. At this stage lateral roots have just been initiated or are not yet initiated. Initiation of new roots is necessary for exponential root growth to continue. For the bulk density of 1.10 Mg m^{-3} the predicted values are too high causing the slope of the regression equation to be much less than one. For oxygen stress at six days, the actual stimulation of root growth at a θ_v of 0.30 $m^3\ m^{-3}$ causes this point to be separated from the other values. The root length of the control varies with experiment, yet the predicted value should be the same.

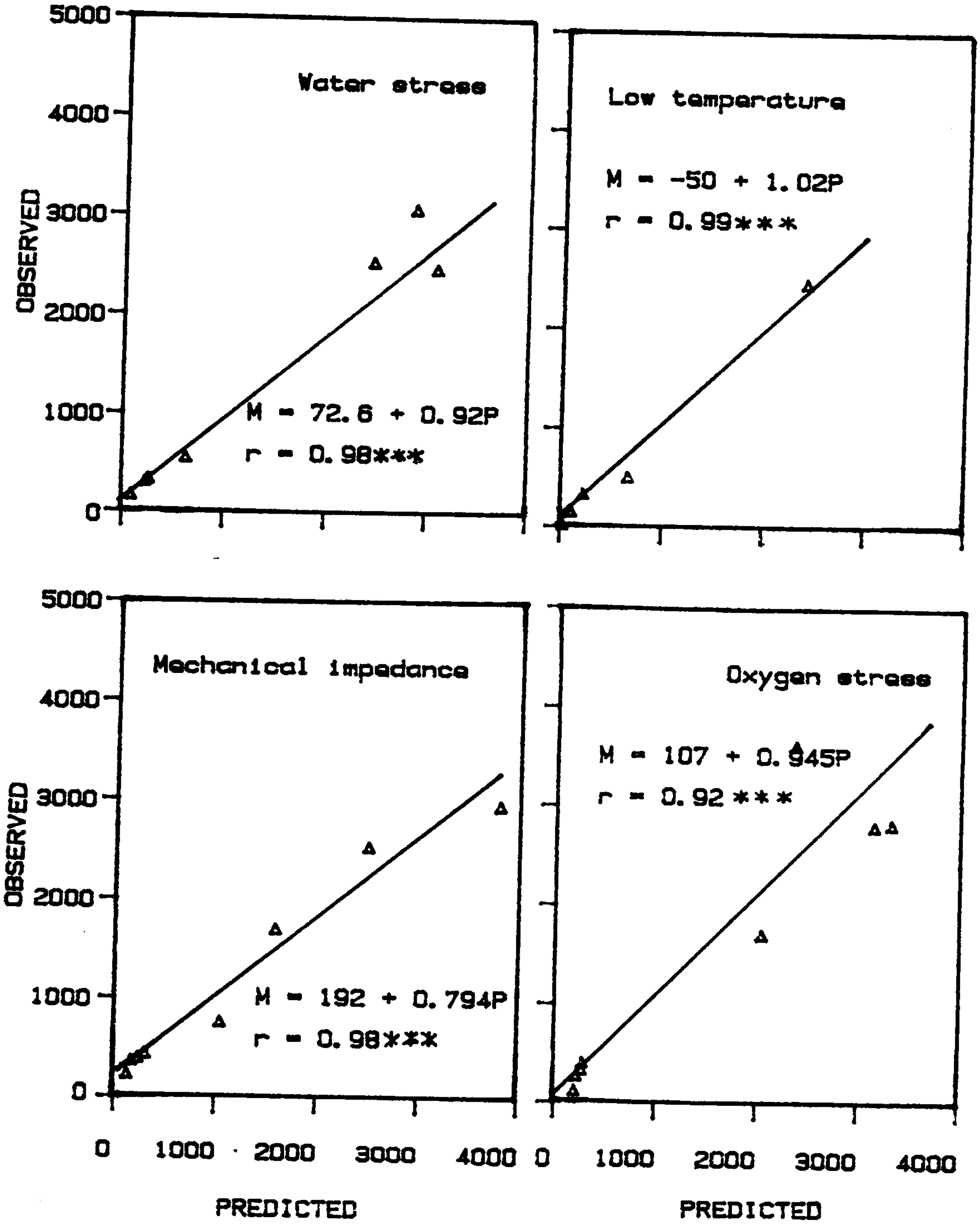


Fig. 29. Correlations of observed corn root lengths and those predicted by model 1. *** denotes significance at the 0.001 probability level.

In light of these problems, another root growth model was developed. First an ideal root growth pattern was developed based on the linear growth of individual root members as follows:

1. At the end of the day of its initiation, a new root axis is 5 mm in length. Thereafter each axis elongates at a constant maximum rate of 45 mm day^{-1}. Stresses will reduce the elongation rate.
2. At the end of its day of initiation, a lateral root is 1 mm in length. Thereafter each lateral root elongates at a maximum rate of 8 mm day^{-1}. Stresses will reduce the elongation rate.
3. The radicle is initiated on day one, two seminal roots on day two, and one seminal root on day three.
4. Fourty five lateral roots per day are initiated from each axis, starting 3 days after initiation of that axis.
5. Four nodal roots are initiated on day seven.

These elongation rates are not measured values but have been made to fit data for length of axes and laterals at 4 and 6 days. This pattern of root growth is only valid for 6 to 8 days. After that, the elongation rate of seminal roots slows and eventually ceases, and second order laterals are initiated. This pattern of root growth is summarized in Table 25. Model 2 helps to explain the over prediction of root length at 4 days when exponential growth was assumed.

Using measured values of axis and lateral root length, the average growth rates between 0 and 4 days, and between 4 and 6 days were calculated for mechanical impedance, moisture stress, and oxygen stress (Table 26). The average overall growth rates were proportioned according to the length of time of each component of growth (0-4 or 4-6 days). Lateral root elogation rates are the average for 4 to 6 days, assuming no lateral roots are initiated before 4 days.

Problems with prediction for oxygen stress are apparent. In wet soil up to 4 days, oxygen stress is the main factor affecting root growth; but after 4 days, root growth is stimulated in wet soil. For this reason only the root elongation rates for 0 to 4 days were used for oxygen stress. Root growth beyond 4 days could not be predicted.

Regression equations were developed to describe the reduction in root growth rate caused by various stresses. For oxygen stress the elongation rate (E) of a root axis (to 4 days) is given by:

$$E = -7.81 + 4.36\ \mathrm{ODR} \qquad r = 0.95\mathrm{NS} \quad \text{(axes)}$$

For water stress the elongation rates for axes and laterals are:

$$E = 42.1 - 0.0244\ \psi \qquad r = -0.97\mathrm{NS} \quad \text{(axes)}$$

Table 25. Predicted length of corn root members each day.

Day	Radicle	2 seminal	1 seminal	Laterals	Total
0	0	0	0	0	0
1	5	0	0	0	5
2	50	10	0	0	60
3	95	100	5	0	200
4	130	190	50	45	415
5	175	280	95	540	1090
6	220	370	130	2160	2880

Table 26. Average growth rate of corn axes and laterals.

Level	Growth Rate (mm day^{-1})[1] Axes 0-4 d	Axes 4-6 d	Axes avg.	Laterals
Mg m^{-3}		Bulk density		
1.1	45	45	45	7.8
1.22	40	33	38	6.7
1.35	37	32	35	3.5
1.45	22	23	22	0.6
kPa		Water potential		
200	34	48	39	6.2
240	33	48	38	8.6
330	31	29	30	3.2
1 090	15	17	16	0.2
mg m^{-2} s^{-1}		ODR		
5.05	11	55	--	3.8
6.82	27	57	--	10.8
11.05	42	41	--	6.9
10.40	34	42	--	6.4
° C		Temperature		
17.0	9	14	11	---
21.6	32	35	33	0.0
25.0	--	--	45	8.0

---

[1] These values assume the root number and initiation pattern described in the text.

$E = 7.94 - 0.0076\ \psi$ $r = -0.84NS$ (laterals)

For mechanical impedance the equations are:

$E = 109 - 57.9\ \rho_b$ $r = -0.96NS$ (axes)

$E = 32.2 - 21.6\ \rho_b$ $r = -0.99{**}$ (laterals)

The same system cannot be used for lower temperature stress because initiation of roots is also delayed. For 17° C initiation of axes is assumed to be delayed 2 days, and laterals 4 days; and at 21.6° C axes are delayed 1 day and laterals 2 days. From this the assumed delay in root initation (I) as a fuction of temperature can be calculated.

$I = 6.26 - 0.248\ T$ (axes)

$I = 12.52 - 0.596\ T$ (laterals)

An equation describing elongation rate of axes as a function of temperature is:

$E = -61.1 + 4.28\ T$ $r = 0.997NS$

An equation cannot be developed for lateral root elongation because there are not enough points. The equation for laterals is only valid between 21.6 and 25.0°C.

Comparison of observed and predicted root length of axes and laterals at 4 and 6 days (Fig. 30) shows fairly good agreement with small intercepts and slopes close to one. The measured high root length at ψ = 240 kPa increases the slope a little. These low values of ψ_m are in the range where measurement is not accurate with a thermocouple psychrometer. Root lengths are generally underpredicted for mechanical impedance.

Although this second model is more physically based, the ultimate physical cause of root growth has not been explained. Is the action of these soil factors on root growth direct, indirect, or both? The ultimate physical basis of root growth lies at the cellular and subcellular levels. The interaction of the environment and plant hormones and their effects on root growth are not fully understood at the present time.

The time steps in this model are large, and the growth rates are conjectural. The elongation rates of roots in an ideal environment are not the maximum possible elongation rates. The growth rates can actually be increased by plant hormones. Model 2 assumes all factors to act independently, although in a field, increased ψ_m increases impedance. Prebble (1970) has shown root penetration of smeared soil was greatly reduced at ψ_m above 10 kPa, which is much wetter

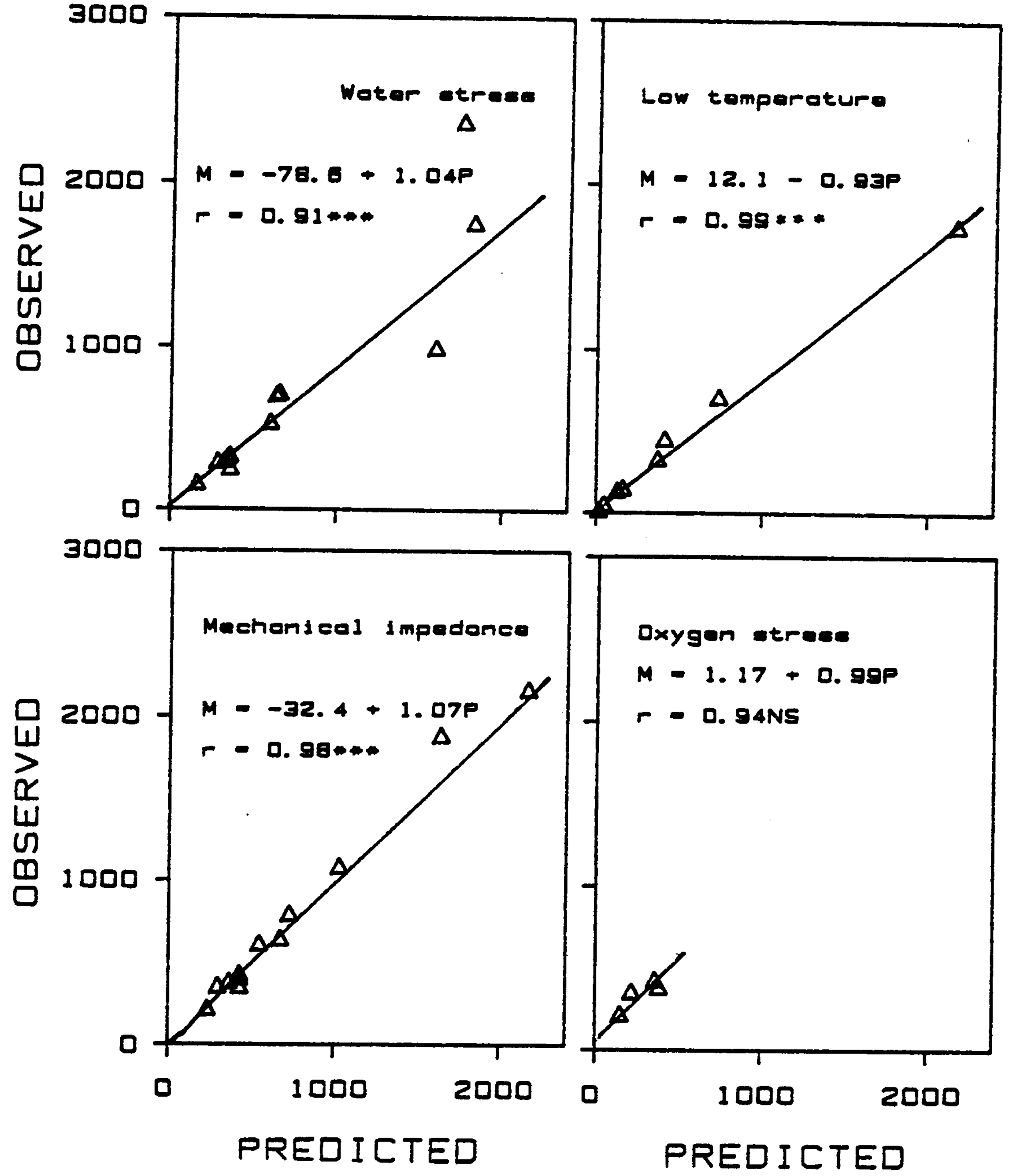


Fig. 30. Correlation of observed corn root lengths and those predicted by model 2. *** denotes significance at the 0.001 probability level.

than the controls in these experiments. In these studies individual aggregates were not penetrated much by roots because even moist soil is dry enough to be an impedance to roots. Use of small, unclumped aggregates permitted water stress to be studied independently of mechanical impedance. Model 2 would only apply to similar conditions, not to consolidated field soil.

Model 2 assumes homogeneous soil. If soil conditions are not uniform in the root zone, compensatory root growth will result. Although the decreased root growth in an unfavorable environment can be predicted, the increased root growth in a more favorable environment cannot be predicted. Compensatory growth may be a hormonal response (Crosett et al., 1975).

In conclusion, mechanical impedance, oxygen stress, lower temperature, and water stress all reduced corn root elongation to some extent, but lower temperature had the most dramatic effect. Mechanical impedance, lower temperature, and water stress led to thicker roots; but only mechanical impedance and lower temperature increased the diameter of individual root members. Influences of these stresses on root diameter would have been more detectable if root systems at the same stage of development had been compared rather than comparing plants of a specific age. Water stress and low temperature reduced shoot growth while mechanical impedance and oxygen stress did not.

At first glance similar responses suggest similar mechanisms for reduced root growth; however, enough differences occur in response to these physical stresses to suggest different or multiple mechanisms. In each trial we could not eliminate the possibility of hormones as part of the ultimate mechanism controlling root length and diameter. Empirical regression equations were developed to describe the exponential root elongation rate as a linear function of bulk density, matric potential, or temperature. Oxygen stress was not linearly related to the exponential growth rate. A somewhat more physically based model was developed to describe the reduction in the elongation rate of each root member in response to these stresses. Root elongation as a function of oxygen stress could not be predicted beyond 4 days due to possible hormonal interaction. The model could be used to predict root growth to 6 or 8 days for the other stresses assuming each stress is isolated. Low temperature delays initiation of roots as well as slowing elongation. Application of the model to field situations is cautioned because of interactions between ϕ_m and impedance. Much study remains to be done before the ultimate underlying factors affecting root growth can be fully understood.

Chapter VI

POLYETHYLENE GLYCOL INDUCED WATER STRESS

Polyethylene glycol (PEG) is often used as an osmoticum for studying plant water relations, and many suggest PEG adequately simulates dry soil (Kaufmann and Eckard, 1971; Lawlor, 1970; Parmar and Moore, 1968; Thrill, 1979). Problems can develop which might affect results. If a low molecular weight PEG (400) is used, the PEG may be taken up by the plant (Lawlor, 1970; Janes,1974). Large molecular weight PEG's (>4000) can be taken up if roots are damaged (Lawlor, 1970). Resnik (1970) detected PEG 6000 mainly in roots but also in shoots. The PEG in the roots was mainly absorbed in the apoplast. Large molecules of PEG can block pathways of water movement reducing water absorption. Using PEG 6000 as an osmoticum led to decreased xylem pressure potential of pepper plants (*Capsicum frutescens* L.) as the solution osmotic potential (ϕ_s) decreased, yet the ϕ_s of the xylem sap remained constant (Kaufmann and Eckard, 1971). In contrast, PEG 400 decreased the ϕ_s of the xylem sap as the solution ϕ_s increased due to increased cation uptake. Guttation still occurred even when the solution ϕ_s was -480 kPa. Only at low solution ϕ_s did the xylem pressure potential become negative.

The viscosity of PEG presents problems. Nutrient uptake and translocation may be reduced. When the PEG solution is not agitated, a nutrient concentration gradient may develop around roots, slowing diffusion (Kaul, 1966). Translocation of P may be inhibited (Resnik, 1970). High molecular weight PEG solutions froth when aerated (Lawlor, 1970). Oxygen is sparingly soluble in PEG solutions, and the viscosity of PEG slows oxygen transport to the root (Mexal, 1975). The ϕ_s of PEG does not follow Van't Hoff relationships (McClendon, 1981; Michel and Kaufmann, 1973). The ϕ_s varies with temperature due to changes in the structure of the macromolecule. As the temperature increases, the ϕ_s of PEG solutions increases.

The ϕ_s can also change with time (Thrill, 1979), although the change is not usually critical. Water uptake and evaporation can lower ϕ_s (Berkat and Buske, 1982).

Impurities in PEG may be a problem. Lagerwerff et al. (1961) mention the possibility of toxic heavy metals and suggest passing through an ion exchange column. Reid et al. (1978) mention P contamination.

PEG-induced water-stress leads to shorter (Ciamporova and Luxova, 1976; Lawlor, 1973; Murin, 1979), thicker roots (Ciamporova and Luxova, 1976). Is this the effect of water-stress or of PEG? Can PEG simulate dry soil for the roots growing directly in the medium? The purpose of this study was to examine the effects of PEG on corn roots and to compare the results of this study with the results of dry soil-induced water stress.

MATERIALS AND METHODS

For the first experiment Corn plants 'SS-727' were grown in nutrient solution, and water stress was induced by using PEG as an osmoticum. Plastic 1 L cartons were used for containers, and a 20 mm thick styrofoam sheet was cut to fit in the top of the containers. Air was passed through rubber tubing and bubbled into the nutrient solution. Air was supplied to each pot by a 26 gauge syringe needle, connected to plastic tubing and joined to the main rubber tubing by a 20 gauge syringe needle.

Corn seeds were germinated in paper towels for 5 days. Foam strips (5 x 20 x 80 mm) were wrapped around each seedling just above the first node. Each seedling was then pushed through a 20 mm diameter hole in the center of the styrofoam and placed in nutrient solution having the following concentrations (µM): Ca-3750 NO_3-N-11,200; NH_4-N-1180; K-4420; Cl-1800; Mg-1500; S-1500; P-64.5; Fe-204; Mn-9.15; B-36.8; Zn-0.766; Cu-0.301; Mo-0.111; EDTA-204. The solutions were changed twice a week.

Day temperature was about 28° C and night temperature about 17° C. Day length was 16 h. Relative humidity was about 62% during the day. Problems with the temperature control developed, resulting in abnormally cool conditions (and resulting in the growth chamber shutting off). This slowed the growth of the corn plants.

Treatments were applied when the plants were 23 days old. Four plants were taken to determine dry weights of roots and shoots. The four levels of water stress had the following concentrations of PEG 6000 initially: 0, 150, 200, and 250 g per kg H_2O. The initial ϕ_s (including nutrients) as measured by a thermocouple psychrometer chamber (of paper discs dipped in solution) were -50, -330, -490, and -800 kPa. The ϕ_s decreased as water was transpired. The lowest ϕ_s for the three water stress levels were -490, -700, and -850 kPa. The treatments were randomly arranged and rotated daily. Twice a day the containers were refilled to the original volume, not counting volume of roots, to try to keep ϕ_s more constant. The containers were not completely filled since aerated PEG froths over the top. This resulted in some roots not being submerged in solution and was accentuated with increasing transpiration.

Transpiration was measured from the volume of water needed to refill the containers to a mark. (This does not account for the increase in the volume of roots.) There were also seven blanks (containers without plants) to measure evaporation. Leaf area of each plant was measured once on the day after applying the treatments. Leaf water potentials were measured in-situ with a thermocouple psychrometer.

The plants were water-stressed for 4 days before terminating the experiment. Then water potentials of leaf discs were measured with a thermocouple psychrometer chamber. Root and shoot dry weight were again measured. Root lengths were measured by the modified intersection method (Tennant, 1975).

For the second experiment Corn 'Becks 60X' was grown in paper towels for 4 days at about 28° C at the following PEG induced ϕ_s: 0, -100, -200, -240, -330, -390, and -1090 kPa corresponding to ϕ_m in the soil (Chapter V). To achieve these levels PEG was added at the rates of 0, 78, 119, 131, 159, and 309 g per kg H_2O. Root length was measured by the modified intersection method (Tennant, 1975), and root diameter was calculated from root weight assuming the fresh root density to be 1 Mg m^{-3}. The containers were loosely covered with saran wrap, which was removed for 1 min a day to ensure adequate gas exchange.

RESULTS AND DISCUSSION

Shoot weight, leaf area, and transpiration rate decreased as osmotic pressure was increased (Table 27, Figs. 31 and 32). Root dry weight increased with slight water stress even when length decreased (Figs. 31 and 33) due to thickening of roots. Root to shoot ratio increased as osmotic pressure increased (Fig. 33). Measured water potential of leaf discs were too high perhaps due to inadequate equilibration time and low battery charge.

Ciamporova and Luxova (1976) also noticed thickening of roots grown in PEG whereas Bar Yosef and Lambert (1979) observed that lower ϕ_s resulted in a greater number of thinner roots. The increase in root to shoot ratio was also shown by Malik et al., (1979). Gales (1979) observed a reduced root to shoot ratio initially, then an increased ratio as drought continued, whether induced by dry soil or by solution ϕ_s.

The ϕ_s used to moisten the paper towels (measured in a thermocouple psychrometer chamber) were as follows: -240, -290, -280, -320, -420, and -1090 kPa. The values at the wet end were higher than expected indicating the inaccuracy of thermocouple psychrometers at low ϕ_w. The amount of decrease in root length with increasing ϕ_s was more rapid than the rate of decrease for soil at the same ϕ_w (Tables

Table 27. Root and shoot growth of soution grown corn seedlings as influenced by polyethylene glycol (PEG) induced water stress.

Osmotic potent.	Leaf area	Dry weight[1]			Root length	Transp. rate
		Shoots	Roots	Total		
kPa	mm^2	-------- g --------			m	$mg\ m^{-2}s^{-1}$
-50	57 000c*	7.12bc*	3.71a*	10.83	232c*	61.0bc*
-410	51 700bc	7.25bc	4.38ab	11.63	172b	38.5ab
-600	45 600ab	5.93b	4.70bc	10.63	165b	31.9a
-820	41 400a	3.55a	3.56a	7.01	116a	13.9a

*Means followed by the same letter are not significantly different at the 0.05 level by Duncan's multiple range test.

[1] Root and shoot parameters are of corn grown in nutrient solution for 23 days before adding PEG for 4 days. At 23 days shoot weight was 2.87 g and root weight was 1.83 g.

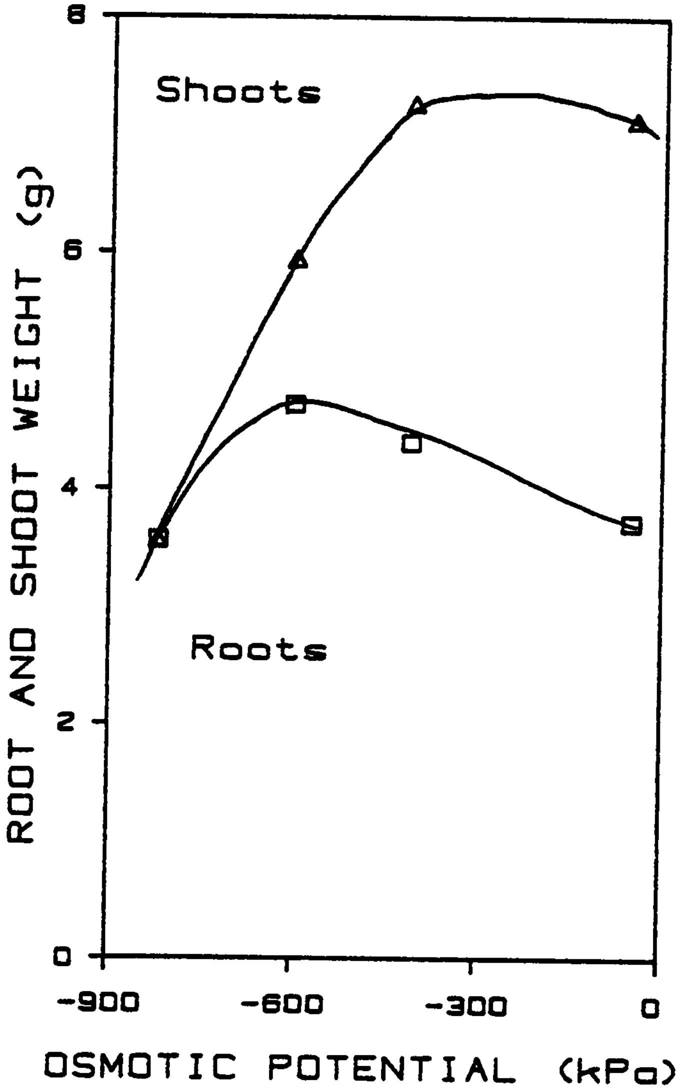


Fig. 31. Corn root and shoot weights as influenced by polyehtylene glycol (PEG) in solution. The corn was grown for 23 days in solution before being placed in PEG for 4 days.

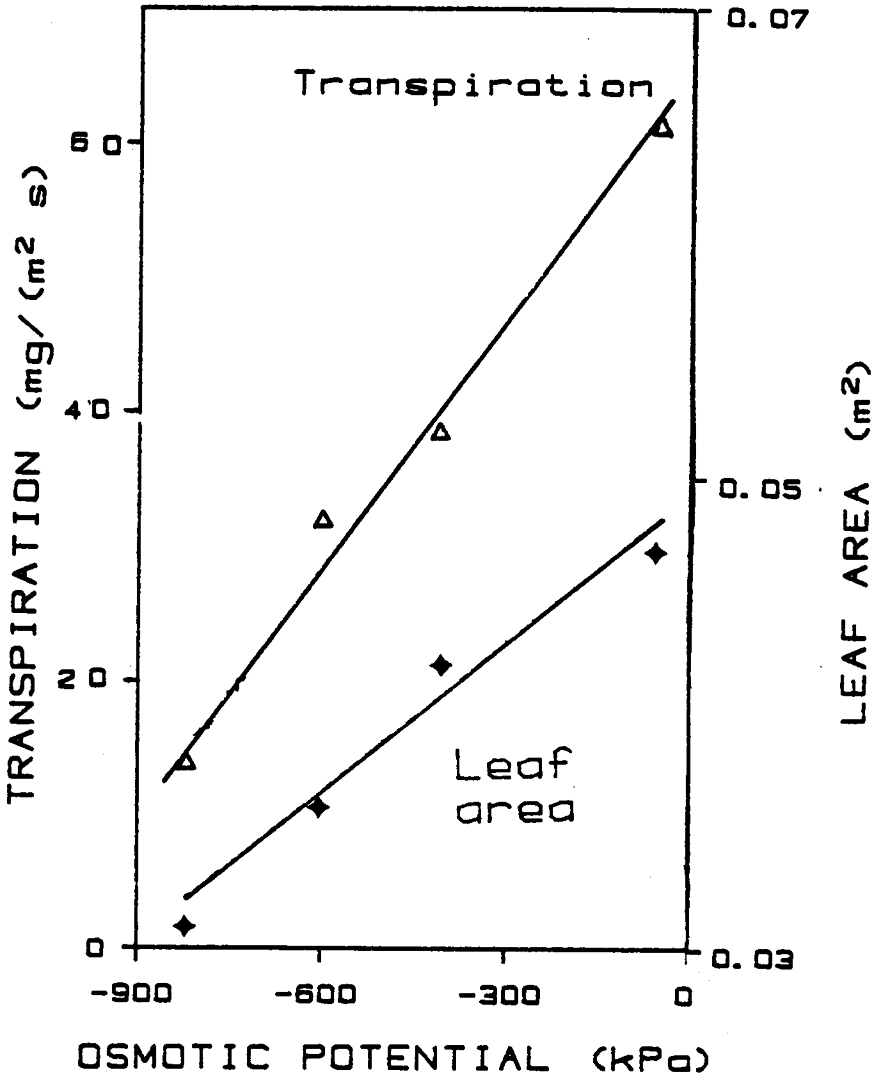


Fig. 32. Transpiration rate and leaf area as influenced by polyethylene glycol (PEG) in solution. The corn was grown for 23 days in nutrient solution before being placed in PEG for 4 days.

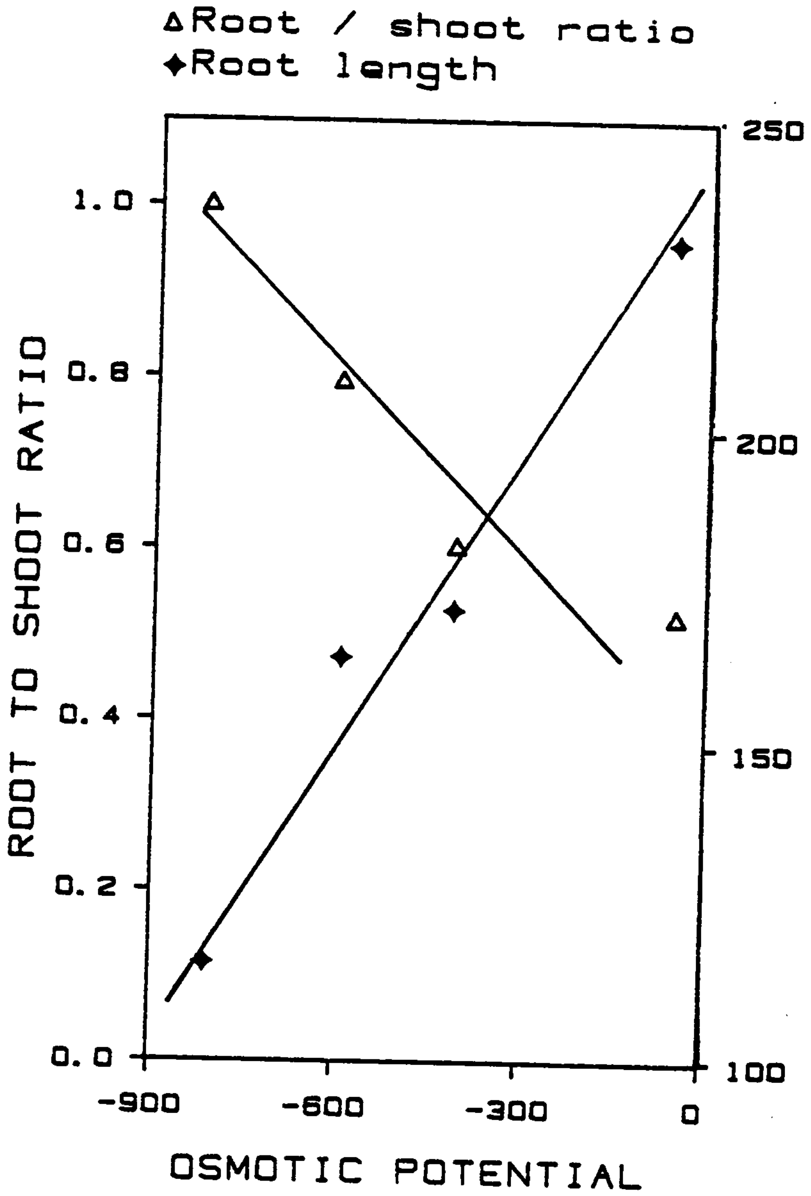


Fig. 33. Corn root length and root to shoot ratio as influenced by polyethylene glycol (PEG) in solution. The corn was grown for 23 days in nutrient solution before being placed in PEG for 4 days.

23, 28). All the roots grown in paper towel were shorter than roots of a similar age grown in soil, perhaps due to less accurate temperature control. The seedlings grown without PEG (the control) had etiolated coleoptiles, but none of the seedlings from the other treatment did. PEG did not affect the diameter of 4 day old corn seedlings when they were grown in moist paper towel.

The behavior of corn seedlings to ϕ_m in soil, ϕ_s in solution, and ϕ_s of solution-moistened paper towel was not similar. PEG in solution led to thickened individual roots while soil ϕ_m only altered the proportion of different root members. Seedlings grown in paper towel did not have thickened roots. Although high molecular weight PEG is considered to be the perfect osmoticum for inducing water stress, other factors may be involved in root response. Further study is needed to determine if the effects due to PEG are solely due to water stress, or if ethylene, toxic impurities, or other factors are also involved. This study indicated that PEG might not be the best medium for simulating root response to water stress.

Table 28. Corn seedlings grown in paper towel for 4 days as influenced by polyethylene glycol induced water stress.

Osmotic potential	Root length	Root diameter[1]
kPa	----- mm	-------
-0	290	0.81
-100	200	0.72
-200	153	0.78
-240	149	0.81
-330	74	0.78
-390	67	0.80
-1090	8	0.92

[1] Root diameters are averaged per root system.

Chapter VII

CONCLUSIONS

In a humid climate, altered corn root distribution during a dry period appeared to be important for sustaining plants through the drought. If subsoil conditions do not inhibit root growth, roots will proliferate in these deeper layers which partially compensates for the decrease of roots in the surface horizons. Perhaps for water uptake, the distribution and depth of root penetration is more important than root length. If this is true, prediction of compensatory root growth, and of the effects of subsurface compaction, acidity, etc, on root growth would be of utmost importance for water-uptake models on a field scale.

Large aggregates were a slight impedance to corn roots as roots were deflected around the aggregates. The impedance was more pronounced for laterals which have a smaller diameter than axes, hence less root pressure. Roots were able to push smaller aggregates out of their path. An equation was developed to describe root pressure as a function of aggregate size, root diameter, and angle of incidence. If used with Dexter's (1978) equation describing percent root penetration, his model describing soil structure, and a modification of his description of the pattern of root growth; perhaps the pattern of root growth in structured soil could be predicted.

Mechanical impedance, water stress, oxygen stress, and lower temperature all reduced corn root elongation, but the reduction at lower temperature was the most dramatic. Mechanical impedance and lower temperature also may have increased the diameter of individual roots. After 4 days, high θ_v was associated with increased root elongation rate, perhaps as a result of low levels of ethylene (Konings and Jackson, 1979). If the ultimate cause of the response to these stresses is at least partially hormonal, the development of physically-based models will be difficult until the mechanisms of hormonal responses are better understood.

The knowledge of root elongation may or may not be very critical for prediction of water and nutrient uptake. A steep perirhizal ϕ_w gradient near the root does not occur (Dunham and Nye, 1976a; Newman, 1969a, b). If the resistance of water movement to the root is not large, perhaps root elongation rate is not very critical for water uptake. A steep nutrient gradient does develop, however, and root density is important for nutrient uptake (Dunham and Nye, 1976b; Mackay and Barber, 1984; Silverbush and Barber, 1983). Since nutrient uptake relies on root elongation, knowledge of the effects of soil factors on root growth is important.

Aggregate size and θ_v affect the soil-root interface resistance. Herkelrath (1977) has shown that decreasing moisture films on the roots surface decrease water uptake due to a reduced "effective" surface area. Aggregate size also affects the soil-root contact. As aggregate size increases, the surface area of the root in contact with the soil decreases. This reduced "effective" surface area decreases nutrient uptake (Cornforth, 1968; Dexter, 1978; Tabatabai and Hanway, 1968; Wiersum, 1962).

Current models of root growth are generally inadequate because of insufficient data necessary to develop the assumptions of the models. Crop models can be developed at different levels of detail (Loomis et al., 1979): 1. community/ecosystem level (field scale), 2. organ/organism level (root system of an isolated plant), or 3. cell/tissue level (meristematic and elogation regions). At the ecosystem level, one aspect of the system can be detailed, but other aspects must be dealt with in a rudimentary manner (Loomis et al., 1979). At the organ level, Loomis et al. (1979) have stated, "Modeling the initiation, growth, and development of individual organs in an explanatory way is not always easy or in some cases even possible. Limited information exists about the mechanisms controlling the morphogenesis of individual organs. In many cases, the modeling becomes descriptive." It is not advantageous to develop root growth models from first principles (cell and subcellular level) if we are to obtain a useful model of root growth at the field scale (ecosystem level). Simplifying assumptions must be accepted.

Although a useful, general root growth model has not been developed, new directions for research are suggested:

1. Study the altered distribution of roots under drought by collecting root data from many locations, years, weather conditions, and management practices. From this develop a semi-empirical, field-scale model of root growth.
2. Reduce the variability of field root samples by decreasing the vertical dimension of a sample and increasing the horizontal cross sectional area. This can be accomplished by mixing together several small cores at the same depth.
3. Modify the root washing technique. Field-moist, fine-textured soil peds do not disperse in sodium hexametaphosphate. This greatly increases the washing time. Air-drying the peds before soaking in a dispersing agent will allow the clay clods to slake. Although this will also dry the roots, rehydrated root length is not significantly different from fresh root length.

4. Modify Dexter's (1978) and Hewitt and Dexter's (1979) root growth models to allow for root branching, aggregate size, layered soil, nongeotropic root growth, and stresses. Perhaps this could provide the physical framework for suggestion (1) above.
5. Use plants of the same stage of development rather than the same age to study the effects of environmental factors on root diameter.
6. Use pregerminated seeds to separate the influence of soil physical factors on germination from their effects on root and shoot growth.
7. Ascertain whether the effects of PEG on root morphology are solely due to water stress or if other factors are involved.

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Appendix A. Corn root length density data comparing mechanical and hand sampling for the first sampling on 8 June 1983.

	Root length density: by hand					
	Reps					
Depth[1]	1	2	3	4	5	6
	---------------- $km\ m^{-3}$ ----------------					
1a[2]	12.9	12.5	13.2	17.3	9.5	17.8
1b	11.9	6.1	12.4	14.5	10.2	6.3
2a	1.8	5.9	4.6	6.1	2.0	18.7

	Root length density: mechanical					
	Area A[3]			Area B		
	Reps			Reps		
Depth	1	2	3	1	2	3
1a	25.0	17.3	18.7	12.1	14.5	29.3
1b	----	10.9	12.7	5.1	----	6.8
2a	6.3	16.6	05.9	8.1	4.4	4.8

[1] Depths are in 0.15 m increments.

[2] Location 'a' is next to plants and 'b' is between rows.

[3] The areas were within the overall site at the edge.

Appendix B. Corn root length densities at various depths and dates in 1983.

	Root length density					
	Area A[2] Reps			Area B Reps		
Depth[1]	1	2	3	1	2	3
	km m^{-3}					
	21 June					
1a[3]	29.3	19.1	24.1	20.1	10.9	20.7
1b	6.5	14.0	14.3	11.2	15.0	16.1
2a	9.3	11.1	14.6	9.5	10.2	5.6
3a	7.0	10.2	5.1	6.0	6.6	3.7
4a	4.7	3.0	2.9	3.0	1.9	1.2
	6 July					
1a	28.3	38.8	46.9	31.5	34.8	27.1
1b	9.1	15.0	16.3	15.4	9.2	9.4
2a	21.6	13.5	10.9	14.4	15.3	10.7
3a	12.8	3.9	5.5	1.6	2.8	1.8
4a	7.5	3.6	4.4	0.8	1.2	0.9
5a	0.9	3.1	2.5	0.2	1.7	0.5
	20 July					
1a	16.1	29.3	29.1	25.8	27.6	22.7
1b	11.5	17.5	16.3	9.5	18.2	4.3
2a	7.0	10.1	14.9	17.0	15.9	7.3
3a	12.6	12.2	16.9	9.9	15.6	9.3
4a	2.4	9.0	9.9	0.5	2.2	1.3
5a	1.1	0.3	1.1	0.8	0.5	0.4

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[1] Depths are in 0.15 m increments.

[2] The areas are within the overall site at the edge of the field.

[3] Location 'a' is next to plants and 'b' is between rows.

Appendix C. Corn root length density at various depths and dates in 1983 (cont.).

	Root length density					
	Area A[2] Reps			Area B Reps		
Depth[1]	1	2	3	1	2	3
	km m^{-3}					
	3 August					
1a[3]	28.7	32.9	35.6	28.0	33.9	37.2
1b	10.5	7.6	18.5	7.2	4.9	5.5
2	9.1	13.6	11.4	7.5	4.5	10.1
3	7.6	10.4	9.0	0.2	4.9	4.4
4	3.9	7.7	11.6	0.6	0.5	4.5
5	0.7	2.1	1.0	0.4	0.7	1.8
	24 August					
1a	39.7	35.8	26.7	13.5	26.9	2.5
1b	3.1	3.6	5.6	2.9	0.9	3.7
2	8.2	12.6	5.8	7.8	15.4	4.9
3	5.6	7.5	5.9	1.0	4.1	1.7
4	5.4	3.3	0.9	0.1	0.5	0.4
5	0.4	0.2	1.3	0.0	0.1	0.1
	14 September					
1a	6.1	6.5	4.0	6.6	13.1	5.0
1b	2.4	8.0	0.4	1.5	4.2	0.7
2	4.2	5.5	3.2	6.8	2.9	2.1
3	7.7	10.7	6.5	9.2	9.8	4.1
4	3.6	12.3	4.6	1.6	2.4	0.3
5	1.9	8.7	0.2	0.0	0.2	0.0

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[1] Depths are in 0.15 m increments.

[2] The areas are within the overall site at the edge of the field.

[3] Location 'a' is next to plants and 'b' is between rows.

Appendix D. Grain and dry matter corn yields for 1983.

Area[1]	Yield	Total dry matter
	------ kg ha^{-1}	-------
1	8 678	22 910
2	8 480	18 040
3	8 222	21 510
4	8 731	19 970

[1] The areas measured 3.05 x 0.98 m.

Appendix E. Corn shoot weights during the growing season and final grain and dry matter yields for 1984.

Shoot weights per plant						
8 July	25 July		2 August		17 August	
	C[1]	N[1]	C	N	C	N
g						
15.96	125	60	107	125	161	198
13.87	136	87	115	78	186	135
4.28	76	70	127	69	152	132
1.65	78	60	94	141	160	102

Final yields							
Rep. 1		Rep. 2		Rep. 3		Rep. 4	
C	N	C	N	C	N	C	N
kg ha^{-1}							
Grain yield							
9 670	8 600	9 420	10 610	10 420	9 040	10 670	11 110
Shoot yield							
14 770	13 460	14 730	16 150	16 450	15 450	20 240	17 250

---

[1] Plots covered with plastic are designated by 'C' and noncovered plots are designated by 'N'.

Appendix F. Corn leaf water potentials for 1984.

	Leaf water potentials							
	Covered[1]				Noncovered			
	a[2]		b		a		b	
Rep	P[3]	H[3]	P	H	P	H	P	H
	kPa							
1	-485	-500	-632	-639	-765	-728	-709	-640
2	-727	-722	-602	-591	-805	-793	-713	-744
3	-726	-719	-963	-1021	-572	-584	-675	-707
4	-643	-648	-988	-978	-694	-664	-494	-571

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[1] Covered plots were covered with plastic.

[2] Letters 'a' and 'b' designate leaves.

[3] The psychrometric mode is designated by 'P' and the hygrometric mode is designated by 'H'.

Appendix G. Corn root length density data in 1984.

	Root length density							
Rep:	1		2		3		4	
Location[1]: Depth[2]	a	b	a	b	a	b	a	b
	km m^{-3}							
	8 July							
1	31.7	7.5	19.1	22.2	25.4	4.9	6.1	0.2
2	11.8	7.2	7.0	8.5	4.2	2.5	0.5	5.0
3	7.2	5.7	5.0	6.0	2.8	6.9	2.8	4.7
4	3.3	9.1	1.8	4.5	6.0	7.6	4.5	7.0
	25 July - noncovered							
1	19.7	19.3	20.7	16.5	26.0	8.9	34.6	16.3
2	8.7	16.3	8.0	8.0	6.1	6.0	1.6	5.2
3	5.5	8.5	1.6	5.4	4.4	6.2	2.0	3.8
4	5.0	3.5	0.7	0.0	5.3	7.9	11.1	7.2
5	3.4	2.0	3.7	5.8	4.0	11.9	3.1	8.3
	25 July - covered[3]							
1	32.9	17.6	24.9	4.3	12.8	2.6	24.0	20.9
2	16.8	10.4	4.4	1.6	2.3	2.2	4.4	10.1
3	3.4	3.7	4.0	1.2	2.0	0.8	7.3	9.2
4	2.6	4.9	4.6	7.8	5.6	1.5	8.0	10.0
5	6.2	4.2	4.2	3.8	10.5	2.8	2.7	1.7

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[1] Location 'a' is next to plants and 'b' is between rows.
[2] Depths are in 0.15 m increments.
[3] Covered plots are covered with plastic.

Appendix H. Corn root length density data for 2 August 1984.

	Root length density							
Rep:	1		2		3		4	
Location[1]: Depth[2]	a	b	a	b	a	b	a	b
	km m^{-3}							
	Noncovered							
1	47.9	16.0	18.0	7.1	30.5	8.0	22.0	14.6
2	7.1	10.9	1.5	4.5	4.0	2.3	4.8	7.3
3	6.3	6.4	0.7	1.7	3.8	2.7	6.8	3.1
4	6.7	6.9	5.0	3.1	8.1	1.8	9.2	2.2
5	12.4	11.9	3.7	1.6	3.4	6.7	4.7	12.4
6					2.1			
	Covered[3]							
1	21.7	26.8	25.0	2.0	25.3	26.3	16.3	11.8
2	10.9	13.5	5.9	6.2	6.6	5.3	2.5	7.1
3	9.1	2.9	3.0	2.5	4.5	5.2	3.4	3.1
4	7.1	0.2	8.7	1.6	8.7	8.3	3.1	4.8
5	0.8	1.7	4.9	13.3	9.4	3.8	0.5	0.2
6	0.4					0.8		

---

[1] Location 'a' is next to plants and 'b' is between rows.
[2] Depths are in 0.15 m increments.
[3] Covered plots are covered with plastic.

Appendix I. Corn root length density data for 17 August 1984.

	Root length density							
Rep:	1		2		3		4	
Location[1]: Depth[2]	a	b	a	b	a	b	a	b
	km m^{-3}							
	Noncovered							
1	32.7	15.1	22.0	7.3	38.5	0.9	22.4	9.7
2	4.5	7.1	15.1	15.8	7.1	3.7	5.5	5.4
3	1.6	3.9	4.1	0.2	3.2	1.2	1.8	2.9
4	4.3	5.9	0.9	1.7	7.2	8.8	2.2	2.1
5	2.2	4.0	0.1	2.0	8.1	4.1	0.0	1.8
	Covered[3]							
1	22.3	7.5	24.6	3.8	22.4	9.1	22.3	2.7
2	20.2	5.6	7.2	10.7	3.3	4.3	11.1	0.9
3	1.8	0.0	2.2	2.4	3.9	4.5	2.7	2.3
4	2.8	7.9	1.5	1.1	6.4	10.5	2.8	4.7
5	4.5	7.4	0.3	3.3	6.1	6.5	1.9	4.8
6	0.0	4.5		4.8				

---

[1] Location 'a' is next to plants and 'b' is between rows.

[2] Depths are in 0.15 m increments.

[3] Covered plots are covered with plastic.

Appendix J. Soil volumetric moisture contents of Groseclose silt loam in 1984.

	Volumetric moisture contents							
	Covered[1] (reps)				Noncovered (reps)			
Depth[2]	1	2	3	4	1	2	3	4
	$m^3\ m^{-3}$							
	2 August 1984							
1	0.25	0.28	0.19	0.21	0.23	0.23	0.21	0.21
2	0.31	0.26	0.27	0.21	0.29	0.24	0.30	0.21
3	0.31	0.33	0.34	0.29	0.41	0.27	0.33	0.29
4	0.40	0.43	0.40	0.30	0.41	0.32	0.45	0.30
5	0.49	0.49	0.38	0.45	0.43	0.41	0.48	0.45
	21 August 1984							
1	0.30	0.30	0.17	0.23	0.31	0.28	0.24	0.24
2	0.27	0.27	0.25	0.25	0.27	0.31	0.28	0.28
3	0.36	0.33	0.39	0.25	0.37	0.26	0.37	0.27
4	0.46	0.41	0.47	0.35	0.47	0.30	0.46	0.31
5	0.54	0.47	0.44	0.44	0.48	0.37	0.43	0.34

---

[1] The covered plots were covered with plastic.

[2] The depths are in 0.15 m increments.

Appendix K. Root growth of 4-day-old corn seedlings as influenced by aggregate size of Groseclose silt loam.

Aggregate size	Rep	Root length	Root diameter
mm		----- mm	------
<1	a	502	0.86
	b	403	0.91
	c	483	0.89
	d	452	0.87
1-2	a	440	0.93
	b	425	0.90
	c	---	----
	d	446	0.93
2-3	a	249	0.88
	b	424	0.92
	c	386	1.00
	d	411	0.92
3-6	a	313	0.95
	b	348	0.99
	c	369	0.98
	d	456	0.94

Appendix L. Root and shoot growth of 6-day-old corn seedlings as influenced by aggregate size of Groseclose silt loam.

Aggregate size	Rep	Leaf area	Root length			Root rehyd. diam.
			Total	Axes	Laterals	
mm		mm^2	------	m	-------	mm
<1	a	1150	1.79	0.61	1.18	0.37
	b	1530	2.42	0.58	1.84	0.36
	c	1440	1.71	0.62	1.09	0.35
	d	1625	2.55	0.56	1.99	0.28
	e	2070	4.18	0.72	3.46	0.31
	f	1775	3.55	0.76	2.79	0.29
	g	1475	2.45	0.64	1.81	0.31
1-2	a	1390	4.31	0.72	3.59	0.30
	b	1990	5.72	0.86	4.86	0.28
	c	1695	4.49	0.73	3.76	0.31
	d	1960	4.05	0.86	3.21	0.32
	e	1680	3.30	0.80	2.50	0.32
	f	1930	1.89	0.64	1.25	0.32
	g	1580	2.62	0.68	1.94	0.30
2-3	a	670	1.07	0.47	0.50	0.33
	b	1040	1.34	0.57	0.77	0.38
	c	1420	3.99	0.65	3.24	0.32
	d	1390	4.97	0.58	3.39	0.18
	e	----	----	----	----	----
	f	1370	4.51	0.84	3.31	0.30
	g	1380	1.23	0.49	0.74	0.38
3-6	a	725	0.97	0.64	0.33	0.49
	b	990	1.57	0.59	0.98	0.42
	c	1670	3.83	0.61	3.22	0.31
	d	1550	2.12	0.66	1.46	0.39
	e	1810	2.26	0.73	1.53	0.38
	f	1900	2.39	0.67	1.62	0.43
	g	2110	3.96	0.75	3.21	0.37

Appendix M. Root and shoot growth of 7-day-old corn seedlings as influenced by aggregate size of Groseclose silt loam.

Aggregate size	Rep	Leaf area	Shoot dry weight	Root length			Root rehyd. diam.
				Total	Axes	Laterals	
mm		mm²	g	------	m	-------	mm
<1	a	2930	0.18	7.13	1.23	5.90	0.27
	b	2750	0.15	8.23	1.18	7.05	0.25
	c	2715	0.19	8.08	1.27	6.81	0.29
	d	2800	0.13	6.57	0.96	5.61	0.27
1-2	a	2000	0.11	4.27	0.91	3.38	0.32
	b	3240	0.17	8.30	1.43	6.87	0.31
	c	3135	0.13	6.41	1.04	5.37	0.32
	d	3510	0.15	10.43	1.05	9.38	0.24
2-3	a	1190	0.09	2.92	0.80	2.12	0.39
	b	2280	0.15	3.43	1.18	2.25	0.37
	c	2930	0.11	7.20	0.99	6.21	0.32
	d	2610	0.13	4.93	0.91	4.02	0.29
3-6	a	2220	0.09	2.58	0.62	1.96	0.36
	b	960	0.06	1.52	0.44	1.08	0.38
	c	2430	0.13	6.00	1.01	4.99	0.37
	d	2700	0.12	5.85	1.12	4.73	0.32

Appendix N. Root growth of 4-day-old corn seedlings as influenced by bulk density of Groseclose silt loam.

Bulk density	Rep	Root length	Root diameter
Mg m^{-3}		------ mm ------	
1.10	a	433	0.82
	b	409	1.01
	c	475	0.94
	d	382	0.89
1.22	a	459	0.91
	b	332	0.95
	c	475	0.93
	d	250	0.81
1.35	a	268	0.84
	b	311	0.90
	c	433	0.89
	d	397	0.96
1.47	a	130	1.33
	b	278	0.88
	c	249	1.15
	d	205	1.09

Appendix O. Root and shoot growth of 6-day-old corn seedlings as influenced by bulk density of Groseclose silt loam.

Bulk density	Rep	Leaf area	Root length			Root diameter
			Total	Axes	Laterals	
Mg m^{-3}		mm^2	------	m	-------	mm
1.10	a	2090	3.98	0.86	3.12	0.49
	b	1110	3.55	0.72	2.83	0.41
	c	1960	3.08	0.77	2.31	0.49
	d	1490	2.18	----	----	0.51
	e	1980	3.46	0.93	2.52	0.49
	f	1040	1.46	0.68	0.78	0.62
1.22	a	1740	3.14	0.75	2.40	0.51
	b	1900	2.81	0.65	2.16	0.55
	c	2110	2.67	0.68	1.99	0.54
	d	1790	3.27	----	----	0.54
	e	1010	1.67	0.58	1.08	0.48
	f	1660	1.59	0.54	1.04	0.65
1.35	a	1660	1.37	0.56	0.81	0.66
	b	1710	1.04	0.65	0.39	0.74
	c	1670	1.34	0.63	0.46	0.55
	d	1370	2.22	0.54	1.67	0.47
	e	1800	2.22	0.64	1.56	0.49
	f	1660	2.01	----	----	0.63
1.47	a	1020	0.60	0.18	0.42	0.68
	b	----	----	----	----	----
	c	1340	0.86	0.41	0.45	0.67
	d	----	0.46	0.39	0.08	0.84
	e	1310	0.60	----	----	0.77
	f	1450	1.24	0.69	0.54	0.78

Appendix P. Root growth of 4-day-old corn seedlings as influenced by high soil moisture induced oxygen stress.

Moisture content	ODR[1]	Rep	Root length	Root diam.
m^3 m^{-3}			---- mm	---
0.24	62.9	a	333	0.96
	56.1	b	356	1.09
	72.1	c	351	1.03
	53.7	d	262	0.91
0.27	59.0	a	401	0.93
	67.5	b	444	0.93
	66.7	c	443	0.97
	60.6	d	307	0.91
0.30	81.8	a	394	0.86
	34.6	b	414	0.74
	26.6	c	248	1.06
	18.0	d	13	1.40
0.33	3.0	a	29	1.15
	58.4	b	237	0.93
	29.4	c	39	0.80
	39.3	d	169	0.95

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[1] ODR is oxygen diffusion rate measured with a platinum microelectrode (Lemon and Erickson, 1952) having units of g cm^{-2} min^{-1}.

Appendix Q. Root and Shoot growth of 6-day-old corn seedlings as influenced by high-soil-moisture-induced stress.

Moisture content	Rep	ODR[1]	Leaf area	Plant height	Root length			Root diam.
					total	axes	laterals	
$m^3\ m^{-3}$			mm^2	mm	----- m ------			mm
0.24	a	54.8	1040	74	1.70	0.55	1.15	0.64
	b	63.4	1500	105	2.51	0.76	1.75	0.54
	c	58.3	1550	112	3.52	0.61	2.91	0.41
	d	63.5	1050	76	0.68	0.49	0.19	0.67
	e	59.2	1830	107	3.99	0.85	3.14	0.49
	f	80.2	1650	114	2.42	0.71	1.71	0.46
0.27	a	62.3	1750	136	3.71	0.70	2.01	0.45
	b	68.2	1500	111	2.29	0.79	1.50	0.49
	c	71.8	1690	137	2.95	0.84	2.11	0.52
	d	78.3	1030	102	1.02	0.50	0.52	0.51
	e	67.1	2040	136	4.37	0.86	3.51	0.50
	f	61.8	1650	120	2.58	0.69	1.89	0.48
0.30	a	59.9	1960	140	5.31	0.86	4.55	0.42
	b	58.3	1350	178	2.86	0.72	2.14	0.52
	c	44.6	2250	151	4.78	1.06	3.72	0.43
	d	7.2	860	81	0.55	0.31	0.24	0.64
	e	27.2	1820	120	4.40	0.72	3.68	0.36
	f	50.8	1630	132	3.77	0.68	3.09	0.43
0.33	a	18.1	1350	96	1.36	0.57	0.79	0.60
	b	6.0	1400	204	2.39	0.61	1.78	0.46
	c	66.2	1540	75	0.81	0.45	0.36	0.66
	d	31.4	1620	120	2.64	0.49	2.15	0.47
	e	4.3	2310	157	2.29	0.78	1.55	0.55
	f	52.9	510	63	0.72	0.46	0.26	0.69

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[1] ODR is oxygen diffusion rate measured with a platinum microelectrode (Lemon and Erickson, 1952) having units of $g\ cm^{-2}\ min^{-1}$.

Appendix R. Root growth of 4-day-old corn seedlings as influenced by soil temperature[1].

Soil temp.				
Night	Day	Rep	Root length	Root diameter
°C			------ mm	------
24.4	26.1	a	411	0.91
24.5	24.8	b	282	1.00
24.5	25.1	c	266	0.79
24.4	25.4	d	348	1.01
20.3	22.3	a	95	0.97
19.9	22.7	b	215	0.88
20.7	21.9	c	160	0.80
19.9	21.1	d	168	0.95
15.2	17.8	a	9	2.06
15.1	18.5	b	12	1.46
15.0	17.5	c	20	1.38
15.1	18.2	d	15	1.30

[1] Soil temperature was measured with thermocouples at the center of each pot.

Appendix S. Root and shoot growth of 6-day-old corn seedings as influenced by soil temperature[1].

Soil temp.					Root length			
Night	Day	Rep.	Leaf area	Plant height	Total	Axes	Laterals	Root diam.
°C			mm^2	mm	------	m	-------	mm
24.5	26.1	a	1530	107	3.33	0.75	2.58	0.47
24.4	24.9	b	1270	100	2.40	0.82	0.58	0.52
24.4	25.4	c	1430	92	1.60	0.66	0.94	0.61
24.5	25.1	d	1150	91	2.26	0.79	1.47	0.56
23.3	25.8	e	290	60	0.41	0.30	0.11	0.50
24.0	24.5	f	1260	84	2.71	0.56	1.15	0.47
20.1	22.9	a	0	51	0.45	0.49	0.01	1.12
19.9	22.3	b	0	50	0.35	0.34	0.01	0.95
19.7	21.8	c	0	43	0.39	0.39	0.00	0.94
20.1	23.2	d	620	64	0.57	0.48	0.09	1.02
20.3	21.6	e	0	62	0.52	0.50	0.02	0.97
19.9	24.0	f	380	65	0.71	0.57	0.92	0.52
15.3	18.7	a	0	0	0.17	0.17	0.00	1.05
15.1	18.3	b	0	0	0.17	0.17	0.00	1.03
15.2	17.6	c	0	0	0.16	0.16	0.00	1.06
15.1	17.0	d	0	0	0.09	0.09	0.00	0.98
15.1	17.9	e	0	0	0.08	0.08	0.00	1.08
15.2	18.7	f	0	0	0.13	0.13	0.00	1.02

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[1] Soil temperature was measured with thermocouples at the center of each pot.

Appendix T. Root growth of corn seedlings at 3.75 days as influenced by mild water stress.

Moisture content	Rep	Root length	Root diameter
$m^3\ m^{-3}$		------ mm	------
0.24	a	281	0.90
	b	256	0.86
	c	322	1.86
	d	244	0.76
0.22	a	276	0.80
	b	334	0.78
	c	234	1.01
	d	264	0.78
0.20	a	241	0.95
	b	251	0.84
	c	256	0.90
	d	258	0.71
0.18	a	331	0.94
	b	270	0.82
	c	332	0.63
	d	199	0.87

Appendix U. Root and shoot growth of corn seedlings at 6.5 days as influenced by mild water stress. mild water stress.

Moisture content	Rep	Soil water tens.[1]	Leaf area	Root length			Root diam.
				Total	Axes	Laterals	
m^3 m^{-3}		kPa	mm^2	------	m	-------	mm
0.24	a	0	1895	5.63	0.93	4.70	0.41
	b	67	2300	5.19	0.93	4.26	0.42
	c	41	2120	4.05	0.69	3.36	0.45
	d	0	1780	1.82	0.62	1.20	0.51
	e	138	2090	5.19	1.02	4.17	0.45
	f	306	2190	4.15	1.04	3.11	0.46
0.22	a	121	1720	2.80	1.02	1.76	0.54
	b	84	1810	2.86	0.55	2.31	0.45
	c	0	1440	0.83	0.49	0.34	0.64
	d	0	2240	6.07	0.96	5.01	0.43
	e	60	2020	6.76	0.79	5.97	0.40
	f	0	1510	1.85	0.65	1.20	0.48
0.20	a	157	1545	1.40	0.56	0.84	0.52
	b	340	1470	3.30	0.75	2.55	0.44
	c	116	----	0.93	0.42	0.51	0.61
	d	165	1730	2.81	0.49	2.32	0.44
	e	235	1665	4.24	0.85	3.39	0.46
	f	315	840	2.47	0.59	1.88	0.43
0.18	a	286	1460	3.80	0.65	3.15	0.49
	b	330	1110	3.11	0.61	2.50	0.36
	c	403	1565	3.05	0.65	2.40	0.47
	d	403	1760	4.71	0.70	4.01	0.46
	e	432	1110	3.52	0.57	2.95	0.45
	f	485	1080	4.53	0.63	3.90	0.45

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[1] Soil water tension was measured psychrometrically in a sample chamber.

Appendix V. Root growth of 4-day-old corn seedlings as influenced by moisture stress.

Moisture content	Rep.	Root length	Root diam.
$m^3\ m^{-3}$		------ mm	------
0.24	a	411	0.91
	b	282	1.00
	c	266	0.79
	d	348	1.01
0.21	a	390	1.02
	b	286	0.97
	c	207	0.82
	d	320	0.96
0.18	a	378	0.95
	b	264	0.96
	c	202	0.87
	d	335	0.85
0.15	a	243	0.89
	b	93	1.28
	c	227	1.00
	d	266	1.00

Appendix W. Root and shoot growth of 6-day-old corn seedlings as influenced by moisture stress.

Moisture content	Rep	Soil water tens.[1]	Leaf area	Plant height	Root length			Root diam.
					Total	Axes	Laterals	
$m^3\ m^{-3}$		kPa	mm^3	mm	------ m -------			mm
0.24	a	200	1530	107	3.33	0.75	2.58	0.47
	b	130	1270	100	2.40	0.82	0.58	0.52
	c	200	1430	92	1.60	0.66	0.94	0.61
	d	---	1150	91	2.26	0.79	1.47	0.56
	e	230	290	60	0.41	0.30	0.11	0.50
	f	230	1260	84	2.71	0.56	1.15	0.47
0.21	a	---	1650	132	5.00	0.72	4.28	0.42
	b	230	1320	94	----	0.68	----	----
	c	320	1340	109	3.03	0.89	2.14	0.53
	d	230	1450	100	3.39	0.66	2.73	0.47
	e	180	560	68	2.17	0.65	1.52	0.54
	f	220	783	72	1.70	0.60	1.10	0.57
0.18	a	210	620	65	2.70	0.57	1.13	0.46
	b	300	610	71	3.08	0.57	2.51	0.47
	c	486	590	58	3.55	0.35	3.20	0.31
	d	310	510	59	1.19	0.47	0.72	0.51
	e	390	370	62	1.73	0.55	1.18	0.60
	f	260	1440	96	2.89	0.69	2.20	0.52
0.15	a	750	0	14	0.35	0.28	0.07	0.64
	b	1280	57	66	0.68	0.42	0.26	0.75
	c	770	0	47	0.80	0.31	0.49	0.60
	d	1530	0	0	0.23	0.10	0.13	0.71
	e	110	0	41	0.79	0.38	0.41	0.66
	f	---	0	24	0.40	0.25	0.15	0.64

[1] Soil water tension was measured psychrometrically in a sample chamber.

Appendix X. Root and shoot growth and transpiration rate of solution grown corn plants as influenced by polyethylene glycol (PEG)-induced water stress.

PEG	Solution water potential	Leaf water potential		Leaf area	Dry mass		Root length	Trans. rate (avg)	
					Shoots	Roots			
kg	kPa	MPa		mm^2	---- g ----		m	$\text{mg m}^{-2}\text{ s}^{-1}$	
		Psy.	D.P.					24h	16h
	pre				2.96	1.73			
					1.84	1.92			
					2.81	1.13			
					3.88	2.54			
0.000	-50	1.08	1.05	62 000	5.63	3.15	191	39.5	54.2
		1.03	1.04	48 300	7.85	3.95	262	69.9	95.7
		1.19.	1.15	61 300	7.68	4.03	246	34.2	46.8
		1.16	1.07	56 500	7.32	3.71	228	34.6	47.3
0.175	-410	1.11	1.05	54 000	8.81	5.40	206	36.4	26.6
		1.12	1.14	43 100	4.95	3.05	145	26.6	36.4
		1.26	1.20	58 800	8.41	4.60	187	63.5	32.2
		1.05	0.89	50 800	6.84	4.46	151	26.1	35.7
0.200	-600	1.30	1.24	40 800	7.30	5.51	152	32.8	46.2
		1.17	1.28	47 700	3.71	3.70	201	17.6	24.2
		1.07	1.05	51 400	6.65	4.80	142	19.7	27.0
		1.23	1.20	44 700	5.93	4.95	160	21.2	29.0
		1.20	1.02	43 500	6.06	4.46	171	24.3	33.3
0.225	-820	1.37	1.48	31 600	3.59	3.78	119	11.3	15.5
		1.12	1.35	35 000	4.02	3.63	105	13.1	17.9
		1.34	1.44	30 900	3.52	3.74	140	9.7	13.3
		1.58	1.53	39 900	3.42	3.31	109	7.1	9.8
		1.37	1.47	28 000	3.18	3.33	107	9.4	12.9

Appendix Y. Root growth of paper towel grown corn plants at 4 days as influenced by polyethylene glycol induced water stress.

Solution osmotic pressure						
kPa						
0	100	200	240	330	390	1090
Root length						
mm						
421	259	217	141	142	21	8
218	198	191	139	112	18	68
279	271	123	175	67	92	0
359	262	305	53	157	43	0
288	242	213	123	130	35	0
328	139	140	205	56	53	0
325	136	54	210	24	84	0
254	193	113	151	18	84	0
211	100	63	125	35	101	0
218	205	112	166	0	90	0
					114	
Root diameter						
mm						
0.82	0.70	0.77	0.80	0.79	0.78	1.26
0.94	0.80	0.77	0.86	0.83	0.84	0.61
0.77	0.78	0.85	0.80	0.87	0.83	----
0.78	0.79	0.71	0.98	0.75	0.77	----
0.80	0.83	0.73	0.85	0.77	0.85	----
0.76	0.68	0.67	0.75	0.83	0.69	----
0.77	0.61	0.84	0.89	0.73	0.87	----
0.81	0.63	0.75	0.71	0.83	0.67	----
0.83	0.74	0.89	0.73	----	0.80	----
					0.82	