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IMPEDANCE AND AERATION

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GHOLAM HOSSEIN ASADY

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MODELING SPATIAL AND TEMPORAL RESPONSES OF PHASEOLUS VULGARIS, L.
ROOTS AND SHOOTS TO SOIL MECHANICAL IMPEDANCE AND AERATION

By

Gholam Hossein Asady

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ABSTRACT

MODELING SPATIAL AND TEMPORAL RESPONSES OF PHASEOLUS VULGARIS, L. ROOTS AND SHOOTS TO SOIL MECHANICAL IMPEDANCE AND AERATION

By

Gholam Hossein Asady

Understanding the spatial and temporal responses of plant cultivars to the dynamically changing soil environments is important for the development of a comprehensive plant and soil production system. The purpose of this study was to obtain experimental information regarding plant root responses to a mechanically impeding clay soil and put those results into a model.

A soil core seedling test was developed which could be used as a fast and inexpensive method of studying root responses to multiple levels of mechanical impedance and aeration under a constant soil water potential. Root penetration ratios (RPR) were measured 14 days after planting (DAP) without destroying seedling viability. RPR and root lengths declined linearly with decreasing air filled porosity. The maximum dry matter accumulations and yields occurred at RPR values of approximately 0.65. The xylem flow rates of plants grown in high bulk density soils were also reduced to values as low as 5 nL s^{-1} . Transpiration and photosynthetic rates were inversely and diffusive resistance was directly correlated to mechanical impedance, respectively.

Severe mechanical impedance reduced total root length by approximately 80 and 74% after 20 and 30 days of growth, respectively. The average root length density was reduced to less than 1 cm cm^{-3} in high density soils. Extension of the roots into deeper layers was greatly reduced by severe mechanical impedance. Approximately 90% of the roots grown in severely compacted treatment remained in the surface 2.5 cm compared to 15% in the control, at 20 DAP.

Greater pathway resistances of the soil pores appeared to influence the reduced oxygen and increased carbon dioxide concentrations of the soil more than the reduced aeration treatments of this study. In addition, nearly 12% of the air filled pores in the surface layers of the compacted soil were plugged by the roots, at 30 DAP, further contributing to greater pathway resistances.

A model of shoot growth is proposed which includes the dynamic relative growth rate and biological growth capacity of the environment. A model of root growth and water uptake was modified which includes soil mechanical impedance. This modified, PHASOL model dynamically calculates the mechanical resistance, aeration porosity, and root growth responses in different soil layers. Penetration of the roots completely ceased as the mechanical resistance approached a critical value of 5.5 MPa. Predicted root and shoot growth, leaf water potential, and cumulative water use responses of dry edible beans were parallel to experimental data, for a 20 day period of simulated growth.

To

My new-born daughter Beeta

whose arrival gave my life

a new dimension

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INTRODUCTION

Limited natural resources and growing world populations have placed an unprecedented demand on contemporary agricultural research programs. The agriculture industry is now faced with developing available technologies in order to cope with the ever increasing problems associated with food and fiber production. Therefore, it is imperative that our research be directed toward the problems needing attention. Unfavorable soil physical conditions are known to be one of the major limiting factors in agricultural production systems. Mechanization of agriculture, including utilization of heavy machinery and associated equipment, coupled with poor management practices have resulted in compacted soils.

The compaction of soils affects those physical properties which influence the storage and conduction of water, diffusion of gases, uptake of nutrients, and the soil mechanical resistance to root penetration. These adverse physical consequences of soil compaction cause soil particles to be in closer contact with each other, consequently increasing the angle of soil internal friction and cohesive forces, creating smaller mean pore diameters and reducing total soil porosity which imposes a mechanical barrier to root development.

The growth and distribution of plant roots determines their efficiency in water and nutrient uptake and ultimately controls plant

production. Although root development is genetically controlled, soil environmental conditions modify the root development of different genotypes. Soil compaction appears to directly and indirectly influence the ontogenetic development of plant root systems through certain soil physical conditions (eg. temperature, aeration, mechanical impedance, and water potential). The direct influence of soil compaction appears to be an increasing mechanical resistance to root penetrations. Soil compaction indirectly affects plant growth by creating an oxygen stressed environment which promotes anaerobic root respiration and the formation of toxic anaerobic compounds. The shallow rooting generally associated with soil compaction results in reduced anchorage of plants.

Expansion of the computer industry and the wide scale availability of digital processors has provided scientists from different disciplines a new avenue to organize their thoughts and implement their ideas through the development of simulation models. Models have become established as a means for understanding concepts which elude the brain's unaided ability (Radford, 1968). Models developed for simulating a system or organism are designed to represent the mechanisms which control the activities of that system or organism. A model is usually amenable to manipulation which would be otherwise impossible, too expensive, or impractical to perform on the entity it portrays (Naylor et al., 1966). A fundamental rationale for developing simulation models is our increasing quest for knowledge concerning the future. Computer simulation models for predicting crop production systems appear to provide researchers with an additional analytical tool. Application of plant growth simulation models has great potential in forecasting yields of large areas which could provide valuable

information at the local, state, and federal levels of decision making.

The primary objective of this study was to evaluate the effects of mechanical impedance and associated stresses on the growth and development of the dry edible beans (Phaseolus vulgaris, L.) root system. Other objectives include development of a quick and inexpensive method of studying plant-root system grown under multiple levels of soil physical environments. The experimental data which quantitatively describes the underlying relationships is put into a feasible model to predict the drybean root growth and distribution under a given set of conditions. This, both summarizes what we already know about the drybean and also projects what is not yet known. The model needs more testing against field data and parameter estimations before it could be used for management decisions.

CHAPTER 1

LITERATURE REVIEW

Plant Responses to Root Environments

Crop production is often limited by prevailing environmental conditions, i.e. by the existing complex of physical, chemical and biological factors (Feddes et al., 1978). Plants, as a whole, live in two realms, the atmosphere, and the soil, each of which has its own characteristics and complexity, of these two, the soil seems to be much more complex. Terrestrial portions of plant root systems are confined to the soil and exposed to multiple chemical, physical and biological environments. The paucity of information concerning the root-soil interface and the many environmental conditions which influence this interface are of prime importance to the tolerance of plants to soil related stresses .

Plant growth is an integration of two principle factors with time. Those which genetically control development of the different plant characteristics, and the environmental conditions which appear to modify this genetic behavior. Most of the changes in plant characteristics may be an expression of ontogenetic drift (Hunt, 1978). This is due to developments which occur within the plant with the passing of time. These developments occur against the background of changing environments. In order to obtain a greater understanding of

the relative importance of these two effects, plants should be grown in constant or controlled environments.

Basically shoot and root functions remain the same, even though their relative contributions to the whole growth process may be altered by the environment. Shoots are specialized to convert the chemical energy into metabolites through the complex biochemical process of photosynthesis on which the whole plant growth depends. It is not exaggerated to say that the biological capacity of the earth is ultimately dependent upon the energy received from the sun through many natural light detectors and sensors (Hunt 1978). In contrast, the major functions of root systems include absorption of water and nutrients, anchorage, and synthesis of some of the plant growth regulators (Russell, 1977), all of which are coordinated with the components of the shoot. One of the main functions of the root system is uptake and fixation of nitrogen. The daily nitrogen requirements for growth of a plant or plant part with dry matter W , and its associated respiration cost are defined as

$$F_n \, dW/dt \quad (1)$$

and

$$a \, F_n \, dW/dt \quad (2)$$

respectively, where F_n is the fractional nitrogen content of plant dry weight (eg. Kg N/Kg dry wt.), a is the respiration cost per unit nitrogen taken up (eg. Kg CO₂/Kg N), and dW/dt is the time rate of dry matter production (Johnson, 1983). Another metabolic activity of the root system is the utilization of carbohydrate. An efficient root

system appears to be one which can support the minimum metabolic demands during periods of maximum stress without putting excessive demands on the limited quantities of photoassimilates. The metabolic investments for developing and maintaining a functional root system subjected to adverse environments are much greater than in nonstressed environments (Smucker, 1984). Complete analysis of the growth and functions of either roots or shoots is impossible without considering the interrelationship between both organs (Russell, 1977).

Interactions between root and shoot activities has been the subject of considerable research by those scientists (Fischer and Turner, 1978; Huber, 1983; Moony, 1972; Novoa and Loomis, 1981; Russell, 1977; Thornley, 1977; Wareing and Patrick, 1975) who tried to quantitatively describe the processes of growth in a whole plant system. Charles Edwards (1976) model of shoot-root activities during steady state exponential growth, describes and relates the growth constants to the specific activities of both shoot and roots. Reynolds and Thornley (1982), expressed this functional relationship between the size and activity of the roots and the size and activity of the shoots as

$$\sigma_C W_{sh} \propto \sigma_N W_r \quad (3)$$

where σ_C is the specific shoot activity (i.e. the net rate of carbon uptake per unit of shoot structural dry matter), W_{sh} is shoot structural dry matter, σ_N is specific root activity with respect to nitrogen (i.e. the rate of nitrogen uptake per unit of root structural dry matter), and W_r is root structural dry matter. The value of the specific shoot activity (σ_C) is dependent on environmental variables

such as light flux density, CO_2 concentration, and temperature. Specific root activity (σ_N) might be determined by factors such as soil temperature, and soil nitrogen concentration. Based up on these principles, Reynolds and Thornley (1981) developed a two compartment (shoot and root), two substrate (carbon and nitrogen) semi-mechanistic, semi-empirical shoot:root partitioning model.

Understanding the consequences of metabolic activities of roots on the whole plant is necessary in order to assess the integrated growth behavior at the whole plant level. This is a central problem, however, as little is known concerning the carbohydrate requirements of root growth into a new soil volume. Although the absorption of nutrients increases, additional photosynthates, which could have been used in the shoot growth are required by the root. Novoa and Loomis (1981) reported that the leaves have first priority in the use of carbon supply, largely because of their proximity to the photosynthate source. Roots on the other hand, are considered to have a similar priority in nutrient and water uptake. The balance operates to restrict root or shoot growth depending upon whether shoot- or root-supplied factors are more limiting at the moment.

Huck and Hillel (1983) considered carbohydrate partitioning between the root and shoot to be a function of plant water potential. When abundant water is available, shoot growth will be stimulated with little change in the formation of new roots. According to Huber (1983), dry matter distribution between the shoot and root may be related to photosynthate partitioning into soluble carbohydrates and starch. Increased partitioning of the daily photosynthates into starch is inversely related to the relative dry weight of roots in several plant

species. Carbon partitioned into leaf starch was preferentially utilized for growth of shoots at night. This relationship didn't appear to change with the nutritional status of the plant. As growth proceeds, development of the different parts of the plant and their consistent relative sizes are evidence of the close coordination which exists in plant growth processes. Brouwer (1963) showed that if half the leaves or roots of bean plants are removed, the original root/shoot ratio will soon recover, provided that the meristemic tissues remain on both parts of the plant. Some of the root produced hormones (i.e., cytokinins) may be involved in this coordination (Russell, 1977). Dependence of the shoot function on the roots in a number of perennial plants has been indicated by the straight line relationship between the incremental dry weight and incremental mineral uptake rates under many different environmental conditions (Richards, 1980).

Plant organs are continuously competing for the available carbohydrate produced in the leaves. A simple analysis would suggest that to have the highest rate of shoot growth, there is a minimum diversion of carbohydrate to the roots which are currently providing adequate water and nutrients. In this situation, greater root growth would seem to dissipate those metabolites which otherwise could be invested in the photosynthetic apparatus. This analysis may seem reasonable for plants growing under favorable environments, but seldom occurs under natural conditions. Therefore it is believed that successful plant growth strategies are those that provide for the instantaneous needs of the entire plant system. In this situation then, plant productivity may be determined by the development of a root system that is adequate to support plant growth during the time of

maximum stress.

Adverse physical and chemical root environments are a major cause of plant physiological stresses. Soil properties such as temperature, water, aeration and mechanical impedance are manifestations of the resultant dynamic physical forces acting on the soil body. It is these forces which determine to a large extent the physical characteristics of the soil-root interface and the degree of contact between the root and the soil.

Root Responses to Soil Environments

The soil and root interface could be classified into three major categories, chemical, physical, and biological. Although it is recognized that there is a dynamic interaction among these three categories, this report will emphasize the physical factors which primarily influence root growth. In spite of the many chemical stresses which may be eliminated by soil fertility and leaching, physical inadequacies are difficult to eliminate and at best may be temporarily alleviated. Therefore, it is important to continuously maintain the physical condition of the soil.

Adverse physical conditions which roots experience may be categorized into four major classes: mechanical impedance, shortage of oxygen (excessive water), water stress (inadequate water) and unfavorable soil temperature regimes. All of these may cause an adverse environment which stresses the growing roots depending on the degree of their severity. Boyer (1982) describes stress as, plants growing in natural environments which are often prevented from expressing their full genetic potential for reproduction. In order to understand the

mechanisms of physical restraints, we must comprehend the soil structure and its corresponding constituents.

Soil is a three phasic dynamic body consisting of solids (eg. mineral matter derived from parent rock), liquid (eg. water) and gases (eg. oxygen, carbon dioxide, nitrogen and other trace gases). Between 40 to 60 percent of the total soil volume commonly consists of its solid phase including the organic matter (Russell, 1977). The solid phase is penetrated by a network of irregularly shaped pores, filled with air and/or water. The distribution of pores is an important factor in describing the physical state of the soil. For a steady state condition an ideal soil porosity for good root penetration is when 50% of the soil volume is occupied by the solid phase ,25% by water, and 25% by air (Vomocil and Flocker, 1961). From the mechanical point of view, a soil satisfactory for root growth might be visualized as a deformable storage tank which contains liquids and gases and at the same time acts as a conductor of these fluids .

Attempts to describe the physical state of the soil by a single index has led to definitions like, bulk density, void ratio, soil strength, soil compaction, etc. The definition of soil compaction could be described as the increasing of soil bulk density. Although this definition might be satisfactory for agronomic use, it should be realized that soil bulk density only reflects the total volume of pores and does not consider the more important criteria of pore size distributions. Bulk density is generally a confusing term when comparing the porosity of contrasting soil textures, as coarse textured sandy soils normally have higher bulk densities. Too much compaction strengthens the soil, impeding root growth and reducing crop yields

(Dunlap and Weber, 1971). Soil compaction must be characterized in terms of both soil and plant related conditions. Symptoms of soil compaction in plant systems include the presence of horizontal root systems above the compacted zone (Steinhardt, 1982), thicker roots (Goss, 1977), a reduction in dry weight (Asady et al., 1985), and reduced mycorrhizal infections (Mulligan et al., 1985).

Pore Size

The size and continuity of soil pores determines the water potential of the soil and the energy required to extract that water. In a simulated wheel-track experiment, where the average pore size was smaller, the hydraulic potential values were more negative in the wheel-track area than those in the nonwheel-track area (Reicosky et al., 1981). Pore size distribution not only depends upon the state of compaction, but also on the soil texture. Compacted clayey soils generally have smaller pores, consequently the water is more tightly held. The saturated hydraulic conductivity of a compacted soil is usually reduced due to a reduction in total pore volume, with ancillary changes in the size, shape, and continuity of pores. Sinclair et al. (1974) estimated nonsteady state permeability from soil water desaturation data which is the direct consequence of soil porosity.

Russell (1977) classifies the soil pores into three broad categories. Pores which drain freely under forces of gravity so that they are air filled when the soil is at or close to field capacity. The minimum size of the pores in this class is 30-60 μM . Because the diffusion coefficient of oxygen in water is 10000 times less than in

air, soil aeration at field capacity largely depends upon these small water filled pores. The second class of pores are the ones which hold water against gravitational forces but in which the water potential is sufficiently high for absorbing roots to withdraw from it. That is to say, the water potential is above -15 bar (less negative). The minimum size of such pores is $0.2 \mu\text{m}$. The quantity of pores between 0.2 and $60 \mu\text{m}$ is a major factor which determines the reserves of available water. The third class are fine pores which hold water at potentials less than -15 bars (more negative) so that it is essentially inaccessible to roots.

Mechanical Resistance

Root penetration into the soil may be considered from at least two perspectives. First, root penetration is primarily a function of the difference between mean pore diameter and mean root diameter. The second model ignores the direct influence of pore diameter and considers the soil strength as a determinant factor. If a growing root encounters a pore which has a smaller mean diameter than the root tip, it would either have to apply ample pressure to expand the pore or decrease its diameter to be able to penetrate. The later alternative seems unreal, because the diameter of mechanically impeded roots usually increases. Goss (1977) and Wiersum (1957) indicated that plant roots are unable to reduce their diameters when they encounter pores with small mean diameters and mechanical impedance caused their diameter to increase. However, mechanically impeded roots start proliferating and generating fine laterals which penetrate the smaller pores. The increased growth of laterals may then result in the total

root dry weight being unaffected by the mechanical resistance. This compensatory growth of roots is analogous to those observed when part of a root system is subjected to other restraints. For example, when barley roots were grown in rigid ballotini sand having pores with diameters midway between that of the axis and lateral roots, so that the laterals were unimpeded, the total weight of the root was unaffected (Goss, 1977). These smaller branches might be the source of confusion by some workers occasionally reporting a reduction in diameter of mechanically impeded roots (Russell, 1974).

Expansion of the soil pores is a function of root tip pressure and soil resistance to external pressure. Soil is a heterogeneous medium and the enlargement of pores by roots can vary due to either the displacement of the particles or to their deformation. Results of studies on effects of mechanical impedance on root growth using rigid mediums (Gill and Miller, 1956; Goss, 1977; Wiersum, 1957; Goss and Russell, 1980) has demonstrated that rigidity of pore structure is also a factor governing mechanical resistance to root penetration. As long as the roots can displace or deform soil particles they can force through pores originally smaller than themselves. Results of interactions between pore diameter, rigidity of pore structure and root penetration indicated that when the pore size was sufficient to allow penetration by the narrower roots, the depth of penetration increased as the rigidity of the pore structure diminished (Wiersum, 1957). It is generally believed that soil compaction adversely affects plant root growth by (1) increasing the mechanical impedance and (2) altering the extent and configuration of the pore space. A major difficulty in studying the effects of mechanical impedance on root penetration in the

soil is that compacting the soil not only increases mechanical resistant to penetration, but also changes the balance of water and aeration. Aside from the direct influence of mechanical impedance on the supply of oxygen to the soil it is implicated that mechanical impedance induces physiological changes in the root system which predisposes them to greater oxygen deficiencies (Schumacher and Smucker, 1981). The observed responses of root morphology may, therefore, be the consequence of complex interactions of these variables.

Barley (1962), indicated that corn roots can exert longitudinal pressure as high as 12 atmospheres per unit area when subjected to pressures within a flexible diaphragm. The maximum pressure, however, is not as important as the minimum soil mechanical pressure which can appreciably reduce root growth. Other investigations whose experimental systems provided an opportunity to measure the direct affects of the pressures which roots experience have reported that the elongation of root axes is reduced when they are subject to root pressures of 0.5 bar or less (Barley, 1972 ; Gill and Miller, 1956; Abdalla et al., 1969). Greacen and Oh (1972) attribute the sensitivity of root growth to mechanical impedance and relative insensitivity of root growth to changes in soil water potential, to partial osmoregulation of roots against the variable external pressure and complete osmoregulation against the soil water potential.

There are evidences suggesting that the resistance to root extension can not be due solely to the physical effects of external pressure on the elongation of cells. Goss and Russell (1980) conducted an experiment in which the tip of barley root seedlings were subjected

to a small external pressure. There was an appreciable time lag, three or more days, from the time of relief of the external pressure until the rate of root elongation increased to that of unimpeded roots. They suggested that physical restraints imposed on the enlargement of the vacuolating cells was not the only factor responsible for root responses to small external pressures. This information suggests that root responses to mechanical stresses depend upon a complex of many interacting physiological processes.

Morphological effects of mechanical resistance on root growth can include reducing the length of the axes and thickening of laterals. Goss and Russell (1980) reported that when mechanical resistance caused barley roots to curve laterals were initiated on the convex or tension side of the curve and root hairs were more abundant on the concave side. Less impeded roots are much thinner than the roots grown at a high mechanical resistant (Boone and Veen, 1982). Goss(1977) indicated that the rate of root elongation in a number of agronomically important crop plants, including barley, was reduced considerably by small mechanical resistances, when other characteristics of the rooting medium and environmental conditions were favorable to growing roots. Schumacher and Smucker (1981) reported that drybean root systems grown on 1 mm rigid matrix had larger root tissue densities than 3 mm matrix. They also reported that the finer soil matrix reduced porosity of the roots. Wilson et al. (1977) indicated that the diameter of the steele, near the apex of the barley roots, grown under mechanical stress, exceeded that of unimpeded roots by as much as 22% . The increased diameter was not fully accounted for by the shorter roots indicating a reduction in volume by about 40%. There was also a significant increase

in the total number of cells in the steele of apical barley root tips.

Attempts to characterize soil properties such as soil strength and its effect on plant root growth has led to the wide use of soil penetrometers (Bradford, 1980; Voorhees et al., 1975; Blanchar et al., 1978). Koolen and Kuipers(1983) believes that penetrometers can be used for quick determination of soil mechanical or physical properties such as cohesion, angle of soil internal friction, pore space, moisture content, or soil water suction. There are three principle characteristics of the root, however which are quite different from penetrometers and cannot be simulated. These are : (1) the root apex is quite capable of deformation and (2) can curve round the obstacles which they may encounter, and (3) the lubricating effects of the mucigel sheath at the surface of the root cap. It is these considerations, which has caused scientists to use many different static and dynamic penetrometers varying from cone shape and angle to metal and plastic.

Correlation of root elongation rates and penetrometer resistances, has indicated that primary root elongation of pea seedlings were more closely corelated to a 10 degree probe than a 60 degree probe (Voorhees et al., 1975). Close correlation between root elongation rates and soil resistance normal to the probe, which does not include soil-metal friction, may therefore suggest that the root-soil friction is negligible. The complexity of the soil system appears to be the main factor responsible for lack of mechanistic approaches to the problem of soil strength and root growth. Gerard et al. (1982) derived regression equations describing penetrometer resistance and root growth. The critical soil strength at which root elongation stopped was found to

be 60-70 bars in coarse textured soils to 25 bars in clay soils.

Changes in environmental factors such as soil aeration, soil water potential and soil temperature, may modify the response of roots to mechanical resistance. Gill and Miller (1956) indicated that the reduction in root elongation can be enhanced if the concentration of oxygen in the gaseous phase around the roots is reduced to less than 10%. They managed to demonstrate that the ability of roots to overcome mechanical resistance is related to the amount of oxygen available. Rickman et al. (1966) indicated that limiting oxygen concentrations in the root zone of tomato plants reduced the rate of water uptake by the roots almost equally in mechanically compacted and noncompacted soils, even though root growth was quite different. This indicates that in oxygen deficient environments, the rate limiting factor is primarily oxygen partial pressure rather than mechanical impedance. Many investigators (Gill and Miller, 1956; Barley, 1962; Eavis, 1972; Schumacher and Smucker, 1981) have attempted to differentiate the effects of mechanical resistance from aeration in mechanically impeded soils. Eavis (1972) introduced an aeration deficiency index as

$$ADI = (1 - E_1/E_2) * 100 \quad (4)$$

where E_1 is the effects obtained when mechanical impedance and aeration effects are both operating. E_2 is the effects obtained when only mechanical impedance operating.

Aeration Stress

The effects of oxygen stresses on root growth might be due to diffusion resistance in either soil or plant pathways. A third possibility might be the presence of toxic anerobic materials accumulated in the root zone by the high diffusion resistances in the escape pathways (Eavis, 1972). Plant roots growing in the soil may receive their oxygen requirements through two pathways: soil pathway includes diffusion of oxygen through the soil pores and eventually the cell walls. The plant pathway is the diffusion of oxygen in intracellular gas spaces of plants. This pathway appears to be less important for field crops than it is for bog plants (Luxmoore and Stolzy, 1972). Consequently it is generally believed that the soil aeration is the primary factor responsible for diffusion of oxygen into, and carbon dioxide out of the root zone of upland crops.

The rate at which oxygen can diffuse into a porous media may be described by the partial differential equation (Lemon, 1962)

$$\frac{\partial C}{\partial t} = D \nabla^2 C \quad (5)$$

in which C is the concentration or partial pressure of oxygen, t is time and D is the coefficient of gas diffusion in the diffusing medium. The gas diffusion coefficient appears to be the predominate factor controlling the rate of oxygen supply to the soil and describes the resistance of soil pathways to diffusion processes. Therefore, the pore size distribution is an important soil characteristic defining the diffusion pathway. Reducing the size of the pores beyond the mean free path of diffusing oxygen molecules increases the chance of collisions

between the gas molecules and the pore walls resulting in a reduction in the number of molecules transferred. Many investigators (Lemon, 1962; Luxmoore et al., 1970; Luxmoore and Stolzy, 1972; Woolley, 1965; Jensen et al., 1967) have tried to integrate the oxygen demand characteristics of the plant and oxygen supplying power of the soil in a unified model. Lemon (1962) solved the general equation of gas diffusion and derived the following equations

$$C_i = C_R - (q/4D_i)(R^2 - r_i^2) \quad (6)$$

where

$$C_R = C_p + (qR^2/2D_e)\ln(R/r_e) \quad (7)$$

C_i is the oxygen concentration (g cm^{-3}) inside the root at the radial distance r_i (cm) from the root axis, q is the rate of oxygen consumption per unit volume of the root tissues ($\text{g cm}^{-3} \text{ s}^{-1}$), C_R is the concentration (g cm^{-3}) of oxygen at the root surface at the distance of R (cm) from the root center, C_p is the oxygen concentrations (g cm^{-3}) in the liquid at the gas-liquid interface, some radial distance, r_e from the root axis. D_i and D_e are coefficients of gas diffusion ($\text{cm}^2 \text{ s}^{-1}$) inside the root and at the liquid-solid interface, respectively.

Lemon's model does not take into account the longitudinal diffusion of oxygen within the roots. Luxmoore et al. (1970) described a model which accounts for longitudinal as well as radial oxygen diffusion, and considers root respiration to be a function of oxygen concentration and position along the root. Lemon (1962) defined the critical oxygen concentration as the oxygen concentration at the root surface below which the oxygen consumption rate by the root is

reduced. It appears that the soil diffusion is the rate limiting factor below the critical oxygen level. The critical oxygen concentration can be estimated by the equation

$$C_R' = qR^2/4D_i \quad (8)$$

where C_R' is the critical oxygen concentration at the root surface at radial distance (R) from the root center, q is the oxygen consumption rate, and D is the coefficient of gas diffusion inside the root. Schumacher and Smucker (1981) used Lemon's equation to calculate the different critical oxygen concentration for the drybean roots under various mechanical stresses. The calculated C_R' was 0.04, 0.05, and 0.09 atm. when roots were in the solution culture, 3mm and a 1mm matrix of glass beads respectively, at 25C temperature.

Eavis (1972) reported that root elongation of pea seedlings were reduced progressively when the O₂ partial pressure fell below 0.16 atm. He attributes this decline in root elongation rates to the shorter individual cells, since the total number of cells remained the same at this range. The rate of cell division declined when the partial pressure of O₂ reached 0.03 atm.

Water Uptake

Plants growing in the soil may maintain their water uptake, as water is extracted, by either exploring a large volume of the soil or exploiting the particular volume to a greater extent. This could be achieved by roots growing deeper or proliferating within the particular volume and increasing the root density. In both situations it is

necessary to have a soil zone loose enough to allow such root activities. From a physical point of view, this simple analysis seems reasonable. However, larger root systems do not always translate into higher water uptake rates. The hydraulic resistances across the soil-plant pathways must be low enough to permit the water to flow freely within the plant system.

The integrated view of the water transport processes within the soil-plant system has led to considerable research in the area of soil-plant water movement (Arya et al., 1975; Biscoe et al., 1976; Elston et al., 1976; Feddes et al., 1978; Fiscus and Markhart, 1979; Gardner, 1960; Gardner, 1964; Hillel, 1977; Hillel and Talpaz, 1976; Isdo, 1982; Taylor and Klepper, 1978). Many mathematical models have been proposed to quantitatively describe these processes (Huck and Hillel, 1983; Hillel et al., 1976; Lomen and Warrick, 1978; Neuman et al., 1975; Rowse et al., 1983; Warrick and Lomen, 1983; Warrick et al., 1980). All of these models have one thing in common ie., the driving force is the water potential gradient and movement is in the direction of decreasing energy resulting from resistances present along the water flow pathways. Passioura (1981) classifies the flow of water from the soil to the plant as consisting of five major sections: (1) Pararhizal, which starts from a distant soil to the soil close to the roots; (2) perirhizal, from soil close to the roots to the soil-root interface; (3) flow across soil-root interface ; (4) radial flow through cortex and steele to the xylem and (5) axial flow along the xylem.

The flow of an incompressible fluid in a rigid, homogenous, isotropic, and isothermal porous medium can be described by a combination of two equations. The first is Darcy's law, namely

$$q = - K \nabla \theta \quad (9)$$

which describes the flux of water (q) to be proportional to and in the direction of the driving force, and hydraulic conductivity (K) of the porous medium. The second is the conservation of mass principle

$$\frac{\partial \theta}{\partial t} = \nabla \cdot q \quad (10)$$

which states that the time rate of change of water content (θ) in a controlled volume must be equal to the divergence ($\nabla \cdot$) of the flux (q) (Hillel, 1977). When describing the flow of water across a soil-root interface and into the plant, modifications of the basic flow equations are necessary to account for the hydraulics of the root system. Hillel et al. (1976) used such an equation to simulate the pattern of soil water depletion and the spatial distribution of soil-water potentials in the presence of a nonuniform growing root system. This transient state one-dimensional flow equation may be described as

$$\frac{\partial \theta}{\partial t} = \frac{\partial}{\partial z} \left\{ K(\theta) \frac{\partial (h_m - z)}{\partial z} \right\} - S_w \quad (11)$$

where $K(\theta)$ is the hydraulic conductivity of the soil as a function of the soil volumetric water content (θ), h_m is matric potential head, S_w is the sink term for roots, and z and t are the space and time dimensions respectively. Many equations have been proposed to simulate the sink term. Nearly all are driven by the water potential gradient. Gardner (1964) defined the water extraction rate from a unit soil

volume to be

$$S_w = (H_s - H_p) / (R_s + R_p) \quad (12)$$

where subscript s and p represent the soil and plant, H is the total water potential and R is the resistance to flow. The impedance of soil to water movement (R_s) may be a function of unsaturated soil hydraulic conductivity (K) and root length density (L) such that

$$R_s = 1/B K L \quad (13)$$

where B is a constant representing the efficiency of the roots to water uptake. Rowse et al. (1983) derived the impedance to water movement in the soil to be

$$R_s = (-\ln(L \pi r^2)) / (4 L \pi K) \quad (14)$$

where L is the root length density, r is the root radius, K is the hydraulic conductivity. Tinker (1976) described the root water uptake assuming a cylindrical shape root growing into a cylindrical shape hollow of soil whose inner radius (a) is that of the root and whose outer radius is b. Water flows into the root radially at a constant rate per unit length of the root as follows

$$\bar{\theta} - \theta_a \approx \frac{I_w}{2 \pi D_w} \ln\left(\frac{b}{2.1 a}\right) \quad (15)$$

where $\bar{\theta}$ is the average water content of the soil, θ_a is water content

at the root surface, I_w is the water uptake rate per unit length of the root, and D_w is the water diffusivity.

Feddes et al. (1978) considerations of the root system as a sink for soil water differs from the others in that the water uptake rate is not a constant function of water potential gradients over the whole range of soil water potentials observed. They defined three soil-water potential intervals, each having different water uptake rates. The first is from saturation (ψ_0) to an anaerobic point (ψ_1) where the water uptake rate is either zero or reaches zero very quickly. The second is from ψ_1 to a limiting point (ψ_2) where the water uptake rate is maximum. The third is from ψ_2 to a wilting point (ψ_3) where the water uptake decreases linearly to zero. It is within the first and third regions where plants generally suffer the most from water stress. Boyer et al. (1980) also indicated that water deficits of soybeans may develop during the mid-day period especially where roots are shallow regardless of soil water status. This period represent a period of high solar radiation and rapid photosynthesis. Their observations reiterate the inhibitory role of pathway resistances in meeting the evapotranspiration demands of the atmosphere. When the leaf water potential dropped below a threshold value of -11 bars, the photosynthesis rate dropped sharply.

Soil temperature is known to be one of the major components of the soil physical conditions affecting plant growth. Although the thermal conductivity and diffusivity of soils appears to be adversely affected by soil compaction, this variable will not be considered in this study.

LITERATURE CITED

- Abdalla, A.M., D.R.P. Hettiartchi and A.R. Reece. 1969. The mechanics of root growth in granular media. *J. Agric. Eng. Res.* 14:236-248.
- Arya, L.M., G.R. Blake and D.A. Farrell. 1975. A field study of soil water depletion patterns in presence of growing soybean roots. III. Rooting characteristics and root extraction of soil water. *Soil Sci. Soc. Am. Proc.* 39:437-444.
- Asady, G.H., A.J.M. Smucker and M.W. Adams. 1985. Seedling test for the quantitative measurement of root tolerances to compacted soil. *Crop Science* 25:802-806.
- Barley, K.P. 1962. The effect of mechanical stress on the growth of roots. *J. Exp. Bot.* 13:95-110.
- Biscoe, P.V., Y. Cohen and J.S. Wallace. 1976. Community water relations. Daily and seasonal changes of water potential in cereals. *Philo. Trans. Roy. Soc. London. Ser. B.* 273:565-581.
- Blanchar, R.W., C.R. Edmonds and J.M. Bradford. 1978. Root growth in cores formed from fragipan and B2 horizons of Hobson soil. *Soil Sci. Soc. Am. J.* 42:437-440.
- Boone, F.R. and B.W. Veen. 1982. The influence of mechanical resistant and phosphate supply on morphology and function of maize roots. *Neth. J. Agric. Sci.* 30:179-192.
- Boyer, J.S. 1982. Plant productivity and environment. *Science*, 218:443-448.
- Boyer, J.S., R.R. Johnson and S.G. Saupe. 1980. Afternoon water deficits and grain yields in old and new soybean cultivars. *Agron. J.* 72:981-985.
- Bradford, J.M. 1980. The penetration resistance in a soil with well-defined structural units. *Soil Sci. Soc. Am. J.* 44:601-606.
- Brouwer, R. 1962. Distribution of dry matter in the plant. *Neth. J. Agr. Sci.* 10:361-376.
- Charles-Edwards, D.A. 1976. Shoot and root activities during steady-state plant growth. *Ann. Bot.* 40:767-772.
- Dainty, J. 1981. The movement of water across the plant root. *Plant and Soil.* 63:11-14.

- Dunlap, W.H. and J.A. Weber. 1971. Compaction of an unsaturated soil under a general state of stress. *Trans. of The ASAE*. 601-607.
- Eavis, B.W. 1972. Soil physical conditions affecting seedling root growth. I. Mechanical impedance, aeration and moisture availability as influenced by bulk density and moisture levels in a sandy loam soil. *Plant and Soil*. 36:613-622.
- Eavis, B.W. 1972. Soil physical conditions affecting seedling root growth. III. Comparisons between root growth in poorly aerated soil and at different oxygen partial pressures. *Plant and Soil*. 37:151-158.
- Elston, J., A.J. Karamanos, A.H. Kassam and R.M. Wadsworth. 1976. The water relation of the field bean crops. *Philo. Trans. Roy. Soc. London. Ser. B*. 273:581-591.
- Feddes, R.A., P.J. Kowalik and H. Zaradny. 1978. Simulation of field water use and crop yield. John Wiley and Sons. New York. pp:1-10.
- Fischer, R.A. and N.C. Turner. 1978. Plant productivity in the arid and semi-arid zones. *A. Rev. Plant Physiol*. 29:277-317.
- Fiscus, E.L. and A.H. Markhart III. 1979. Relationship between root system water transport properties and plant size in *Phaseolus*. *Plant Phys*. 64:770-773.
- Gardner, W.R. 1964. Relation of root distribution to water uptake and availability. *Agron. J*. 56:41-45.
- Gardner, W.R. 1960. Dynamic aspects of water availability to plants. *Soil Sci*. 89:63-73.
- Gerard, C.J., P. Sexton and G. Shaw. 1982. Physical factors influencing soil strength and root growth. *Agron. J*. 74:875-879.
- Gill, W.R. and R.D. Miller. 1956. A method for study of the influence of mechanical impedance and aeration on the growth of seedling roots. *Soil Sci. Soc. Am. Proc*. 20:154-157.
- Goss, M.J. 1977. Effects of mechanical impedance on root growth in barley (*Hordeum Vulgare* L.). I. Effects on the elongation and branching of seminal root axes. *J. Exp. Bot*. 28:96-111.
- Goss, M.J. and R.S. Russell. 1980. Effects of mechanical impedance on root growth in barley (*Hordeum Vulgare* L.). III. Observations on the mechanism of response. *J. Exp. Bot*. 31:577-588.
- Greacen, E.L. and J.S. Oh. 1972. Physics of root growth. *Nature New Biol*. 235:24-25.
- Gupta, S.C. and W.E. Larson. 1979. A model for predicting packing density of soil using particle-size distribution. *Soil Sci. Soc. Am. J*. 43:758-764.

- Hillel, D. 1977. Computer simulation of soil water dynamics. A compendium of recent work. Box. 8500, Ottawa, Canada K1G 3H9.
- Hillel, D. and H. Talpaz. 1976. Simulation of root growth and its effect on the pattern of soil water uptake by a non-uniform root system. *Soil Sci.* 307-312.
- Hillel, D., H. Talpaz and H. Van Kuelen. 1976. A microscopic-scale model of water uptake by a non-uniform root system and of water and salt movement in the soil profile. *Soil Sci.* 121:242-255.
- Huber, S.C. 1983. Relation between photosynthetic starch formation and dry -weight partitioning between the shoot and the root. *Can. J. Bot.* 61:2709-2716.
- Huck, M.G. and D. Hillel. 1983. A model of root growth and water uptake accounting for photosynthesis, respiration, transpiration, and soil hydraulics. In *Advanced In Irrigation*. ed. D. Hillel . 2:273-333.
- Hunt, R. 1978. *Plant growth analysis*. Edward Arnold (Publisher) Limited. 41 Bedford Square. London. WC1B3DP.
- Isdo, S.B. 1982. Non-water stressed baselines: A key to measuring and interpreting plant water stress. *Agric. Meteo.* 27:59-70.
- Jensen, C.R., L.H. Stolzy and J. Letey. 1967. Tracer studies of oxygen diffusion through roots of barley, corn and rice. *Soil Sci.* 103:23-29.
- Johnson, I.R. 1983. Nitrogen uptake and respiration in roots and shoots : a model. *Physiol. Plant.* 58:145-147.
- Koolen, A.J. and H. Kuipers. 1983. *Agricultural Soil Mechanics*. Springer-Verlag, Berlin, Heidelberg, New York, Tokyo. pp.139-170.
- Lemon, E.R. 1962. Soil aeration and plant root relations. I. Theory. *Agron. J.* 54:167-170.
- Lemon, E.R. and C.L. Wiegand. 1962. Soil aeration and plant root relations. II. Root respiration. *Agron. J.* 54:171-175.
- Lomen, D.O. and A.W. Warrick. 1978. Linearized moisture flow with loss at the soil surface. *soil Sci. Soc. Am. J.* 42:396-400.
- Luxmoore, R.J. and L.H. Stolzy. 1972. Oxygen diffusion in the soil-plant system. VI. A synopsis with commentary. *Agron. J.* 64:725-729.
- Luxmoore, R.J., L.H. Stolzy and J. Letey. 1970. Oxygen diffusion in the soil-plant system. I. A model. *Agron. J.* 62:317-322.
- Mooney, H.A. 1972. The carbon balance of plants. *A. Rev. Ecology and Systematics.* 3:315-346.

- Mulligan, M.F., A.J.M. Smucker and G.F. Safir. 1985. Tillage modifications of dry edible bean root colonization by VAM fungi. *Agron. J.* 77:140-144.
- Naylor, T.H., J.L. Balintfy, D.S. Burdick and K. Chu. 1966. Computer simulation techniques. John Wiley and Sons. New York.
- Neuman, S.P., R.A. Feddes and E. Bresler. 1975. Finite element analysis of two-dimensional flow in soils considering water uptake by roots. I. Theory. *Soil Sci. Soc. Am. Proc.* 39:224-230.
- Novoa, R. and R.S. Loomis. 1981. Nitrogen and plant production. *Plant And Soil.* 58:177-204.
- Passioura, J.B. 1981. Water collection by roots. In : *Physiology and Biochemistry of Drought Resistance in Plants*. L.G. Paleg and D. Aspinall.(eds.) pp.39-55. Academic Press.
- Radford, P.J. 1968. Systems, models and simulation. In : *Annal Report of the Grassland Research Institute*. pp.77-85. GRI. Hurley, Berkshire.
- Reicosky, D.C., W.B. Voorhees and J.K. Radke. 1981. Unsaturated water flow through a simulated wheel track. *Soil Sci. Soc. Am. J.* 45:1-8.
- Reynolds, J.F. and J.H.M. Thornley. 1982. A shoot:root partitioning model. *Ann. Bot.* 49:585-597.
- Richards, D. 1980. Root-shoot interactions: effects of cytokinin applied to the root and/or shoot of apple seedlings. *Scientia Hort.* 12:143-152.
- Rickman, R.W., J. Letey and L.H. Stolzy. 1966. Plant responses to oxygen supply and physical resistance in the root environment. *Soil Sci. Soc. Am. Proc.* 30:304-307.
- Rowse, H.R., W.K. Mason and H.M. Taylor. 1983. A microcomputer simulation model of soil water extraction by soybeans. *Soil Sci.* 136:218-225.
- Russell, R.S. 1977. *Plant root systems : their function and interaction with the soil*. Mc Graw-Hill Book Co.(UK) Ltd. pp:9-27.
- Russell, R.S. and M.G. Goss. 1974. Physical aspects of soil fertility: The response of roots to mechanical impedance. *Neth. J. Agric. Sci.* 22:305-318.
- Schumacher, T.E. and A.J.M. Smucker. 1981. Mechanical impedance effects on oxygen uptake and porosity of drybean roots. *Agron. J.* 73:51-55.
- Sinclair, L.R., D.W.Fitzsimmons and G.L.Bloomsburg. 1974. Permeability of unsaturated field soils calculated from laboratory desaturation data. *Trans. of The ASAE.* 399-405.

- Smucker, A.J.M. 1984. Carbon utilization and losses by plant root systems. In: Roots, Nutrient and Water Influx and Plant Growth.(eds.) Barber and Bouldwin. ASA. Special Pub. Madison Wisconsin. pp27-45.
- Steinhardt, G.C. 1983. Soil compaction : a hidden problem. Better Crops With Plant Food.
- Taylor, H.M. and B. Klepper. 1978. The role of rooting characteristics in the supply of water to plants. *Adv. In Agr.* 30:99-128.
- Tinker, P.B. 1976. Roots and water. Transport of water to plant roots in soil. *Philos. Trans. Roy. Soc. London. Ser. B.* 273:445-461.
- Thornley, J.H.M. 1977. Root:shoot interactions . *Symp. Soc. Exp. Biol.* 31:367-389.
- Vomocil, J.A.,and W.J. Flocker. 1961. Effect of soil compaction on storage and movement of soil air and water. *Trans. of The ASAE.* 242-245.
- Voorhees, W.B., D.A. Farrell and W.E. Larson. 1975. Soil strength and aeration effects on root elongation. *Soil Sci. Soc. Am. Proc.* 39:948-953.
- Wareing, P.F. and J. Patrick. 1975. Source-sink relations and the partition of assimilates in the plant.In: Photosynthesis and Productivity in Different Environments. (ed.) J.P. Cooper. pp481-499.
- Warrick, A.W. and D.O. Lomen. 1983. Linearized moisture flow with root extraction over two-dimensional zones. *Soil Sci. Soc. Am. J.* 47:869-873.
- Warrick, A.W., D.O. Lomen and A. Amoozegarfard. 1980. Linearized moisture flow with root extraction for three-dimensional steady conditions. *Soil Sci. Soc. Am. J.* 44:911-914.
- Wiersum, L.K. 1957. The relationship of the size and structural rigidity of pores to their penetration by roots . *Plant and Soil.* 9:75-85.
- Wilson, A.J., A.W. Robards and M.J. Goss. 1977. Effects of mechanical impedance on root growth in barley (*Hordeum Vulgare* L.). II. Effects on cell development in seminal roots. *J. Exp. Bot.* 28:1216-1225.
- Woolley, J.T. 1965. Drainage requirements of plants. Drainage for effecient crop production. *Conf. Proc. ASAE.* St. Joseph, Mich. PP:2-5.

CHAPTER 2

SEEDLING TEST FOR THE QUANTITATIVE MEASUREMENT OF ROOT TOLERANCES TO COMPACTED SOIL

ABSTRACT

Root responses of plant genotypes to compacted soils have not been well defined. This experiment was conducted under controlled environments using a soil core seedling test consisting of an experimentally compacted soil having air filled porosities of 31, 18, and 6%. Root penetration ratios were measured 14 days after planting without destroying seedling viability. Root penetration ratios and root lengths declined linearly with decreasing air filled porosity. Xylem accumulations of toxic anaerobic metabolites were directly correlated with soil bulk density and inversely related to oxygen diffusion rates in the soil. High correlations ($R=0.91$) were observed between root penetration ratios of this rapid test and the growth and yield of field grown dry edible beans.

INTRODUCTION

Root penetration and exploration of the soil horizons are essential if maximum crop yields are to be achieved. Plant root growth is generally reduced by the soil matrix, especially if the soil particles are compacted by traffic or tillage. Excessive tillage and traffic generally reduce both the size and abundance of soil pores through which plant root systems develop (Cassel, 1982). Root systems stunted by compacted soils generally reduce plant vigor and crop yield. The selection of crop cultivars having some tolerance to certain compacted soils is expensive using conventional plant breeding field programs (Ghaderi et al., 1984). It is also very difficult to quantify root morphological responses of plant populations grown in the field. Furthermore, we believe that more quantitative information relating specific root responses to compacted soils must be available before improved selection programs can be established.

Bohm (1979) reported that several container experiments have been designed to measure the influence of soil bulk densities on the growth of roots. Those approaches demonstrate the adverse effects of greater soil bulk densities on the growth of roots, but are not designed to provide rapid and quantitative root responses to multiple levels of soil compaction. The objective of this study was to examine some of the primary morphological and physiological root responses of several cultivars to soil compaction using a rapid and nondestructive soil core seedling test.

MATERIALS AND METHODS

Polyvinyl chloride cylinders, having inside diameters of 7.6, and a wall thickness of 0.64 cm were used to establish the layered soil containers consisting of a stack of three cores. Each three layered container consisted of top and middle cores which were 2.5 cm in height and a bottom core which was 7.6 x 7.6 cm. The cores of this study were filled with Charity clay, an illitic, calcareous, mesic, Aeric Haplaquept soil containing 53% clay and having a consistency ranging from very elastic when wet, to very hard when dry. Soil aggregates sieved to a range of 0.25-2.0 mm, were equilibrated to a constant gravimetric soil moisture content of 18% and uniformly compacted to the desired bulk densities. The soil was compressed into 2.5 cm high cores by a piston (7.6 cm diameter) attached to a hydraulic press (Carver Type, Model 20505-11). Initial bulk density levels of 1.1, 1.4, and 1.7 Mg m⁻³ were established by pressing a specific quantity of soil into the middle 2.5 cm core. Compacted cores were sandwiched between the top and the bottom cores which had approximate bulk densities of 1.1 Mg m⁻³. The three cores were sealed together into one air and water-tight soil container by wrapping them with 5 cm wide plastic impregnated duct tape. Each soil container was saturated for 48 h, drained, and seedlings were transplanted into the surface soil. Each experimental unit of soil consisted of one core assembly containing two plants. Soil moisture contents were

determined by weighing the experimental units daily and adjusting the moisture content as directed by the water retention curve (Richards, 1965). Oxygen diffusion of the soil at an equilibrium matric potential of -8 kPa was measured by the D/D_0 method of Taylor (1949). Oxygen diffusion rates were measured at the same water potential by the platinum microelectrode method of Lemon and Erickson (1955). Aeration status, water content and bulk density of the soil in each treatment are reported in Table 1.

Seeds of Phaseolus vulgaris L. cultivars 'Black Turtle Soup', 'NEP-2', 'Swan Valley', and 'Domino' were surface sterilized with 0.1% sodium hypochlorite and germinated on wet paper surfaces @ 25° C. 'Swan Valley' (a small white seeded cultivar) and 'Domino' (a small black seeded cultivar) are progeny of the cross between 'NEP-2' (a small white seeded cultivar) and 'Black Turtle Soup' (a small black seeded cultivar). Two uniform seedlings were transplanted to each core and grown for 14 days in the growth chamber at a constant humidity of $65 \pm 5\%$, day/night temperatures of 24/18°C and a 16 h photoperiod with a light intensity of $640 \text{ mol m}^{-2} \text{ s}^{-1}$. Water was applied twice daily to maintain an average soil water potential of $-8 \pm 2 \text{ kPa}$. Nutrient solution, 10 ml of a 50% Hoaglands, was applied daily during the second week of growth. The experimental design was a randomized complete block which was replicated four times. Each experiment was repeated once and the data combined for the analysis of variance.

Two weeks after transplanting, leaf abaxial diffusive resistance was measured by a LICOR Model 3000 diffusion porometer. Then seedlings were harvested by cutting the stems at the first

cotyledonary node, stems were blotted and fitted with a latex rubber tube which accumulated the xylem exudate for one hour. Acetaldehyde and ethanol contents in the xylem exudate were determined by gas-liquid-chromatography (Smucker and Erickson, 1976). Morphological plant parameters measured were shoot and root fresh and dry weights, leaf area, root length and root penetration ratios. The root penetration ratio (RPR) is defined as a ratio of the number of roots which exit the compacted middle core divided by the number of roots which penetrate the same core. Values of the RPR were determined for the central 20.3 cm^2 area of the middle core to eliminate any influence the soil and container interface could have on root growth. Roots in each layer of the soil container assembly were determined by cutting the system into its three primary components and washing the roots from the soil of each layer by the hydropneumatic elutriation method of Smucker et al. (1982). Root length for each layer was approximated by the line intercept method of Newman (1966).

Plant dry weight and yield values from the field are the average of a three year study at the Michigan State University Research Farm near Saginaw, Michigan. The Charity clay soil on this farm was compacted to a depth of 7-10 cm by multiple passes of wheel traffic and secondary tillage (Smucker, 1985) which resulted in bulk densities similar to those reported above for the soil core seedling test.

RESULTS AND DISCUSSION

Reduced air filled porosity, resulting from greater compression of soil in the middle core, caused a reduction in the root penetration ratios of the four dry edible bean cultivars evaluated in this study (Figure 1). Root growth at 14 days was directly related to the aeration status of the soil (eg., air filled porosity and oxygen diffusion rate) and inversely related to the mechanical resistance of the soil. Mechanical impedance of the soil, approximated by the penetrometer (Table 1), reduced root penetration and root length densities in both the middle and bottom soils of the core assembly, Table 2. Although more roots accumulated in the top soil, as compaction of soil in the middle cores increased (Table 2), the total length of roots which accumulated in the entire core assembly was significantly reduced by soil compaction, Table 3. Root growth in the middle and bottom cores of the most compacted soil was greatly inhibited by mechanical impedance and oxygen exclusion (Tables 1 and 3). Greater soil bulk densities not only created an oxygen stressed environment for the roots, but also reduced the mean diameter of air filled pores. Assuming macroscopic pore continuity and applying capillary theory, one can approximate the air filled pore diameters to be ≥ 0.03 mm at a soil matric potential of -8 kPa. As the soils became more compacted, the air filled porosities for the same water potential were reduced to 18 and 6% for the intermediate and most

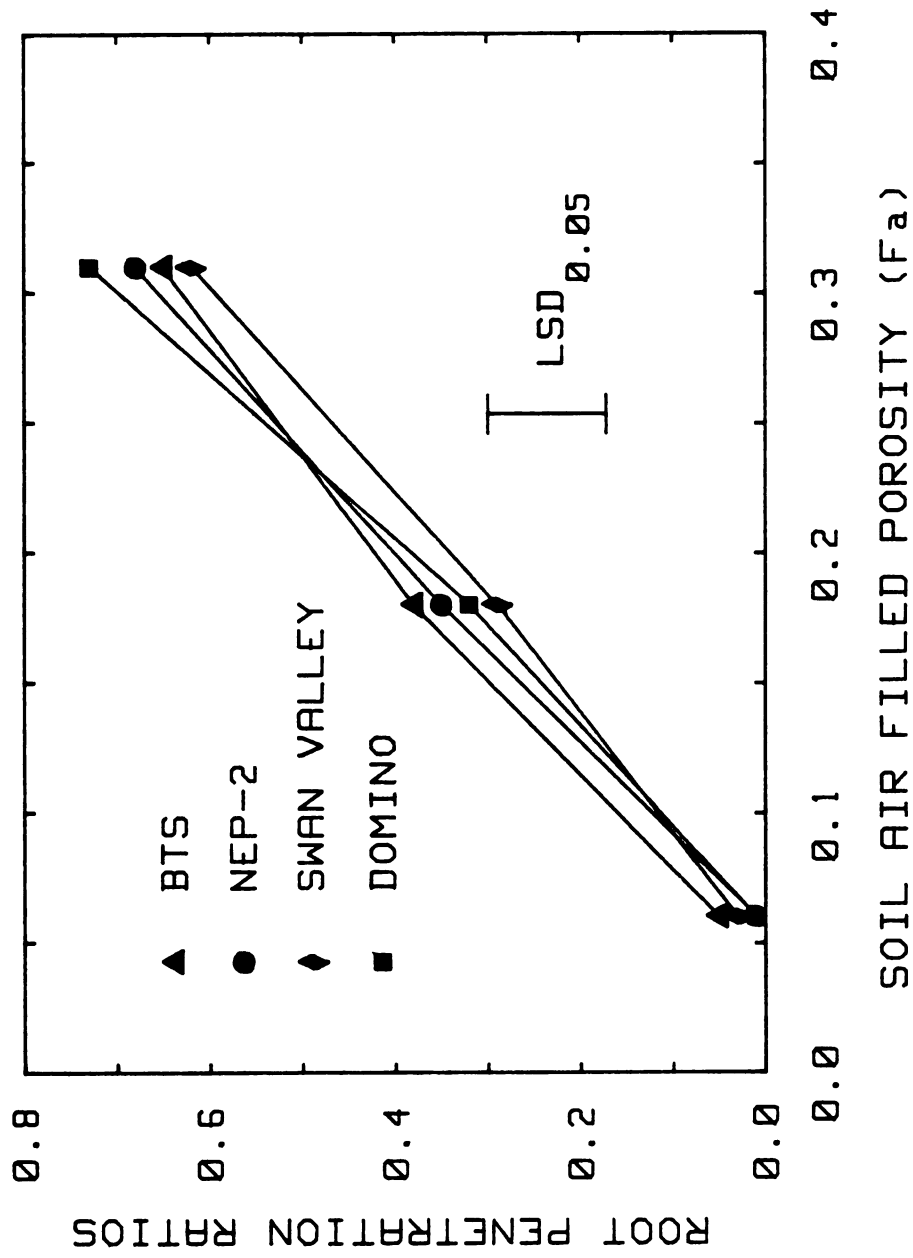


Figure 1. Root penetration ratio responses of four dry edible bean cultivars to air filled porosities of a clay soil at -8 ± 2 kPa water potential. Each data point represents the mean of eight replications.

Table 1. Influence of soil compression on the soil bulk density, water retention, penetrometer resistance, and aeration status of an expanding clay soil at several soil water contents. Each value is the average of five to eight replications.

Saturation	Soil bulk density		Soil water content at -8kPa	Penetrometer resistance at -8kPa	Air filled porosity at -8kPa	ODR at -8kPa	D/D ₀ at -8kPa
	0.18†	Oven dry					
- - - -	Mg m ⁻³	- - - -	m ³ m ⁻³	MPa	%	μg m ⁻² s ⁻¹	
1.15	1.10	1.39	0.26	0.43	31	81.7	0.27
1.30	1.40	1.70	0.33	2.10	18	25.0	0.18
1.52	1.70	2.10	0.37	5.46	6	16.7	0.04

† Gravimetric soil moisture content.

Table 2. Root length density in the top, middle, and bottom cores when the middle core was subjected to three levels of soil compaction.

Air filled porosity	Cultivars	Root length density			
		Weighted average	Top	Middle	Bottom
%		----- km m ⁻³ -----			
31	Black Turtle	45 g†	43 ab	57 de	42 d
	NEP-2	43 fg	41 a	62 e	36 c
	Swan Valley	41 def	46 ab	44 b	37 cd
	Domino	42 efg	45 ab	57 de	35 c
18	Black Turtle	41 def	70 de	52 cd	28 b
	NEP-2	34 c	54 bc	48 bc	23 b
	Swan Valley	38 cde	62 cd	44 b	28 b
	Domino	37 cd	68 d	45 bc	24 b
6	Black Turtle	19 b	89 f	7.3 a	0 a
	NEP-2	11 a	50 abc	5.2 a	0 a
	Swan Valley	17 b	80 ef	7.0 a	0 a
	Domino	13 a	59 cd	4.1 a	0 a

† Values in each column followed by the same letter are not significantly different at the 0.05 level of probability according to the Least Significant Difference.

Table 3. Total and relative root lengths in the top, middle, and bottom cores when the middle core was subjected to three levels of soil compaction.

Air filled porosity	Cultivars	Total root length	Relative root length		
			Top	Middle	Bottom
%		m	- - - - - % - - - - -		
31	Black Turtle	26.34 g†	19.1 a	25.4 bcd	55.5 d
	NEP-2	24.71 fg	19.4 a	29.5 e	51.1 d
	Swan Valley	23.50 def	22.9 a	21.8 b	55.3 d
	Domino	24.09 efg	21.6 a	27.6 cde	50.8 d
18	Black Turtle	23.83 def	34.4 bc	25.3 bcd	40.3 bc
	NEP-2	19.86 c	31.4 b	28.3 de	40.3 bc
	Swan Valley	22.16 cde	32.1 b	23.0 b	44.9 c
	Domino	21.50 cd	36.7 c	24.1 bc	39.2 b
6	Black Turtle	11.15 b	92.4 d	7.6 a	0.0 a
	NEP-2	6.41 a	90.4 d	9.6 a	0.0 a
	Swan Valley	10.05 b	91.7 d	8.3 a	0.0 a
	Domino	7.32 a	93.4 d	6.6 a	0.0 a

† Values in each column followed by the same letter are not significantly different at the 0.05 level of probability according to the Least Significant Difference.

compacted soils, respectively. These changes may be attributed to the reduction in the number of pores with diameters ≥ 0.03 mm in the compacted soil. Since the weighted mean diameters of dry edible bean roots are reported to range from 0.3 to 0.8 mm (Schumacher, 1979 and Fiscus, 1981), the proportion of air filled pores having diameters smaller than roots is greatly increased. Consequently, the roots of plants growing in highly compacted soils are more likely to be impeded by the smaller pores. This, along with anaerobic conditions created by soil compaction, suggests that most of the roots in this experiment were unable to penetrate due to their large diameters and low metabolic energy (Russell, 1977). The greater percentage of roots in the surface soil of this study (Table 3), is very similar to field observations and a previous report of soybean root distribution in compacted clay soils (Smucker, 1985). These phenomena, combined with reductions in total plant root length, reduce plant tolerances to short-term dry surface soils.

Smaller root systems of the physically stressed 14 day-old seedlings appear to cause lower rates of xylem accumulation and greater leaf diffusive resistances (Figure 2 and Table 4) even though soil matric potentials were similar. These root-related stresses caused a general reduction in the dry weight and leaf area of seedling shoots when the soil was compacted (Table 4). Shoot growth rates of dry edible beans grown on the most compacted soil began to decline 6-8 days after transplanting (Figure 3). Shoot growth during the first 14 days of this soil core seedling test was similar to the power function described by Fiscus (1981). Our data indicate that coefficients of those equations must be different for each level of soil compaction.

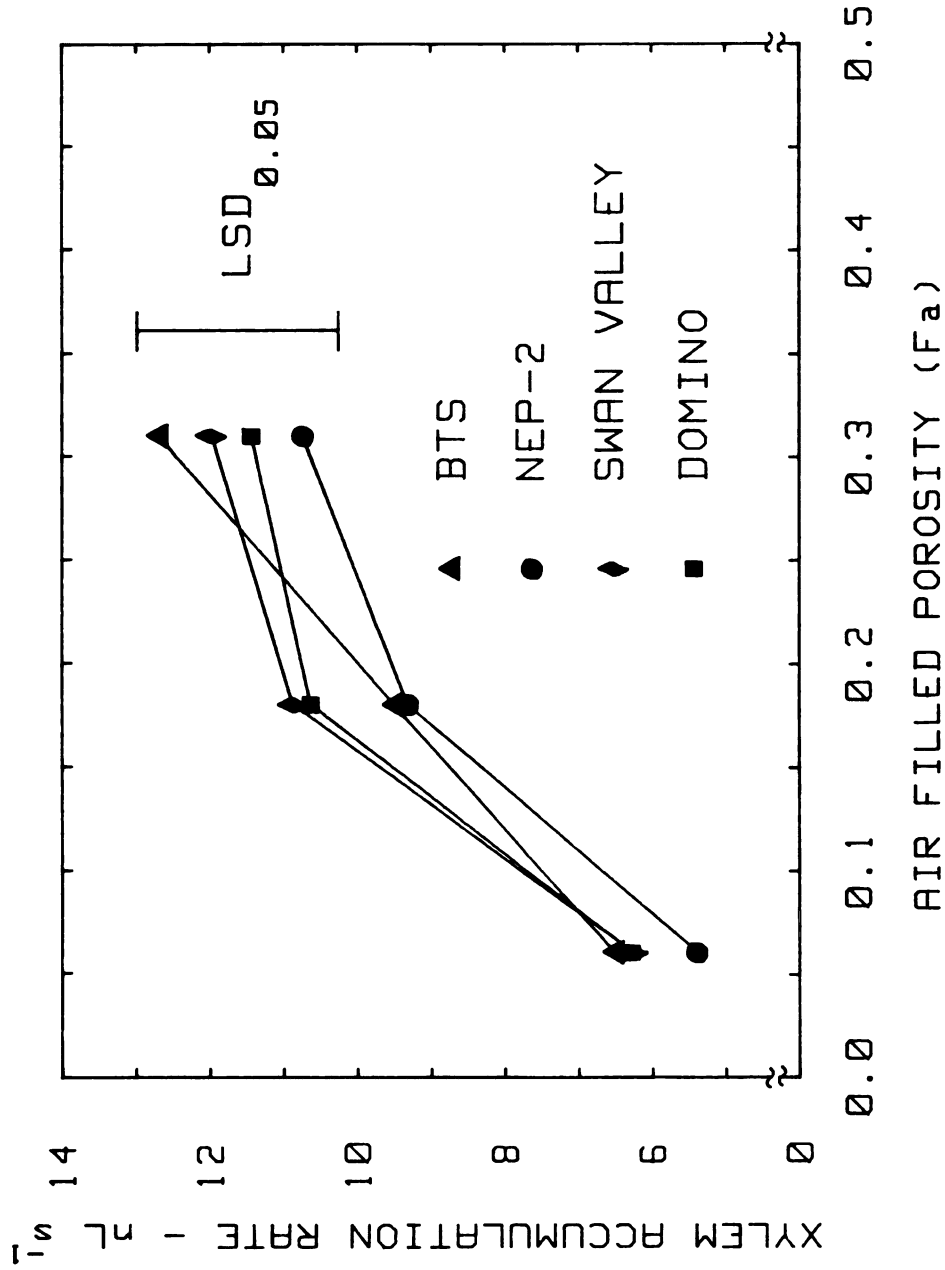


Figure 2. Xylem accumulation rates of dry edible beans grown in compacted clay soils. Each data value is the mean of eight replications.

Table 4. Influence of air filled porosity on shoot weight, leaf area and stomatal diffusive resistance of four dry edible bean cultivars at 14 days in the soil core seedling test.

Air filled porosity	Cultivars	Shoot dry mass	Leaf area	Diffusive resistance
%		g	cm ²	s m ⁻¹
31	Black Turtle	1.08 d†	198.0 c	910 a
	NEP-2	0.96 bcd	174.2 bc	870 a
	Swan Valley	0.79 ab	166.7 bc	1150 ab
	Domino	1.01 cd	186.0 c	1140 ab
18	Black Turtle	1.02 cd	179.8 bc	1210 ab
	NEP-2	0.88 abcd	151.4 ab	1320 ab
	Swan Valley	0.84 abc	176.2 bc	980 a
	Domino	1.02 cd	185.7 c	1050 a
6	Black Turtle	0.84 abc	128.4 a	1710 ab
	NEP-2	0.82 abc	132.7 a	2330 b
	Swan Valley	0.70 a	123.5 a	2370 b
	Domino	0.94 bcd	127.2 a	4040 c

† Values for each column followed by the same letter are not significantly different at the 0.05 level of probability according to the Least Significant Difference.

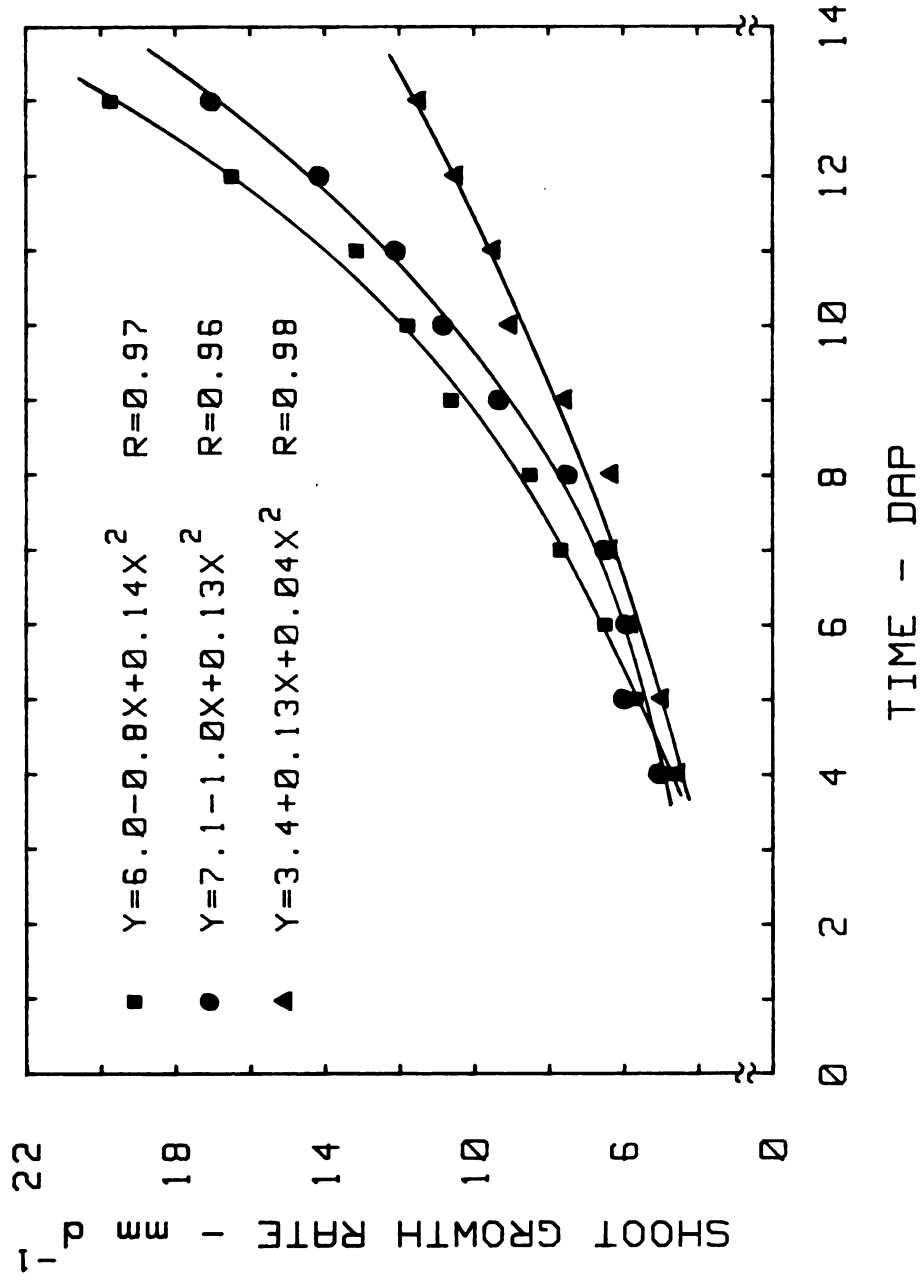


Figure 3. Shoot growth responses of dry edible beans to three levels of compacted clay soil cores during two weeks of growth. The square, circle, and triangle symbols represent air filled porosities of 0.31, 0.18, and 0.06, respectively. Each data point is the mean of four cultivars replicated eight times.

Internal aeration of the soils in this study was inversely related to the extent of compaction (Table 1). As the air filled porosity decreased to 6% the diffusion of oxygen was too low to support optimum aerobic root growth (Erickson, 1982). Declining oxygen availability decreases oxidative phosphorylation causing more of the photoassimilate carbon of roots to be converted to ethanol via acetaldehyde (Russell, 1977). Acetaldehyde and ethanol accumulations in the xylem exudates of Phaseolus cultivars appeared to be inversely related to the aeration status of the soil treatments (Table 5). Although there were no significant differences for the cultivar 'Black Turtle Soup', acetaldehyde and ethanol accumulations of the cultivar 'NEP-2' were significantly greater when grown on the most compacted soils.

Total length of accumulated root growth appeared to be the most significantly different growth variable among the four cultivars grown in the phytotron conditions of this study. 'Black Turtle' had a significantly greater root length than 'Swan Valley' at the lowest level of soil compaction. This difference was reduced with increasing bulk density. The root length of 'Black Turtle' was significantly greater than 'NEP-2' at the intermediate level of compaction and significantly greater than both 'NEP-2' and 'Domino' at the greatest level of soil compaction (Table 3). The cultivar 'Black Turtle' appeared to have the greatest values for root length, root length density, shoot weight and leaf area for nearly all levels of soil compaction. Root penetration ratios were significantly different between 'Domino' and 'Swan Valley' at the lowest level of soil compaction (Figure 1). This difference was negated, however, by

Table 5. Influence of air filled porosity on the accumulation of toxic anaerobic metabolites by black and white dry edible beans grown for 14 days in the soil core seedling test.

Air filled porosity	Cultivars	Acetaldehyde	Ethanol
%		$\mu\text{g L}^{-1}\text{s}^{-1}$	$\mu\text{g L}^{-1}\text{s}^{-1}$
31	Black Turtle	2.14 a†	1.50 a
	NEP-2	1.86 a	1.05 a
18	Black Turtle	1.89 a	1.53 a
	NEP-2	3.22 ab	1.36 a
6	Black Turtle	2.86 ab	7.33 a
	NEP-2	5.75 b	15.03 b

† Values for each column followed by the same letter are not significantly different at the 0.05 level of probability according to the Least Significant Difference.

increasing levels of soil compaction.

Although the soil core seedling test provides the experimental conditions for morphological and metabolic measurements, the real test of this method is how well these results from the growth chamber may be correlated with those of field studies. A quadratic function of RPR was highly correlated ($R=0.92$) with plant dry weights of field samples (Figure 4). Figure 5 reports an excellent multiple correlation ($R=0.91$) between a quadratic function of RPR values from the soil core seedling test and the yields of dry edible bean cultivars grown on the same soil type having similar bulk densities. The close correlation between these two plant variables and the RPR values suggest that the soil core seedling test could be used to determine specific genotype responses to soil compaction. In addition, these data suggest that RPR values from multiple field samples could be used to develop a RPR index for evaluating dry edible bean and other cultivar responses to specific soil and tillage conditions. It further indicates that when RPR values approach 0.65 the growth and yield of dry edible beans appear to be no longer affected by soil physical conditions which control root penetration (Figures 4 and 5). Since RPR measurements can be made without destroying the entire root system, soil core seedling tests in the laboratory and field should be useful to breeding programs for determining the inheritance of root tolerance to compacted and other specific soil conditions.

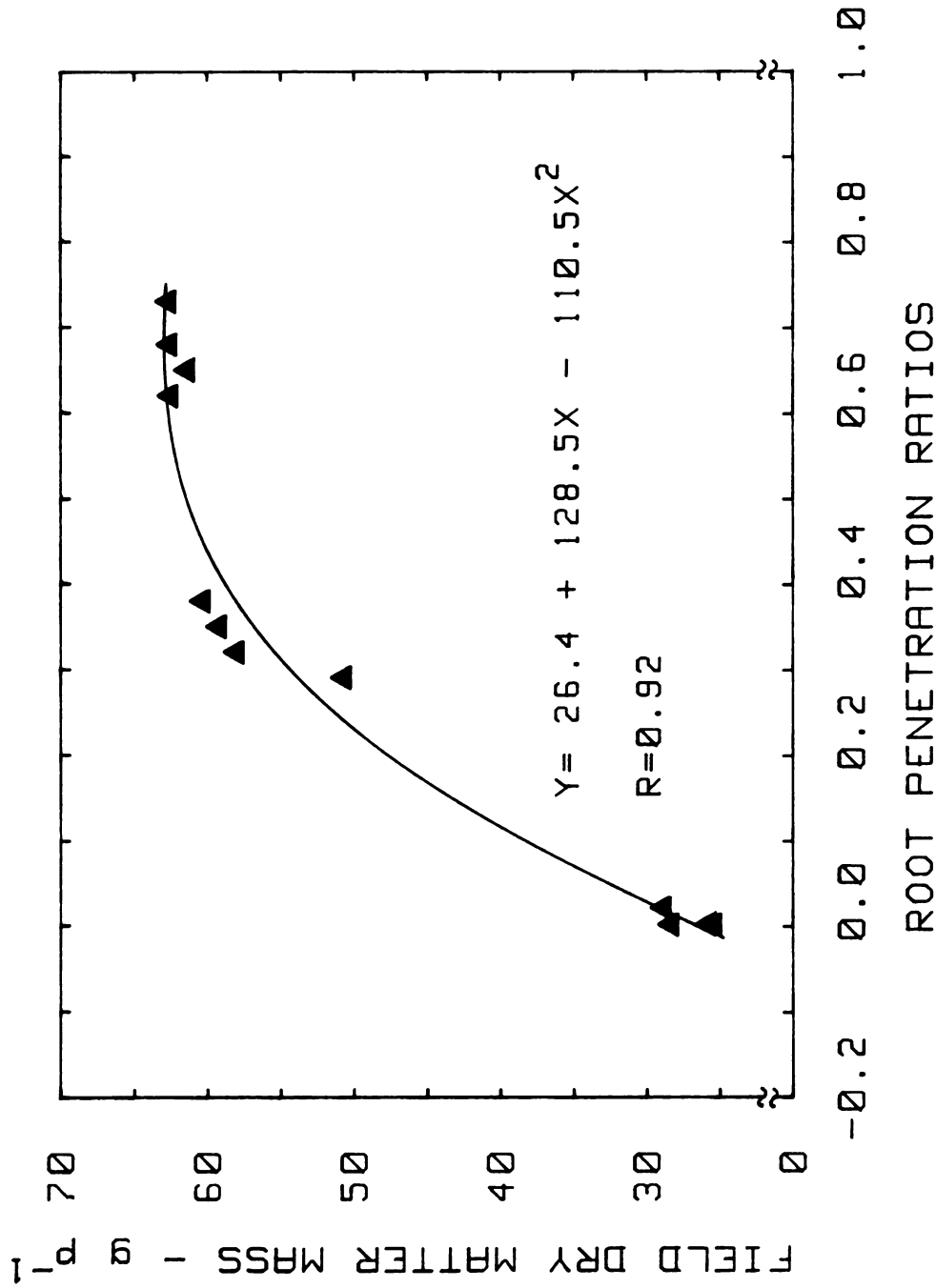


Figure 4. Multiple correlation of a quadratic function of root penetration ratios of four dry edible bean cultivars grown in three levels of a compacted clay soil core to the dry matter accumulation of the same cultivars grown on similarly compacted clay soils in the field. Each data point is the mean of four replications for each cultivar.

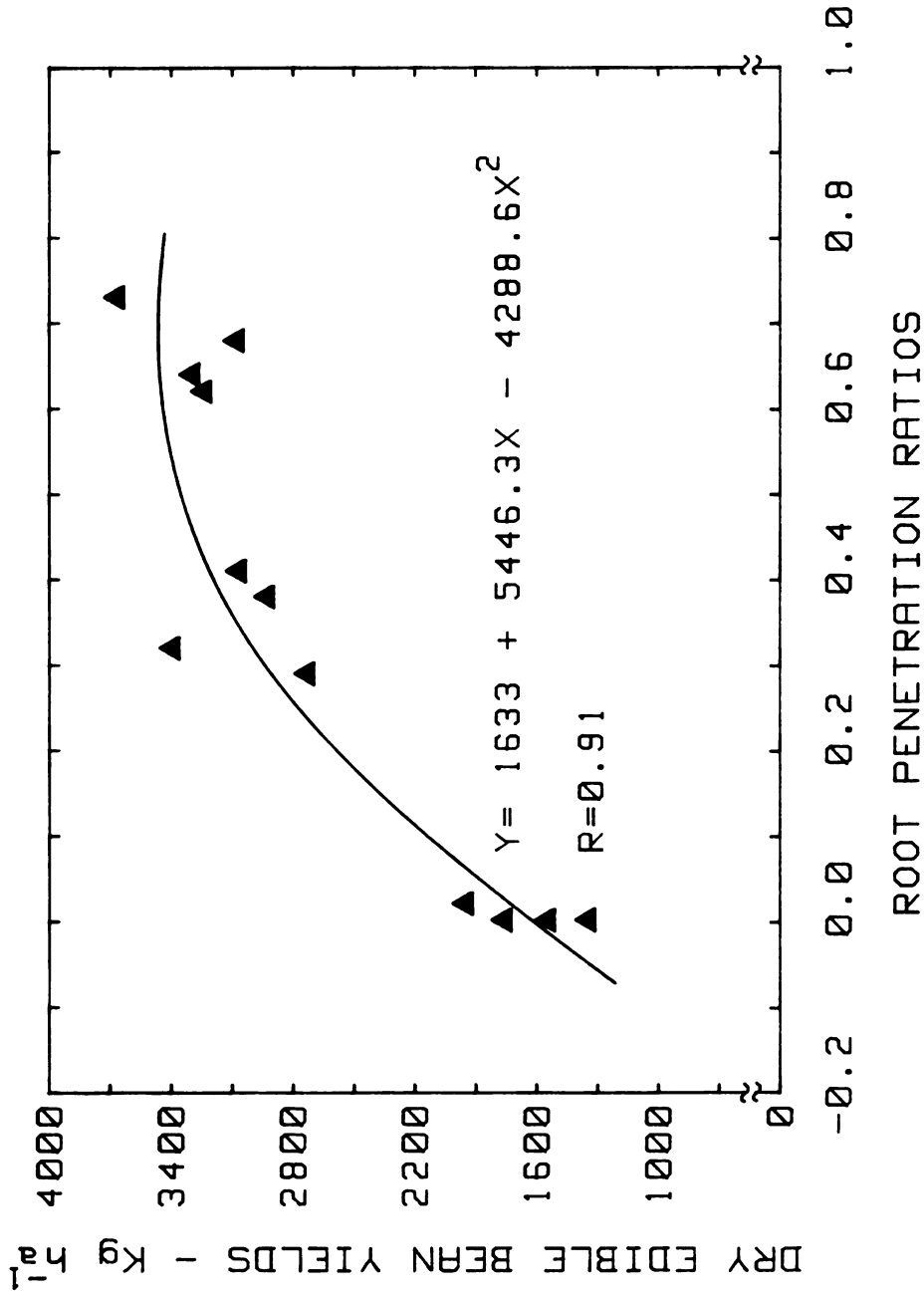


Figure 5. Multiple correlation of a quadratic function of root penetration ratios of four dry edible bean cultivars grown in three levels of a compacted clay soil core to the yield of the same cultivars grown on similarly compacted clay soils in the field. Each data point is the mean of four replications for each cultivar.

LITERATURE CITED

- Bohm, W. 1979. Container methods. In: Methods of Studying Root Systems. Springer-Verlag. Berlin.
- Cassell, D.K. 1982. Tillage effects on soil bulk density and mechanical impedance. In: Predicting Tillage Effects on Soil Physical Properties and Processes. ASA Spec. Pub. No. 44 pp. 45-67.
- Erickson, A.E. 1982. Tillage effects on soil aeration. In: Predicting Tillage Effects on Soil Physical Properties and Processes. ASA Special Pub. No. 44. pp. 91-104.
- Fiscus, E.L. 1981. Analysis of the components of area growth of bean root systems. Crop Sci. 21:909-913.
- Ghaderi, A., A. J. M. Smucker, M. W. Adams and A. W. Saettler. 1984. Breeding implications of stress induced by soil compaction. Euphytica 33:377-385.
- Lemon, E. R. and A. E. Erickson. 1955. Principle of the platinum microelectrode as a method of characterizing soil aeration. Soil Sci. 79:383-391.
- Newman, E.I. 1966. A method of estimating the total length of root in a sample. J. Appl. Ecol. 3:139-145.
- Richards, L. A. 1965. Physical condition of water in soil. In: Methods of Soil Analysis, Physical and Mineralogical Properties. Part I. Agronomy 9:128-152. C. A. Black (ed.).
- Russell, R. S. 1977. Effects of anaerobic soil conditions. In: Plant Root Systems Their Function and Interaction with the Soil. McGraw-Hill, London.
- Schumacher, T. E. 1979. The influence of mechanical impedance and short term anoxia on respiration, growth and structure of Phaseolus vulgaris L. roots. M.S. Thesis. Michigan State Univ. p. 52.
- Smucker, A.J.M. 1985. Soybean crop responses to soil environmental stresses. (R. Shibles, ed.) Proceedings World Soybean Research Conference III. Ames, Iowa 15 pp.
- Smucker, A. J. M. and A. E. Erickson. 1976. An aseptic mist chamber: A method for measuring root processes of peas. Agron. J. 68:59-63.

- Smucker, A. J. M., S. L. McBurney and A. E. Srivastava. 1982.
Quantitative separation of roots from compacted soil profiles
by the hydropneumatic elutriation system. Agron. J. 74:500-503.
- Taylor, S. A. 1949. Oxygen diffusion in porous media as a measure
of soil aeration. Soil Sci. Soc. Am. Proc. 14:55-61.

CHAPTER 3

EFFECTS OF MECHANICAL IMPEDANCE AND AERATION ON DRY BEAN ROOT GROWTH

ABSTRACT

Spatial and temporal responses of dry edible beans (Phaseolus vulgaris L.; cv. Seafarer) grown under different compaction and aeration treatments were studied in a greenhouse environment. Extreme soil compaction resulted in mechanical resistances as high as 5500 kPa. This mechanical impedance reduced total root length by 80 and 71% in the aerated treatments, and 81 and 77% in the nitrogen treated treatments for 20 and 30 days after planting (DAP) respectively. Root extension into deeper layers was practically halted at a depth of 10 cm, with approximately 90% of the roots being at the surface 2.5 cm, 20 DAP.

Oxygen diffusion into and carbon dioxide out of the soil was significantly curtailed by high mechanical impedance. Oxygen concentration depressions and carbon dioxide elevations within the soil reached as much as 5 and 10% respectively. Oxygen diffusion rate (ODR) and D/D_o characterization of the soil aeration status, both indicated that anaerobic soil conditions resulted from the high bulk densities. Approximately 12% of the air filled pores of the surface

layers were plugged by the compensatory root growth in this layer due to high mechanical resistance of the compacted soil. These deleterious effects of soil compaction on plant growth necessitate cultural practices which avoid traffic of heavy machinery on the field.

INTRODUCTION

Studies of the physical factors which influence root growth often include the characterization of those physical and biological soil processes which are associated with bulk density (Gupta and Larson, 1982). One of the major reasons for manipulating agricultural soil is to create a physical condition of the soil which favors root growth. The development of this condition includes minimization of the mechanical barriers to root growth, and optimization of soil aeration, soil water content, and soil temperature.

Soil compaction may be described as the manifestation of excessive physical forces acting on a soil body resulting in a relatively static condition which influences the dynamic responses of plants to soils. The degree of soil compaction depends very much on the biophysical state of the soil. For instance, when a tillage tool is pulled across a field, conditions of the moving soil are changed. Soil properties such as size and distribution of particles, water content, soil structure and organic matter content respond to the applied forces. Soil compaction usually changes the existing balance between the liquid, gas, and solid phases in a given unit of soil volume. The net result usually is a reduction of liquid and gas in the pores, an increase in the proportion of the solid phase, an increase in the pore water and air pressures, and a rearrangement of the particles. All of these changes contribute to the increasing mechanical resistance of a

compacted soil.

Mechanical resistance may be characterized by several methods which assess the different mechanical properties of a soil. These include, penetrometers, modulus of rupture, shear planes, and triaxial tests, all of which give empirical results. These values should be calibrated against specific plant growth variables before they can be used for prediction equations (Bowen, 1981). Since plant growth is dependent upon mechanical as well as physio-chemical soil properties, penetrometer results should be calibrated against plant growth variables only when all other soil properties are optimum and plant growth response is largely due to mechanical soil properties. Some physical soil properties such as water content strongly affects the mechanical behavior of a given soil.

Mechanical resistance of the soil is a constraint to both root growth and plant production. Root responses to mechanical impedance can vary from the bending of root tips to abrupt changes in root diameters and direction. Voorhees et al. (1975) reported that the root length density of peas, grown on mechanically compacted soils, increased due to an increase in the root length of first order laterals of primary roots. This mechanical impedance usually resulted in the reduction of plant growth and yield. Carmi and Heuer (1981) characterized plants with restricted roots as being smaller and having leaves with smaller surface areas and shorter internodal distances. They attributed these differences to be hormonally regulated and suggested that mechanically impeded roots may control the balance of hormones.

Mechanical impedance appears to be inversely related to the root elongation rates and directly related to the root diameters in many

annual plants. Penetrometer resistance of 580 to 1150 kPa appeared to severely reduce the elongation rates of cotton roots (Taylor and Ratliff, 1969a,b). Mechanical impedance as low as 25 kPa reduced the root elongation rates of maize and peas by 69%, and barley by 43%. Russell and Goss (1974) reported that the extension rate of barley roots was reduced 50% by 20 kPa, and 80% by 50 kPa external pressures. Voorhees et al. (1975) reported an inverse relationship between root elongation rates and penetrometer resistances. They obtained a better correlation when the penetrometer tip had an angle of 10 degrees than 60 degrees. This suggests that normal point resistance is a better indicator of soil resistance to root penetration than total point resistance. Mechanical impedance appears to increase root diameter. Taylor et al. (1972) reported that when the root tips encountered resistance, their elongation regions increased in diameter .

Root growth pressure is known to be the main driving force behind penetrating roots. It is therefore logical to assume that the higher the root growth pressure, the higher the elongation rates for a given soil condition. Maximum root growth pressure for cotton has been reported to be less than 1300 kPa (Taylor and Ratliff, 1969a). Even though there are cultivar differences in these root responses to external pressures, there is a general agreement that maximum longitudinal root growth pressures seldom exceed 1500 KPa for most common crops (Taylor and Ratliff, 1969a; Russell and Goss, 1974; Kibreab and Danielson, 1977).

An adequate supply of oxygen to the roots is essential if maximum growth of plants is desired. Lack of sufficient oxygen in the soil is perhaps one of the greatest limiting factors in the development of an

extensive root system. Since active surfaces of the roots are covered with a film of water and the diffusion of oxygen in water is 10^{-4} that in air, the composition of air in the rhizosphere is not as important as oxygen fluxes toward the roots. Consequently, the oxygen supplying power of a soil is complicated by the distributions of capillary and noncapillary pores and the degree of saturation.

A low internal aeration capacity is usually accompanied by those soil conditions which mechanically impede root growth. Vomocil and Flocker(1961) reported that when the soil moisture content was at field capacity root growth was inhibited when the soil aeration porosity fell below 10%. Crop yields are often reduced when the non-capillary pore space drops below 10% (Erickson, 1982). Hence, it is generally believed that the lower limit of aeration porosity of most soils is around 10% for common crops (Stolzy, 1974; Erickson, 1982).

Aeration intensity, or composition of air in the rhizosphere is another factor which might influence the development of a root system. Taylor et al. (1972) and Armstrong (1979) however, indicated that the rate of oxygen supplied to the root surface is more accurately estimated by measuring oxygen flux to an oxygen sink, than by oxygen concentration. Furthermore, oxygen flux depends not only on oxygen concentration gradients, but also on the resistance of a soil matrix to diffusion (Blackwell and Wells, 1983).

Gas diffusion pathway resistances can be divided into three distinguishable regions. One, the region in which diffusion is taking place in a gas-gas system (ie., diffusion of oxygen through air filled porosity). Two, the aqueous pathway where diffusion occurs in a gas-liquid system (eg., where oxygen diffuses into water films surrounding

the roots). Three, diffusion through cell walls and into the plant. Interactions of the heterogenous and porous soil further complicates the study of these three phases. Tackett and Pearson (1964a,b) indicated that the penetration of cotton roots through low bulk density soil cores was not affected until oxygen partial pressures dropped below 10% or carbon dioxide concentrations reached 24%. They also reported that root penetrations were unaffected by oxygen or carbon dioxide partial pressures of high bulk density soils.

Diffusion is defined as the net transport of a substance from one region to another within the same medium in the absence of mixing (Reid and Sherwood, 1966). This transport may be due to thermal diffusion, pressure diffusion, molecular diffusion or to convective mixing. Taylor (1949) introduced a technique for measuring the oxygen diffusion coefficient in the porous medium (D), and in the stirred air (D_o). The ratio of D/D_o is then used to evaluate the diffusion characteristics of the porous medium. It indicates the degree of resistance which the medium offers to incoming oxygen from the atmosphere. Diffusion of oxygen to the root surfaces appears to be limited most by the liquid phase surrounding the roots. The ODR method of Lemon and Erickson (1955) thus, appears to be more realistic index of soil aeration capacity. Erickson(1982) concludes that, plant roots will not grow at ODR's below $0.20 \text{ ug cm}^{-2} \text{ min}^{-1}$, and their growth could be retarded at $0.2\text{--}0.4 \text{ ug cm}^{-2} \text{ min}^{-1}$.

MATERIALS AND METHODS

Seeds of dry edible beans (Phaseolus vulgaris, L. cv; Seafarer) were surface sterilized with a 0.5% sodium hypochlorite solution for ten minutes, rinsed with distilled water 5 times and germinated at 25 °C on trays containing wet cheesecloth covered with wet paper towels. After four days, uniform seedlings were transplanted into experimental units containing a Charity clay soil (illitic, calcareous, mesic, Aeric Haplaquept) prepared and compacted by the soil core seedling test method of Asady et al. (1985). Several modifications were made in preparing the experimental units for this experiment. Each experimental unit was made up of four primary cores. The cores were cut from schedule 80 PVC drainage pipes. The top core was 2.5 cm and succeeding lower cores were each 7.5 cm high. A 5 mm diameter access port was drilled in the center of each 7.5 cm core and sealed by a rubber serum which provided a means for sampling soil gases. The three 7.5 cm cores were sealed together into one gas- and water-tight cylinder by wrapping them with 5 cm wide plastic impregnated duct tape.

Three levels of bulk density were established by a hydraulic press equipped with a plunger 7.5 cm diameter as described by Asady et al. (1985). A 2.5 cm high core was then placed on the top and sealed as described above. Therefore, each experimental unit consisted of a cylinder, 25 cm in height, with three access ports 7.5 cm apart. Filter paper and cheesecloth prevented the soil from being lost at the base of

the container. After compaction each experimental unit was saturated by distilled water for 48 hours and the free water drained for 24 hours at a matric potential of -6 kPa. Seedlings were transplanted to the top core, covered with loose soil, and irrigated.

Four porous plate tension tables (Hillel, 1980) were established on the greenhouse bench. Each consisted of a fine mesh screen and regular desk top blotting paper. Experimental units were placed on the blotting paper equilibrated at -6 KPa of water potential which was applied to the base of the experimental units. A modified tension table (Figure 1) which included a burette and manometer, also provided a method for measuring water use. The graduated burett served as a water supply reservoir for the tension tables. Each tension table was covered with black plastic film having water tight ports for the cores to prevent direct evaporative losses. Four days after transplanting (DAP) the experimental units were sealed in the top using plastic impregnated cardboard container caps and cutting a small hole at the middle for the plant stems. The caps were sealed using parawax to minimize the air exchange with the atmosphere.

Two aeration treatments were applied by continuously flushing the space above the soil surface with saturated compressed air or nitrogen gas at the rate of 40 ml/min per experimental unit. Gas sampling from the top of the cores indicated that this reduced the oxygen concentrations to $14 \pm 1\%$ at the soil surface.

The experimental design was a 3 factor factorial, randomized complete block, replicated four times. The three factors were : (1) three levels of bulk density (1.1, 1.4, and 1.7 Mg m^{-3}) at 18% gravimetric water content, (2) two levels of aeration (air and nitrogen

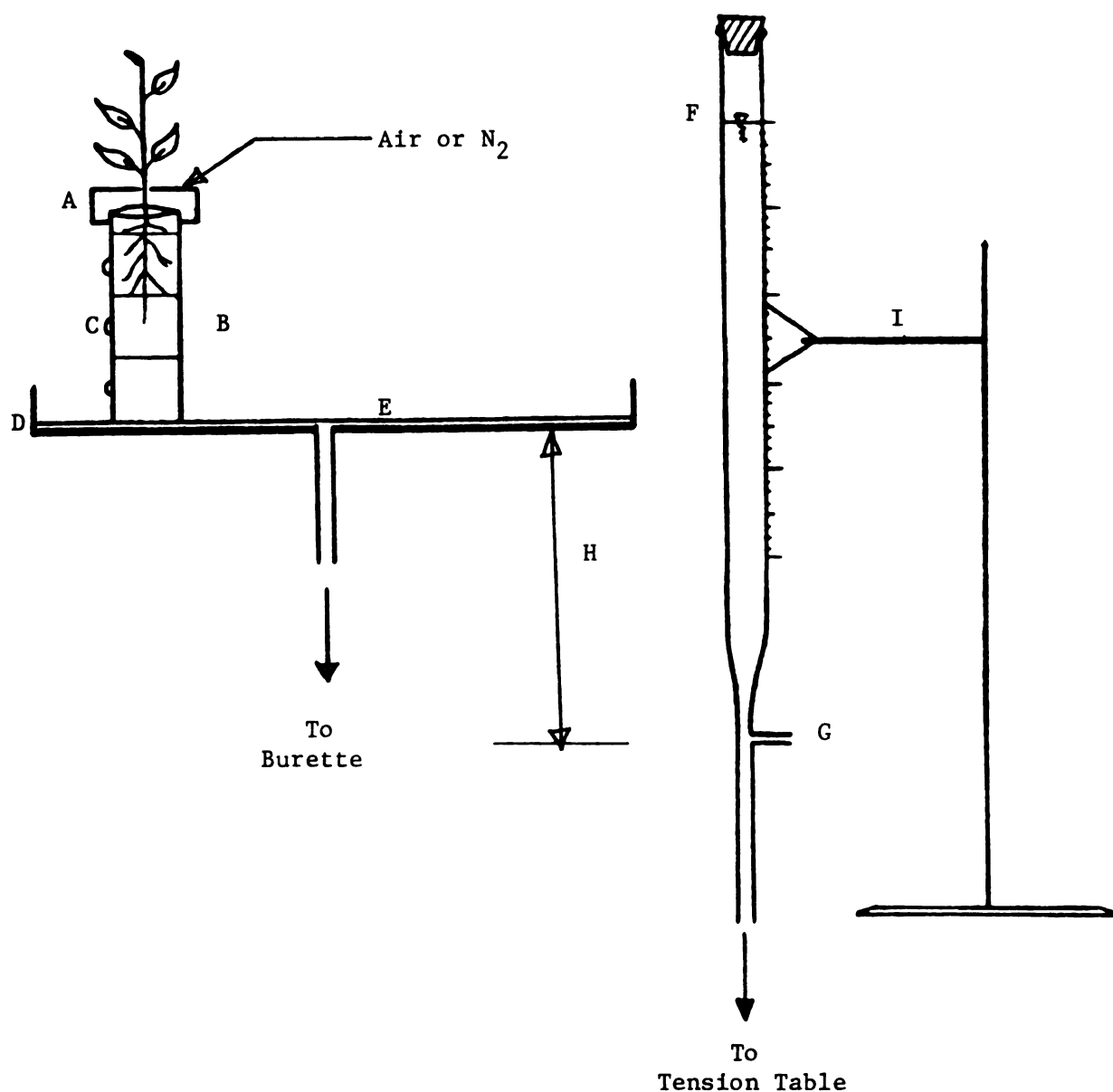


Figure 1. Schematic view of the root chamber and tension table apparatus. A is the surface aeration chamber, B is the experimental unit, C is the access port for gas sampling, D is the tension table, E is the porous plate over the tension table, F is the burette, G is the air entry point, H is the applied matric potential head, and I is the burette support.

gas), (3) and three harvest times (10, 20, and 30 DAP) giving the study a total of 72 experimental units. A modified 25% Hoagland's nutrient solution was supplied to plants each week beginning with the second week of growth. The greenhouse conditions were set to humidity of $65 \pm 5\%$, day/night temperature of $24/18^\circ\text{C}$, and a 16 h photoperiod with light intensity of $640 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$.

Several plant and soil measurements were taken during the experiment and at each harvest. Plant physiological measurements included abaxial diffusive resistance of the leaf, transpiration rate, and leaf temperature using a steady state leaf porometer, model Licor LI-1600. Leaf water potentials were measured with a Scholander model 3005 pressure bomb (1965) and plant water contents by the gravimetric method. Morphological measurements included fresh and dry shoot weights, leaf area by the optical method using a Licor model LI-3000, stem dry weights and water contents. Root measurements were root length and dry weight distributions in the soil containers.

The carbon exchange rate was measured by placing a 4.5 liter, cylindrical shaped, plexiglass chamber over the plant for one minute. Hypodermic syringes were used to extract 7.5 ml gas samples from the chamber, 10 and 60 seconds after a pump started stirring the gas inside the chamber. The carbon dioxide concentrations in the samples were measured by an infrared gas analyzer(IGA). The carbon exchange rate was determined to be the CO_2 depression for 50 seconds.

During the course of this experiment several gas measurements were taken for a period of 6-7 hours. Point source sampling of gases was achieved by extracting one ml of air samples from the rhizosphere through the access ports. Concentrations of oxygen, carbon dioxide and

nitrogen at three different depths in the rhizosphere were then measured. Hypodermic syringes (1cc tuberculin type B-D) equipped with 3.8 cm, 18 gauge needles, provided a means for the point source gas sampling. The gas samples were injected into a gas chromatograph (Carle Instruments, model 8500) equipped with a conductivity detector and a 200 cm by 3.2 mm internal diameter column filled with Porpak Q (PQ) in parallel with a molecular sieve (MS) column having the same dimensions. Columns were maintained at 40 C. The He carrier gas was at the flow rate of 30 ml/min. The detector temperature was maintained at the low setting. Detector polarity switching allowed alternate sides of the parallel column arrangement to act as the reference. For instance, the PQ column could either bypass or be put in a series with the MS column. This provided a method for separating the three gases from the same sample. The component peaks were electronically integrated by a computer integrator (Autolab, system I) and compared with standards prepared using an exponential dilution flask held at 25 C and atmospheric pressure. Normal atmospheric levels of CO₂, O₂ and N₂ were 300 ppm v/v, 20.8×10^5 ppm v/v and 78×10^5 ppm v/v respectively. The PQ column separated CO₂ from O₂ and N₂ and MS separated O₂ from N₂ gases. The oxygen diffusion rates were also measured using the modified method of Lemon and Erickson (1955) where microelectrodes were radially inserted 3.8 cm into the soil through the three access ports. Soil temperatures were also measured through the access ports using a portable digital thermocouple (STI type K model A2501).

RESULTS AND DISCUSSION

Mechanical impedance was simulated under greenhouse environments by exposing the growing dry edible bean root tips to a compacted soil layer similar to that of a plow pan in the field. The average penetrometer resistances in the compacted soil layers were approximately 430, 2140, and 5500 KPa for the bulk density levels of 1.1, 1.4, and 1.7 Mg m⁻³, respectively. These values are within the bulk range of critical soil strengths reported for different crops. Gerard et al. (1982) reported that cotton root elongations stopped when the mechanical resistance reached 2500 kPa in clay soils and 6000–7000 KPa in sandy soils.

Root growth was inversely related to soil bulk density. Less root growth in the compacted layers resulted in the accumulation of roots in the overlying layers. Total accumulations of root length were significantly greater after 20 days for plants growing in the least compacted soil (Table 1). After 10 days, there were 48 and 46% reductions in the root growth of Phaseolus beans grown on the aerated Charity clay soils compressed to bulk densities of 1.4 and 1.7 Mg m⁻³. Total root growth was reduced 80 and 71%, and 81 and 77% in the two most compacted soils after 20, and 30 days of growth, respectively. The accumulations of roots in the overlying layers of compacted soils were significantly higher than the control.

The cumulative total root length distributions in the soil

Table 1. Root length distribution responses of Phaseolus vulgaris to soil compaction, time, and aeration treatments.

Treatments		Total	Soil Depth cm			
Gas	Bulk Density	Time	0-2.5	2.5-10	10-17.5	17.5-25
	Mg m ⁻³	DAP	cm plt ⁻¹			
Air	1.1	10	751.8 ab ⁺	299.5 b	308.0 b	28.0 a
		20	3768.5 f	986.5 d	1086.0 d	1592.8 d
		30	5419.8 g	991.0 d	1335.5 e	3006.0 f
Air	1.4	10	392.5 a	40.5 a	1.5 a	0.0 a
		20	1363.3 c	580.0 c	247.5 b	79.8 a
		30	2511.0 d	650.5 c	748.5 c	737.0 b
Air	1.7	10	408.5 a	41.5 a	0.0 a	0.0 a
		20	742.5 ab	186.3 ab	0.0 a	0.0 a
		30	1044.8 bc	199.3 ab	0.0 a	0.0 a
N ₂	1.1	10	710.1 ab	308.5 b	236.8 b	11.5 a
		20	2946.8 de	749.0 c	1038.5 d	1044.3 c
		30	5236.3 g	1125.5 d	1319.3 e	2613.8 e
N ₂	1.4	10	422.8 a	151.5 ab	2.3 a	0.0 a
		20	1463.5 c	636.0 c	276.3 b	88.5 a
		30	3002.2 e	54.8 d	732.8 c	779.8 bc
N ₂	1.7	10	392.0 a	40.8 a	0.0 a	0.0 a
		20	838.3 ab	142.5 ab	0.0 a	0.0 a
		30	1179.5 bc	309.5 b	0.0 a	0.0 a

+ Values in each column followed by the same letter are not significantly different at the 0.05 level by the Least Significant Difference.

containers indicate a significant reduction in total root length with increasing mechanical impedance (Table 1). The direct relationship observed between soil compaction at the lower soil layers and root growth at the surface soils (Table 1) are similar to those obtained for maize (Shierlaw and Alston, 1984). These data illustrate the inhibitory effects of soil compaction on root penetration. The direct relationship between harvest times and root growth in all treatments and depths, is a natural consequence of the dynamics of root growth. Root length present at the surface 2.5 cm of 1.1 Mg m^{-3} soil treatment, at 20 DAP, was 11% lower than 10 DAP. At 30 DAP, root growth was 14% lower than 20 DAP. These results though not significantly different may be due to root turn over in the soil. Five to seven percent reduction in oxygen concentration at the surface soil in the nitrogen treated samples appeared to have no significant effects on the root growth for most treatments. These results are similar to those of Gill and Miller (1956) who reported that root growth was significantly reduced only when oxygen partial pressures fell below 10%.

Root growth at the 2.5–10 cm depth, was significantly lower when the soil was compacted to a bulk density of 1.7 Mg m^{-3} , than when the bulk density was 1.4 Mg m^{-3} for nearly all treatments. Similar results were observed at lower soil depths. Comparisons between root growth in soils compacted to a bulk density of 1.1 and 1.4 Mg m^{-3} indicate that the mechanically impeded root growth of this study became significantly different at approximately 20 DAP. At the extreme bulk density, practically no roots penetrated beyond the depth of 10 cm. This bulk density corresponds to a penetrometer resistance of 5500 KPa, and is much greater than the 1000 KPa reported to be the limiting resistance

for pea roots (Voorhees et al., 1975), and the 2500 KPa which is reported to limit cotton (Gerard et al., 1982). The reduction of root growth in the intermediate bulk densities indicates that the limiting pressure for Phaseolus vulgaris root growth appears to be somewhat less than 2140 KPa.

Root length density (RLD), defined as root length per unit soil volume may be one of the most important factors effecting water and nutrient uptake. RLD appeared to be inversely related to soil compaction with no significant aeration effects (Figure 2). This inverse relationship, however, didn't become significant until 20 DAP. Compression of soil to a bulk density of 1.4 Mg m^{-3} reduced root length density more severely than 1.7 Mg m^{-3} for both aeration treatments. This is additional evidence that the limiting mechanical resistance for Phaseolus vulgaris is below 2140 KPa. The average rate of RLD increases during the second 10 days of growth ranged from 37.6 %/day, 24.7 %/day, and 9.7 %/day for the none, intermediate, and most compacted treatments respectively. These values were reduced to 6.2 %/day, 11.2 %/day, and 4.1 %/day for the same treatments, during the third 10 day period of growth.

Spatial distributions of RLD within the soil containers after 10 days of growth indicate that the maximum RLD was 0.8 cm cm^{-3} at a depth of 5-10 cm for the noncompacted treatments (Figure 3). At the same region of soil containers, the maximum RLD was 0.3 and 0.1 cm cm^{-3} for the intermediate and most compacted treatments, respectively. After 20 days, the maximum RLD increased to 3.6, 1.6, and 0.4 cm cm^{-3} , for the none, intermediate, and most compacted treatments respectively (Figure 4). The region of maximum root growth occurred at a depth of 15-20 cm

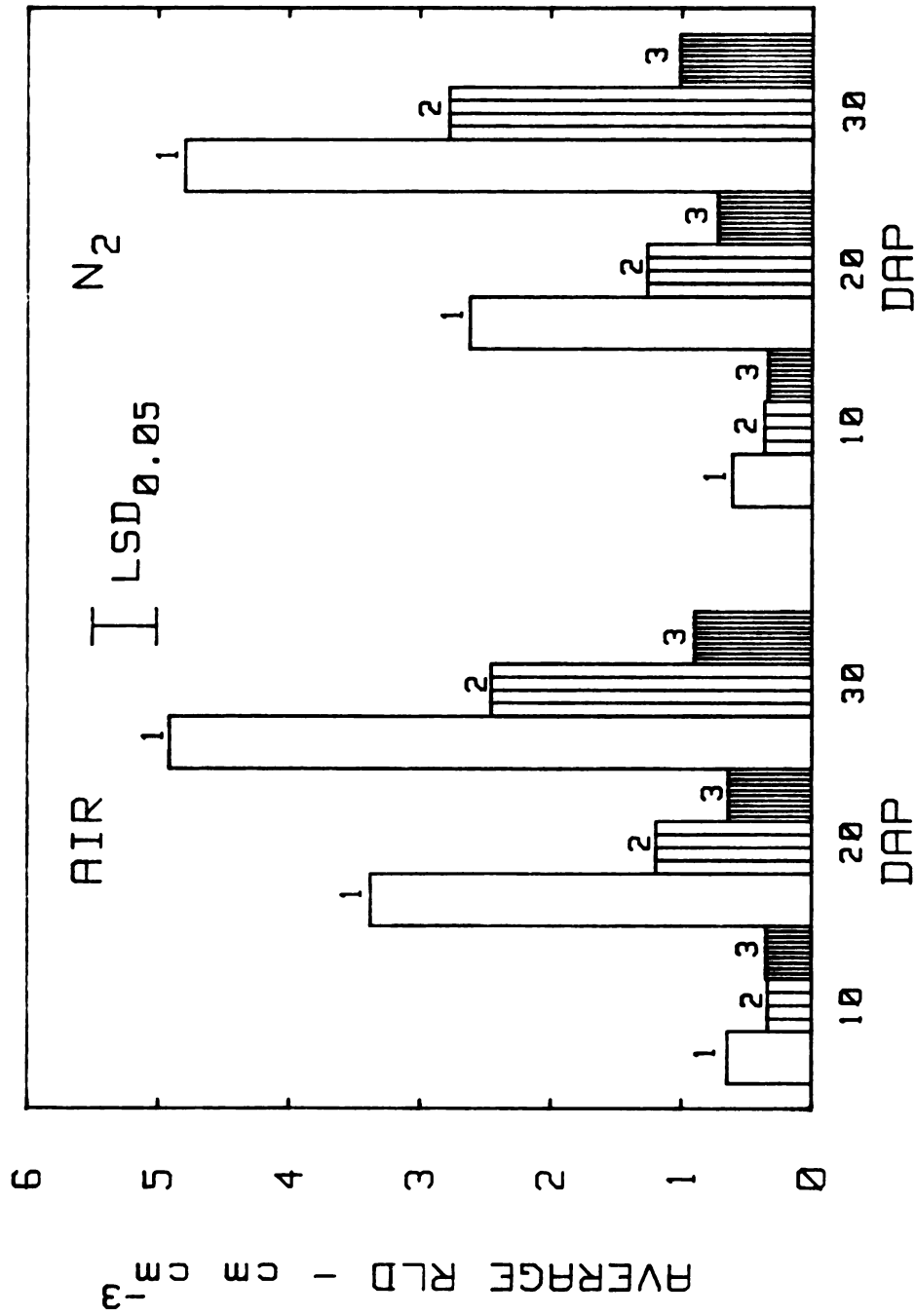


Figure 2. Influence of soil compaction, aeration, and time on root length density of dry edible beans grown in 25 cm cores. 1, 2, and 3 represent bulk densities of 1.1, 1.4, and 1.7 Mg m⁻³, respectively.

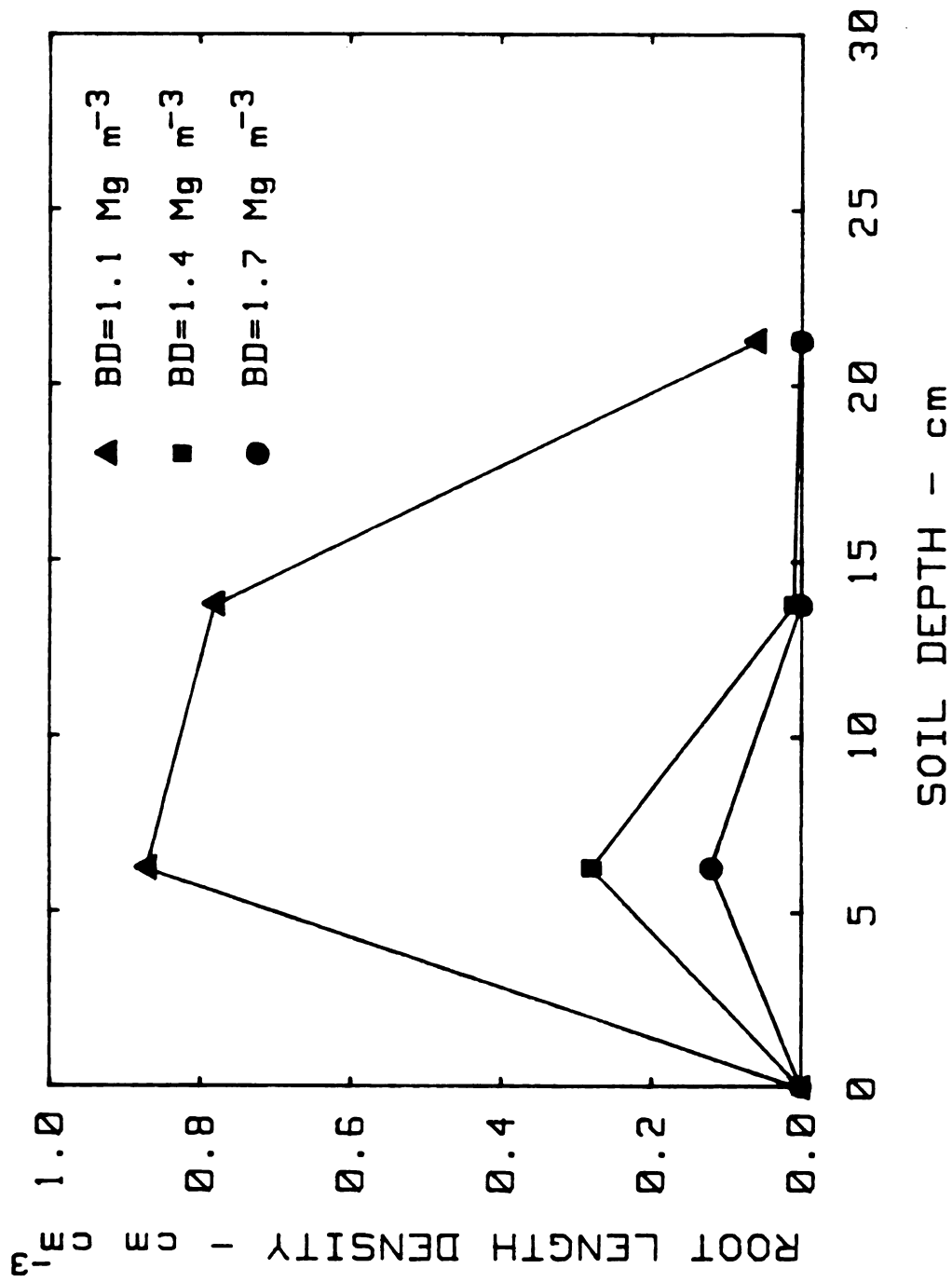


Figure 3. Influence of soil compaction on root length density distribution of dry edible beans after 10 days of growth.

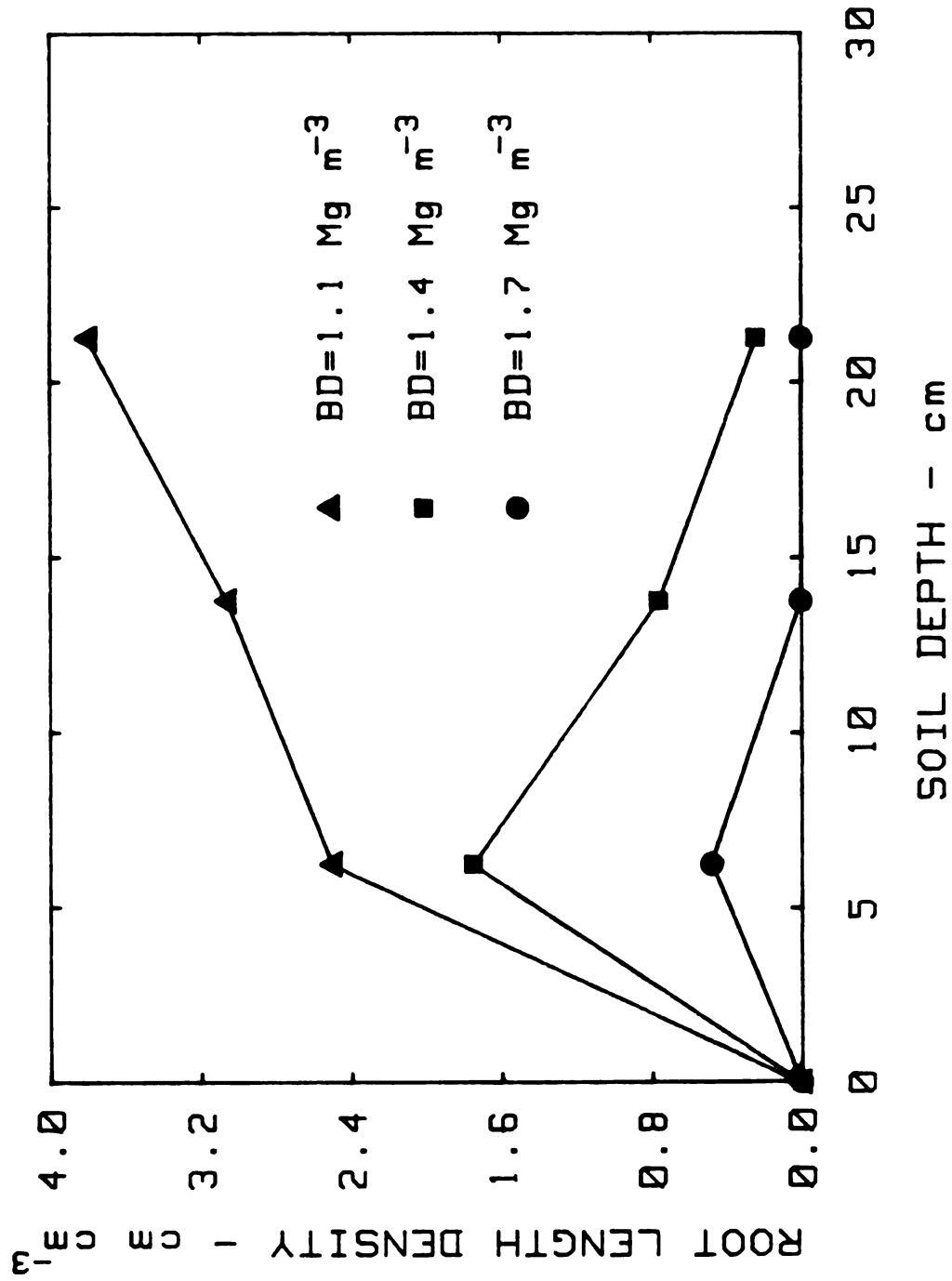


Figure 4. Influence of soil compaction on root length density distribution of dry edible beans after 20 days of growth.

for the control and didn't change for the other treatments. At 30 DAP, the maximum RLD increased to 8.0 cm cm^{-3} and 2.1 cm cm^{-3} , at the depth of 20 cm for the none and intermediate compaction treatments, respectively (Figure 5). Severe mechanical resistance resulted in RLD values which were less than 1 cm cm^{-3}

Relative root length (RRL) is defined as the ratio of root length present in each soil compartment to total root length. It represents the relative distribution of roots within each depth of soil and appears to be an appropriate index for normalizing root growth data which may be used in models. RRL distributions after 20 days of growth, indicate that 90% of the bean roots were within the surface 2.5 cm soil, when the underlying layers were severely compacted (Figure 6). Soil compaction apparently reduced the number of macro-pores which were similar in size to plant roots. This is shown in Figure 7 where the air filled porosity was severely reduced for a given pore diameter, at high soil bulk densities. This mechanical barrier slowed down or completely stopped the movement of roots downward. At the same time, only 15% of the roots were within the surface and 85% were below 2.5 cm depth, in the noncompacted treatments. These data demonstrate that drybean roots grown under noncompacted soil conditions have grown downward with little external mechanical forces limiting their development. As a result, plant roots grown in the noncompacted soil penetrated deeper into the profile. RRL within the surface 2.5 cm soil generally decreased with time. The rate of decline was most significant for the none and intermediate compaction treatments. RRL increased with time in the bottom soil compartment because root extension was limited to proliferation within this section of the soil.

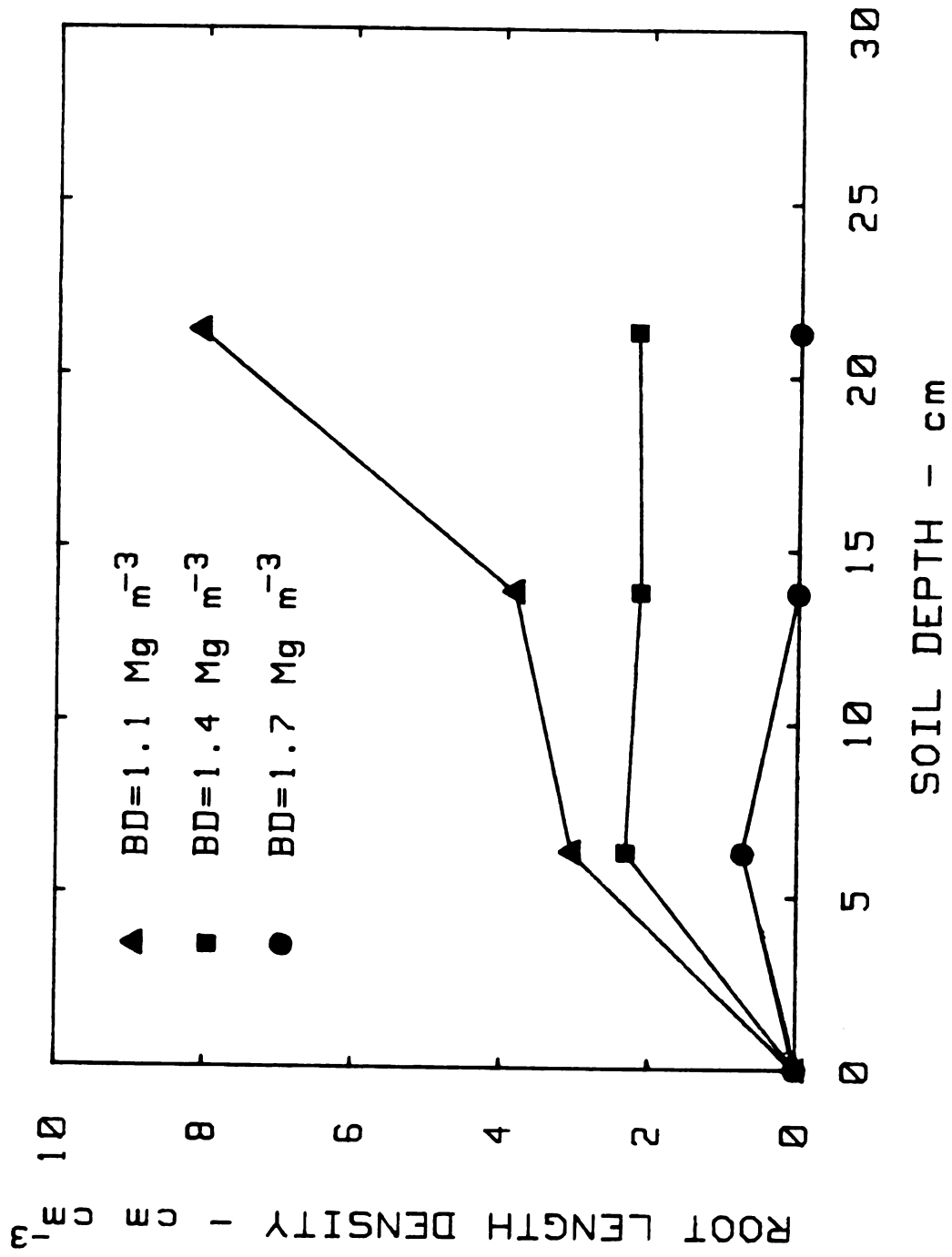


Figure 5. Influence of soil compaction on root length density distribution of dry edible beans after 30 days of growth.

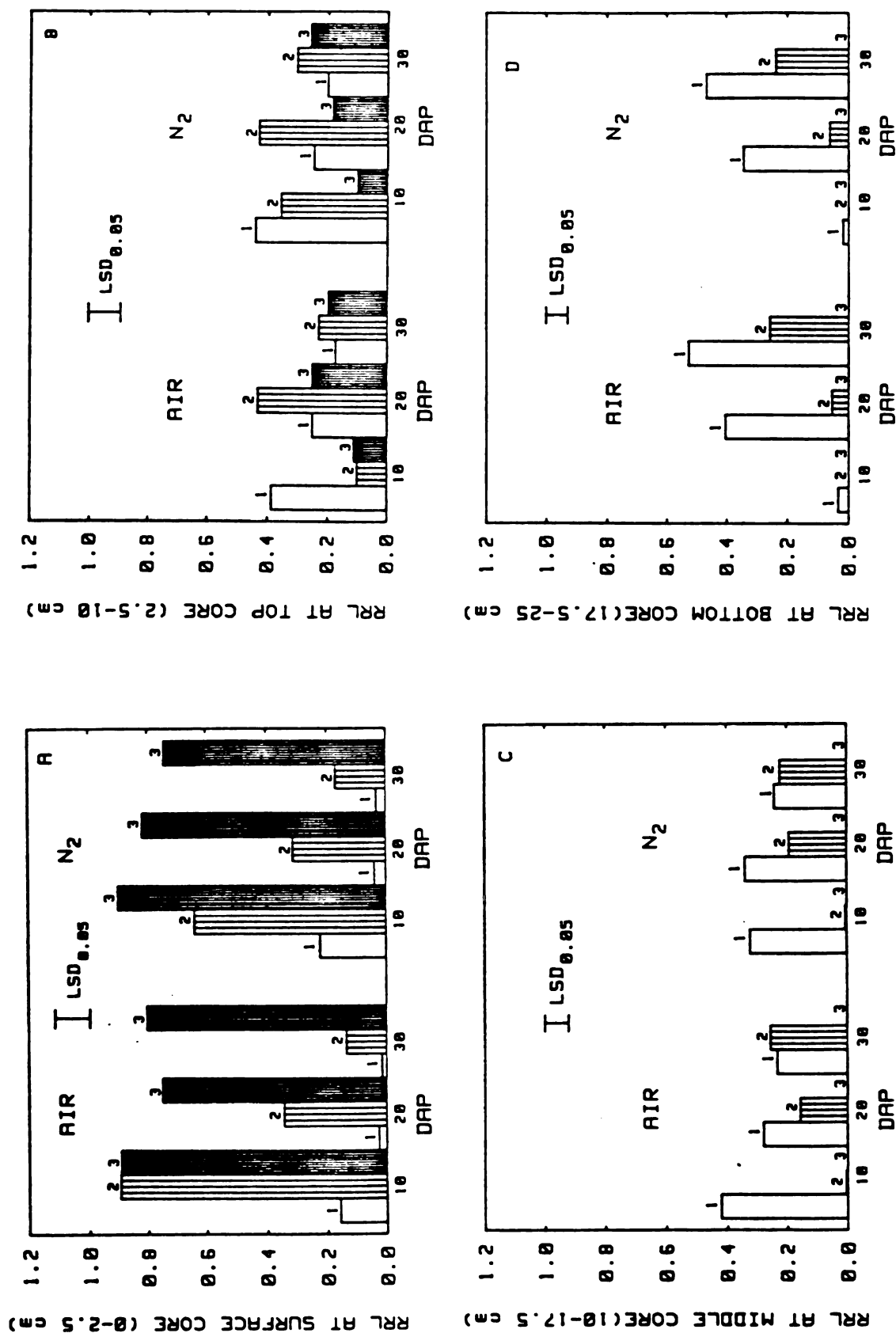


Figure 6. Influence of soil compaction, aeration and time on relative root length of dry edible beans. The bulk density treatments 1-3 are: 1.1, 1.4, and 1.7 Mg m⁻³, and A, B, C, and D represent surface, top, middle, and bottom cores, respectively.

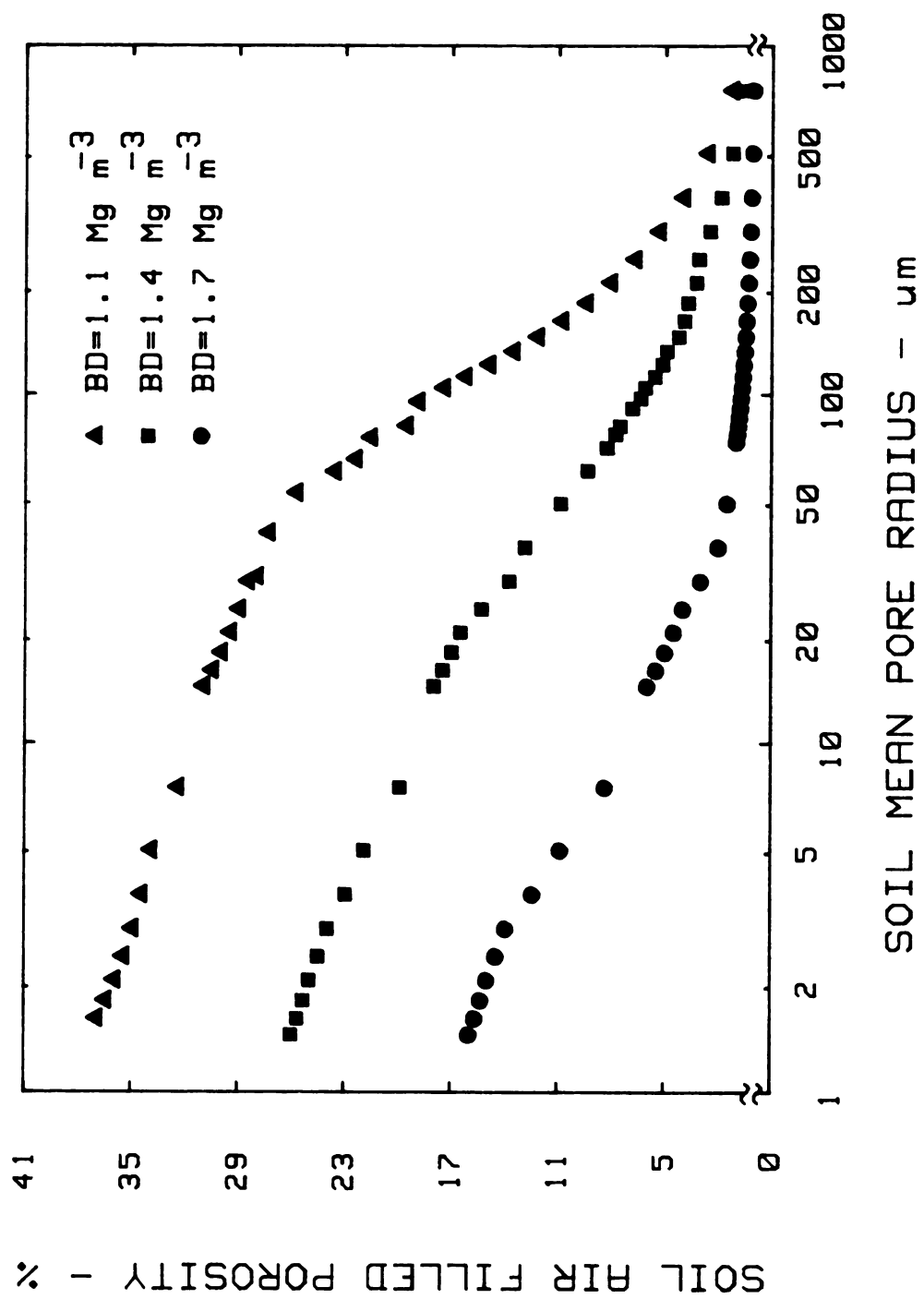


Figure 7. Air filled porosity contained in the pores larger than the mean pore radius.

Soil aeration stresses in this study may have resulted from either oxygen shortages due to high diffusion resistances in soil, or carbon dioxide accumulations due to high resistances in the escape pathways. Oxygen diffusion rate (ODR) was significantly reduced with increasing levels of soil compaction for most treatments (Table 2). Aeration treatment appeared to have no significant effects on the ODR, when the soil was extremely compacted. These along with the low oxygen and high carbon dioxide concentrations present in the lower layers of highly compacted soils (Figures 8-11) may therefore suggest that the high pathway resistance to gases is the main obstacle to diffusion of oxygen into the soil. Lower oxygen concentrations in the N_2 treated samples had significant effects on the ODR for some treatments (Table 2). Intermediate soil compaction decreased ODR due to a reduction of the mean pore diameter (Figure 7) and an increase in the thickness of water films. The pathway resistance probably was not high enough to prevent diffusion of oxygen into the soil, because the oxygen concentrations were similar (Figures 8 and 9).

The Relationship between soil compaction, pathway resistances, and the thickness of water films can be described in Figure 12. At the regions of high bulk density the rate of increase in ODR per unit increase in D/D_0 (eg., slope of the curve) is small, because the air filled porosity is predominately comprised of micro-pores, the thickness of the water film is high, and the soil has a high resistance to diffusion of oxygen. This region of the curve has a gentle slope and ODR is mainly controlled by the porosity. As decompression proceeds, the pore diameters increase, the resistance to diffusion decreases, and the ODR is no longer entirely controlled by porosity. This region of

Table 2. Oxygen diffusion rate responses of Charity clay soil measured at three soil depths and at three different times.

Treatments			Time of measurements		
Gas	Bulk Density	Depth	10 DAP	20 DAP	30 DAP
	Mg m ⁻³	cm	- - - - - ug m ⁻² s ⁻¹ - - - - -		
Air	1.1	6.25	88.7 g ⁺	79.4 ghi	78.7 f
		13.75	81.9 fg	84.6 hi	57.8 de
		21.25	79.1 ef	88.0 i	59.1 de
Air	1.4	6.25	81.7 fg	56.4 de	86.3 f
		13.75	51.6 cd	60.3 def	67.7 ef
		21.25	71.0 e	73.6 fghi	69.4 ef
Air	1.7	6.25	20.9 a	32.6 abc	29.5 ab
		13.75	21.8 a	26.4 ab	28.3 a
		21.25	32.5 b	46.8 cd	38.3 abc
N ₂	1.1	6.25	82.2 fg	73.2 efghi	57.8 de
		13.75	70.5 e	60.9 def	40.6 abcd
		21.25	76.3 ef	69.9 efgh	48.0 bcd
N ₂	1.4	6.25	78.8 cd	65.9 efg	57.8 de
		13.75	49.6 c	64.6 efg	36.8 abc
		21.25	60.7 d	67.7 efg	55.4 cde
N ₂	1.7	6.25	21.9 a	21.8 a	34.5 ab
		13.75	17.2 a	32.3 abc	32.0 ab
		21.25	24.6 ab	39.1 bc	36.9 abc
LSD _{0.05}			9.3	16.6	11.2

*Values in each column followed by the same letter are not significantly different at 0.05 level of probability according to the Least Significant Difference.

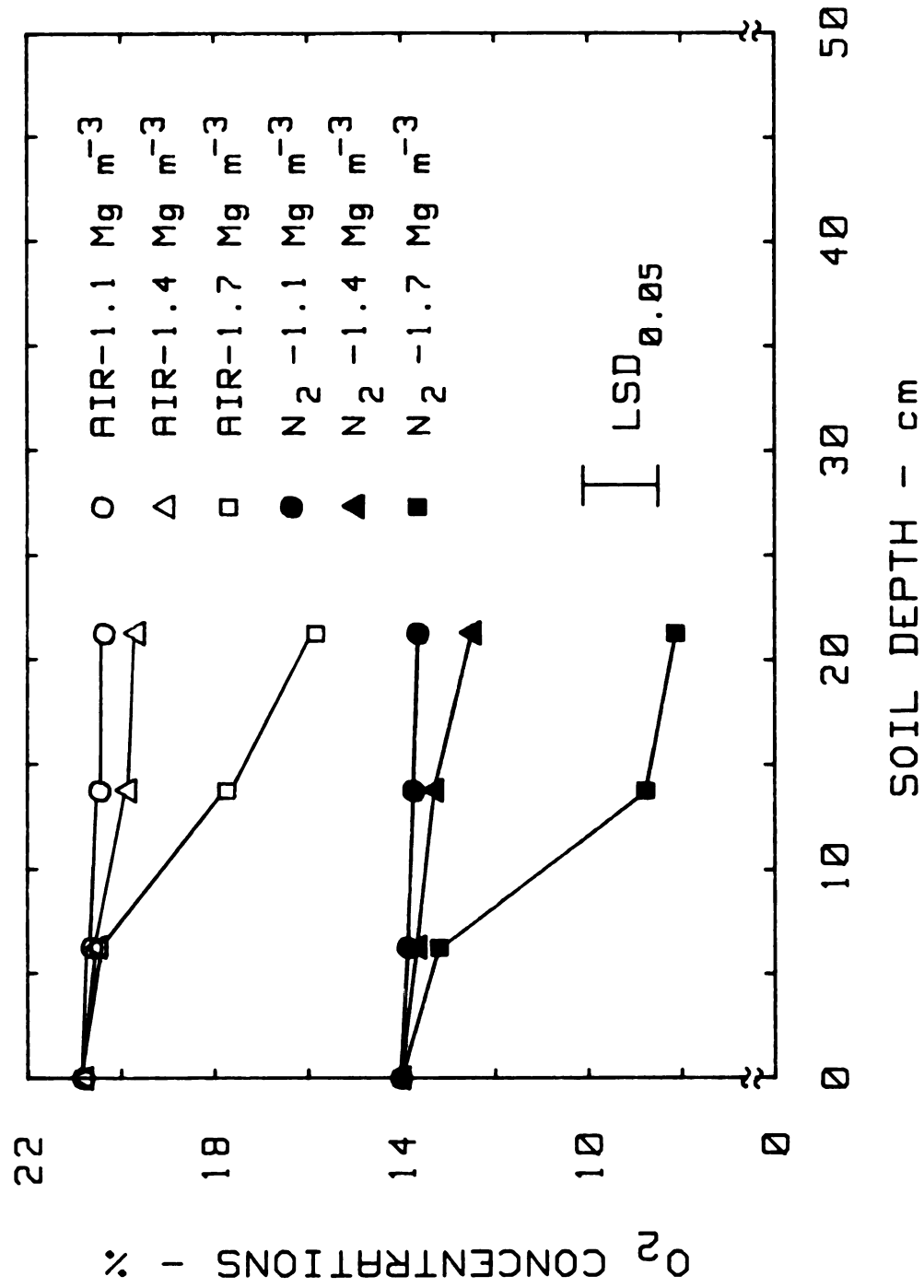


Figure 8. Influence of soil compaction and aeration on oxygen concentration distributions 20 days after planting.

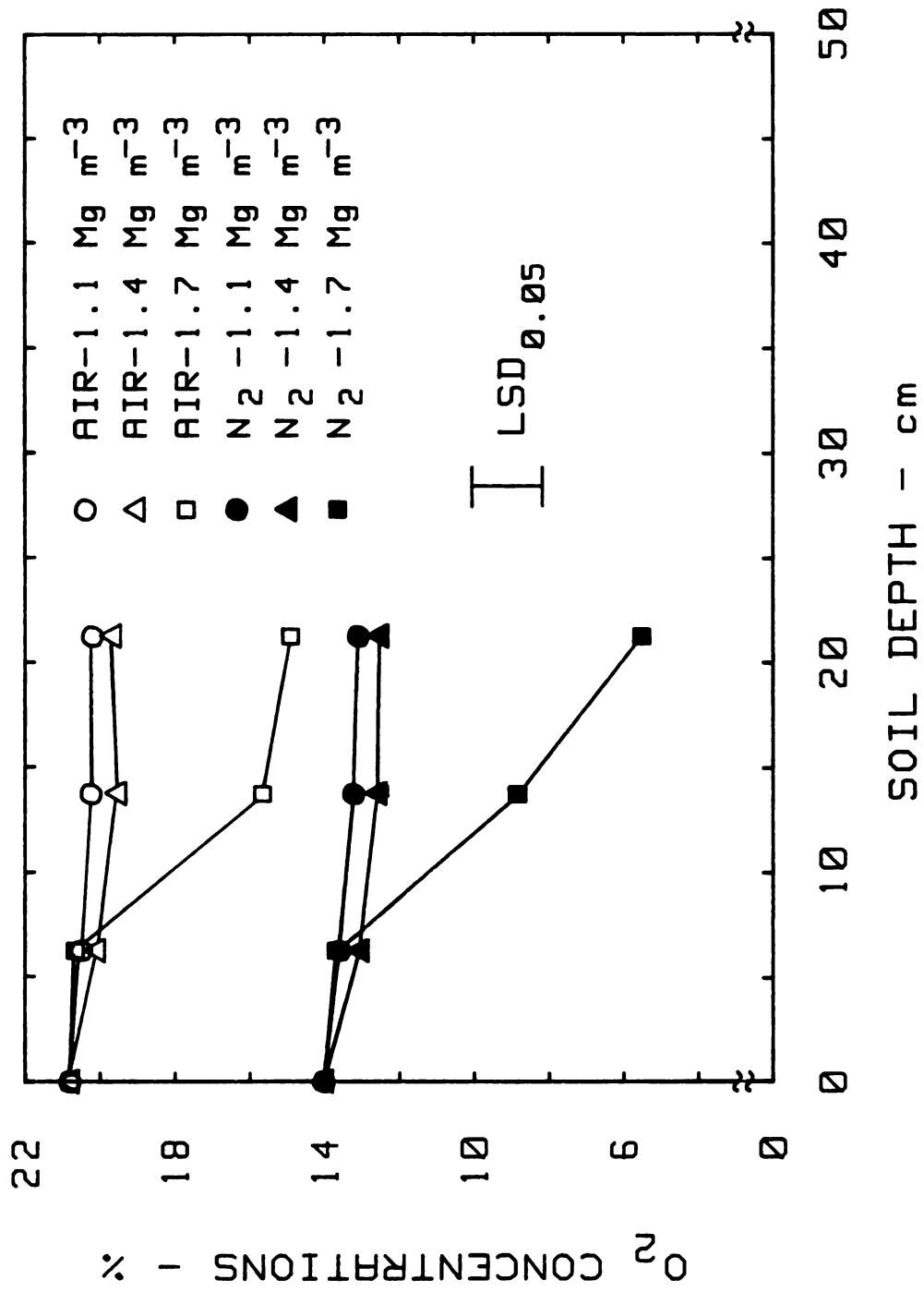


Figure 9. Influence of soil compaction and aeration on oxygen concentration distributions 30 days after planting.

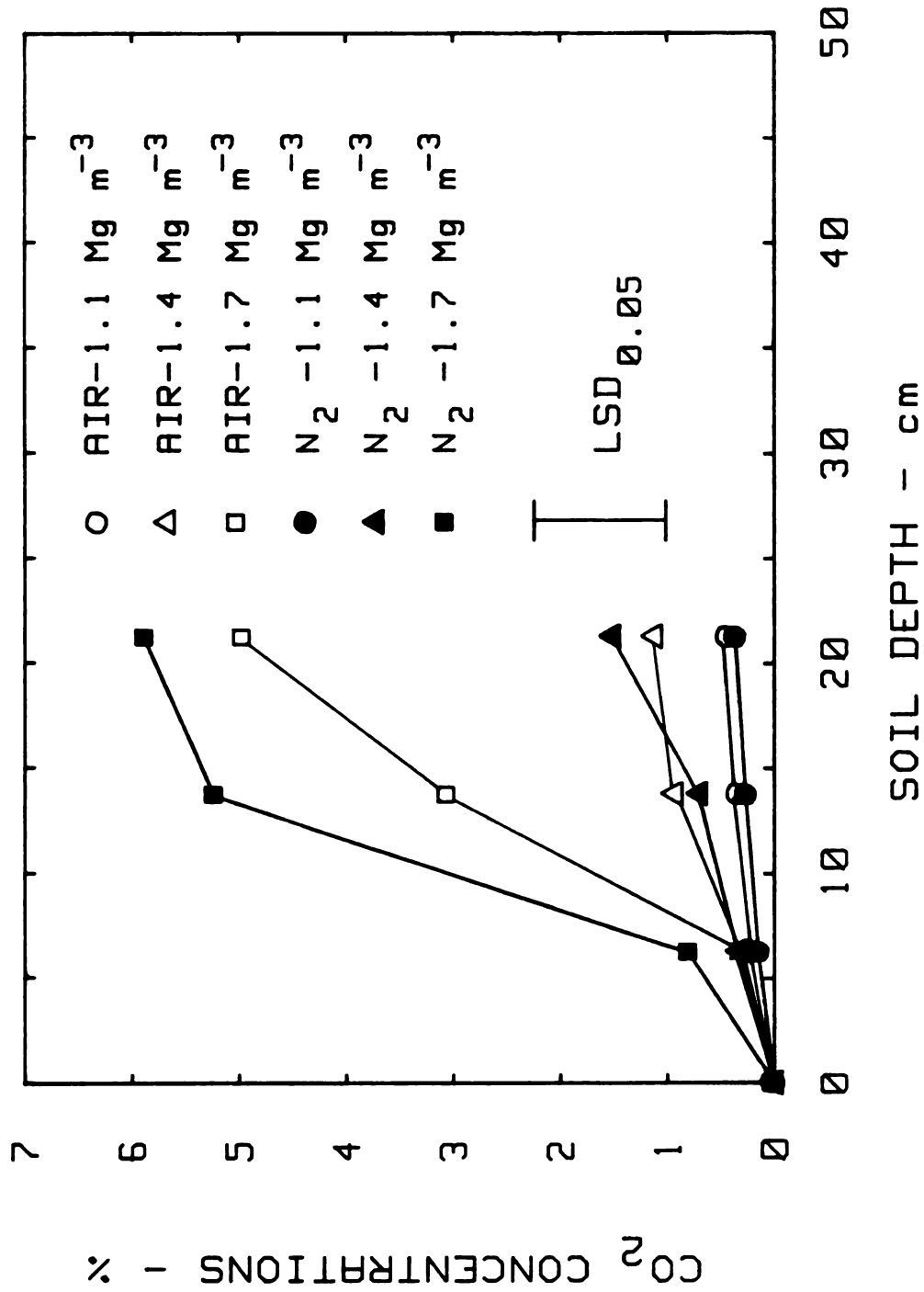


Figure 10. Influence of soil compaction and aeration on carbon dioxide concentration distributions 20 days after planting.

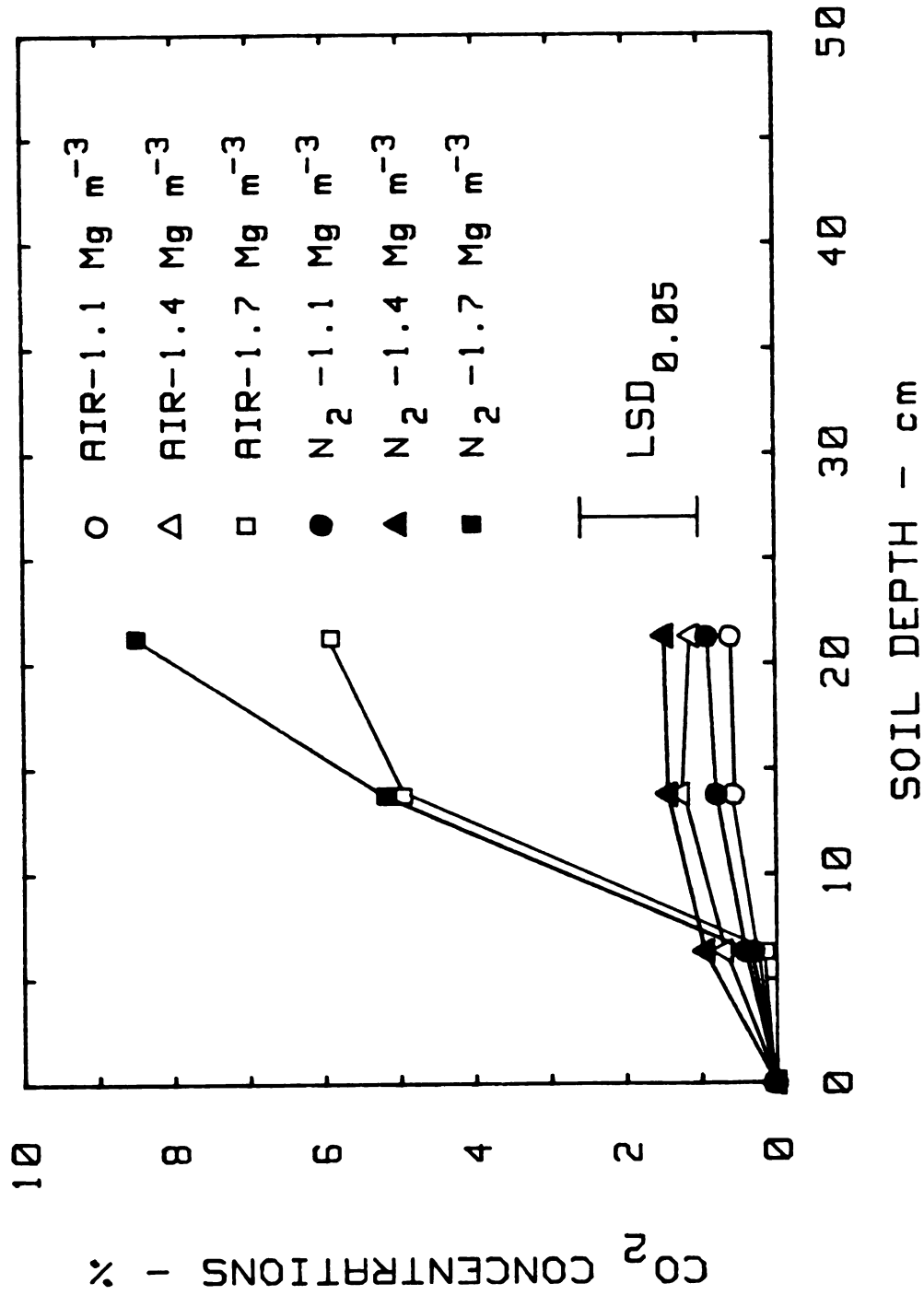


Figure 11. Influence of soil compaction and aeration on carbon dioxide concentration distributions 30 days after planting.

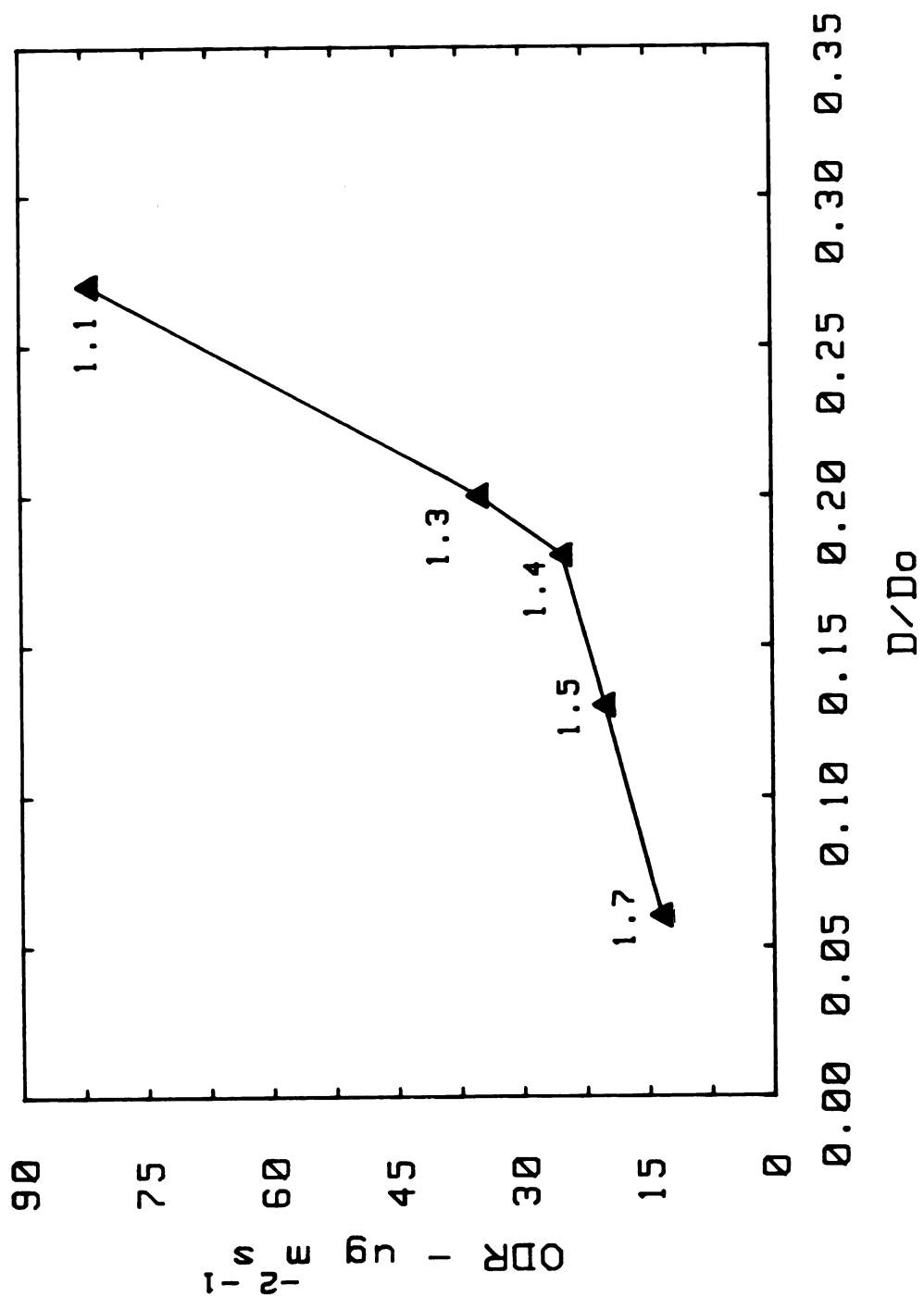


Figure 12. Relationship between ODR, D/D_0 , and bulk density of Charity clay soil at -6 kPa soil matric potential.

the curve has a sharp slope and the ODR appears to be controlled by the thickness of the water films.

It appears that the ODR of the soils in this experiment is controlled by the thickness of the water film for soil bulk densities as high as 1.4 Mg m^{-3} . This is supported by the fact that oxygen concentrations were not significantly affected by soil compaction up to bulk densities of 1.4 Mg m^{-3} (Figures 8 and 9). The ODR, however, was significantly reduced for most treatments (Table 2). The oxygen partial pressure and ODR values significantly dropped with depth due to high diffusion resistances in the soil resulting from high bulk densities. The practical implications of these phenomena might be that ODR would provide little information about the thickness of water film in highly compacted soils, if such information is desired, and D/D_o would likewise be a poor index of oxygen availability to roots. These data also indicate that the 6-8% reductions in oxygen partial pressures due to aeration treatments did not significantly effect the root growth of dry edible beans. Results of experiments on pea seedlings (Eavis, 1972) indicated that root elongation rates of pea seedlings did not change until the oxygen concentration fell below 16%. Carbon dioxide accumulations in the soil containers were parallel to the reduction of oxygen partial pressures (Figures 10 and 11), suggesting that high resistances in the escape pathway were probably responsible for CO_2 concentrations which approached 10%.

Pores plugged by growing roots may significantly decrease the internal aeration of the highly compacted soils. In order to demonstrate how the diffusion pathway is affected by root plugging, we introduced the concept of root filled porosity (RFP). RFP is defined as

the ratio of the volume of pores occupied by roots to the volume of pores occupied by air at a given water potential. After 10 days of growth, RFP was highest at the surface 2.5 cm soil, and ranged from 2% in the control to about 5% in the most compacted soil (Figure 13). As growth proceeded, the percentage of root filled pores in the surface layers of the compacted soils increased to 9 and 12% after 20 and 30 days of growth, respectively (Figures 14 and 15). These data suggest that the plugging effects of the roots on the aeration status of a soil may become significant in severely compacted soils where root growth is confined to the surface layers.

All biomass accumulations by plants ultimately depend upon the net carbon exchange rate. The effects of soil compaction on photosynthetic rates were determined by measuring the amount of CO_2 exchanged by the total plants. Processes accompanying photosynthesis, such as, respiration and translocation, however, can be major deterrents to plant productivity. Photosynthetic activity is strongly dependent upon the incoming solar radiation intensity as well as the openings of the stomatal aperture. Thus, the carbon exchange rate is a dynamic process which is determined by the instantaneous conditions of the soil and atmosphere at the time of measurements.

Mechanical impedance appeared to have no significant effect on the specific carbon exchange rate of most treatments, at 20 DAP (Table 3). Increased mechanical impedance, however, increased the specific photosynthetic activity, at 30 DAP (Table 3). The photosynthetic activity of the total plant, grown under high mechanical impedance, was significantly decreased for the air and N_2 treated treatments at 20 and 30 DAP, respectively (Table 4). The carbon exchange rate responses of

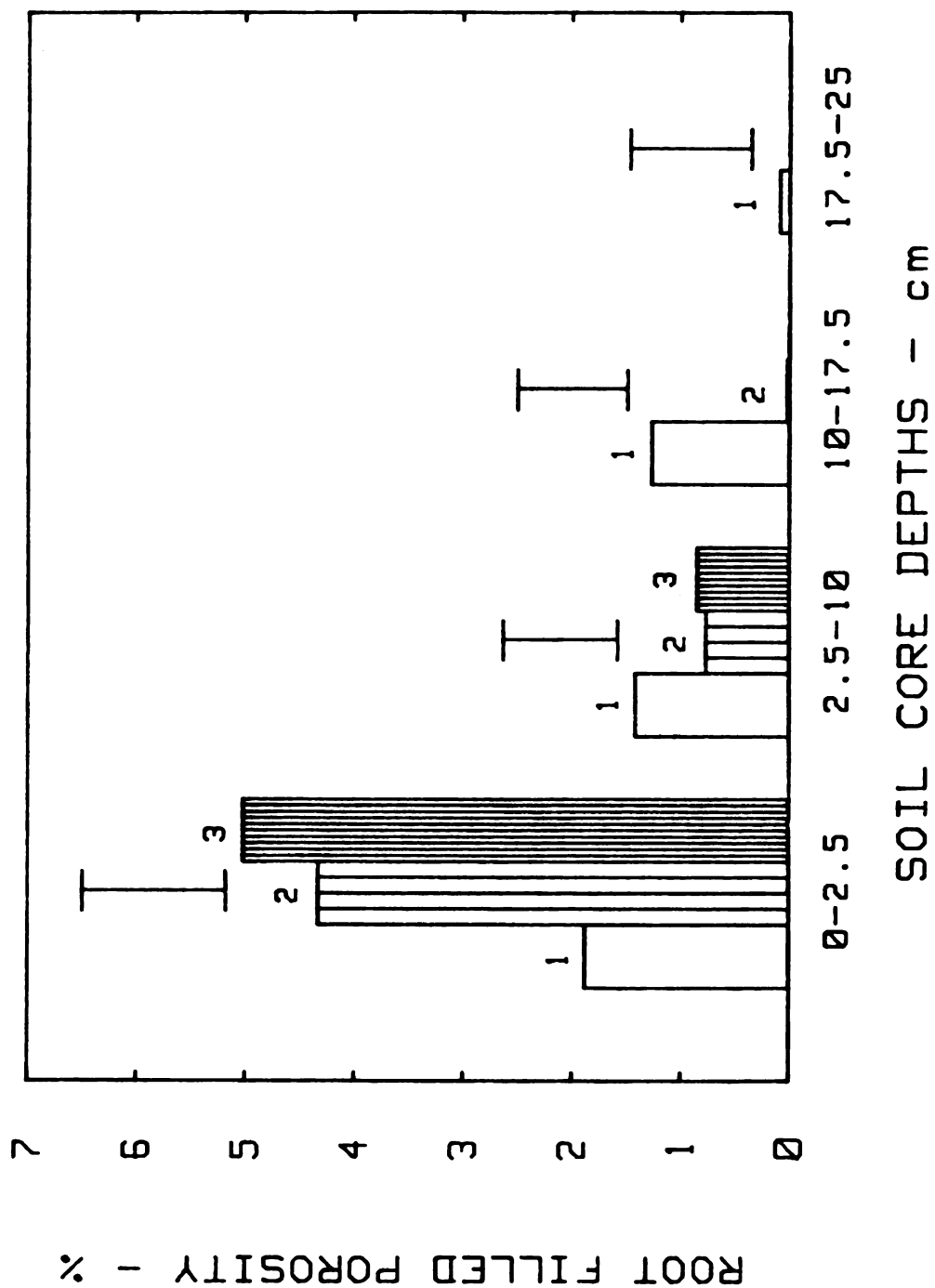


Figure 13. Root filled porosity distribution of dry edible beans after 10 days of growth. 1, 2, and 3 represent bulk densities of 1.1, 1.4, and 1.7 Mg m⁻³, respectively. The bar over each core depth represents LSD at 0.05 level of probability.

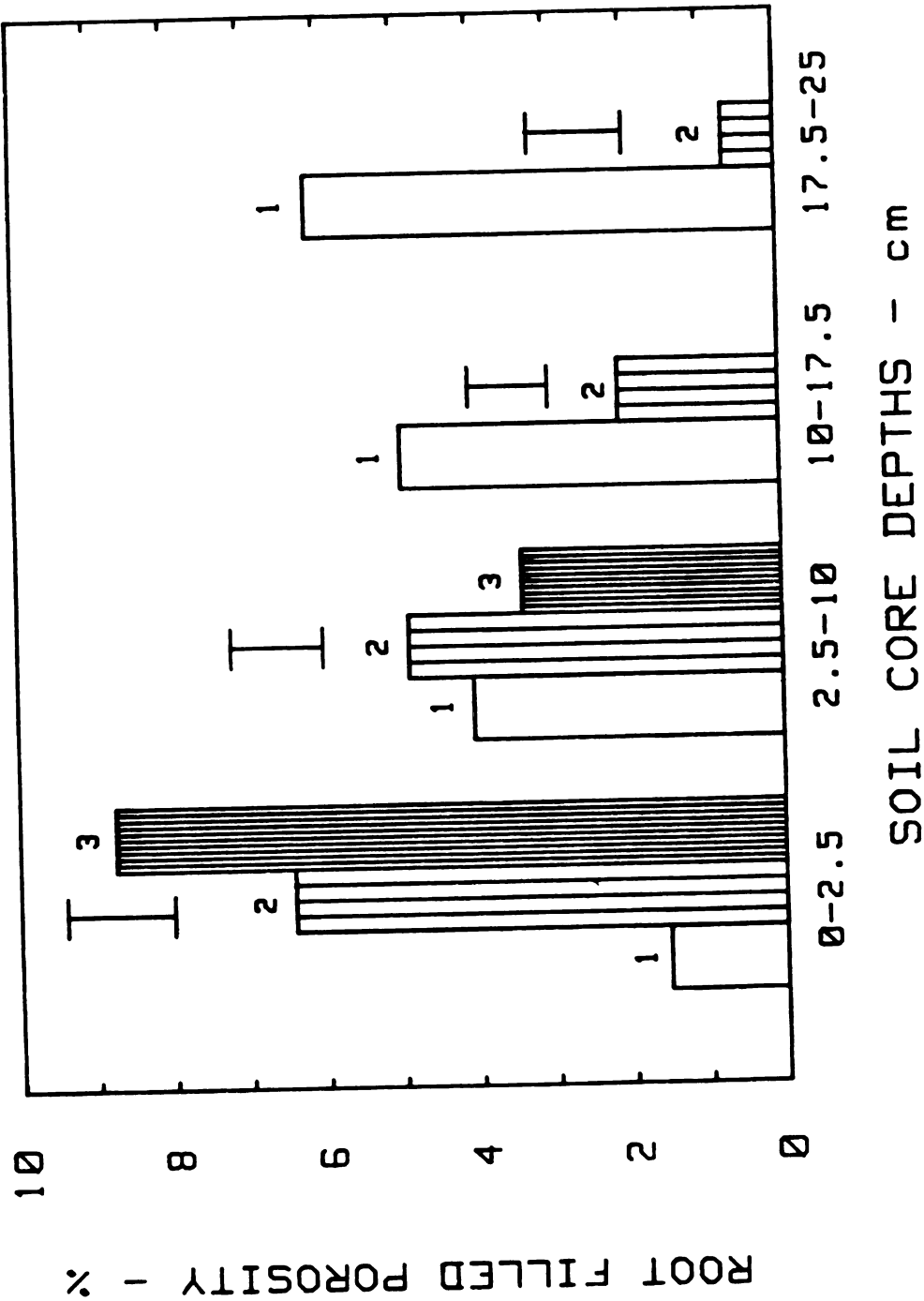


Figure 14. Root filled porosity distribution of dry edible beans after 20 days of growth. 1, 2, and 3 represent bulk densities of 1.1, 1.4, and 1.7 Mg m⁻³, respectively. The bar over each core depth represents LSD at 0.05 level of probability.

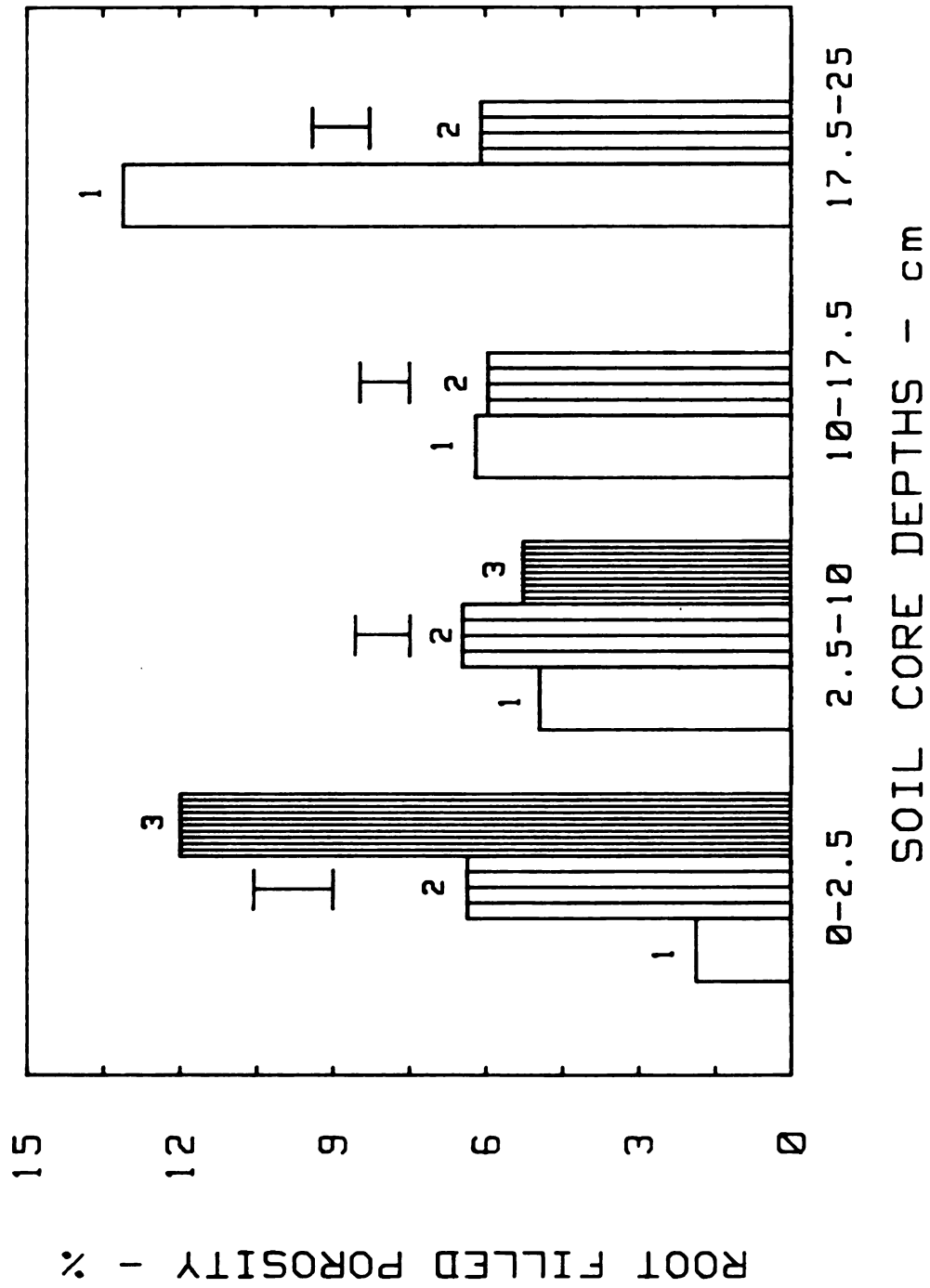


Figure 15. Root filled porosity distribution of dry edible beans after 30 days of growth. 1, 2, and 3 represent bulk densities of 1.1, 1.4, and 1.7 Mg m⁻³, respectively. The bar over each core depth represents LSD at 0.05 level of probability.

Table 3. Specific carbon exchange rate responses of Phaseolus vulgaris to soil compaction and aeration treatments.

Treatments		Days After Planting - DAP	
		20	30
Gas	Bulk Density		
	Mg m ⁻³	- - - - mg dm ⁻² h ⁻¹ - - - -	
Air	1.1	29.9 ab ⁺	10.5 a
	1.4	38.2 ab	16.8 ab
	1.7	35.4 ab	20.6 b
N ₂	1.1	26.4 ab	14.5 ab
	1.4	39.1 b	18.6 b
	1.7	21.2 a	20.7 b
LSD _{0.05}		17.2	7.9

⁺Values in each column followed by the same letter are not significantly different at 0.05 level of probability according to the Least Significant Difference.

Table 4 Total carbon exchange rate responses of Phaseolus vulgaris to soil compaction and aeration treatments.

Treatments		Days After Planting	
		20	30
Gas	Bulk Density		
	Mg m ⁻³	- - - - mg h ⁻¹ plt ⁻¹ - - - -	
Air	1.1	34.9 c ⁺	24.1 bc
	1.4	25.3 bc	26.7 c
	1.7	13.8 ab	11.5 ab
N ₂	1.1	22.4 abc	29.7 c
	1.4	27.7 c	28.3 c
	1.7	9.5 a	11.1 a
LSD _{0.05}		13.5	12.7

*Values in each column followed by the same letter are not significantly different at 0.05 level of probability according to the Least Significant Difference.

the intermediate and low bulk densities were similar. The increased specific carbon exchange rate with high mechanical impedance on the one hand, and the decreased total plant photosynthetic rate on the other hand, therefore supports the hypothesis that plants grown under environmental stresses have a leaky root system (Smucker, 1984).

In conclusion, soil compaction reduced root growth and dry matter accumulation of dry edible beans. Highly compacted soils prevented roots from penetrating downward and causing high accumulations of roots in the upper layers of the soil profile. The root length density was significantly reduced by severe soil compaction. The aeration status of the soil was curtailed by greater resistances to gas movement by the smaller and plugged pores. Plants growing in severely compacted soils appear to have a leaky root system as was suggested by Smucker (1984). In lieu of these detrimental effects of soil compaction on root growth and plant development, crop production systems should devise management practices which would require minimum traffic across the field.

LITERATURE CITED

- Armstrong, W. 1979. Aeration in higher plants. *Adv. Bot. Res.* 7:225-332.
- Asady, G.H., A.J.M. Smucker and W. Adams. 1985. Quantitative measurements of root tolerances to compacted soil. *Crop Science* 25:802-806.
- Blackwell, P.S. and E.A. Wells. 1983. Limiting oxygen flux densities for oat root extension. *Plant Soil* 73:129-139.
- Bowen, H.D. 1981. Alleviating mechanical impedance. In: G.F. Arkin and H.M. Taylor (eds.). *Modifying the Root Environment to Reduce Crop Stress*. ASAE. Monograph No. 4.
- Carmi, A. and B. Heuer. 1981. The role of roots in control of bean shoot growth. *Ann. Bot.* 48:519-527.
- Eavis, B.W. 1972. Soil physical conditions affecting seedling root growth. III. Comparisons between root growth in poorly aerated soil and at different oxygen partial pressures. *Plant Soil* 37:151-158.
- Erickson, A.E. 1982. Tillage effects on soil aeration. In: *Predicting Tillage Effects on Soil Physical Properties and Processes*. ASA Special Publication # 44:91-105.
- Gerard, C.J., P. Sexton and G. Shaw. 1982. Physical factors influencing soil strength and root growth. *Agron. J.* 74:875-881.
- Gill, W.R., and R.D. Miller. 1956. A method for study of the influence of mechanical impedance and aeration on the growth of seedling roots. *Soil Sci. Soc. Am. Proc.* 20:154-157.
- Gupta, S.C., and W.E. Larson. 1982. Modeling of soil mechanical behavior during tillage. In: *Predicting Tillage Effects on Soil Physical Properties and Processes*. ASA Special Pub. # 44:151-179.
- Hillel, D. 1980. *Foundamentals of Soil Physics*. Academic Press Inc. pp 123-165, 195-232.
- Kibreab, T. and R.E. Danielson. 1977. Measurement of radish root enlargement under mechanical stress. *Agron. J.* 69:857-860.
- Lemon, E.R. and A.E. Erickson. 1955. Principle of the platinum microelectrode as a method of characterizing soil aeration. *Soil*

Sci.79:383-391.

Reid, C.R. and T.K. Sherwood. 1966. The Properties of Gases and Liquids. McGraw-Hill Book Co. pp 520-567.

Russell, R.S. and M.G. Goss. 1974. Physical aspects of soil fertility - The response of roots to mechanical impedance. Neth. J. Agric. Sci. 22:305-318.

Scholander, P.F., H.T. Hammel, E.D. Bradstreet, and E.A. Hemmingsen. 1965. Sap pressure in vascular plants. Science. 148:339-346.

Shierlaw, J. and A.M. Altson. 1984. Effect of soil compaction on root growth and uptake of phosphorus. Plant Soil. 77:15-28.

Smucker, A.J.M. 1984. Carbon utilization and losses by plant root systems IN: Roots, Nutrient and Water Influx, and Plant Growth. (eds.) Barber and Bouldwin. pp27-45. ASA Special Pub. Madison Wisconsin.

Stolzy, L.H. 1974. Soil atmosphere. In: E.W. Carson(ed.). The Plant Root and Its Environment. Univ. Press of Virginia, Charlottesville. pp 335-361.

Tackett, J.L. and R.W. Pearson. 1964a. Oxygen requirements of cotton seedling roots for penetration of compacted soil cores. Soil Sci. Soc. Am. Proc. 28:600-605.

Tackett, J.L. and R.W. Pearson. 1964b. Effect of carbon dioxide on cotton seedling root penetration of compacted soil cores. Soil Sci. Soc. of Am. Proc. 28:741-743.

Taylor, H.M. and L.F. Ratliff. 1969a. Root growth pressures of cotton, peas and peanuts. Agron. J. 61:398-402.

Taylor, H.M. and L.F. Ratliff. 1969b. Root elongation rates of cotton and peanuts as a function of soil strength and soil water content. Soil Sci. 108:113-119.

Taylor, H.M., M.G. Huck and B. Klepper. 1972. Root development in relation to soil physical conditions. In: D. Hillel(ed.). Optimizing the Soil Physical Environment Toward Greater Crop Yields. Academic Press, N.Y. pp 57-77.

Taylor, S.A. 1949. Oxygen diffusion in porous media as a measure of soil aeration. Soil Sci. Soc. Am. Proc. 14:55-61.

Vomocil, G.A. and W.J. Flocker. 1961. Effects of soil compaction on storage and movement of soil, air, and water. Trans. Am. Soc. Agric. Eng. 4:242-246.

Voorhees, W.B., D.A. Farrell and W.E. Larson. 1975. Soil strength and aeration effects on root elongation. Soil Sci. Soc. Am. Proc. 39:948-953.

CHAPTER 4

A MATHEMATICAL MODEL OF GROWTH IN ANNUAL PLANTS

ABSTRACT

A model of plant growth was introduced which simulates the growth of plants from seedling to physiological maturity. It takes into account the dynamic relative growth rate with the upper limit being treated as a constant and equal to that of the exponential growth. This model has the advantage of both the classical approach, where the model variables have biological meaning, and the functional approach where the instantaneous values of variables are calculated. Potential use of the model includes curve fitting and predicting the plant responses beyond the range of the data base. The model was used to evaluate the dry mass accumulations of two dry edible bean cultivars grown under two soil management practices. It accounts for a biological growth capacity and competition effects among plant organs subjected to environmental stresses.

INTRODUCTION

Plant growth analysis has received a great deal of attention for many years. The methodology has evolved from classical approaches, where the plant variables were evaluated on the basis of mean values of such variables as relative growth rates, absolute growth rates, unit leaf area, etc., which were calculated for an interval between two harvest times. The instantaneous value of these variables can be calculated if there is an approximate mathematical function to describe the experimental data. Hunt (1979) describes advantages of the functional approach which summarizes data in a convenient way and replaces the original and often scattered data with a smooth, continuous function.

Considerable research has been devoted to developing the appropriate methodology for the functional approach (Duchateau et al. 1972; Elias and Causton, 1976; Hunt and Parsons, 1977; Hunt, 1978, 1979; Hunt and Evans, 1980; Hurd, 1977; Parsons and Hunt, 1981; Sivakumar and Shaw, 1978). Duchateau et al. (1972) fitted parabolic curves to segments of growth progression data. Polynomial equations of varying degrees were used to fit each segment of the experimental data. They used both sliding parabola and parabolic splines to describe the entire data range. Similar analysis was devised by Hunt and Parsons (1977). Sivakumar and Shaw (1978) applied both classical methods and a functional approach to analyze soybean growth and concluded that the latter is preferred.

Other investigators have used polynomial exponentials, where polynomial equations have been fitted to logarithmic transformations of the experimental data (Hughes and Freeman, 1967; Hunt and Parsons, 1974; Parsons and Hunt, 1981). All of these methods have arisen from the fact that many investigators had an incomplete mathematical function to describe a complete time series of data. Although, polynomial equations may adequately describe the experimental data, they nevertheless lack the biological basis and their constants have no biological meaning (Hurd, 1977). Hurd (1977) also objected to the use of polynomial equations on the grounds that they may easily overfit the experimental data. Based on these arguments Hurd (1979) attempted to use a general purpose equation which was derived by Richards to describe the complete range of plant growth progression data. The purpose of this report is to introduce a model of plant growth which simulates all stages of growth. The model variables have biological meaning, and offer a new approach to plant growth analysis.

EXPONENTIAL GROWTH

In 1879 Kreusler and colleagues demonstrated that growth of an annual plant under natural conditions follows the law of exponential growth. Blackman (1919) was the first to describe the mathematics of an annual plant growth by applying the principles of compound interest. This process has come to be known as typical of many plants. The process can be described by a linear first order differential equation such as

$$dP(t)/dt = K_1 P(t) \quad (1)$$

where $P(t)$ is a growth variable at time t , and K_1 is the proportionality constant. Separating the variables

$$dP/P = K_1 dt$$

and integrating between times t_1 and t_2

$$\ln(P_2/P_1) = K_1(t_2 - t_1)$$

Then

$$P_2/P_1 = \text{EXP}(K_1(t_2 - t_1)) \quad \text{or}$$

$$P_2 = P_1 \text{EXP}(K_1(t_2 - t_1)) \quad (2)$$

where P_2 and P_1 are growth variables at times t_2 and t_1 , a scalar quantity eg. mass (M), and K_1 is the proportionality factor (t^{-1}).

In plant growth analysis K_1 is called specific growth rate (SGR), relative growth rate (RGR), or what Blackman (1919) called efficiency index of dry weight production, when applied to biomass accumulations. In the classical approach K_1 is calculated as a mean value across a harvest time, for instance

$$\bar{K}_1 = \frac{\ln(P_2) - \ln(P_1)}{(t_2 - t_1)} = \frac{\Delta \ln(P)}{\Delta t} \quad (3)$$

which is a value calculated for the time interval Δt . The instantaneous RGR is mathematically defined as

$$K_1 = \lim_{\Delta t \rightarrow 0} \frac{\Delta \ln(P)}{\Delta t} = \frac{d \ln(P)}{dt} \quad (4)$$

which is the slope of the graph of natural log transformations of the growth variable P versus time. The growth of many annual plants is exponential for a given phase of development. Therefore, the plot of the natural logarithms of P ($\ln(P)$) versus time will be a straight line relationship where the instantaneous and mean RGR are equal and constant (Hunt, 1978). As plants grow, the proportion of assimilates invested into structural material increases. Thus, RGR can not remain constant and would decline as more and more photoassimilates are diverted from photoassimilate metabolism to the development of structural compounds. This is indeed the essence of applying the functional approach to plant growth analysis.

The true RGR is thus a time variant variable with the upper limit being equal to RGR at the exponential period of growth and lower limit equal to zero. The true differential equation of growth thus becomes

$$\frac{dP(t)}{dt} = K(t) P(t) \quad (5)$$

If we assume that RGR deviates from the upper limit proportionately to the quantity of growth, then the dynamic RGR changes as

$$K(t) = K_1 - K_2 P(t) \quad (6)$$

where K_2 is the proportionality constant. Substituting this into equation (5) results in

$$\frac{dP(t)}{dt} = K_1 P(t) - K_2 P(t)^2 \quad (7)$$

Gold (1977) used this equation in describing the competition effects in populations of organisms growing in an environment where the growth components are limited. He called parameter K_2 , the competition factor. The relative magnitude of parameters K_1 and K_2 in eq. (6), is such that at the early stages of development where P is small, $K_2 P$ is much smaller than K_1 . Therefore RGR is controlled primarily by K_1 . As plant growth continues, P increases and the effects of $K_2 P$ becomes increasingly significant, until a steady state condition is reached then

$$K_1 = K_2 P(t)$$

and

$$P(t) = K_1/K_2 \quad (8)$$

At this point the absolute growth rate, eq.(5), and RGR, eq.(6) are zero. If the value of P at which a steady state condition of growth is achieved is denoted by p^{ss} , then eq.(8) becomes

$$p^{ss} = K_1/K_2 \quad (9)$$

Applying these principles to the growth of microorganisms, Gold (1977) called p^{ss} the carrying capacity of the environment. Feddes et al. (1978) used a similar concept to describe the effects of radiation, temperature, and CO_2 on the rate of plant growth. They stated that every set of environmental conditions bears a biological growth capacity or potential growth. I integrated equation (7) with the initial conditions of $P(t)=P_i$ at $t=t_i$, as

$$P(t) = \frac{P_i e^{K_1 t}}{e^{K_1 t_i} + \frac{K_2}{K_1} P_i (e^{K_1 t} - e^{K_1 t_i})} \quad (10)$$

where P_i is the initial value of the plant growth variable at initial time t_i . If $P_i=P_o$ at $t_i=0$, then eq. (10) reduces to

$$P(t) = \frac{P_o e^{K_1 t}}{1 + \frac{K_2}{K_1} P_o (e^{K_1 t} - 1)} \quad (11)$$

The mean value of K_2 over a time interval t_1 to t can be estimated by

$$K_2 = K_1 \frac{\frac{e^{K_1 t}}{P(t)} - \frac{e^{K_1 t_1}}{P_1}}{(e^{K_1 t} - e^{K_1 t_1})} \quad (12)$$

In order to derive the equation's parameters from experimental data, and test the model we used the shoot dry matter accumulation of dry edible bean cultivars which were grown on mechanically compacted soil as the growth variable (P). A time series of data was generated by harvesting 10 plants every 3-7 days for each treatment. Two dry edible bean cultivars, Black Turtle Soup (BTS), and Seafarer (SEA) combined with two soil compaction treatments, no secondary tillage (NST) and excessive secondary tillage (EST) produced four growth progression curves (Figure 1). These curves indicate that soil compaction significantly reduced the growth potential of both cultivars. Growth potential of the Seafarer cultivar appeared to be greater than BTS for both environmental soil conditions of this experiment.

Soil compaction apparently delayed plant growth about equally for both cultivars. If we plot the natural logarithms of dry matter mass versus time (Figure 2) we observe that plants either showed no change or lost mass during the first 10 days of growth. The straight line segment of the curves is representative of the exponential phase of growth where RGR was maximum and equal to the slope of the lines. These values were calculated to be 0.159 and 0.130 day⁻¹ for the SEA, and 0.154 and 0.120

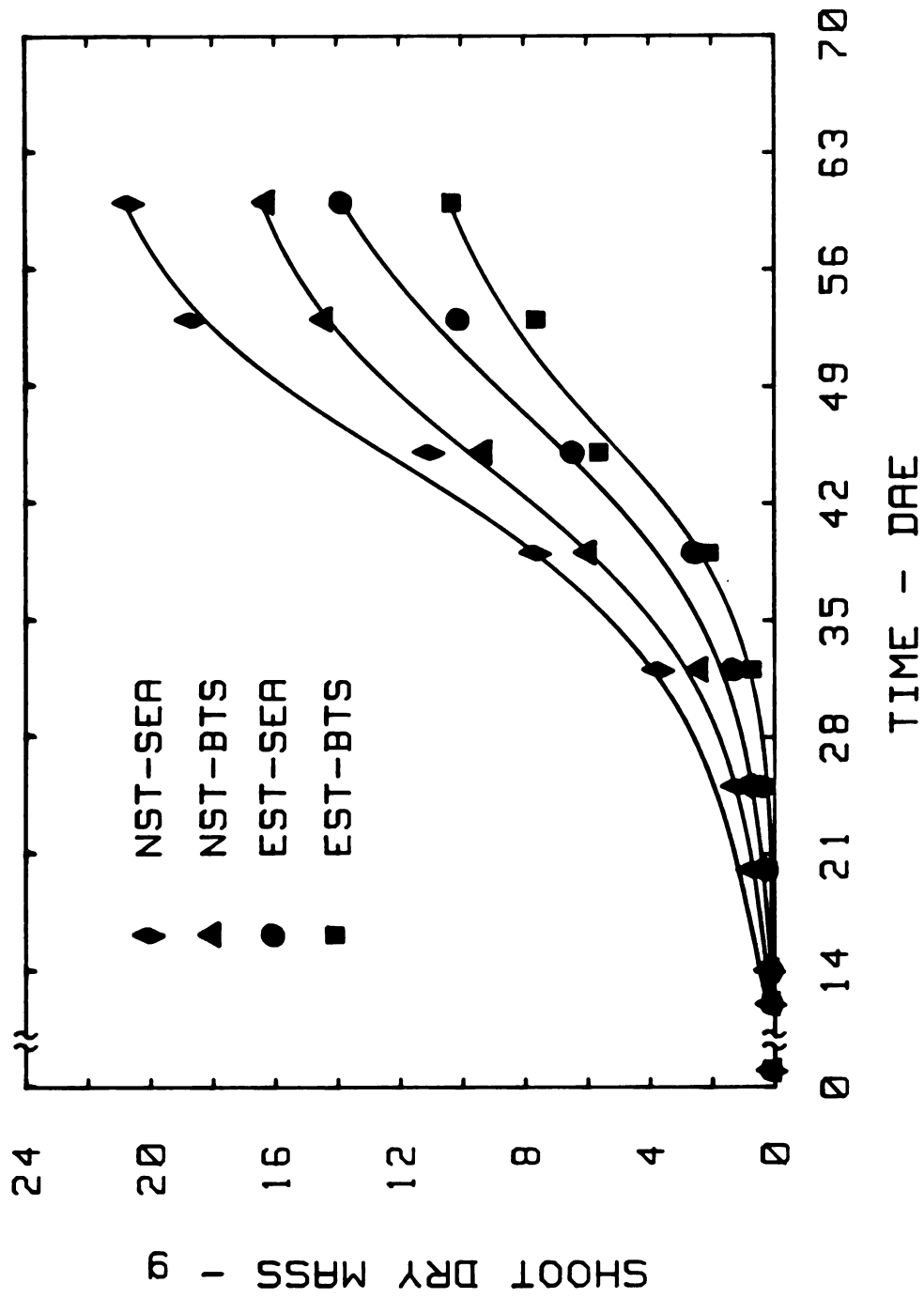


Figure 1. Measured shoot dry mass accumulations of dry edible beans grown on Charity clay soil.

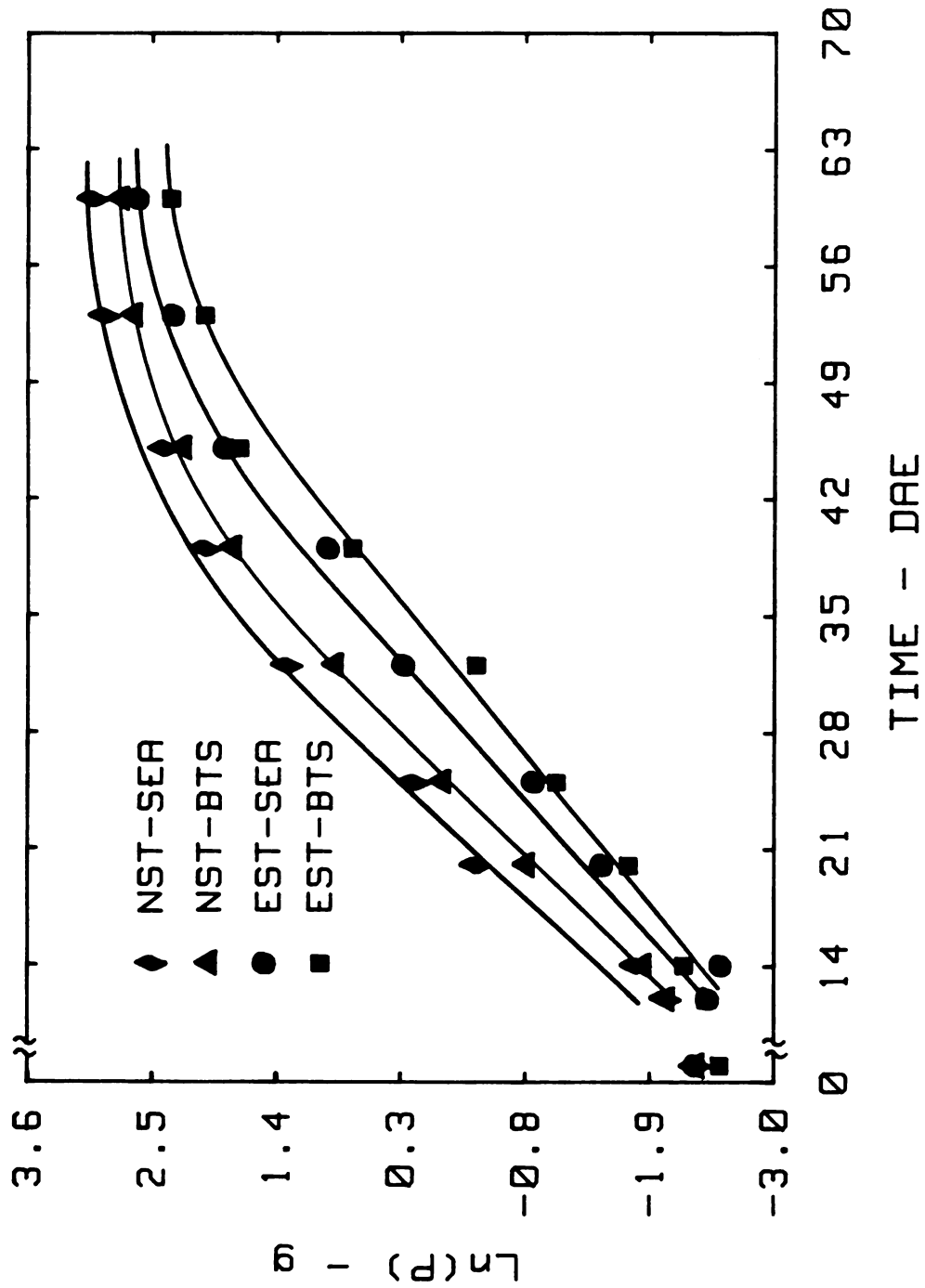


Figure 2. Natural log transformations of measured shoot dry mass accumulations of dry edible beans grown on Charity clay soil.

day⁻¹ for the BTS cultivar grown under NST and EST soil treatments, respectively. The end of this phase of growth corresponds to the inflection point in Figure 1, and the maximum points in Figures 3 and 4. The second stage of growth thus ended approximately 42 and 52 days after emergence (DAE) for NST and EST soil treatments respectively (Figure 3). The accumulated dry matter mass at this time was, however, roughly 11 and 9 g/plt for the SEA, and 9 and 6.5 g/plt for BTS cultivars grown under NST and EST soil treatments, respectively (Figure 4).

The third stage of growth started when the competition for limited carbohydrates among plant organs and reproduction systems forced RGR to deviate from linearity in Figure 2 and a descending trend in Figures 3 and 4. The points at which graphs in Figures 3 and 4 crossed the X axes, represent the steady state conditions where RGR is equal to zero. The biological capacity or potential growth of these plants were approximately 21.5 and 18.0 g/plt for SEA and 17.0 and 13.5g/plt for BTS cultivars grown under NST and EST treatments, respectively (Figure 4). Plant physiological maturity was delayed similarly for the two cultivars. Plants grown under the EST soil treatment reached physiological maturity about 100 DAE. These same cultivars matured 85-90 DAE when grown under NST soil treatment (Figure 3).

The competition factor, K_2 , may now be calculated using eq.(9) and knowing the biological growth potential and maximum RGR. These values are calculated to be 0.0073 and 0.0072 g⁻¹ d⁻¹ for the SEA, and 0.0090 and 0.0089 g⁻¹ d⁻¹ for BTS, cultivars grown under NST and EST treatments respectively. Substituting these values into eq.(7) and numerically

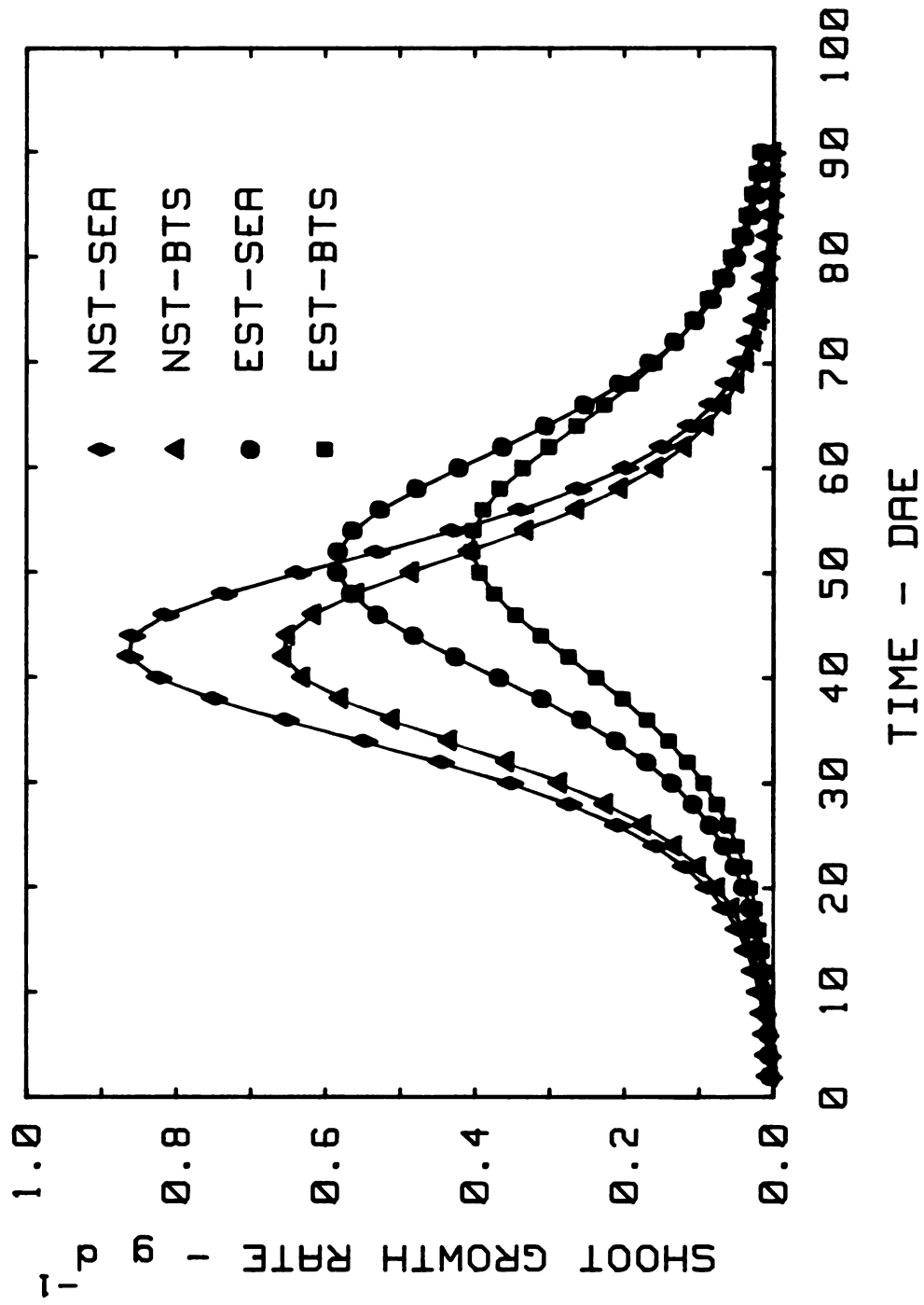


Figure 3. Absolute growth rate of dry edible bean shoots grown on Charity clay soil as a function of days after emergence (DAE).

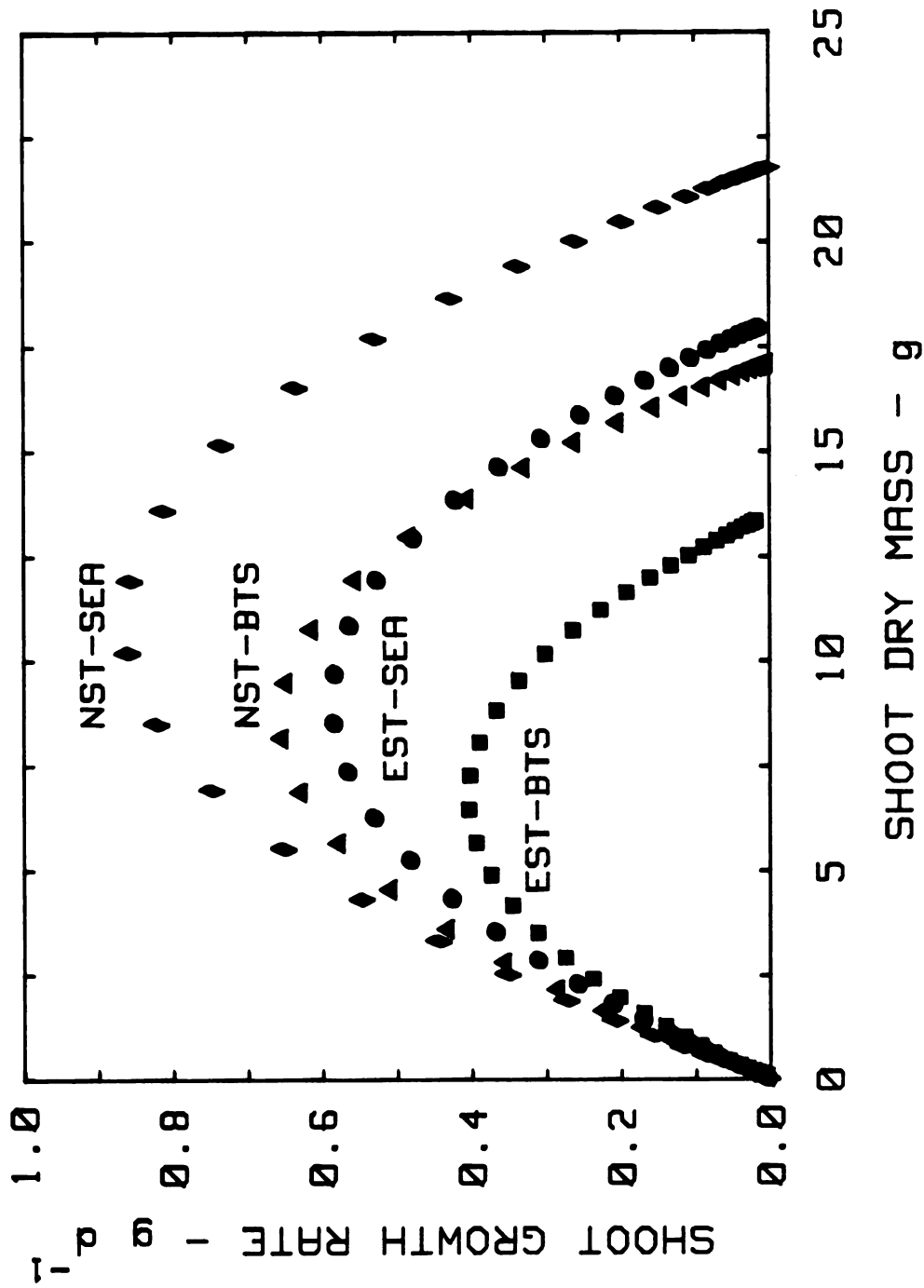


Figure 4. Absolute growth rate of dry edible bean shoots grown on Charity clay soil as a function of shoot dry mass.

integrating or into eq.(10) and calculating, produced the simulated values of plant dry weight (Figure 5).

Soil compaction apparently reduced the efficiency index of dry matter productions for both cultivars. The competition factors however remained unchanged for the same cultivars but were different for each cultivar. Based upon these experimental data one might suggest that the competition effects may be genetically controlled. The effects of RGR and competition factor on final plant growth are analogous to the effects of interest and taxation rates on the final income. One has a positive and the other a negative effect. Numerical integration of eq.(7) with initial conditions of $P(0)=0.0245$ g produced shoot dry mass progression data presented in Figure 5. The measured and calculated dry masses are overlayed in Figure 6 to indicate how this model simulates the actual field data. This graph along with Figure 7 indicates a good agreement between the calculated and actual data.

The methodology presented here can be used in two ways depending upon availability of a complete range of experimental data, or having limited growth information. In the first case derivation of equation parameters include extraction of maximum RGR from graphs similar to Figure 2, and the steady state growth potential from the maximum point of graphs similar to Figure 1. The competition factor, K_2 is then calculated from eq.(9). In this case we are primarily involved in curve fitting and producing a smooth set of growth progression data from which plant growth analysis can proceed.

If experimental data are limited but still have some points in the region of exponential growth, like our data presented here, then we can

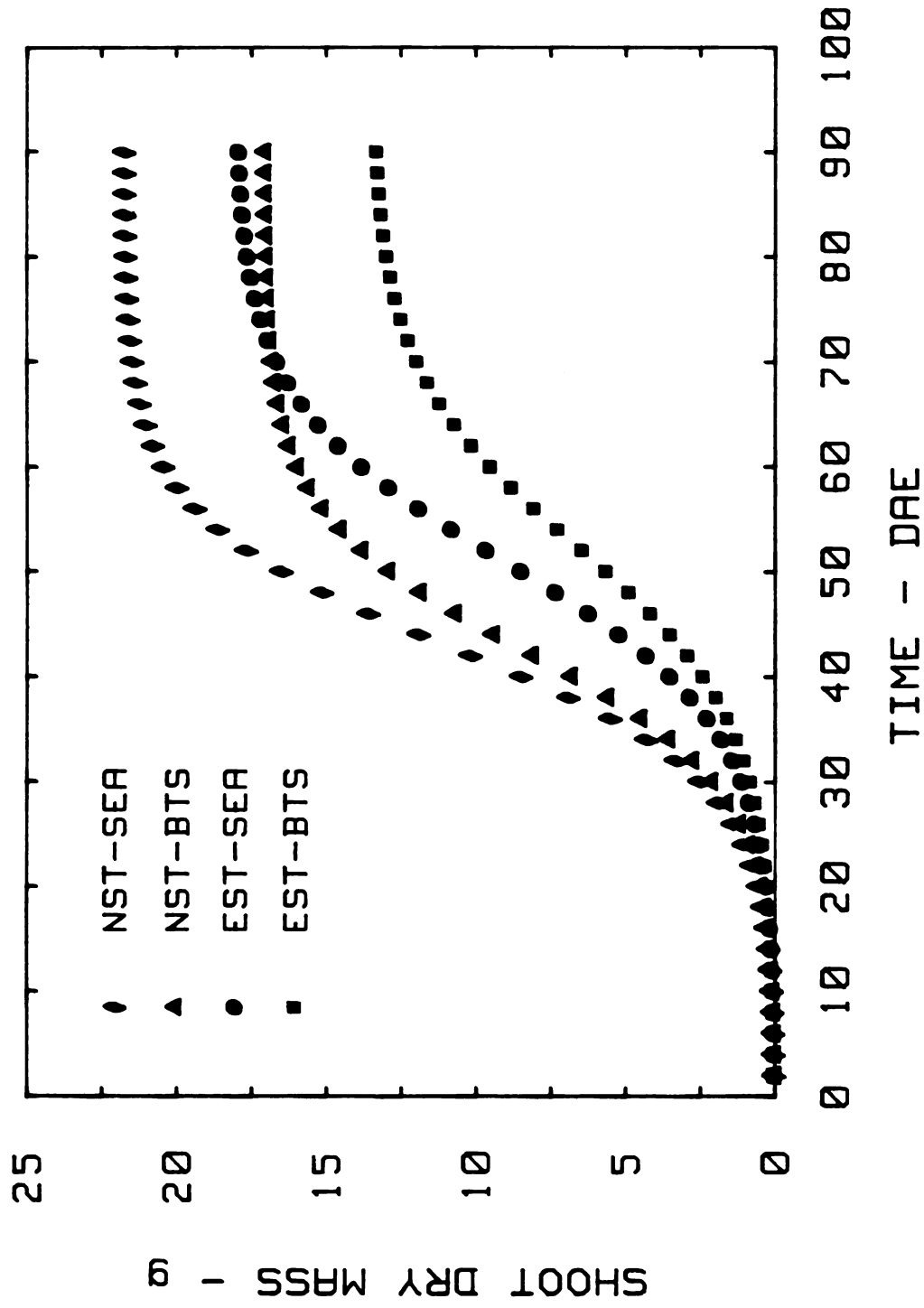


Figure 5. Simulated shoot dry mass accumulations of dry edible beans grown on Charity clay soil.

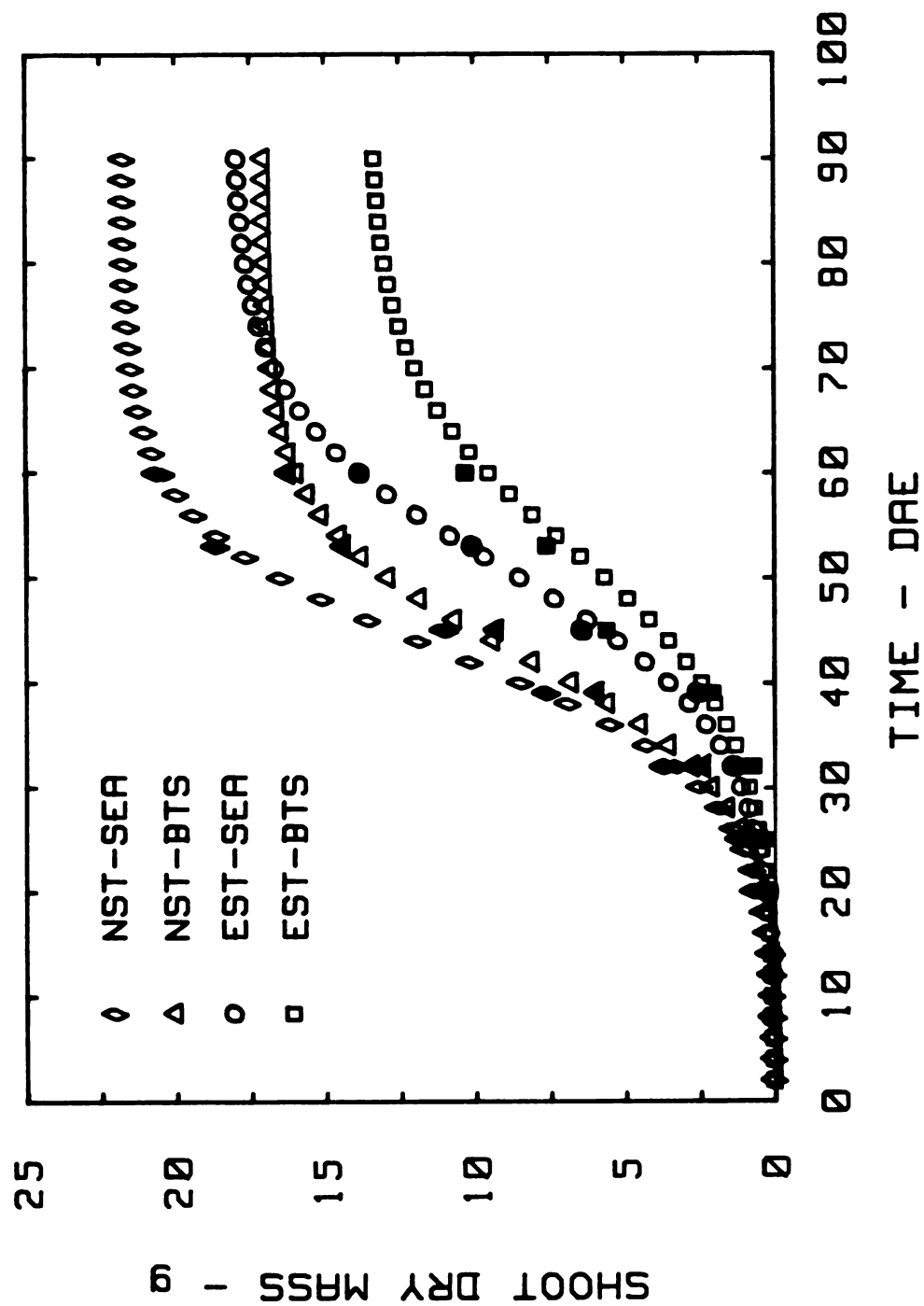


Figure 6. Simulated and measured shoot dry mass accumulations of dry edible beans grown on Charity clay soil. The solid symbols represent measured observations.

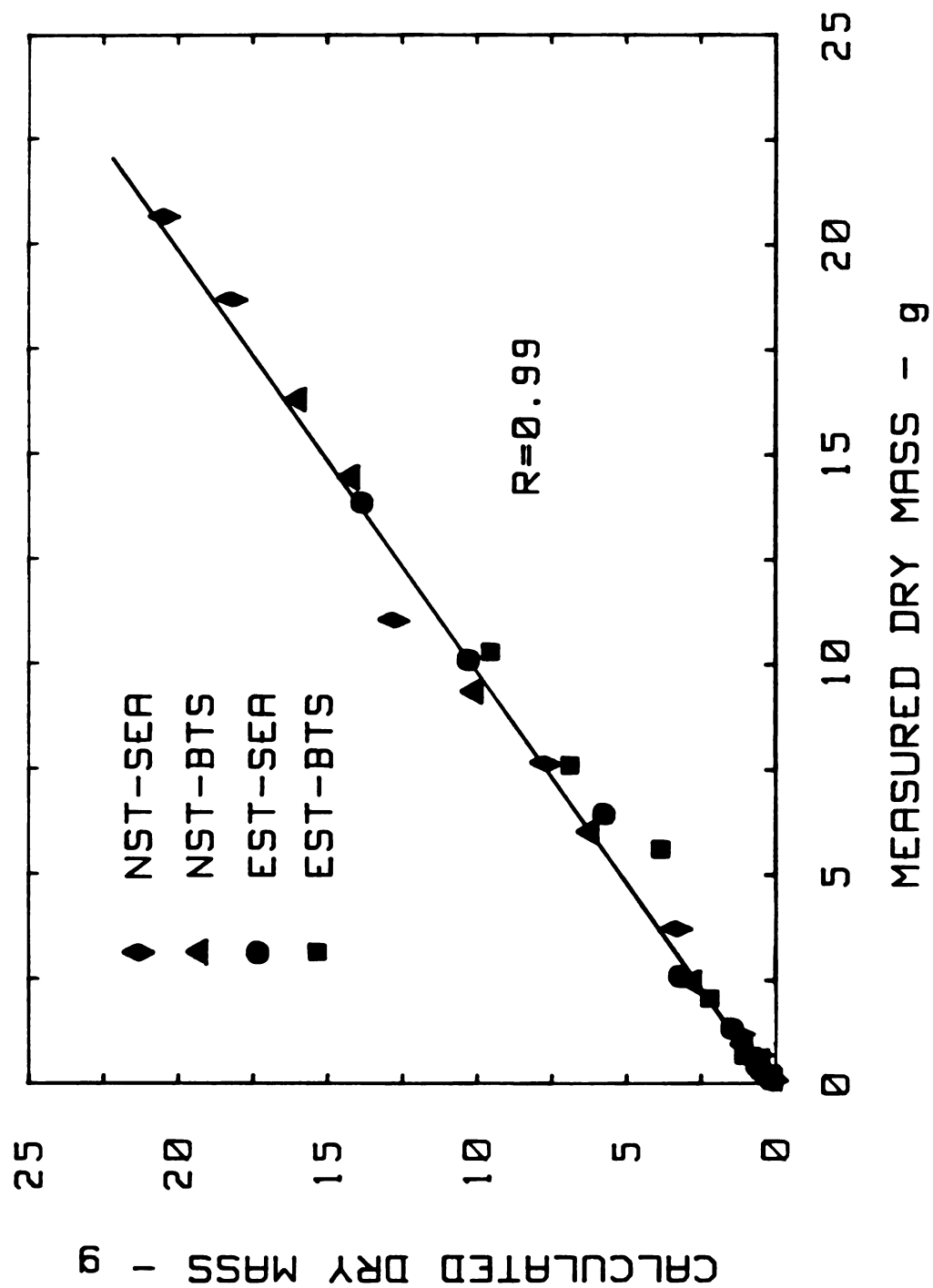


Figure 7. Correlation between the simulated and measured shoot dry mass of dry edible beans grown on Charity clay soil.

estimate the maximum RGR, K_1 from Figure 2 as described above. The task is now to find that value of K_2 which would best simulate the existing experimental data by trial and error. Using one of the points as the initial condition and eq.(12), the approximate value of K_2 can be obtained. We may then generate a complete range of data like those presented in Figs. 3-5. In this case our model has prediction capabilities and we were able to estimate not only the existing data but also go beyond the data base and gain new information. The data presented in Figure 6 predicts that accumulated shoot dry mass in the SEA cultivar grown under EST soil treatment would probably exceed that of BTS grown under NST after 70 DAE. This might be attributed to the compaction induced delayed maturity of the SEA cultivar.

In conclusion, the concept of carrying capacity or potential growth may provide a convenient way to integrate the combined performances of various parts of plants, when used to compare different species or treatments. New information may be gained from calculating potential growth of each subcomponent. This not only takes into account the efficiency index of plant growth, which is a measure of the economical conversion of its energy to different subcomponents, but also accounts for the competition which exist between subcomponents. It may also be a useful tool in screening plant performances grown under controlled environments. The assumptions made in devising this analysis were (1) that growth has an exponential course at some stage of its development, (2) the growth function resembles a sigmoid curve, and (3) the environmental conditions of the experiment are essentially constant such

that the potential growth does not undergo a drastic change resulting in a relatively constant end point.

LITERATURE CITED

- Blackman, C.V. 1919. *Ann. Bot.* 23:353-
- DuChateau, P.C., D.L. Nofziger, L.R. Ahuja, and D. Swartzendruber. 1972. Experimental curves and rates of change from piecewise parabolic fits. *Agron. J.* 64:538-542.
- Elias, C.O. and D.R. Causton. 1976. Studies on data variability and the use of polynomials to describe plant growth. *New Phytol.* 77:421-430.
- Feddes, R.A., P.J. Kowalik and H. Zaradny. 1978. Simulation of field water use and crop yield. John Wiley and Sons. New York. pp. 1-50.
- Gold, H.J. 1977. Mathematical Modeling of Biological Systems. An Introductory Guide Book. pp. 145-186.
- Hughes, A.P. and P.R. Freeman. 1967. Growth analysis using frequent small harvests. *J. Appl. Ecol.* 4:553-560.
- Hunt, R. 1979. Plant growth analysis: The rationale behind the use of the fitted mathematical functions. *Ann. Bot.* 43:245-249.
- Hunt, R. 1978. Plant growth analysis. Studies in biology no. 96. Edward Arnold, London. 67pp.
- Hunt, R. and G.C. Evans. 1980. Classical data on the growth of maize: Curve fitting with statistical analysis. *New Phytol.* 86:155-180.
- Hunt, R. and I.T. Parsons. 1977. Plant growth analysis: Further applications of a recent curve-fitting program. *J. Appl. Ecol.* 14:965-968. Hunt, R. and I.T. Parsons. 1974. A Computer program for deriving growth-function in plant growth analysis. *J. Appl. Ecol.* 11:297-307.
- Hurd, R.G. 1977. Vegetative plant growth analysis in controlled environments. *Ann. Bot.* 41:779-787.
- Parsons, I.T. and R. Hunt. 1981. Plant growth analysis: A program for the fitting of lengthy series of data by the methods of B-splines. *Ann. Bot.* 48:341-352.

Sivakumar, M.V.K. and R.H. Shaw. 1978. Methods of growth analysis in field grown soy beans (*Glycine Max* L. Merrill). *Ann. Bot.* 42:213-222.

CHAPTER 5

PHASOL: A MODEL OF ROOT GROWTH AND WATER UPTAKE IN A LAYERED-HOMOGENEOUS SOIL PROFILE

INTRODUCTION

A model may be described as an abstract description of a real phenomena in the universal language of mathematics. Plant growth models are built for many different purposes which vary from summarizing the data to predicting plant responses and interpreting those responses. The purpose of a model then, influences its comprehension and degree of universality. The development of a comprehensive mathematical model is one of the most powerful means of describing and analyzing the various ongoing interactions among parameters of a complex system such as the soil-plant-atmosphere continuum. However many models of plant growth and development generally ignore the influence of the soil environment on the physiological processes of growth of the whole plant system.

Modeling soil physical processes is one of the important areas in building any comprehensive plant growth model. Soil physical environments influencing plant growth usually include soil water potential, soil aeration status, soil strength, and soil temperature. It is therefore imperative for plant growth models to quantitatively describe the transport processes involving the movement of liquids and

gases in the soil. A number of models have been constructed which describe the processes of soil water movement in the absence of plant root systems (Beese et al., 1977; James and Larson, 1976; Rowse and Stone, 1978) as well as several which include growing plants (Arya et al., 1975a,b; Hillel, 1977; Huck and Hillel, 1983; Rowse et al., 1978; Warrick et al., 1980; Warrick and Lomen, 1983). The complexity of modeling the physical processes involved in the transport of water in the soil has arisen from the fact that soil is a nonhomogenous highly irregular and tortuous medium. The flow of water through this medium is assumed to be via hypothetical conduits, which are often discontinuous. Thus, flow of water in the soil is limited by many constrictions and at best can be described in a macroscopic continuum approach.

Darcy's law is one of the first equations quantifying the flow of water through a saturated porous medium. This equation can be written as

$$q = - KVH \quad (1)$$

where q is the vector of water flux density, which is directly proportional to the hydraulic gradient vector, VH (Hillel, 1980). The proportionality factor is a scalar quantity called the hydraulic conductivity (K), which depends upon the flowing fluid as well as porous medium. Development of equations describing the flow of water through unsaturated porous media involves combining the equation of continuity with Darcy's law. The assumption is that Darcy's equation is applicable to all flow conditions. Kirkham and Powers (1972) derived this equation for 3 dimensional flow as follows

$$\frac{\partial \theta}{\partial t} = \frac{\partial}{\partial x} \left(K_x \frac{\partial h}{\partial x} \right) + \frac{\partial}{\partial y} \left(K_y \frac{\partial h}{\partial y} \right) + \frac{\partial}{\partial z} \left(K_z \frac{\partial h}{\partial z} \right) \quad (2)$$

where θ is the volumetric water content of the soil, t is the time, h is the soil matric potential, and K_x , K_y , and K_z are the hydraulic conductivity values in the three principle directions. This equation for an isotropic medium may be reduced to

$$\frac{\partial \theta}{\partial t} = \nabla \cdot (K \nabla h) \quad (3)$$

where $\nabla \cdot$ and ∇ are the divergence and gradient operators respectively. In unsaturated conditions the hydraulic conductivity is dependent on soil matric potential or water content.

A major problem encountered in modeling the transport of water in the presence of growing roots is the inherent complicated time-space relationships (Hillel, 1977). Roots are growing in different directions and spacings. Their absorption capacity changes with age creating sectional differences in water uptake. Their elongation rate is further complicated by the soil physical environment. Construction of models describing the transport of water in the presence of growing roots often involves modifications of Darcy's equation which includes the root as a sink. The vertical transient state movement of water in an isotropic and uniform medium containing roots can be described by

$$\frac{\partial \theta}{\partial t} = - \frac{\partial}{\partial z} \left\{ K(\theta) \frac{\partial (h+z)}{\partial z} \right\} - S_w \quad (4)$$

where t is the time, z is the depth, $K(\theta)$ is the hydraulic

conductivity as a function of the volumetric water content (θ), h is the matric potential head, and S_w is the root extraction rate representing the sink term (Hillel, 1977). Therefore, The hydraulic properties of soil and plant are very important in modeling the water transport within the soil-plant system.

Hydraulic soil properties are usually assumed to be defineable in the sense of a macroscopic continuum approach (Klute, 1982). At each mathematical point of this continuum, macroscopic variables such as soil porosity, conductivity, water capacity, water content, and pressure head are assumed to be defineable, and are obtained by averaging the local microscopic variables of the medium over a small control volume. The physical state of a soil however, is not static, rather it is in a dynamic equilibrium with the prevailing environmental conditions. For example the no tillage approach to crop production leaves crop residues in the surface creating a layer of mulch which reduces evaporation losses. The soil water content is then higher than conventional tillage influencing such soil hydraulic properties as soil water potential $h(\theta)$, hydraulic conductivity $K(\theta)$, and soil water capacity $d\theta/dh$ (Phillips et al., 1980). Even though these hydraulic soil properties are important in characterizing the physical state of a soil, the difficulties and complexities involved in sampling and measuring these properties has often discouraged scientists from characterizing the soil directly from these indices. Many investigators have attempted to improve or modify the existing theories and procedures for measuring hydraulic soil properties (Arya et al., 1975; Brakensiek, 1979; Clapp and Hornberger, 1978; Ghosh, 1976; Gupta and Larson, 1979; Mualem, 1976; Nagpal and deVries, 1976).

Two fundamental hydrological soil properties, the soil water retention curve and the hydraulic conductivity are the major components of the quantitative analysis of soil water processes. The soil water characteristic curve is usually determined by desorption of an initially saturated soil to a prespecified pressure and then determining its equilibrium water content (Richards, 1965). The field measurement involves the in situ estimation of soil matrix potential using tensiometers or psychrometers and concurrent measurements of soil water content by gravimetric sampling, neutron probe, or gamma ray attenuation techniques.

Arya et al. (1975) proposed the in situ measurements of hydraulic soil properties by a so called zero-flux method, where a moving plane of zero flux is obtained from the field desaturation data and the soil water pressures are monitored at several depths by tensiometers. The soil hydraulic conductivity then may be calculated from the Darcian flux equation

$$K(h) = \left[\int_{z_0}^z \left(\frac{\partial \theta}{\partial t} \right) dz \right] / \left(\frac{\partial H}{\partial z} \right) z \quad (5)$$

where K is the soil hydraulic conductivity at depth z as a function of soil matrix potential (h), z_0 is the depth of zero-flux plane, θ is volumetric water content, t is the time, and H is the total soil water potential at depth z . Theoretical calculations of unsaturated hydraulic conductivity often involves Poiseuille's law. Most theoretical equations needs the water release curve and the saturated hydraulic conductivity or water content to estimate the unsaturated hydraulic conductivity (Kunze et al., 1968; Jackson, 1972). Jackson

(1972) introduced an empirical component in the form of a matching factor into the theoretical equation

$$K_i = K_s (\theta_i / \theta_s)^c \frac{\sum_{j=1}^m [(2j+1-2i)h_j^{-2}]}{\sum_{j=1}^m [(2j-1)h_j^{-2}]} \quad (6)$$

where K_i is the hydraulic conductivity which corresponds to a volumetric water content of θ_i , K_s is hydraulic conductivity measured at saturation (θ_s), m is the number of intervals in θ , h is the suction head at the midpoint of each θ interval, j and i are summation indices, and c is an arbitrary constant often taken as unity.

A simpler, more easily determined measurement for assessing soil physical conditions including hydraulic properties may be soil bulk density. The Physioempirical model of Arya and Paris (1981) estimating soil moisture characteristic curve from particle size distribution and bulk density is a step toward this approach. The problem with soil bulk density, however, is that it is a crude measure of physical conditions of a soil. It only considers the total pore volume of the soil and ignores the more important criteria of pore size distribution. Pore size distributions have traditionally been determined by applying capillary theory to soil water characteristic curve as follows

$$h = 2 \sigma \cos \theta / r \quad (7)$$

where h is the capillary pressure or suction head with which the water is held in the pores, r is the pore radius, σ is the surface tension of water, and θ is the angle of contact between water and solids. Nagpal et al. (1972) reported a good agreement between this method and mercury

intrusion technique for nonswelling soils.

The purpose of this study was to modify the ROOTSM model of Huck and Hillel (1983), to account for the effects of mechanical impedance on root growth and distribution. Empirical equations were derived from experimental data which describe the processes of water movement and root growth in a layered-homogeneous soil profile.

DESCRIPTION OF THE MODEL

The PHASOL model of root growth and water uptake presented here is a modified version of the ROOTSM model reported by Huck and Hillel (1983). The model takes into account the balance of carbon and the movement of water through plants growing in a one-dimensional multi-compartment soil profile. The present version of the model provides the inclusion of different bulk densities in a 10 layered soil profile. The model is driven by solar radiation, estimated by a solar radiation simulator (SOLSIM) which uses daily maximum and minimum temperatures as well as precipitation to generate daily solar radiations (Hodges et al., 1983). The algorithm is based upon Richardson's (1981) weather simulator. The location specific variables used in this algorithm are available for the continental United States in the form of contour maps. Inputs to the model are soil and plant variables related to the experimental study of this report.

Model Program

The PHASOL model of root growth and water uptake in a layered homogeneous, isotropic soil medium is programmed in FORTRAN V, and run on a CYBER 750 computer. The model consists of a main program and three subprograms. The SOLSIM subroutine is called to generate the daily solar radiation intensities as needed. The other two subprograms are functions INTGRL and AFGEN for rectangular integration and table

function generation, respectively. There are other subprograms which could be used for plotting purposes but are not called by the present model, and their presence in the program listings (APPENDIX), is for documentation only.

Water Balance

The water balance portion of the model takes into account the water supplying power of the soil and roots and the transpiration potential of the atmosphere. The approach considers flow of the water in the transpiration stream to be down a gradient of potential energy from the soil to the roots and to the atmosphere. The gradient-driven concept of water flow within the soil-plant-atmosphere system is originated from the Van den Honert (1948) analogy of the transpiration stream to an electrical circuit. The flow of water within each segment of the stream is directly proportional to the potential gradient and inversely related to the resistance. The water balance flowchart for the PHASOL model is presented in Figure 1. The description of the symbols in these flow charts follows Forrester's (1961) conventions. Rectangular boxes describe the state variables, and the valves represent the rate variables which are usually constrained by some other processes. The water could be supplied to the system through irrigation or rain and may move downward by the Darcian flow and be taken up by the roots simultaneously.

The flow of water in the PHASOL model is considered to be upward within a one-dimensional, 10-layered medium which is isotropic, homogeneous within each layer. This system is hydraulically equivalent to a homogeneous, anisotropic medium. Equation (4) is the flow equation

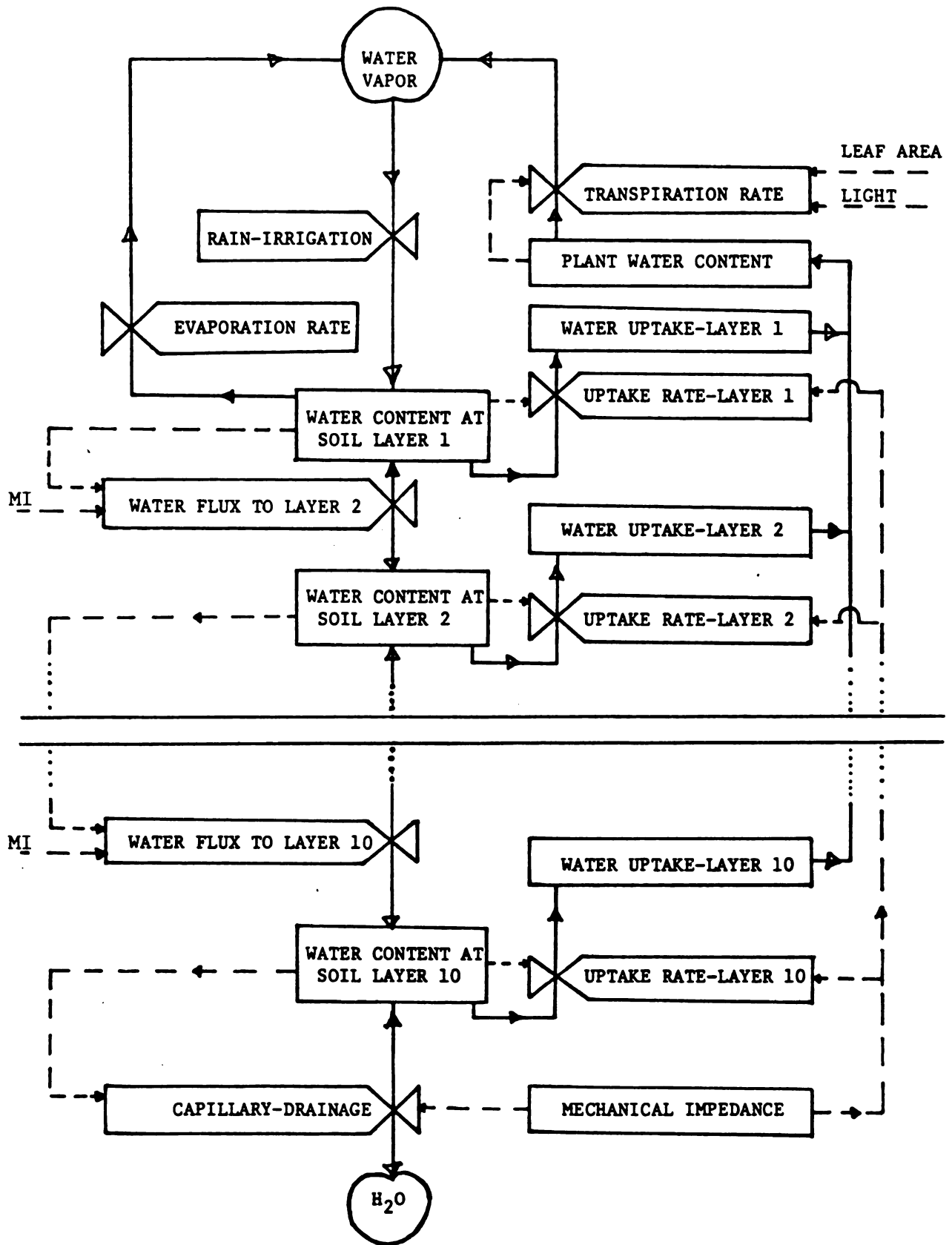


Figure 1. Flowchart representing the water flow processes within the soil-plant-atmosphere system.

which is solved numerically by a finite-difference scheme subject to the following boundary conditions

- | | | | | | |
|-----|----|------------|-----|------------|---------------------|
| (1) | at | $t=0$ | and | $z \geq 0$ | $\theta = \theta_1$ |
| (2) | at | $t \geq 0$ | and | $z = z_b$ | $h = -0.60$ |
| (3) | at | $t \geq 0$ | and | $z = 0$ | $q = 0$ |

The flux is considered to be positive downward with z equal to zero at the soil surface and z equal to z_b at the bottom of the soil profile. The first boundary condition corresponds to an initial soil moisture content (θ_1) within the soil profile. The second boundary condition corresponds to a constant matric potential head of -0.60 meter at the bottom of the soil profile for all times (t). The third boundary condition corresponds to zero evaporation from the soil surface. Other boundary conditions could be used if so desired.

Data on the relationship between soil matric potential head (h), hydraulic conductivity (K), and volumetric water content (θ) in the PHASOL model is limited to those obtained from destructive core sampling. An empirical equation was fitted to the water characteristic curves (Figure 2) which estimates the matric potential head ($POTM(I)$) from the soil bulk densities ($BD(I)$) and the volumetric water content ($THETA(I)$) for each soil layer (I) as follows

$$POTM(I) = -93878.06 * \exp(-37.42 * THETA(I) / BD(I)) \quad (8)$$

where $POTM$ is in m , $THETA$ in $m^3 m^{-3}$, and BD in $Mg m^{-3}$. This equation estimates the matric potential head reasonably well for the range of

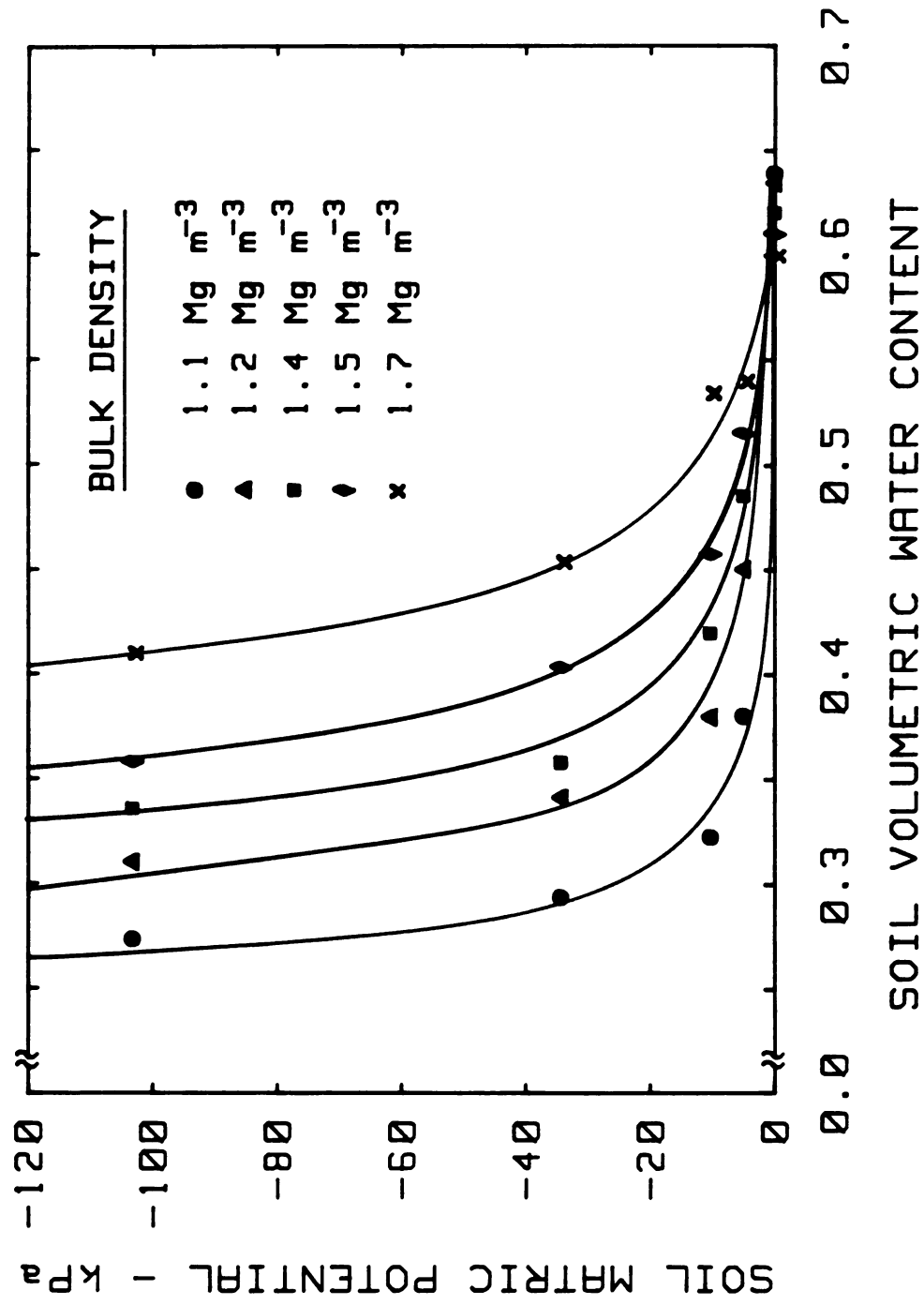


Figure 2. Soil water characteristic modifications of Charity clay soil with bulk density.

soil bulk densities and water contents encountered under most field conditions. The relationship between hydraulic conductivity and matric potential head is more difficult to measure experimentally, especially under different soil bulk densities. The unsaturated hydraulic conductivities for 3 bulk densities (Figure 3) were estimated from eqn.(6). The saturated hydraulic conductivities were measured in the laboratory by applying a constant head permeameter to core samples. An empirical equation was fitted to these data which estimates the hydraulic conductivity (COND(I)) from matric potential head, and soil bulk densities for each soil layer in this model. This equation is

$$\text{COND(I)} = \text{EXP}[6.77 - 4.21 * \text{BD(I)} - 0.93845 * \text{ALOG}(-\text{POTM(I)}) - 0.07445 * (\text{ALOG}(-\text{POTM(I)}))^2] \quad (9)$$

where COND is in cm d^{-1} , POTM in cm of water, and BD in Mg m^{-3} .

The rate of root water uptake (S_w) from the soil-root interface and its transport to plant-air interface is estimated on the basis of Ohm's law analogy with the potential gradient between the transpiring leaves and each soil layer acting as the driving force. The rate of root extraction from each soil layer (RTEX(I)) is thus estimated by ROOTSM in the following equation

$$\text{RTEX(I)} = \text{AMAX1}(0.0, (\text{POTH(I)} - \text{POTCR}) / (\text{RSSL(I)} + \text{RSRT(I)})) \quad (10)$$

where POTH is the hydraulic potential head, POTCR is the leaf water potential, RSSL is soil resistant to water flow, and RSRT is the root resistance to water flow for each soil layer. After summing the initial

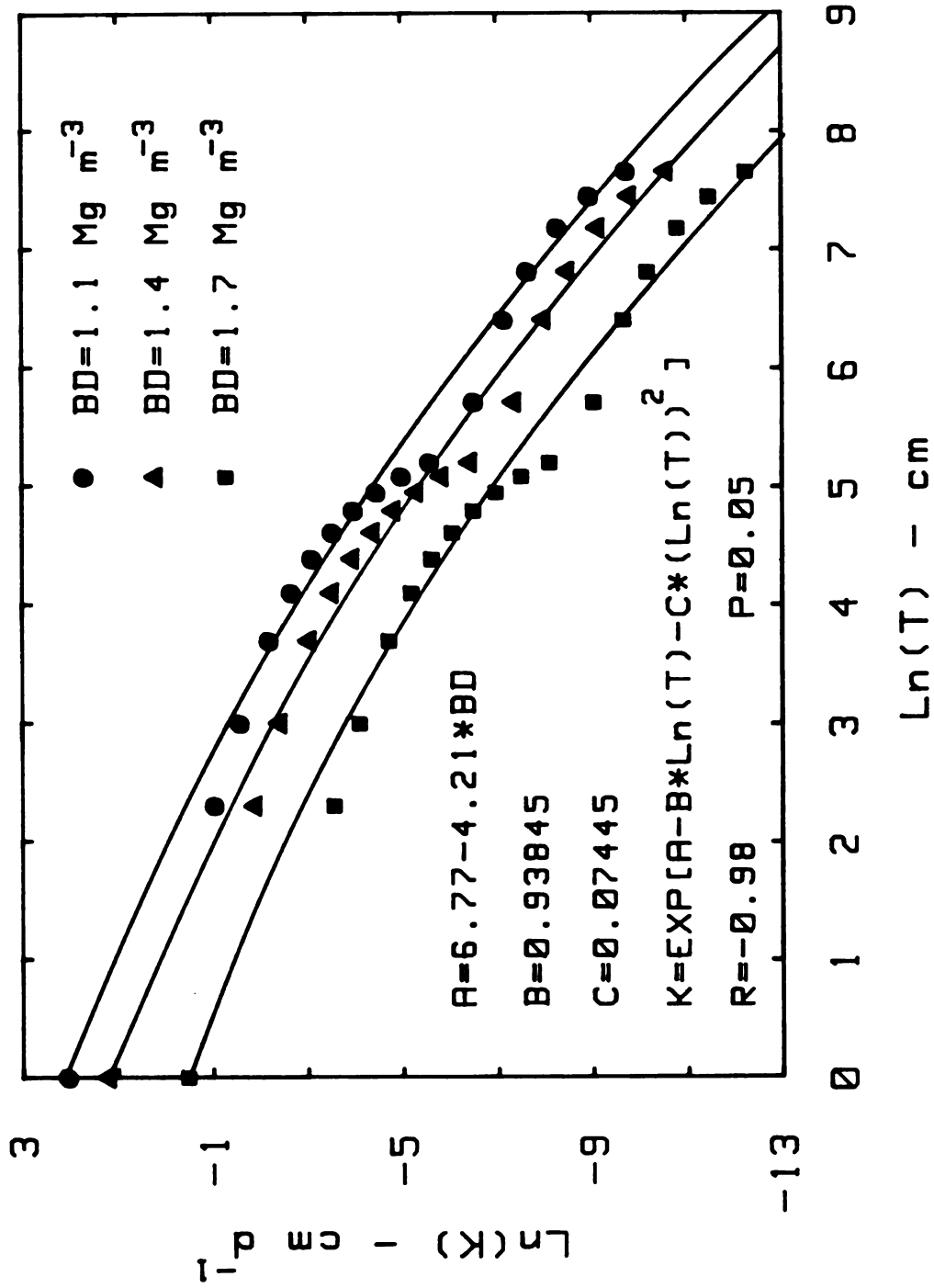


Figure 3. Hydraulic conductivity modifications of Charity clay soil at different bulk densities. T is the soil matric tension and Ln is the natural logarithm.

root water uptake rates over all soil layers, the total (SUMR) is compared to the transpiration rate (TRANSP). The leaf water potential is then adjusted iteratively so that the two are within 1% of one another. Thus, if the transpiration rate is greater than the sum of root removal rate from all soil layers, the leaf water potential would be decreased in order to stimulate more water uptake. This leaf water potential is used as the initial estimate for the next time step.

Evapotranspiration is a name given to the combined process of water loss from the soil (evaporation), and plant (transpiration). The model estimates potential evapotranspiration (PET) from the measured daily pan evaporation (MPANEV) and maximum daily solar radiation (MAXRAD). Thus

$$PET = \text{AMAX1}(0.01 * \text{DTRDEM} / 86400., \text{PI} * \text{RADN} * \text{MPANEV} / \text{MAXRAD}) \quad (11)$$

where PET is considered to be the maximum of either 1% of the daily transpiration demand (DTRDEM) or a daily measured pan evaporation scaled to the incoming solar radiations (RADN). Partition of PET into soil evaporation (SLEVAP), and transpiration (TRANSP) involves leaf area index (LAI). In the absence of a canopy, the water loss is limited to soil evaporation only.

The relative contributions of SLEVAP and TRANSP to PET is modified by the existence of water stress in the plant. If the plant has an adequate water supply the transpiration rate is controlled primarily by the incoming solar radiation. Excess transpiration rate over water uptake rate, however, produces water deficit which decreases plant water potential and stomatal aperture. The ROOTSM

estimation of the transpiration portion of PET is as follows

$$\text{TRANSP} = \text{PET} * \text{WATRST} * \text{LAIFAC} \quad (12)$$

The water stress (WATRST) and leaf area (LAIFAC) factors are variables between 0 and 1 to adjust the transpiration rate for changing plant water potentials and leaf areas.

Changes in stomatal resistance are the most obvious mechanisms by which the leaf water potential influences the transpiration rate. When the turgor pressure of the guard cells fell below a threshold value, the stomatal aperture decreases and stomatal resistance increases. The curvilinear relationship between the leaf water potential (POTCR), and abaxial diffusive resistance (DR) in the PHASOL model (Figure 4) may suggest that the stomatal aperture had changed little so long as the leaf water potential was above -10 meter. A least squares equation was fitted which quantitatively describes this relationship as

$$\text{DR} = \text{EXP}(4.271 - 0.0316 * \text{POTCR}) \quad (13)$$

where DR is in s m^{-1} , and POTCR is in m. Until more objective information is available, which sheds light on the true nature of the transpiration process under a stress environment, it is assumed that environmental stresses including mechanical impedance may indirectly affect transpiration by influencing the mechanisms which control the stomata. In this study, the transpiration rates were the least and diffusive resistances were the greatest on the treatments having very high mechanical impedance (Figure 5). The curvilinear relationship

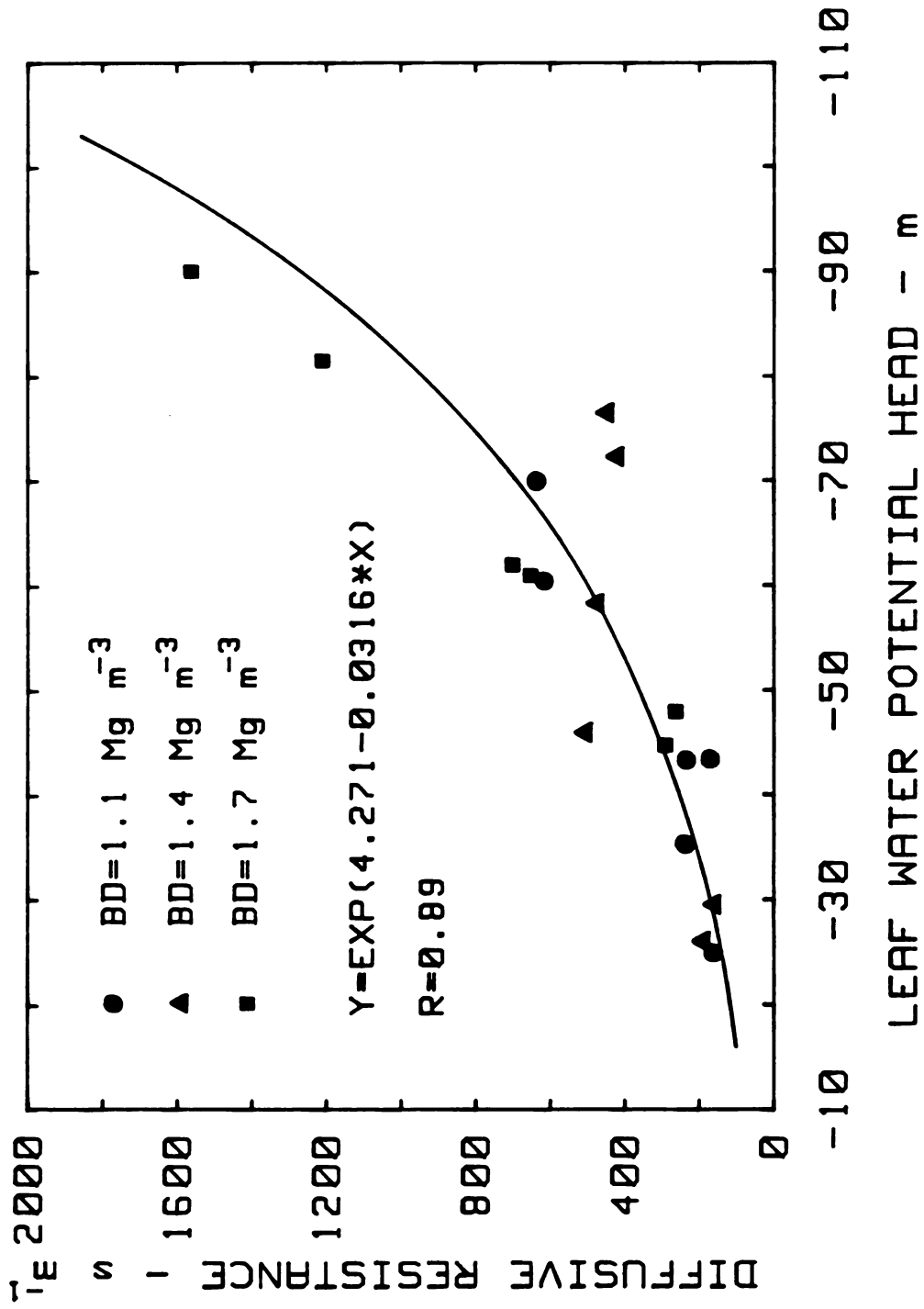


Figure 4. Influence of leaf water potential on the leaf abaxial diffusive resistance of dry edible beans.

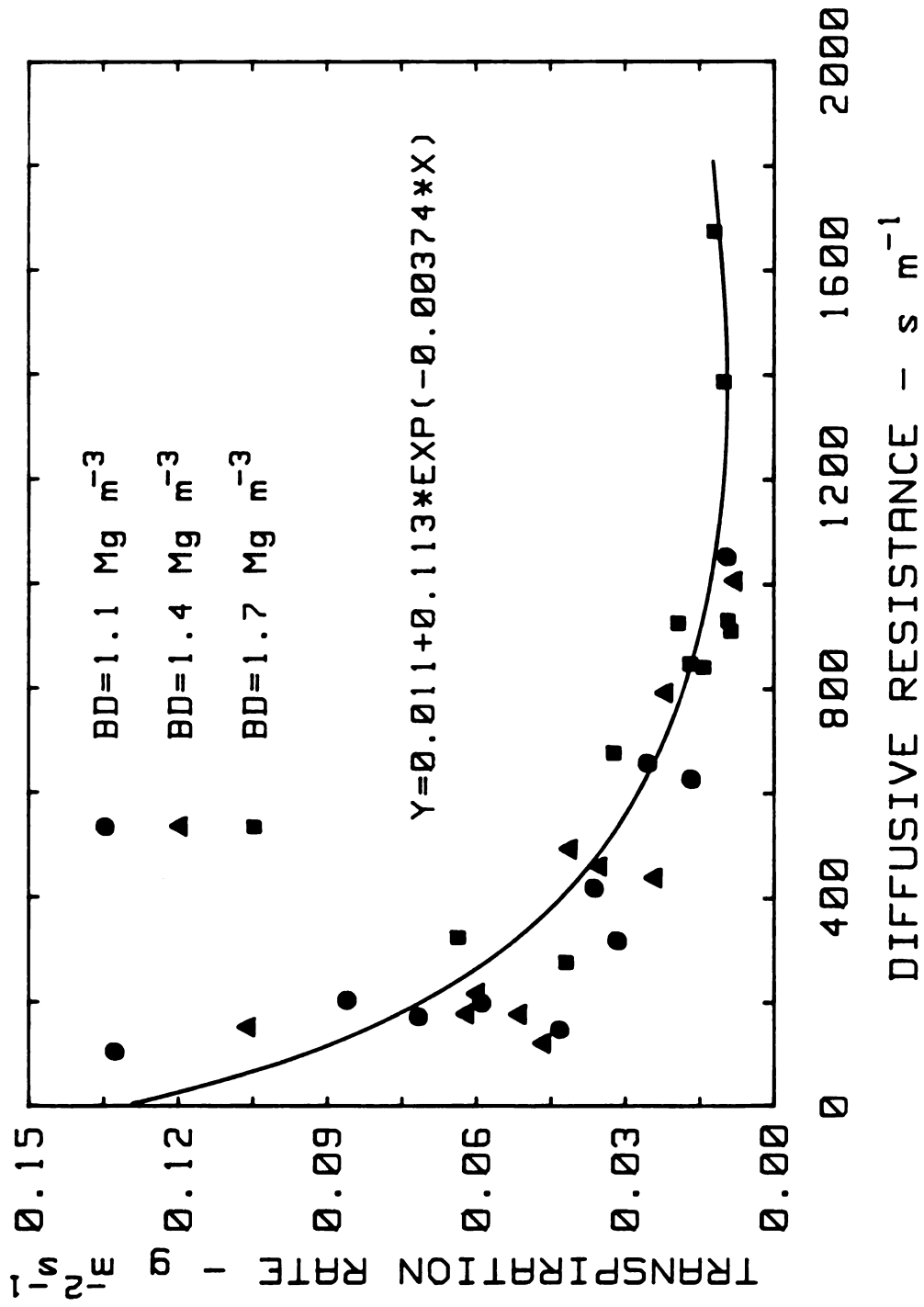


Figure 5. Specific transpiration rate as a function of leaf abaxial diffusive resistance of dry edible beans.

between transpiration rates and diffusive resistances of the PASOL model, approached an asymptotic value for high diffusive resistances. Therefore, it appears reasonable to suggest that the stomatal aperture may not have become completely closed (Figure 5). A least squares equation was fitted to this curve which estimates the specific transpiration rate (SPTRNS) from diffusive resistance (DR) as follows

$$\text{SPTRNS} = 0.011 + 0.113 * \text{EXP}(-0.00374 * \text{DR}) \quad (14)$$

where SPTRNS is given as $\text{g H}_2\text{O m}^{-2}$ of leaf s^{-1} and DR as s m^{-1}

Intuitively, the maximum SPTRNS should occur when the stomata are wide open, the diffusive resistance is minimum, and the potential evapotranspiration (PET) is maximum. The minimum value of DR is the intercept of the curve in Figure 4., which is found to be 72 s m^{-1} in this study. This nonzero intercept appears to be reasonable because the leaf conductance ($1/\text{DR}$) never becomes infinite. The water stress factor (WATRST) of the PHASOL model is calculated as the ratio of the SPTRNS to the maximum SPTRNS as follows

$$\text{WATRST} = \text{SPTRNS} / 0.097 \quad (15)$$

where 0.097 is the maximum SPTRNS, calculated from eqn.(14) for the DR value of 72 s m^{-1} . Substituting eqn.(14) into eqn.(15) results in

$$\text{WATRST} = (0.011 + 0.113 * \text{EXP}(-0.00374 * \text{DR})) / 0.097 \quad (16)$$

which is graphically presented in Figure 6.

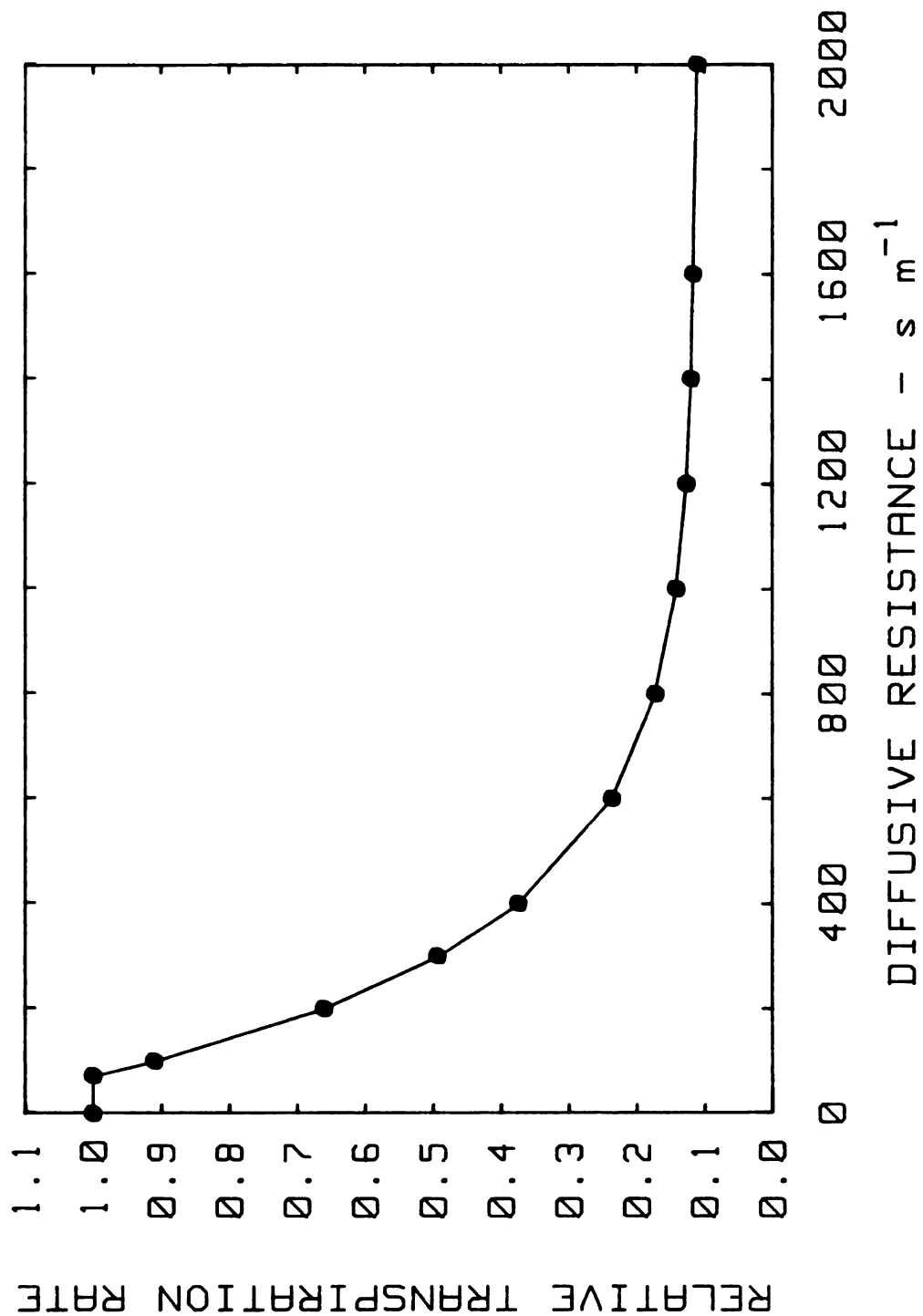


Figure 6. Influence of leaf abaxial diffusive resistance on relative transpiration rate of dry edible beans. This is graph of the water stress factor (WATRST) in the PHASOL model.

The ROOTSM model estimates soil evaporation as

$$\text{SLEVAP} = \text{PET} * (1.0 - \text{LAIFAC}) \quad (17)$$

Soil evaporation in the PHASOL model, however, was zero thus

$$\text{SLEVAP} = 0.0$$

Carbon Balance

A schematic flowchart for the carbon balance portion of the PHASOL model is presented in Figure 7. In this model CO_2 diffuses into the leaf through stomatal apertures and is incorporated into a labile pool which is controlled by photosynthetic carbon fixation processes. Photosynthetic activity is constrained by leaf area, leaf water potential, and the incoming solar radiation or portions of it which are frequently referred to as photosynthetic active radiation. Aside from a shortage of photosynthetic active radiation, the major environmental stresses affecting photosynthesis are unfavorable temperature, inadequate water balance, or nutrient deficiencies (Koller, 1975). All of these environmental stresses appear to be directly related to mechanical impedance. Thus, mechanical impedance is assumed to indirectly influence photosynthesis through impeding water uptake and reducing the canopy water potential. The rate at which carbon dioxide diffuses into the leaf and incorporates into the labile pool is defined by the ROOTSM model of Huck and Hillel (1983) as

$$\text{PHOTSN} = \text{RADN} * \text{MAXFOT} / \text{MAXRAD} * \text{WATRST} * \text{LAIFAC} \quad (18)$$

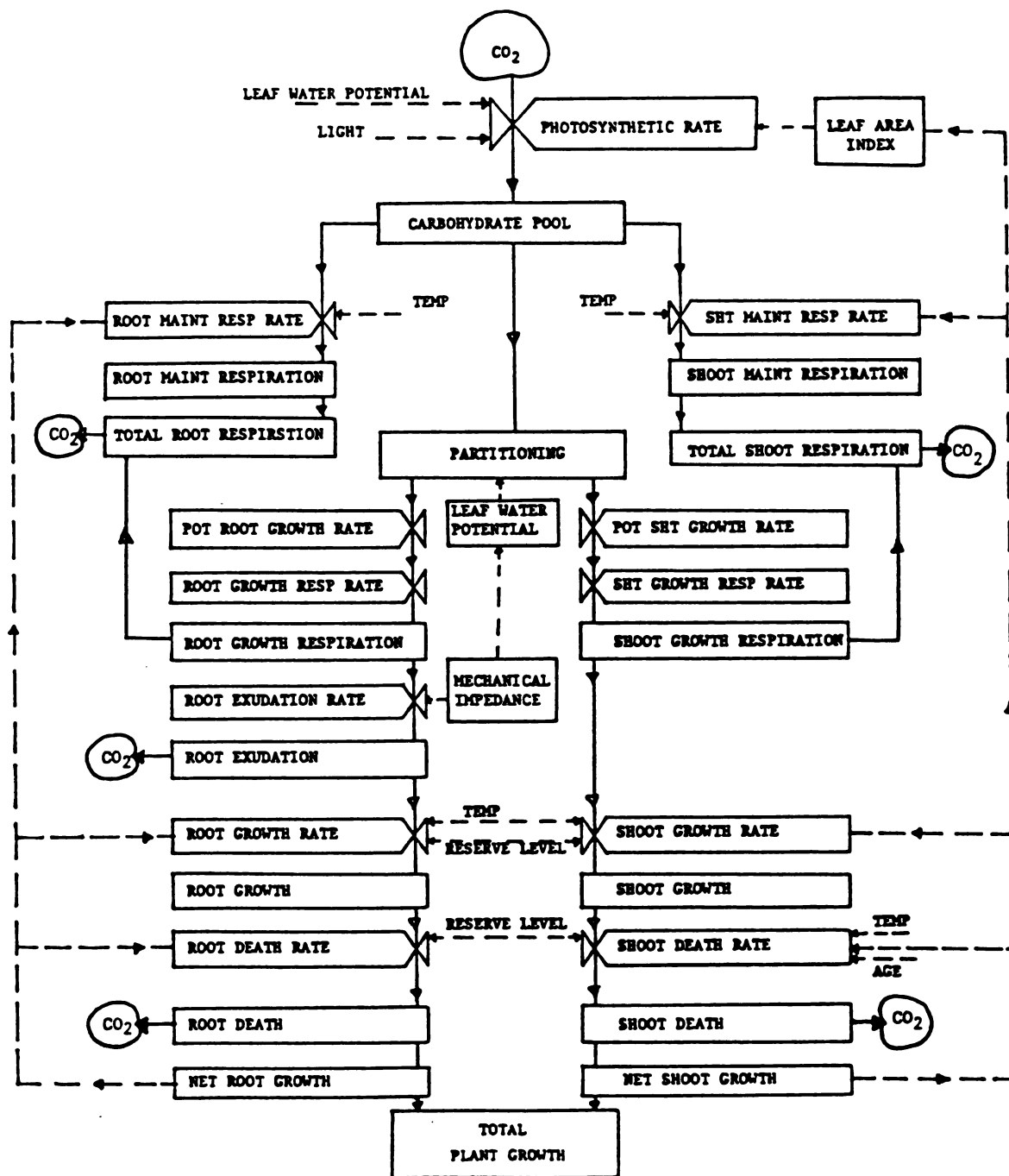


Figure 7. Flowchart representing carbon flow processes within the soil-plant-atmosphere system. RT=root, SHT=shoot, RESP=respiration, TEMP=temperature, MAINT=maintenance, POT=potential.

Where RADN is the instantaneous incoming solar radiation intensity estimated by

$$\text{RADN} = \text{MAXRAD} * (\text{AMAX1}(0.0, \sin(2.0 * \pi * (\text{DAY} - 0.25)))) \quad (19)$$

The MAXRAD is the maximum daily solar radiation intensity estimated by the solar radiation generator (SOLSIM) in the PHASOL model as described earlier. The instantaneous estimation of the solar radiation intensity by a sine function assumes proportionality between the incoming solar radiation and the solar angle, such that the peak radiation is at noon each day. MAXFOT is the maximum photosynthetic rate measured at maximum solar radiation intensity. Since diffusion of CO₂ into, and water vapor out of the leaf is a concurrent process, it seems reasonable to assume that photosynthetic activity and transpiration are similarly affected by plant water stresses and leaf areas. The WATRST and LAIFAC factors thus are the same as those for transpiration.

Allocation of carbohydrates in the labile pool is such that all organs have equal access to the pool. However, maintenance respiration requirements of the plant is assumed to be independent of the pool size. Therefore, maintenance respiration requirements should be satisfied before any carbohydrate can be used for growth. Maintenance respiration is assumed to be a function of the temperature and tissue mass. The model separately calculates the maintenance respirations of the roots and shoots. Hence, shoot maintenance respiration (SHMRES) is assumed to be a function of the shoot mass (SHOOTW) and temperature (Huck and Hillel, 1983). Thus

$$\text{SHMRES} = \text{SHOOTW} * \text{TMPFCS} * \text{RSPFAC} \quad (20)$$

where

$$\text{TMPFCS} = 10.0^{((\text{TEMP} - \text{REFT}) * 0.030103)} \quad (21)$$

The temperature factor of the shoot (TMPFCS) has the effect of doubling SHMRES for each 10 °C rise in temperature. The instantaneous temperature values (TEMP) are calculated by a sine function which makes the peak temperature at 3 PM each day. Hence

$$\text{TEMP} = \text{REFT} + \sin(2.0 * \pi * (\text{DAY} - 0.375)) * \text{RANGE} \quad (22)$$

where REFT is the average daily temperature, and RANGE is the amplitude of the daily maximum and minimum temperatures. The PHASOL model calculates daily values of REFT and RANGE from meteorological data as

$$\text{REFT} = (\text{TMAX} + \text{TMIN}) / 2.0 \quad (23)$$

and

$$\text{RANGE} = (\text{TMAX} - \text{TMIN}) / 2.0 \quad (24)$$

where TMAX and TMIN are the measured daily maximum and minimum temperatures, respectively.

Stress environments adversely affect the development of a functional root system by increasing the respiratory requirements of roots (Smucker, 1984). Our data indicated that increasing mechanical impedance decreased transpiration rates and increased leaf temperature (Figure 8) resulting in increased shoot respiration rates. At high bulk

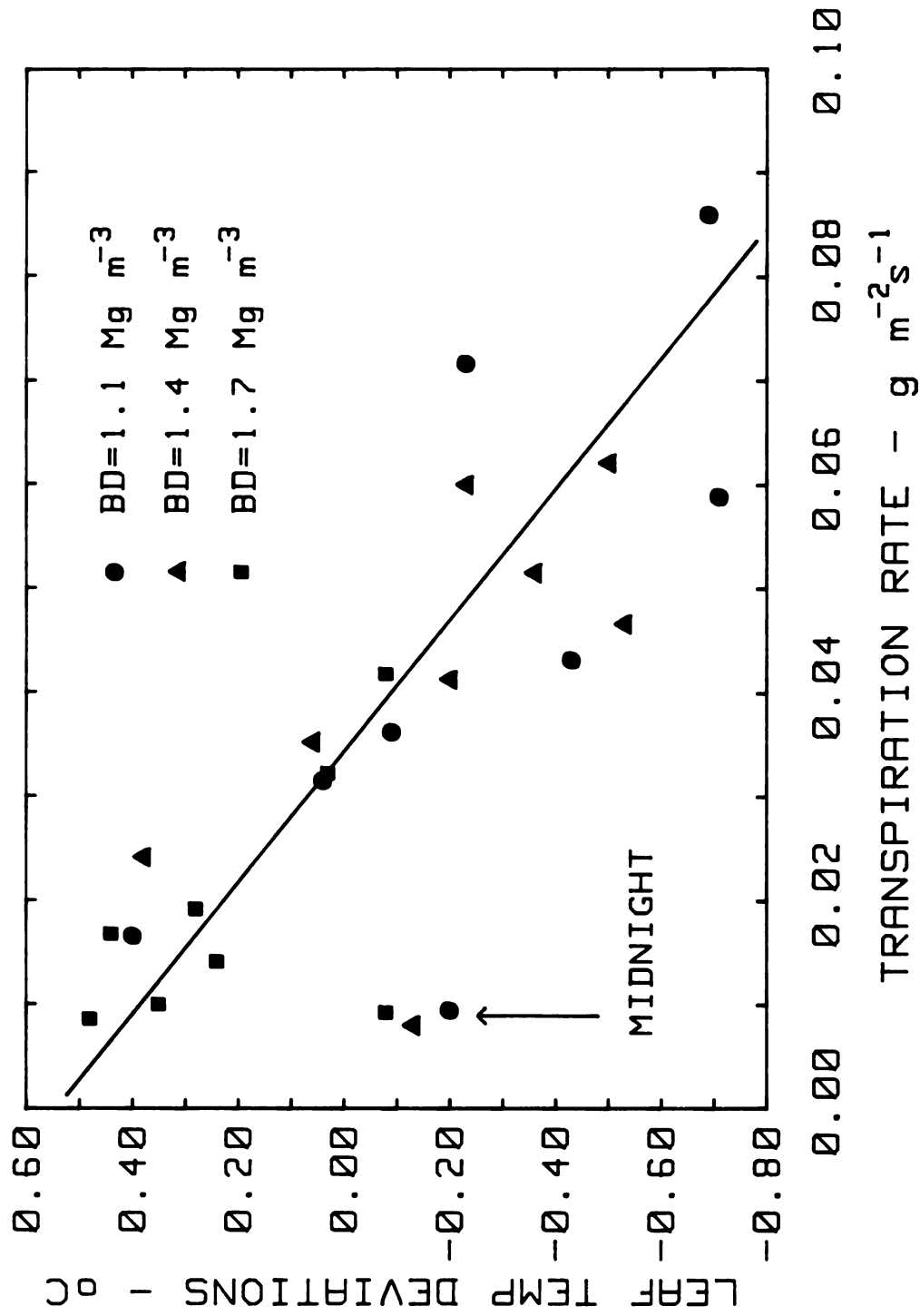


Figure 8. Influence of specific transpiration rate on leaf temperature of dry edible beans.

densities more than 80% of the observed leaf temperatures were higher than the ambient by as much as 0.5 degrees. There appeared to be no correlation between leaf temperature and transpiration at night.

Root Growth and Distribution

The approach of the PHASOL model to carbohydrate partitioning is based more upon a variable partitioning strategy than on a fixed scheme. The fraction of carbohydrate partitioned to root growth is assumed to be dependent upon plant water stress. In fully turgid plants the partitioning strategy favors the shoots. Greater shoot growth however, is accompanied by higher transpiration rates and an increased demand for greater water uptake by the root system. The greater demand for water results in an increase in root growth (Huck and Hillel, 1983). Growth of roots into new layers requires energy which is provided by the carbohydrate partitioning. The model thus calculates the total root growth rate (TOTRG) as

$$\text{TOTRG} = (1.0 - \text{FRAC}) * \text{SOLCHO} * \text{GROFAC} * \text{TMPFCR} \quad (25)$$

where FRAC is the fraction of labile carbohydrates remaining in the shoot as a function of soil water potential, SOLCHO is the available carbohydrate reserve as the labile pool, TMPFCR is the temperature factor of the root which is calculated from eqn.(21) with TEMP being the soil temperature, and GROFAC is the relative consumption rate of carbohydrate reserves (Huck and Hillel, 1983). TMPFCR adjusts the root growth rate for changes in soil temperature and varies between 0 and 1. TOTRG is the total root growth rate representing the maximum amounts of

carbohydrate available for root growth. It has been indicated, however, that appreciable amount of carbohydrates may be lost from the roots of plants growing under stressed environments (Smucker, 1984). The PHASOL model assumes that root exudation losses are proportionate to the level of mechanical resistance in the soil. The total root growth rate is then modified as

$$\text{TOTRG} = (1.0 - \text{FRAC}) * \text{SOLCHO} * \text{GROFAC} * \text{TMPFCR} * \text{MNMIFC} \quad (26)$$

where MNMIFC is the minimum value of mechanical impedance factor (MIFAC) among all soil layers, namely

$$\text{MNMIFC} = \text{AMIN1}(\text{MIFAC}(\text{I}), \text{I}=1,10) \quad (27)$$

With this approach, the root exudation losses are simulated by reducing TOTRG for the highest level of mechanical resistance (lowest MIFAC) in the soil. Modifications of ROOTSM for the effects of mechanical impedance is on the basis of experimental results reported before. When mechanical resistance of a soil layer reached a critical resistance, root growth into that layer completely stopped. The critical mechanical impedance (CRMI) for these experiments were estimated to be approximately 6 MPa. Thus a mechanical impedance factor is introduced which continuously calculates the level of impedance as follows :

$$\text{MIFAC}(\text{I}) = 1.0 - \text{EXP}(-\text{CC} * \text{MIDIF} ** \text{DD}) \quad (28)$$

and

$$\text{MIDIF} = \text{AMAX1}(0.0, (\text{CRMI} - \text{MI}(\text{I}))) \quad (29)$$

MIDIF calculates the difference between the instantaneous mechanical impedance (MI) and critical mechanical impedance (CRMI) in each soil layer. MIFAC is the mechanical impedance factor, ranging from 0 to 1, which adjusts root growth for dynamically changing mechanical resistance in each soil layer. The parameters CC and DD are constants derived from the experimental data such that if mechanical impedance was zero MIFAC would be close to 1, and if mechanical impedance is at or greater than CRMI then MIFAC would be close to zero. For CRMI equal to 6 MPa (600 m of water), the exponential parameters CC and DD were estimated to be 0.102 and 0.502 respectively. AMAX1 and AMIN1 are the maximum and minimum FORTRAN functions, respectively.

Mechanical impedance in this model is evaluated on the basis of resistance of the soil to a dynamic penetrometer. Replicated core samples similar to those used for these studies were sent to the University of Minnesota laboratories in order to evaluate their penetration resistances. These data indicated that mechanical impedance was strongly dependent on soil bulk density and air filled porosity. An empirical equation was derived which estimated mechanical impedance (MI) from soil bulk density (BD) and air filled porosity (FA) as follows

$$MI(I)=521.0-1550.0*BD(I)+912.0*(BD(I)**2.0)+396.0*FA(I) \quad (30)$$

where MI is given in m of water, BD in $Mg\ m^{-3}$, and FA in $m^3\ m^{-3}$. Air filled porosities were calculated from soil desaturation data at different soil matric potentials and bulk densities (Figure 9). A least

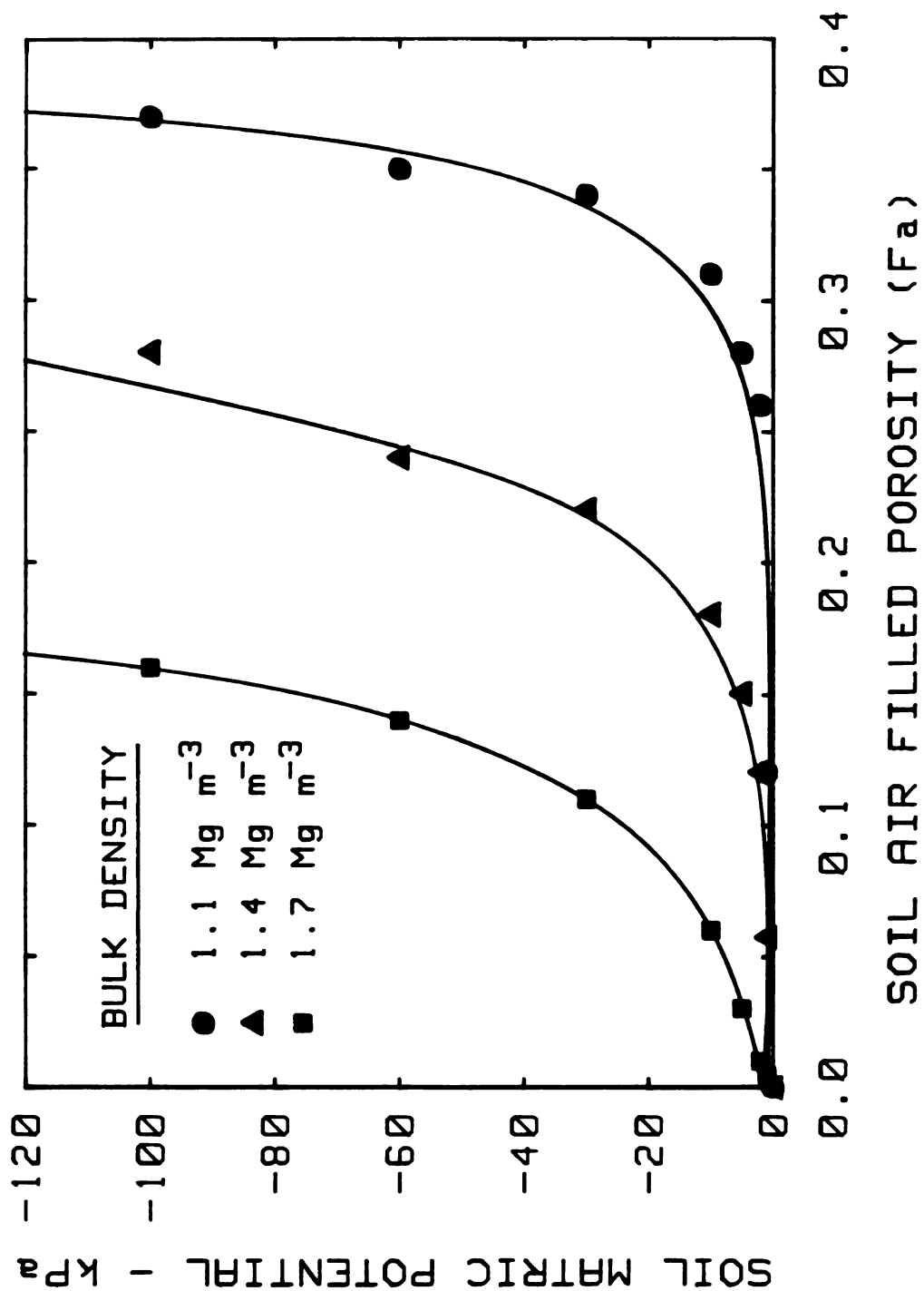


Figure 9. Relationship between soil matric potential and air filled porosity of Charity clay soil for three bulk densities.

squares equation was fitted to these data for calculating air filled porosities from soil bulk densities and matric potentials (POTM) with the PHASOL model as follows

$$FA(I)=(A\text{LOG}(-POTM)+35.1-21.0*BD(I))/52.1 \quad (31)$$

where FA is given in $\text{m}^3 \text{ m}^{-3}$ (air/soil), POTM in cm H_2O , and BD in Mg m^{-3} . TOTRG is the aggregate root growth which has to be distributed among all soil layers.

The PHASOL model takes into account the inhibitory effects of mechanical impedance on root distributions. Experimental data of this study reported earlier (Asady et al., 1985) indicated that root distribution was strongly influenced by mechanical resistance. These data demonstrated that root growth into mechanically impeded soil layers was greatly reduced and increased in the nonimpeded overlying layers. Root growth in the severely compacted soil layers was from proliferation of the existing roots rather than to the extension of the new roots from adjacent layers. Therefore, the root proliferation and extension rates of the PHASOL model are as follows :

$$BIRTH(I)=BR*MIFAC(I)*WTRFCB \quad (32)$$

and

$$EXTENS(I)=EXTNRT*MIFAC(I)*WTRFCE \quad (33)$$

The BIRTH and EXTENS are birth and extension rate factors for each soil layer which are calculated by multiplying the proliferation rate (BR) and extension rate (EXTNRT) of the roots grown under ideal

environmental conditions, with mechanical impedance factor (MIFAC), soil water potential factors for birth (WTRFCB), and extension (WTRFCE). The BR and EXTNRT could be estimated from experimental data to match the overall root growth. The birth rate factor (eqn. (32)) is further modified to increase the root growth in the less impeded layer overlying a more impeded soil as follows :

$$\text{BIRTH}(I-1) = \text{BIRTH}(I-1) * (1.0 + (\text{MIFAC}(I-1) - \text{MIFAC}(I)) / \text{MIFAC}(I-1)) \quad (34)$$

This equation increases the BIRTH factor proportional to the difference in mechanical impedance of the two layers. The PHASOL estimation of the water potential factors is based on the assumption that proliferation and extension rate of the roots may be stopped if the soil water potential head has reached threshold minimum values of -10 (BRMIN), and -100 (EXTMIN) m, respectively. The water potential factors are defined (Huck and Hillel, 1983) as

$$\text{WTRFCB} = (1.0 - \exp(-AA * X^{**}BB)) \quad (35)$$

and

$$\text{WTRFCE} = (1.0 - \exp(-AA * XX^{**}BB)) \quad (36)$$

Where

$$X = \text{AMAX1}(0.0, (\text{POTH}(I) - \text{BRMIN})) \quad (37)$$

and

$$XX = \text{AMAX1}(0.0, (\text{POTH}(I) - \text{EXTMIN})) \quad (38)$$

Where POTH is the hydraulic potential of each soil layer and AA and BB are constants.

The root growth potential of each soil layer (RTGRO(I)) is estimated by multiplying the birth rate factor of that layer (BIRTH(I)) by the partial root length of the same layer (PRTL(I)) and added to the extension rate factor of the same layer (EXTENS(I)) times the partial root length of the overlying layer (PRTL(I-1)) as follows :

$$RTGRO(I) = BIRTH(I) * PRTL(I) + EXTENS(I) * PRTL(I-1) \quad (39)$$

The root growth potential of the whole root system (SUMRG) is the sum of RTGRO for all soil layers. The SUMRG, however, can not be greater than the upper limit for the growth of the entire roots (TOTRG) already established from the available carbohydrates (eq.(26)). In order to bring these two into conformity with one another, the potential root growth in each layer has to be normalized (Huck and Hillel, 1983) to give

$$RTGRO(I) = RTGRO(I) * TOTRG / SUMRG * LNGFAC \quad (40)$$

where LNGFAC is the root length factor which translates the root mass into the root length (eg. root length per unit root mass). The average LNGFAC of dry edible beans in this study was found to be inversely related to soil bulk density (BD), namely

$$LNGFAC = 83100.0 - 26666.0 * BD \quad (41)$$

where LNGFAC is in $m \text{ kg}^{-1}$ and BD in $Mg \text{ m}^{-3}$.

TESTING THE MODEL

To test the overall performance of the model, a series of simulation run was carried out for the experimental conditions of the previous chapters. A dry edible bean plant was assumed to be growing in a 25 cm deep Charity clay soil. The initial time for all simulation runs is julian day 120.

The initial equilibrium condition of soil water was equivalent to a constant soil matric potential of -0.006 MPa at the base of the soil and -0.0085 MPa at the surface of the soil. The lower boundary condition was kept constant throughout the simulation runs. No evaporation losses were allowed from the soil surface. The upward water flux was identical to the root extraction rates.

The initial plant variables were chosen to represent a 10 day old dry bean plant which was already growing in a uniform and nonimpeded soil. The initial shoot (SHOOTW) and root (ROOTW) weights of plants were 0.021 and 0.0095 kg m⁻², respectively (Table 1). The initial carbohydrate reserve (SOLCHO) was assumed to be 3% of the shoot and root masses (Huck and Hillel, 1983). The initial distribution of the roots within the soil were such that 18% of the roots were at the top 2.5 cm, 42% were at 2.5-10 cm, 37% were within 10-17.5 cm, and 3% were below 17.5 cm depth.

Initially, the model was tested to see how plants grow under the original condition of a uniform soil profile with a bulk density of 1.1

Table 1. Simulated shoot and root growth responses of *Phaseolus vulgaris* after 5, 10, and 20 days of simulation, at two soil bulk densities 1.1 and 1.7 Mg m⁻³.

Growth Parameter	Unit	Initial	After 5 days		After 10 days		After 20 days	
			1.1	1.7	1.1	1.7	1.1	1.7
SHOOTW	g m ⁻²	21.0	53.4	49.4	117	88.9	281	167
ROOTW	g m ⁻²	9.5	11.3	10.9	16.8	14.6	39.7	29.6
SOLCHO	g m ⁻²	0.943	10.1	8.2	16.6	9.8	25.5	14.1
ROOTL	m m ⁻²	511.0	609.1	584.0	904.4	782.4	2132.0	1586.8

SHOOTW = Shoot weight per unit land area
ROOTW = Root weight per unit land area
SOLCHO = Soluable carbohydrate pool per unit land area
ROOTL = Root length per unit land area

Mg m⁻³. The model was then run with plants growing in a soil profile with a bulk density of 1.1 Mg m⁻³ at the surface 2.5 cm, and 1.7 Mg m⁻³ at a depth of 2.5–25 cm. Comparison of plant growth variables after 5 and 10 days of simulated growth under two different soil conditions indicated that both shoot (SHOOTW) and root (ROOTW) masses of dry edible beans were reduced at high bulk density soils (Table 1). The soluble carbohydrate reserves in the labile pool (SOLCHO) were also reduced by mechanical impedance. High mechanical impedance reduced total root length (ROOTL) of dry edible beans (Table 1). The thickening effect of mechanical impedance on root growth is not included in root length calculations in these simulation runs because it was assumed all the roots have the same length per unit mass.

Mechanical impedance greatly reduced the root water uptake. The spatial and temporal patterns of simulated root water extraction, under two soil conditions, is characterized by a gradual increase in root water uptake, gradual deepening zones of moisture extractions (Figures 10 and 11), gradual increase in upward water flux (Figures 12 and 13), and gradual steepening of the water potential gradient between the water source at the bottom and water sinks at the top (Figures 14 and 15). The zone of maximum water extraction corresponded to the region of high root density in both soils. Large quantities of water were extracted from the nonimpeded surface layer overlying high bulk density soils (Figures 10 & 11). The root water uptake from the nonimpeded soil layers was about three times greater than from the impeded soil. The upward water flux passing through the bottom of the soil was, however, 6 and 12 times greater after 5 (Figure 12) and 10 (Figure 13) days of simulated growth, respectively. Because maximum water flux had not

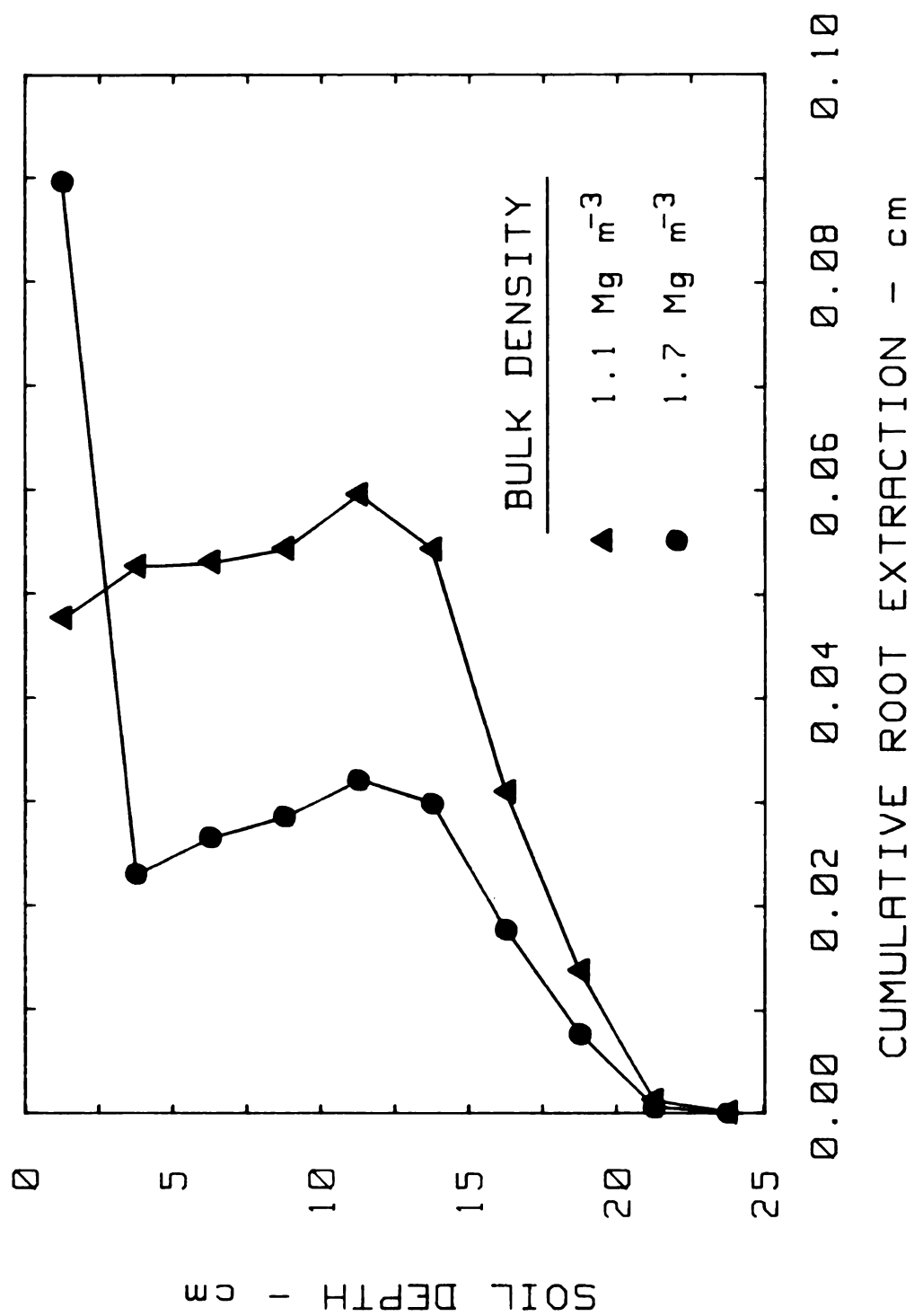


Figure 10. Spatial distribution of root water uptake by dry edible beans after 5 days of simulation.

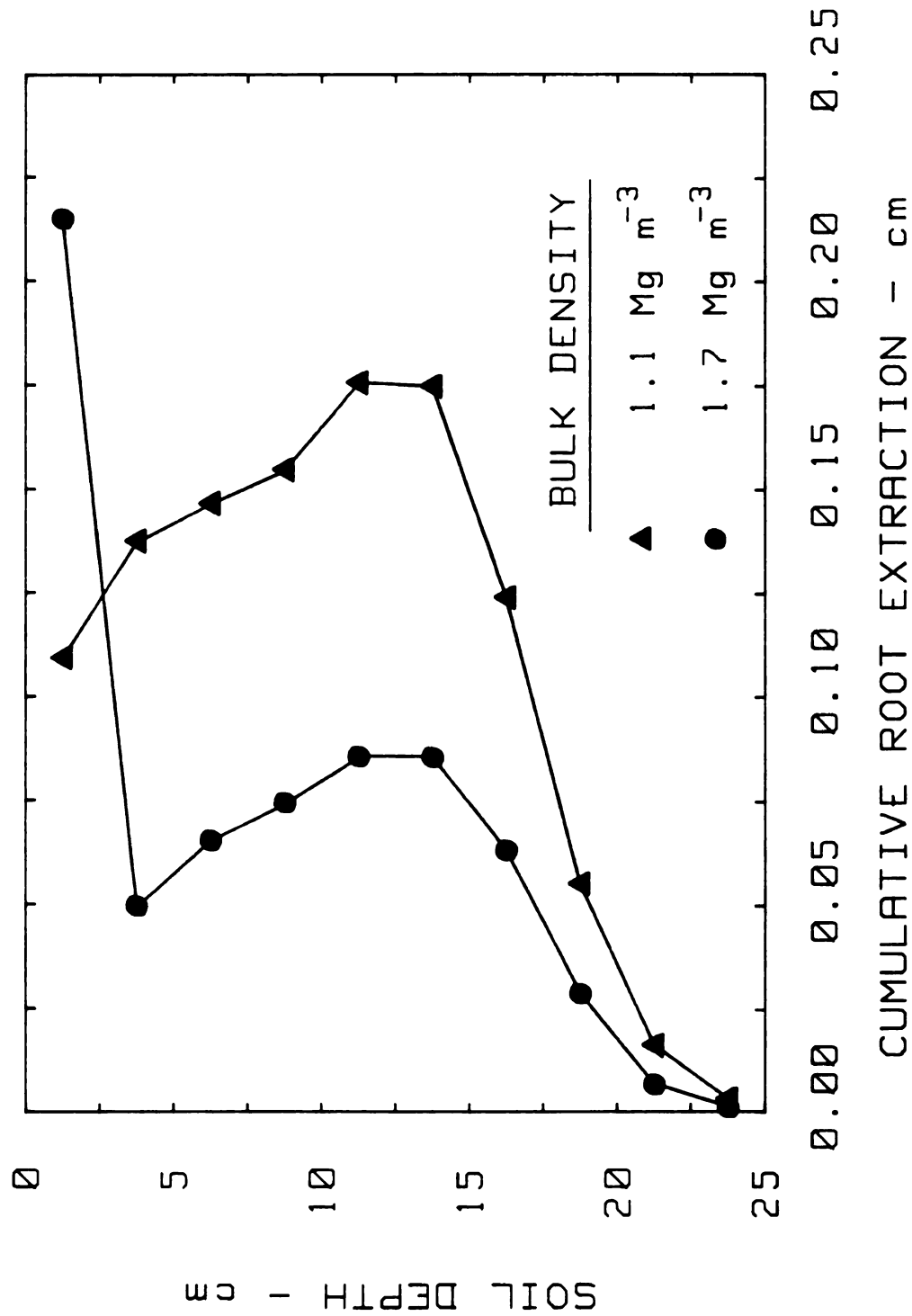


Figure 11. Spatial distribution of root water uptake by dry edible beans after 10 days of simulation.

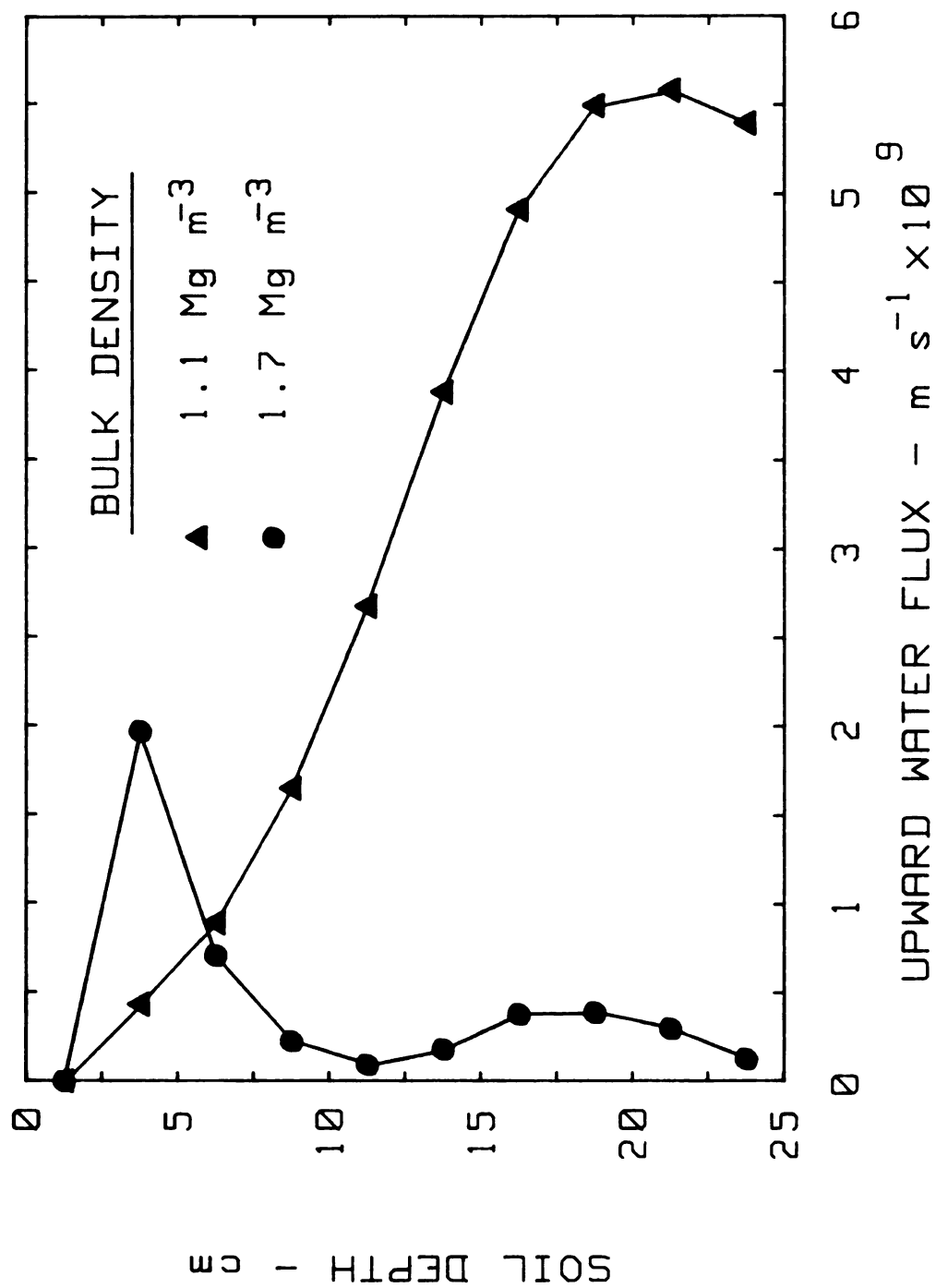


Figure 12. Water flux distribution in a 25 cm deep Charity clay soil after 5 days of simulation.

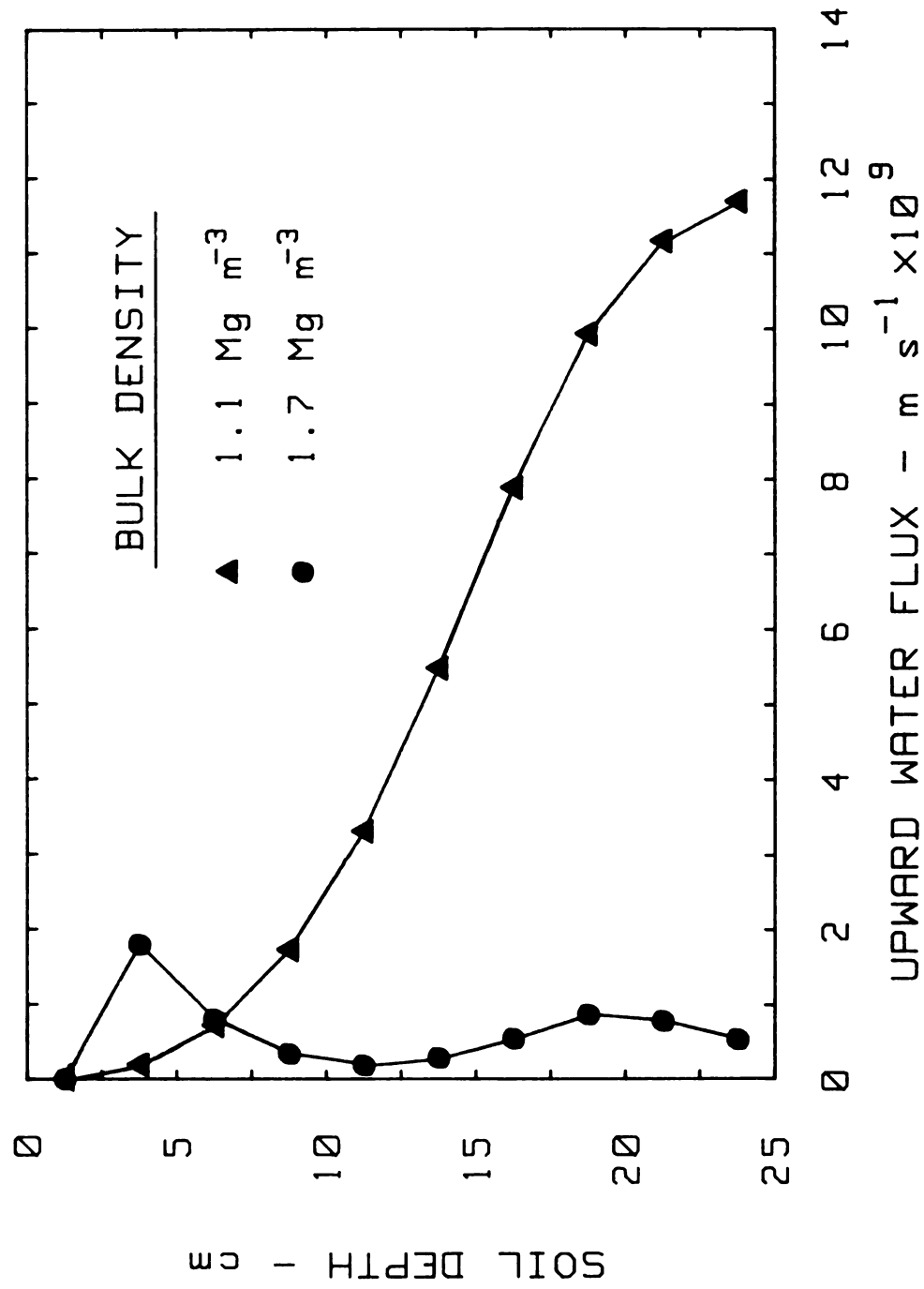


Figure 13. Water flux distributions in a 25 cm deep Charity clay soil after 10 days of simulation.

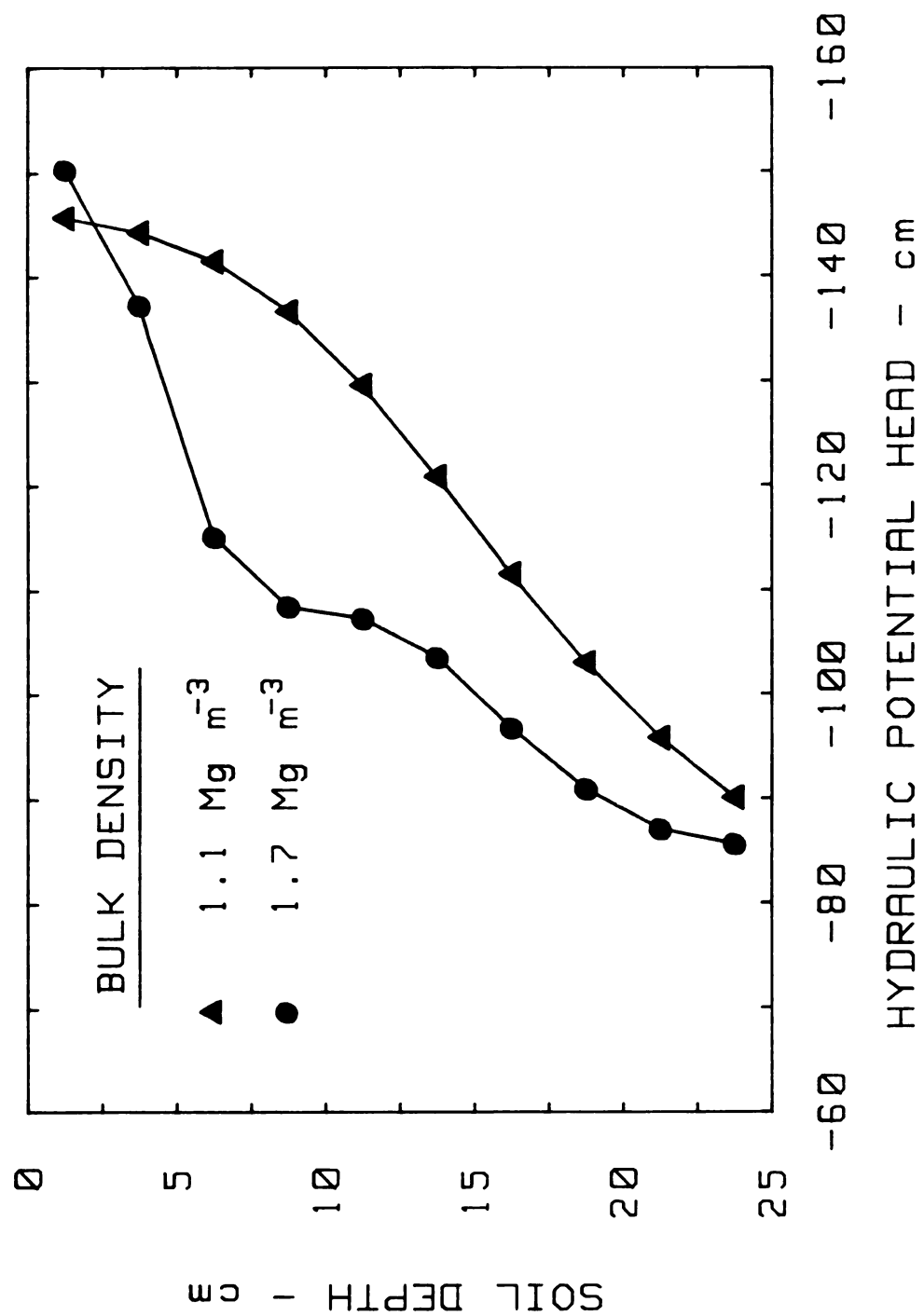


Figure 14. Spatial distribution of soil water potential in Charity clay soil after 5 days of simulation.

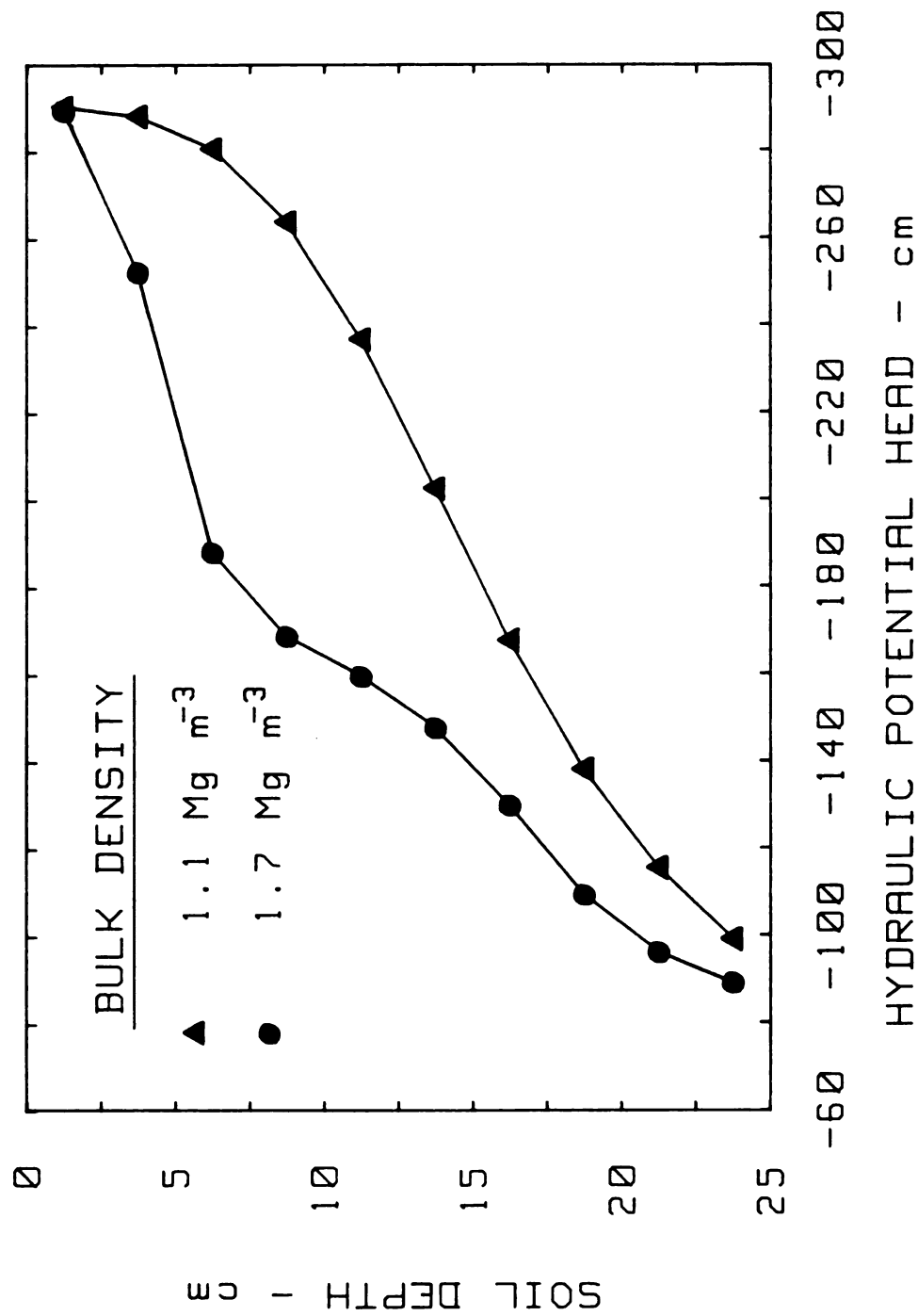


Figure 15. Spatial distribution of soil water potential in Charity clay soil after 10 days of simulation.

occurred at the base of the high bulk density soil (Figures 12 and 13), demonstrated that highly compacted soils were progressively depleted of their water without being recharged. The regions of maximum root density in these soils, were depleted at a faster rate, creating localized spatial water stresses. This is further demonstrated in Figures 14 and 15 where the soil water potential shows a nonequilibrium behavior.

These phenomena are primarily due to very high hydraulic resistances in the soil (RSSL) and in the roots (RSRT) of plants grown under high mechanical impedance (Table 2). Hydraulic resistances of the soil (RSSL(3)) and roots (RSRT(3)) in the third soil layer indicated that soil hydraulic resistances to water uptake increased with time due to a decrease in unsaturated hydraulic conductivity of the soil (Table 2). A decrease in root hydraulic resistance with time, is the result of increase root growth (Table 2). Sum of the soil and root hydraulic resistances, however, increased with time emphasizing a greater importance of the soil rather than root hydraulic resistance.

The transpiration demand often exceeds the water supplying power of mechanically impeded soils. Therefore these soils can not meet the transpiration demands fast enough to prevent water stress. The mid-day water potential of the leaf (POTCR) thus become very low (Table 2). The low leaf water potential activated the control mechanisms of the stomata to reduce their openings, thereby reducing excessive water loss and plant dehydrations. This is accompanied by reducing photosynthetic rate and soluble carbohydrates (Table 1).

In the noncompacted soils, on the other hand, the water flux is maximum at the base and gradually approaches zero at the soil surface

Table 2. Simulated cumulative water uptake, transpiration, plant water potential, and plant and soil hydraulic resistances of *Phaseolus vulgaris* after 5, 10, and 20 days of simulation, for two bulk densities 1.1 and 1.7 Mg m⁻³.

Parameters	Unit	After 5 days		After 10 days		After 20 days	
		1.1	1.7	1.1	1.7	1.1	1.7
CUMREM	mm	3.92	2.91	11.8	7.59	33.8	19.1
CUMTRN	mm	3.38	2.69	10.9	7.23	32.2	18.3
POTCR	meter	-23.39	-43.22	-31.11	-57.92	-27.63	-26.04
RSSL(3)	sec	144X10 ⁷	131X10 ⁸	326X10 ⁷	231X10 ⁸	886X10 ⁷	552X10 ⁸
RSRT(3)	sec	208X10 ⁷	217X10 ⁷	140X10 ⁷	162X10 ⁷	659X10 ⁶	852X10 ⁶
TOTRS(3)	sec	352X10 ⁷	153X10 ⁸	466X10 ⁷	247X10 ⁸	952X10 ⁷	561X10 ⁸

CUMREM = Cumulative water removal from all soil layers.
 CUMTRN = Cumulative transpiration by total plant.
 POTCR = Canopy water potential in meter of water.
 RSSL(3) = Soil resistance to water uptake in the third soil layer.
 RSRT(3) = Root resistance to water uptake in the third soil layer.
 TOTRS(3) = Total resistance to water uptake in the third soil later.

(Figures 12 and 13). The soil hydraulic potential is at quasiequilibrium, with the highest value at the base and the lowest value at the top with a smooth transition (Figures 14 and 15). Therefore, in nonimpeded soils the water supply usually meets the demand, such that localized water shortages would not be developed, and the system may approach equilibrium for most of the time. The cumulative water removal from all soil layers (CUMREM) was slightly greater than the cumulative transpirations (CUMTRN) for both soils (Table 2), indicating a limited potential for storing water in the plant as reported by Huck and Hillel (1983). CUMREM and CUMTRN were both decreased at high soil bulk densities (Table 2).

In conclusion, the PHASOL model of root growth and water uptake presented here simulated the effects of soil mechanical impedance on dry edible beans root growth. Results of several simulation runs demonstrated that the model behaves as expected. Validation of the model against experimental data is necessary, however, before it could be used for management decisions. Further improvement of this model requires more parameter estimations. A complex model of this sort, has many site and plant specific variables which have to be estimated from experimental data. We have derived as much information, regarding the plant, as possible from the experimental data of this study. Those plant parameters which were not available to us, were assumed to be similar to those which were used by M.G. Huck in testing his ROOTSM model (1983) for faba beans in Australia. Stability of this sort of model is dependent upon the magnitude of the time step as well as the thickness of each soil layer. The numerical accuracy of the model decreases if either the time step or the thickness of the soil layers

are increased. The most critical region for error is where there is a large gradient of water content. Thus, it is wise to use as thin of soil layers as possible at those regions. Sensitivity analysis may be necessary to isolate those parameters to which the model is most sensitive, and determine the acceptable range of errors for their estimation. Finally, it should be noted that numerical oscillations were encountered in some simulation runs involving noncompacted soil conditions. The problem was associated with the size of the calculated conductivity 0.5 cured the problem for these calculations.

LITERATURE CITED

- Arya, L.M., D.A. Farrell and G.R. Blake. 1975. A field study of soil water depletion patterns in the presence of growing soybean roots. I. Determination of hydraulic properties of the soil. Soil Sci. Soc. Am. Proc. 39: 424-430.
- Arya, L.M., G.R. Blake and D.A. Farrell. 1975a. A field study of soil water depletion patterns in the presence of growing soybean roots. II. Effect of plant growth on soil water pressure and water loss patterns. Soil Sci. Soc. Am. Proc. 39: 430-436.
- Arya, L.M., G.R. Blake and D.A. Farrell. 1975b. A field study of soil water depletion patterns in the presence of growing soybean roots. III. Rooting characteristics and root extraction of soil water. Soil Sci. Soc. Am. Proc. 39:437-444.
- Arya, L.M., and J.F. Paris. 1981. A physicoempirical model to predict the soil moisture characteristic from particle-size distribution and bulk density data. Soil Sci. Soc. Am. J. 45: 1023-1030.
- Asady, G.H., A.J.M. Smucker and M.W. Adams. 1985. Seedling test for the quantitative measurement of root tolerances to compacted soil. Crop Science 25:802-806.
- Beese, F., R.R. Van Der Ploeg and W. Richter. 1977. Test of a soil water model under field conditions. Soil Sci. Soc. Am. J. 41:979-984.
- Brakensiek, D.L. 1979. Comments on "empirical equations for some soil hydraulic properties" by Clapp & Hornberger. Water, Resource Res. 15: 989-990.
- Clapp, R. B. and G. M. Hornberger. 1978. Empirical equations for some soil hydraulic properties. Water Reso. Res. 14: 601-604.
- Forrester, J.W. 1961. Industrial Dynamics. M.I.T. Press, Cambridge, Massachusetts. (chapters 1-5).
- Ghosh, R. K. 1976. Model of the soil moisture characteristic. J. Ind. Soc. Soil Sci. 24: 353-355.
- Gupta, S. C. and W. E. Larson. 1979. Estimating soil water retention characteristics from particle size distribution, organic matter percent, and bulk density. Water Reso. Res. 15: 1633-1635.
- Hillel, D. 1977. Computer Simulation of Soil Water Dynamics. A compendium of recent work. International Development Research Center. Box 8500, Ottawa, Canada. 214p.

- Hillel, D. 1980. Fundamentals of Soil Physics. Academic press, Inc. pp.123-165, 195-232.
- Hodges, T, V.French and S.LeDuc. 1983. Estimating solar radiation for plant simulation models. Presented at the 6th Annual Workshop of The Biological System Simulation Group . Univ. of Illinois.
- Huck, M.G. and D. Hillel. 1983. A model of root growth and water uptake accounting for photosynthesis, respiration, transpiration and soil hydraulics. Adv. In Irrig. (ed.) D. Hillel. 2:273-333.
- Jackson, R. D. 1972. On the calculation of hydraulic conductivity. Soil Sci. Soc. Am. Proc. 36: 380-382.
- James, L.G. and C.L. Larson. 1976. Modeling infiltration and redistribution of soil water during intermittent application. Am. Soc. Ag. Eng. Trans. 19:482-488.
- Kirkham, D. and W.L. Powers. 1972. Advanced Soil Physics. John Wiley & Sons, Inc. NY. London, Sydney, Toronto. pp46-75, 235-278.
- Klute, A. 1982. Tillage effects on the hydraulic properties of soil: a review. Predicting Tillage Effects on Soil Physical Properties and Processes. ASA. Special publication No.44. ASA, SSSA, 677 South Segoe Road, Madison, Wisconsin 53711.
- Koller, D. 1975. Effects of environmental stress on photosynthesis. Conclusions. In: Photosynthesis and Productivity in Different Environments (ed.) J.C. Cooper. p587-589.
- Kunze, R.J., G. Uehara and K. Graham. 1968. Factors important in the calculation of hydraulic conductivity. Soil Sci. Soc. Am. Proc. 32:760-765.
- Mualem, Y. 1976. A new model for predicting the hydraulic coconductivity of unsaturated porous media. Water Reso. Res. 12: 513-522.
- Nagpal, N. K. and J. deVries. 1976. An evaluation of the instantaneous profile method for in situ determination of hydrologic properites of layered soil. Can. J. Soil Sci. 56: 453-461.
- Nagpal, N. K., L. Boersma and L. W. DeBacker. 1972. Pore size distributions of soils from mercury intrusion porosimeter data. Soil Sci. Soc. Am. Proc. 36: 264-267.
- Phillips, R.E., R.L. Blevins, G.W. Thomas, W.W. Frye and S.H. Phillips. 1980. No-tillage agriculture. Science 208:1108-1113.
- Richards, L. A. 1965. Physical condition of water in soil. In: Methods of Soil Analysis, part I. C. A. Black (ed.) Agronomy 9: 128-152. Am. Soc. of Agron. Madison, Wisconsin.
- Richardson, C.W. 1981. Stochastic simulation of daily precipitation,

- temperature and solar radiation. Water Res. Res. 17:182-190.
- Rowse, H.R. and D.A. Stone 1978. Simulation of the water distribution in soil; measurement of soil hydraulic properties and the model for an uncropped soil. Plant Soil. 49:517-531.
- Rowse, H.R., D.A. Stone and A. Gerwitz. 1978. Simulation of the water distribution in soil ; the model for cropped soil and its comparison with experiment. Plant Soil. 49:533-550.
- Smucker, A.J.M. 1984. Carbon utilization and losses by plant root systems. In: Roots, Nutrients, and Water Influx and Plant Growth. (eds.) Barber and Bouldwin. ASA Special Pub. Madison, Wisconsin.p27-45.
- Van den Honert, T.H. 1948. Water transport in plants as a catenary process. Faraday Soc. Discuss. 3:146-153.
- Warrick, A.W. and D.O. Lomen. 1983. Linearized moisture flow with root extraction over two-dimensional zones. Soil Sci. Soc. Am. J. 47:869-873.
- Warrick, A.W., D.O. Lomen and A. Amoozegarfard. 1980. Linearized moisture flow with root extraction for three-dimensional steady conditions. Soil Sci. Soc. Am. J. 44:911-914.

CHAPTER 6

SUMMARY AND CONCLUSIONS

A soil core seedling test (Asady et al., 1985) was used to obtain multiple data sets which were incorporated into a root growth and water uptake model (Huck and Hillel, 1983). This system could also be used to study the main and interaction effects of several environmental stresses on different cultivars. Root penetration ratios (RPR) of dry edible beans cultured in the soil core seedling test decreased linearly with mechanical impedance. When RPR approached a value of approximately 0.65, growth of plant shoots ceased. The xylem flow rate of stressed plants was greatly decreased. The accumulation of toxic anaerobic metabolites (eg., ethanol, acetaldehyde, etc.) increased with greater mechanical impedance.

Mechanical impedance severely modified growth and distribution of roots in these studies. Total root length of dry edible beans was 80% lower after 30 days of growth in high density soils. Extension of new roots into a deeper, compacted soil layer was significantly reduced, and proliferation of the existing roots in the less compacted overlying soil layers was greatly increased. Critical mechanical resistance values of 5.5 MPa stopped the penetration of dry edible bean roots. The inability of the roots to penetrate the compacted soils on one hand, and the slow water movement in the compacted soils on the other hand,

created localized depletion of water and nutrients which could not be replenished in spite of the large water content gradients.

The localized depletion of O_2 in the root zone, decreased soil pore diameter, slower root growth rate, and increased water film thickness surrounding the roots in the impeded soil resulted in severe plant stress. The O_2 concentrations were low and the CO_2 concentrations were high in the more compacted soils. High diffusive resistance of these soils is attributed not only to smaller pores but also to pore plugging by roots of air filled pores in the less compacted soil layers, overlying the more compacted soil layer.

Severe mechanical resistance reduced the total carbon exchange rate of the leaves but increased their specific carbon exchange rates. The CO_2 concentrations in the rhizosphere of severely impeded soils were 6 to 8 times greater than in the nonimpeded soils.

A mathematical model of growth for annual plants was introduced which describes growth from the seedling stage to physiological maturity. It takes into account the efficiency index of growth as well as the environmental potential of growth. This model provides a new opportunity for plant growth analysis. A mechanistic model of root growth and water uptake in a layered homogeneous soil profile was modified which accounts for the effects of mechanical impedance in the soil. The PHASOL model takes into account the water supplying power of the roots and soils and the evapotranspiration potential of the atmosphere for its water balance. The balance of carbon is the result a mass balance between the atmospheric CO_2 influx through photosynthesis, and the CO_2 efflux through respiration and leakage of soluble root exudates. The effects of mechanical impedance on root proliferation and

extension is simulated via a normalizing function which adjusts root growth for the instantaneous level of mechanical impedance.

The results from several simulation runs demonstrated that this model behaves as expected. The accuracy of the model needs more testing with experimental results before it can be used for management decisions. We, however support the statement forwarded by Huck and Hillel (1983) that " a good model is not one that embodies a perfect depiction of reality, for such is not possible, but one that spurs further efforts toward the aquisition of more knowledge and greater understanding ".

In conclusion, the soil core seedling test appeared to be a quick and inexpensive method for studying plant responses to multiple levels of environmental stresses. This is analoqueous to a small scale physical model that an engineer uses to test his larger scale and real life systems. Biological systems, however, are dynamic and interactive systems which are much more complex. Their linkages and forces which are acted upon are often invisible, even to a trained eye. Their biochemical and enzymatic reactions further complicate the study of these systems. Therefore, plant growth studies under confined environments, such as the soil core seedling test, produce relative results, and interpretations have to be made in the context of two domains, time and space.

A P P E N D I X I

PHASOL MODEL

Computer Program

Input Data

Computer Output

Glossary of Variables

PROGRAM PHASOL 74/175 OPT=1,ROUND= A/ S/ M/-D,-DS FTN 5.1+587 07/29/85 .18.06.28 PAGE 2

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76 DIF=0.0
77 CRON 0 0.01
78 READ(5) THETST, BGNDAV, LOCALE, IYR
79 READ(5) FIATIM, OUTDEL, PRDEL, DELT, DELAY
80 READ(5) NJ, IPOTM(1), I=1, NJ
81 READ(5) RRL(1), I=1, NJ
82 READ(5) TCOM(1), I=1, NJ
83 READ(5) BD(1), I=1, NJ
84 READ(5) IPER(1), I=1, NJ
85 READ(5) ISHOOT, IROOT, LEAFTH
86 READ(5) IPERM, IACRAGE, MCX, GRDFAC, RSPFAC, DTHFAC
87 READ(5) ITRDET, IACRAGE, MCX, GRDFAC, RSPFAC, DTHFAC
88 READ(5) BRMIN, EXTMN, BR, EXTRT
89 READ(5) AA, BB, CC, DD, GRMI
90 READ(5) URAS, UARS, MAXPOT, DUTF
91 READ(5) PCP(1), I=1, 365
92 READ(5) TX(1), I=1, 365
93 READ(5) TN(1), I=1, 365
94 READ(5) MSDPEV(1), I=1, 365
95 DO 5 J=1, NJ
96 WRITE(6,*) J
97 CONTINUE
98 C
99 LMGFAC=83100.-26666.*BD(2)
100 LMGFAC=53767.0
101 RUNS=0
102 FLPELP=-1.0
103 PI=3.14159
104 ICHO={ISHOOT,IROOT}*IPER/(1.-IPER)
105 LA=1.5*ROOT*LEAFTH
106 DEPTH(1)=5*(TCOM(1))
107 DIST(1)=DEPTH(1)
108 DO 20 I=2, NJ
109 DIST(I)=5*(TCOM(I-1)+TCOM(I))
110 DEPTH(I)=DEPTH(I-1)*DIST(I)
111 CONTINUE
112 WRITE(6,52) IRTL
113 WRITE(6,53) IRTL
114 DO 30 I=1, 8530
115 IPR(1)=IRTL*IRL(1)
116 IVOLW(1)=ITHETA(1)*COM(1)
117 RRS(1)=URRS/IPR(1)
118 ARS(1)=UARS/DEPTH(1)/IPR(1)
119 RSRT(1)=RRS(1)+ARS(1)
120 WRITE(6,454) IPR(1), RSRT(1), IVOLW(1), TCOM(1), ITHETA(1),
121 RRL(1), DEPTH(1), BD(1)
122 CONTINUE
123 C
124 POTCR=-2.000
125 DO 10 I=2, 101
126 LINE(I)=18
127 CONTINUE
128 NJ=NJ+1
129 DO 15 I=1, NJ
130 FLW(I)=0.0
131 CONTINUE
132 ICHO=ICHO
133 CUMRS=0.0
134 CRIMRS=0.0
135 SHOOT=ISHOOT
136 POTCR=POTCR
137 POTCRD=POTCRD
138 ROOTW=IROOT
139 CUMPET=0.0
140 DO 37 I=1, NJ
141 VOLW(I)=IPR(1)
142 IPR(1)=IPR(1)
143 NFW(I)=0.0
144 RTEIX(I)=0.0
145 NETGRD(1)=0.0
146 CONTINUE
147 CUMREM=0.0
148 CEVAP=0.0
149 DRAIN=0.0
150
151
152

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PROGRAM PHASOL	74/175	OPT=1,ROUND= A/ S/ M/-D, -DS	FTN 5.1+587	07/29/85 . 18.06.28	PAGE 3
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[illegible]


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307 C CONTINUE
308 IF(POTM(1).GT.-10.0)FLW(1)=-SLEVP
309 IF(POTM(1).LE.-10.0)FLW(1)=FLW(2)
310 C
311 FLW(1)=0.0
312 DO 110 I=1,2,NJ
313   AVCOND(1)=5*(COND(1-1)+COND(1))
314   CL(1)=AVCOND(1)*(POTM(1-1)+POTM(1))/DIST(1)
315 C
316 POTM(NJ)=0.60
317 DEPTHINJ=DEPTH(NJ)+TCOM(NJ)/2.
318 POTH(NJ)=POTM(NJ)-DEPTHINJ
319 FLW(NJ)=COND(NJ)*(POTH(NJ)-POTH(NJ))/DIST(NJ)
320 DO 120 I=1,NJ
321   FLW(1)=FLW(1)+RTEX(1)
322   PRTL(1)=INTGRL (PRTL(1) .NETGRO(1),DELT)
323 C
324   X=AMAX(0.0,(POTM(2)-EXTMIN))
325   MPOT=-POTM(1)*100.
326   FA(1)=AMAX(0.0,(ALOG(MPOT)+35.1-21.*BD(1))/52.1)
327   AIR FILLED POROSITY
328   MI(1)=AMAX(0.0,(521.0-1550.0*BD(1)+912.0*(BD(1)+2.0)
329   +
330   -396.0*FA(1)))
331   MIDF=AMAX(0.0,EXP(-CC*MIDF+.00))
332   MIPAC(1)=1.0-EXP(-CC*MIDF+.00)
333 C
334   MMHIFC=AMTNI(MNHIFC,MIFAC(1))
335   X=AMAX(0.0,(POTM(1)-BRMIN))
336   BIRTH(1)=BR*(1.0-EXP(-AA*X+.88))*MIFAC(1)
337   EXTENS(1)=EXTNRT*(1.0-EXP(-AA*XX+.88))*MIFAC(1)
338 C
339   CONTINUE J=2,NJ
340   IF (MIFAC(J-1).GT. MIFAC(J)) THEN
341     BIRTH(J-1)=BIRTH(J-1)*{1.0*(MIFAC(J-1)-MIFAC(J))/MIFAC(J-1)}
342     ENDIF
343 C
344   CONTINUE
345   RTGRO(1)=PRTL(1)*BIRTH(1)
346   SUMRG=RTGRO(1)
347 DO 647 I=2,NJ
348   RTGRO(I)=PRTL(I-1)*EXTENS(I)+PRTL(I)*BIRTH(I)
349   SUMRG=SUMRG+RTGRO(I)+SUMRG
350 C
351   SUMRTG=0.0
352   DO 648 I=1,NJ
353     IF (SUMRG.NE.0.0) THEN
354       RTGRO(I)=RTGRO(I)+TOTRG/SUMRG*LNCFAC
355       SUMRTG=SUMRTG+RTGRO(I)
356     ENDIF
357 C
358   CONTINUE
359   SUMRTO=0.0
360   DO 649 I=1,NJ
361     RTDTH(I)=PRTL(I)*DTHFAC*TMPFCR
362     SUMRD=SUMRD+RTDTH(I)
363 C
364   SUMRTD=0.0
365   DO 651 I=1,NJ
366     IF (SUMRTO.EQ.0.0) GO TO 651
367     RTDTH(I)=TOTRTH+RTDTH(I)/SUMRD*LNCFAC
368     SUMRTD=SUMRTD+RTDTH(I)
369 C
370   CONTINUE
371   DO 653 I=1,NJ
372     NETGRO(I)=RTGRO(I)-RTDTH(I)
373 C
374   DO 102 I=1,NJ
375     RSSL(1)=1/(B*COND(1)+PRTL(1))
376     PRTL(1)=POTH(1)
377     ARS(1)=URS/DEPTH(1)
378     RSS(1)=ARS(1)*ARS(1)/PRTL(1)
379 C
380   CONTINUE
381   =INTGRL (CUMREM .SUMR .DELT)
382   COUNT=0.0
383   FLPLP=FLPLP
384   IF(RUNS.LE.2) WRITE(6,858)

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PROGRAM PHASOL      74/175  OPT=-1,ROUND= A/ S/ M/-D,DS      FIN 5.1+587      07/29/85  .18.06.28      PAGE 6

C 115      CONTINUE
COUNT=COUNT+1,O
IF(COUNT.LT.50,O)GO TO 116
GO TO 165
116      CONTINUE
SUMR=O,O=1,NJ
DO 150 J=1,NJ
IF(FLPLP.EQ.1,O)I=NJ-J+1
RTEX(I)=AMAX1(O,(POTH(I)-POTCR)/(RSSL(I)+RSRT(I)))
SUMR=SUMR+RTEX(I)
DIFF=SUMR-SUMR
DIFF=(SUMR-TRANSP)/TRANSP
IF(SUMR.LT.1)TRANSP=1
IF(COUNT.GT.2)GO TO 150
IF(COUNT.GT.3)GO TO 50
WRITE(6,854)J,(POTH(I),POTCR,RSSL(I),RSRT(I),RTEX(I),
SUMR,TRANSP,DIFF,DIF,COUNT
CONTINUE
150      CONTINUE
C
IF(RUNS.GT.2)GO TO 118
IF(COUNT.GT.3,O)GO TO 118
WRITE(6,854)TIME,SUMR,TRANSP,DIFF,DIF,POTCR,COUNT
CONTINUE
C 118
CONTINUE
IF(ABS(DIF).LE.ERROR)GO TO 165
IF(ABS(DIF).LE.20*CF=.5
IF(ABS(DIF).LE.10*CF=.1
IF(DIF).60,165,160
POTCR=AMINI(POTCR-DIF,POTCR*CF),MAXPOT)
GO TO 165
160      CONTINUE
DO 170 I=1,NJ
POTR(I)=POTCR+RTEX(I)*RSRT(I)
CONTINUE
SINGLP=POTCR
POTCR=AMINI(POTCR,SINGLP)
SINGLP IS A REAL REPRESENTATION OF POTCRD, FOR THE AMINI FUNCTION
DO 170 I=1,NJ
CRTEX(I)=INTGR(CRTEX(I),RTEX(I),DELT)
CONTINUE
EVAP=AMINI(-FLW(1),SLEVP)
EVAP=AMINI(-INTGR(CVAP,EVAP,DELT)
FLWB=AMAX1(O,O,FLW(8))
DRAIN=INTGR(DRAIN,FLWB,DELT)
FLWB=-AMINI(O,O,FLW(8))
CAPRIS=INTGR(CAPRIS,FLWB,DELT)
CUMTRN=INTGR(CUMTRN,FLWB,DELT)
DRAIN=FLWB
C
IF(RUNS.LE.3)THEN
WRITE(6,274)
WRITE(6,275)TIME,CLOCK,HOURC,SUMR,TRANSP,DIF,POTCR,SOLCHO,CUMREM
ELSEIF(MOD(RUNS,3).EQ.O)THEN
WRITE(6,275)TIME,CLOCK,HOURC,SUMR,TRANSP,DIF,POTCR,SOLCHO,CUMREM
ENDIF
WRITE(6,276)HOURC,(POTH(1),I=1,NJ)
WRITE(6,276)HOURC,(RTEX(1),I=1,NJ)
WRITE(6,276)TIME,CLOCK,POTCR,POTCR,SOLCHO,SHOOTW
+ ROOTS,CUMTRN,CVAP,COUNT
+ Z1014,TRANSP,PHOTN,GROWTH,RESP,Z1003,Z1009,
+ WRITE(6,276)HOURC,EVAP,POTM(2)
+ WRITE(6,276)HOURC,RADN,TEMP,PET,RSSL(3),RSRT(3),CONO(3),
+ RESP,SUMRTG,SUMRTG
CONTINUE
1001      CONTINUE
C
WRITE(6,852){(PRTL(J),J=1,NJ),TIME
WRITE(6,852){(RTGRO(J),J=1,NJ)
WRITE(6,852){(POTM(J),J=1,NJ)
WRITE(6,852){(RTOTH(J),J=1,NJ)
WRITE(6,852){(RTOTH(J),J=1,NJ)

```

PROGRAM PHASOL 74/175 OPT=1,ROUND= A/ S/ M/-D.-DS FTN 5.1+587 07/29/85 .18.08.28 PAGE 7

```

461      WRITE(6,856){NETGRD(J),J=1,NJ}
462      WRITE(6,857)
463      RUNS=0
464      RUT=OUTP+OUTF
465      COUNT=0
466      DO 1000 IFUN=3,6
467      GO TO(500,550,650,700,750,850),IFUN
468      DO 505 I=1,NJ
469      Y(I)=THETA(I)
470      WRITE(6,1505)
471      GO 655 900,1 NJ
472      DO 550 I=1,NJ
473      Y(I)=RST(I)
474      WRITE(6,1555)
475      GO 655 900,1 NJ
476      DO 650 I=1,NJ
477      Y(I)=CRTEX(I)
478      WRITE(6,1655)
479      GO 700 900,1 NJ
480      DO 700 I=1,NJ
481      Y(I)=POT(I)
482      WRITE(6,1705)
483      GO 750 900,1 NJ
484      DO 750 I=1,NJ
485      Y(I)=FLW(I)
486      WRITE(6,1755)
487      GO 850 900,1 NJ
488      DO 850 I=1,NJ
489      Y(I)=POT(I)/TCOM(I)
490      WRITE(6,1855)
491      CONTINUE
492      WRITE(6,905)HOURC, DAY, RUN, IFUN
493      SCALE(IFUN)=(SMAX(IFUN)-SMIN(IFUN))/75.0
494      DO 950 I=1,NJ
495      IL=Y(I)-SMIN(IFUN)/SCALE(IFUN)*2.0
496      IF(IL.LT.2)IL=2
497      IF(IL.GT.10)IL=10
498      J=0.5+COM(I)*100./4.
499      LINE(IL)=IX
500      Y(I)=J
501      GO 925 931,931,925
502      WRITE(6,925)
503      GO 925 931,931,925
504      WRITE(6,935)DEPTH(I),(LINE(K),K=1,101),Y(I)
505      LINE(IL)=IB
506      CONTINUE
507      CONTINUE
508      WRITE(6,276) HOURC, {POT(I),I=1,NJ}
509      WRITE(6,276) HOURC, {FLW(I),I=1,NJ}
510      WRITE(6,276) TIME, CLOCK, POTCR, SOLCHO, SHOOTW
511      ROOT=CUMTRN*EVAP*COUNT
512      + WRITE(6,276) HOURC, PHOTSN, GROWTH, RESP, ZZ1003, ZZ1009,
513      + ZZ1014, TRANSP, EVAP, POTM(2)
514      + WRITE(6,276) HOURC, RADN, TEMP, PET, RSSL(3), RSRT(3), COMD(3),
515      + RESP, SUMRTG, SUMRTD
516      CONTINUE
517      CONTINUE
518      STOP
519      END
520

```



```

1 SUBROUTINE SOLSIM 74/175 OPT=1 ROUND=A/S/M/D-DS FTM 5,1+587 PAGE 1
2 DD=-LONG/-OT,ARG=-COMMON/-FIXED,CS=USER/-FIXED,DB=-TB/-SB/-SL/ER/-ID/-PMD/-ST,PL=50000 .07/29/85 .18.06.28
3 FTM5.
4
5 C SUBROUTINE SOLSIM(JDAY,TX,TN,PCP,SOL,LOCALE,IYR)
6 INPUT DATA ARE IN INCHES AND DEGREES FAHRENHEIT
7 DIMENSION A(3,3), B(3,3), TXM(2), RM(2)
8 DATA A/587.253,-.006,086,504,-.039,-.002,-.05,.244/
9 DATA B/781.328,238.0,...637,...341.0,0,...873/
10 IF (IFLAG.EQ.1000) GO TO 9
11 IF FLAG=LOCALE
12 ATX=27.0
13 TXM(1)=56.7
14 TXM(2)=55.8
15 TXM(3)=0
16 AR=252.0
17 RM(1)=412.0
18 RM(2)=374.0
19 RM(3)=280.0
20 RM(4)=204.0
21 TXBAR=10.
22 TXBAR=10.
23 SRBAR=100.
24 TXL1=1.00
25 TXL1=1.00
26 TXL1=1.00
27 9 CONTINUE
28 I=1
29 IF (PCP GT 0) I=2
30 SRL1=A(3,1)*TXL1+A(3,2)*TXL1+A(3,3)*SRL1
31 DT=COS(.0172*(JDAY-200))
32 DR=COS(.0172*(JDAY-172))
33 TXBAR=TXM(1)*ATX*DT
34 TXBAR=TXM(1)*ATX*DT
35 SRBAR=RM(1)+AR*DR
36 SRSDT=.10*SRBAR
37 TXL1=(TX-TXBAR)/14.
38 TXL1=(TX-TXBAR)/14.
39 SRL1=SRL1+B(3,1)*TXL1+B(3,2)*TXL1
40 IF (SRL1 LT 0) NOISE1=13.2
41 IF (SRL1 GE 0) NOISE1=4.4
42 IF (I.EQ.2) NOISE1=2.6*NOISE1
43 SOL=NOISE1*SRL1+SRSDT*SRBAR
44 IF (SOL GT 770) SOL1=770.
45 IF (SOL LT 0) SOL1=0.
46 RETURN
47 END

```

Notes :

- Line 29 computes first term, right side of eqn. 5 of Richardson, 1981.
 Line 40 adds second term, right side of eqn. 5 of Richardson, 1981.

```

9      SUBROUTINE PLOTS(L,M,N)
        WRITE(6,9)
        FORMAT( ' PLOTTER WAS INITIALIZED AT THIS POINT' )
        RETURN
        END

        SUBROUTINE NEWPEN(I)
        RETURN
        END

        SUBROUTINE LEGEND (X,Y)
        RETURN
        END

        SUBROUTINE PLOT(X,Y,NEW)
        Z = 1
        WRITE(6,9)
        FORMAT( ' * HERE WAS A CALL PLOT COMMAND ' )
        RETURN
        END

9      SUBROUTINE AXIS(X,Y,IBCD,NCHAR,AXLEN,ANGLE,FIRSTV,DELTAF)
        DIMENSION FIRSTV(1), DELTAF(1), IBCD(1)
        Z = 2
        WRITE(6,10)
        FORMAT( ' * SUBROUTINE AXIS WAS CALLED AT THIS POINT' )
        WRITE(6,100) IBCD
        FORMAT( ' * FOR THE AXIS LABELLED ', 20A4)
        RETURN
        END

10     SUBROUTINE LINE(X,Y,NPTS,INC,LINTYP,INTEQ)
        DIMENSION X(30), Y(30)
        Z = 3
        WRITE(6,11) INTEQ
        FORMAT( ' * SUBROUTINE LINE WAS CALLED WITH SYMBOL CODE', I3)
        RETURN
        END

11     SUBROUTINE SYMBOL(X,Y,HEIGHT,IBCD,ANGLE,NCHAR)
        DIMENSION IBCD(1)
        Z = 4
        IF (NCHAR.LT.0) GO TO 18
        WRITE(6,12) IBCD
        FORMAT( ' * $ CALL SYMBOL FOR ', 20A4)
        CONTINUE
        RETURN
        END

12     SUBROUTINE NUMBER(X,Y,HEIGHT,FPN,ANGLE,NCHAR)
        WRITE(6,12) FPN
        FORMAT( ' * $ CALL NUMBER FOR ', G12.3)
        RETURN
        END

```


Computer Output

INITIALIZATION

IRTL= 511. M/M2

I	IPRTL	RSRT	IVOLV	TCOM	ITHETA	RRL	DEPTH	BLK DNS
1	91.9	.194E+10	.00854	.02500	.34179	.18000	.01250	1.1
2	71.5	.249E+10	.00857	.02500	.34268	.14000	.03750	1.1
3	71.5	.249E+10	.00859	.02500	.34360	.14000	.06250	1.1
4	71.5	.249E+10	.00861	.02500	.34455	.14000	.08750	1.1
5	76.6	.232E+10	.00864	.02500	.34553	.15000	.11250	1.1
6	66.4	.268E+10	.00866	.02500	.34654	.13000	.13750	1.1
7	46.0	.387E+10	.00869	.02500	.34759	.09000	.16250	1.1
8	15.3	.116E+11	.00872	.02500	.34868	.03000	.18750	1.1
9	.511E-02	.348E+14	.00875	.02500	.34981	.00001	.21250	1.1
10	.511E-02	.348E+14	.00877	.02500	.35099	.00001	.23750	1.1

TIME	CLOCK	HOURC	SUMR	TRANSP	DIF	POTCR	SOLCHO	CUMREM
0.	0.	0.	0.	0.	0.	-2.000	.9433E-03	0.

*****DYNAMIC SEGMENT OF THE MODEL*****

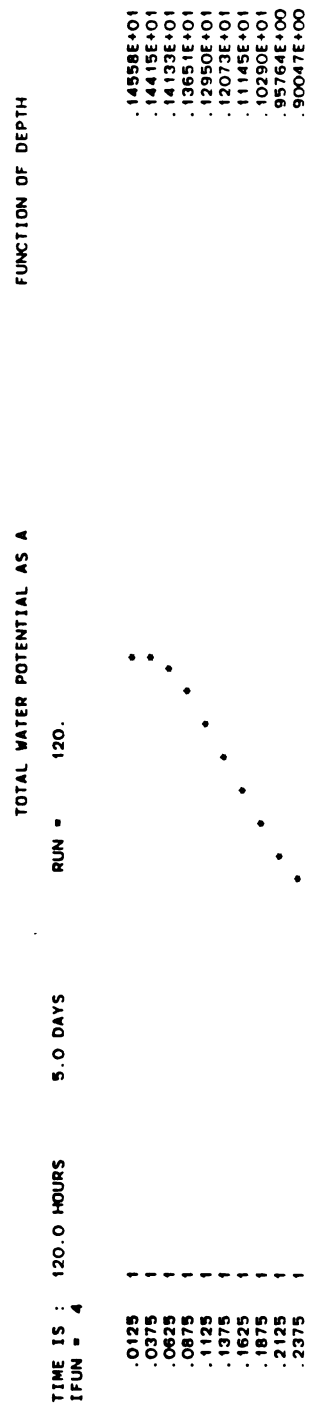
J	I	POTH	POTCR	RSSL	RSRT	RTEX	SUMR	TRANSP	DIF	COUNT
1	10	-.850	-2.00	.673E+13	.348E+14	.277E-13	.277E-13	.167E-09	-1.00	1.00
2	9	-.850	-2.00	.718E+13	.348E+14	.274E-13	.550E-13	.167E-09	-1.00	1.00
3	8	-.850	-2.00	.254E+10	.116E+11	.813E-10	.813E-10	.167E-09	-514	1.00
4	7	-.850	-2.00	.896E+09	.387E+10	.241E-09	.323E-09	.167E-09	.926	1.00
5	6	-.850	-2.00	.656E+09	.268E+10	.345E-09	.867E-09	.167E-09	2.98	1.00
6	5	-.850	-2.00	.600E+09	.232E+10	.393E-09	.108E-08	.167E-09	5.33	1.00
7	4	-.850	-2.00	.678E+09	.249E+10	.363E-09	.142E-08	.167E-09	7.50	1.00
8	3	-.850	-2.00	.713E+09	.249E+10	.359E-09	.178E-08	.167E-09	9.64	1.00
9	2	-.850	-2.00	.750E+09	.249E+10	.355E-09	.214E-08	.167E-09	11.8	1.00
10	1	-.850	-2.00	.612E+09	.194E+10	.451E-09	.259E-08	.167E-09	14.5	1.00

TIME	SUMR	TRANSP	DIF	POTCR	COUNT
.360E+04	.259E-08	.167E-09	-.242E-08	-2.00	1.00

J	I	POTH	POTCR	RSSL	RSRT	RTEX	SUMR	TRANSP	DIF	COUNT
1	1	-.850	-2.00	.612E+09	.194E+10	.451E-09	.451E-09	.168E-09	-284E-09	1.00
2	2	-.850	-2.00	.750E+09	.249E+10	.359E-09	.806E-09	.168E-09	-.639E-09	1.00
3	3	-.850	-2.00	.713E+09	.249E+10	.359E-09	.117E-08	.168E-09	-.998E-09	1.00
4	4	-.850	-2.00	.678E+09	.249E+10	.363E-09	.153E-08	.168E-09	-.136E-08	1.00
5	5	-.850	-2.00	.600E+09	.232E+10	.393E-09	.192E-08	.168E-09	-.175E-08	1.00
6	6	-.850	-2.00	.656E+09	.268E+10	.345E-09	.227E-08	.168E-09	-.210E-08	1.00
7	7	-.850	-2.00	.895E+09	.387E+10	.241E-09	.251E-08	.168E-09	-.234E-08	1.00
8	8	-.850	-2.00	.253E+10	.116E+11	.813E-10	.259E-08	.168E-09	-.242E-08	1.00
9	9	-.850	-2.00	.666E+13	.227E+14	.421E-13	.259E-08	.168E-09	-.242E-08	1.00
10	10	-.850	-2.00	.673E+13	.348E+14	.277E-13	.259E-08	.168E-09	-.242E-08	1.00

TIME	SUMR	TRANSP	DIFF	DIF	POTCR	COUNT	TRANSP	DIF	POTCR	SOLCHO	CUMREM
.720E+04	.259E-08	.168E-09	-.242E-08	14.4	-2.00	1.00	.1677E-09	14.44	-2.000	.9321E-03	.9321E-05
TIME	CLOCK	TRANSP	DIFF	DIF	POTCR		TRANSP	DIF	POTCR	SOLCHO	CUMREM
7200.	2.000		2.000				.1677E-09	14.44	-2.000	.9321E-03	.9321E-05
TIME	CLOCK	TRANSP	DIFF	DIF	POTCR		TRANSP	DIF	POTCR	SOLCHO	CUMREM
.1080E+05	3.000		3.000				.1678E-09	14.40	-2.000	.8172E-03	.1864E-04
.2160E+05	6.000		6.000				.1683E-09	14.29	-2.000	.7018E-03	.4653E-04
.3240E+05	9.000		9.000				.1689E-08	-	-2.541	.2107E-02	.7463E-04
.4320E+05	12.00		12.00				.1695E-08	-	-3.247	.4636E-02	.1234E-03
.5400E+05	15.00		15.00				.1701E-08	-	-2.635	.6404E-02	.1789E-03
.6480E+05	18.00		18.00				.1707E-08	12.91	-2.000	.6084E-02	.2135E-03
.7560E+05	21.00		21.00				.1713E-08	12.51	-2.000	.5182E-02	.2407E-03
.8640E+05	24.00		24.00				.1719E-08	12.23	-2.000	.4538E-02	.2679E-03
.9720E+05	27.00		27.00				.1725E-08	12.03	-2.000	.4032E-02	.2950E-03
.1080E+06	30.00		30.00				.1731E-08	11.85	-2.000	.3567E-02	.3221E-03
.1188E+06	33.00		33.00				.1737E-07	-	-5.691	.4842E-02	.3733E-03
.1296E+06	36.00		36.00				.1743E-07	-	-7.664	.7349E-02	.5122E-03
.1404E+06	39.00		39.00				.1749E-07	-	-6.010	.9016E-02	.6701E-03
.1512E+06	42.00		42.00				.1755E-08	19.25	-2.000	.8382E-02	.7581E-03
.1620E+06	45.00		45.00				.1761E-08	9.538	-2.000	.7147E-02	.7887E-03
.1728E+06	48.00		48.00				.1767E-08	9.339	-2.000	.6267E-02	.8141E-03
.1836E+06	51.00		51.00				.1773E-08	9.196	-2.000	.5573E-02	.8395E-03
.1944E+06	54.00		54.00				.1779E-08	9.074	-2.000	.4937E-02	.8650E-03
.2052E+06	57.00		57.00				.1785E-07	-	-14.05	.6313E-02	.9931E-03
.2160E+06	60.00		60.00				.1791E-07	-	-18.59	.8880E-02	.1362E-02
.2268E+06	63.00		63.00				.1797E-07	46.10	-2.000	.1051E-01	.1766E-02
.2376E+06	66.00		66.00				.1803E-07	-	-2.000	.9727E-02	.1992E-02
.2484E+06	69.00		69.00				.1809E-08	6.122	-2.000	.8294E-02	.2047E-02
.2592E+06	72.00		72.00				.1815E-08	6.061	-2.000	.7272E-02	.2068E-02
.2700E+06	75.00		75.00				.1821E-08	6.028	-2.000	.6468E-02	.2089E-02
.2808E+06	78.00		78.00				.1827E-08	6.008	-2.000	.5729E-02	.2110E-02
.2916E+06	81.00		81.00				.1833E-08	-	-3.252	.4943E-02	.2136E-02
.3024E+06	84.00		84.00				.1839E-08	-	-4.156	.4112E-01	.2197E-02
.3132E+06	87.00		87.00				.1845E-08	-	-3.375	.3533E-01	.2266E-02
.3240E+06	90.00		90.00				.1851E-08	5.400	-2.000	.2544E-01	.2304E-02
.3348E+06	93.00		93.00				.1857E-08	5.286	-2.000	.1070E-01	.2326E-02
.3456E+06	96.00		96.00				.1863E-08	5.228	-2.000	.9385E-02	.2347E-02
.3564E+06	99.00		99.00				.1869E-08	5.197	-2.000	.8351E-02	.2369E-02
.3672E+06	102.0		102.0				.1875E-08	5.176	-2.000	.7402E-02	.2391E-02
.3780E+06	105.0		105.0				.1881E-07	-	-18.10	.9238E-02	.2559E-02
.3888E+06	108.0		108.0				.1887E-07	-	-23.39	.1255E-01	.3036E-02
.3996E+06	111.0		111.0				.1893E-07	9.954E-02	-18.52	.1458E-01	.3547E-02
.4104E+06	114.0		114.0				.1899E-07	43.39	-2.000	.1347E-01	.3836E-02
.4212E+06	117.0		117.0				.1905E-08	2.870	-2.000	.1149E-01	.3901E-02
.4320E+06	120.0		120.0				.1911E-08	2.912	-2.000	.1007E-01	.3917E-02
TIME	ROOT LENGTH, M/SO. M. BY LAYER	ROOT GROWTH RATE	MATRIC POTENTIALS				TIME				
91.9	87.7	85.5	85.3	90.4	81.1	58.9	24.5	3.49	.287	.432E+06	
.188E-11	.388E-04	.370E-04	.361E-04	.360E-04	.362E-04	.343E-04	.249E-04	.104E-04	.148E-05		
-1.44	-1.40	-1.35	-1.28	-1.18	-1.07	-.952	-.842	-.745	-.663		

TIME IS : 120.0 HOURS		5.0 DAYS	CUMULATIVE ROOT EXTRACTION.	METERS VS. DEPTH
IFUN = 3			RUN = 120.	
.0125	1			.47702E-03
.0375	1			.52563E-03
.0625	1			.53000E-03
.0875	1			.54268E-03
.1125	1			.59489E-03
.1375	1			.54186E-03
.1625	1			.30936E-03
.1875	1			.13033E-03
.2125	1			.12485E-04
.2375	1			.73326E-06

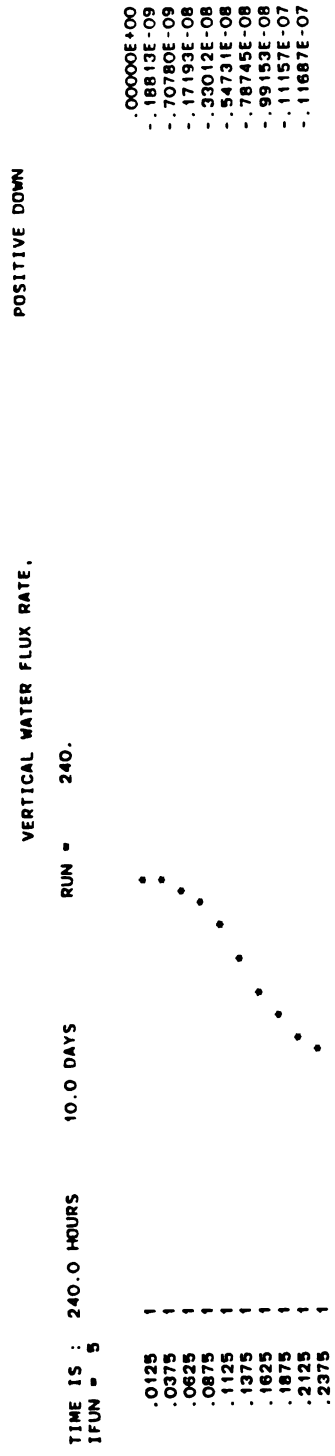


TIME IS : 120.0 HOURS		5.0 DAYS		VERTICAL WATER FLUX RATE.		POSITIVE DOWN	
IFUN = 5				RUN = 120.			
.0125	1						.00000E+00
.0375	1						-.42908E-09
.0625	1						-.88922E-09
.0875	1						-.16453E-08
.1125	1						-.26740E-08
.1375	1						-.38775E-08
.1625	1						-.49059E-08
.1875	1						-.54873E-08
.2125	1						-.55736E-08
.2375	1						-.53861E-08

TIME	CLOCK	HOURC	SUMR	TRANS	DIF	POTCR	SOLCHD	CUMREM
.4392E+06	2.000	122.0	.1502E-08	.3809E-09	2.944	-2.000	.9310E-02	.3928E-02
TIME	CLOCK	HOURC	SUMR	TRANS	DIF	POTCR	SOLCHD	CUMREM
.4428E+06	3.000	123.0	.1514E-08	.3824E-09	2.980	-2.000	.8958E-02	.3933E-02
.4536E+06	6.000	126.0	.1549E-08	.3864E-09	3.008	-2.000	.7933E-02	.3950E-02
.4644E+06	9.000	129.0	.1589E-07	.3905E-07	-18.89	-2.000	.1013E-01	.4117E-02
.4752E+06	12.00	132.0	.4911E-07	.4958E-07	-9437E-02	-24.27	.1399E-01	.4593E-02
.4860E+06	15.00	135.0	.3701E-07	.3666E-07	.9618E-02	-19.29	.1636E-01	.5100E-02
.4968E+06	18.00	138.0	.1512E-07	.3920E-08	37.57	-2.000	.1514E-01	.5387E-02
.5076E+06	21.00	141.0	.9685E-09	.4284E-08	1.267	-2.000	.1291E-01	.5449E-02
.5184E+06	0.	144.0	.1020E-08	.4330E-08	1.355	-2.000	.1132E-01	.5459E-02
.5292E+06	3.000	147.0	.1059E-08	.4379E-08	1.441	-2.000	.1006E-01	.5470E-02
.5400E+06	6.000	150.0	.1116E-08	.4422E-09	1.524	-2.000	.8914E-02	.5482E-02
.5508E+06	9.000	153.0	.2337E-07	.2386E-07	-12.33	-2.000	.1157E-01	.5580E-02
.5616E+06	12.00	156.0	.3127E-07	.3156E-07	-9250E-02	-16.22	.1658E-01	.5874E-02
.5724E+06	15.00	159.0	.2331E-07	.2310E-07	.9087E-02	-12.72	.1977E-01	.6198E-02
.5832E+06	18.00	162.0	.9170E-08	.4608E-08	18.90	-2.000	.1829E-01	.6376E-02
.5940E+06	21.00	165.0	.8614E-08	.4875E-09	.7670	-2.000	.1559E-01	.6416E-02
.6048E+06	0.	168.0	.9178E-09	.4949E-09	.8546	-2.000	.1367E-01	.6425E-02
.6156E+06	3.000	171.0	.9716E-09	.5003E-09	.9420	-2.000	.1216E-01	.6435E-02
.6264E+06	6.000	174.0	.1024E-08	.5050E-09	1.027	-2.000	.1077E-01	.6446E-02
.6372E+06	9.000	177.0	.3789E-07	.3826E-07	-9760E-02	-18.70	.1358E-01	.6608E-02
.6480E+06	12.00	180.0	.4817E-07	.4864E-07	-9611E-02	-24.00	.1857E-01	.7074E-02
.6588E+06	15.00	183.0	.3615E-07	.3582E-07	.9324E-02	-19.07	.2161E-01	.7577E-02
.6696E+06	18.00	186.0	.1472E-07	.5087E-09	28.05	-2.000	.1996E-01	.7851E-02
.6804E+06	21.00	189.0	.5528E-08	.5493E-09	.6367E-02	-2.002	.1702E-01	.7908E-02
.6912E+06	0.	192.0	.6047E-09	.5566E-09	.8627E-01	-2.000	.1491E-01	.7914E-02
.7020E+06	3.000	195.0	.6582E-09	.5620E-09	.1712	-2.000	.1326E-01	.7921E-02
.7128E+06	6.000	198.0	.7116E-09	.5666E-09	.2559	-2.000	.1174E-01	.7929E-02
.7236E+06	9.000	201.0	.5284E-07	.5312E-07	-9126E-02	-25.60	.1471E-01	.8161E-02
.7344E+06	12.00	204.0	.6310E-07	.6370E-07	-9488E-02	-31.72	.1950E-01	.8792E-02
.7452E+06	15.00	207.0	.4777E-07	.4732E-07	.9668E-02	-25.80	.2230E-01	.9441E-02
.7560E+06	18.00	210.0	.2026E-07	.5417E-09	36.39	-2.000	.2060E-01	.9816E-02
.7668E+06	21.00	213.0	.6114E-09	.6055E-09	.9662E-02	-2.275	.1756E-01	.9894E-02
.7776E+06	0.	216.0	.6171E-09	.6124E-09	.7604E-02	-2.221	.1538E-01	.9900E-02
.7884E+06	3.000	219.0	.6218E-09	.6176E-09	.6763E-02	-2.177	.1366E-01	.9907E-02
.7992E+06	6.000	222.0	.6256E-09	.6221E-09	.6080E-02	-2.137	.1209E-01	.9914E-02
.8100E+06	9.000	225.0	.4936E-07	.4986E-07	-9911E-02	-25.05	.1546E-01	.1013E-01
.8208E+06	12.00	228.0	.5946E-07	.6003E-07	-9490E-02	-31.11	.2089E-01	.1072E-01
.8316E+06	15.00	231.0	.4488E-07	.4446E-07	.9522E-02	-25.26	.2410E-01	.1134E-01
.8424E+06	18.00	234.0	.1895E-07	.5928E-09	30.96	-2.000	.2228E-01	.1169E-01
.8532E+06	21.00	237.0	.6641E-09	.6592E-09	.7504E-02	-2.465	.1899E-01	.1176E-01
.8640E+06	0.	240.0	.6714E-09	.6680E-09	.8174E-02	-2.400	.1663E-01	.1177E-01
TIME	ROOT LENGTH, M/50.M, BY LAYER	TIME	ROOT GROWTH RATE	TIME	ROOT GROWTH RATE	TIME	ROOT GROWTH RATE	TIME
91.9	124.	127.	125.	99.1	55.3	18.8	4.27	.864E+06
.135E-11	.433E-04	.585E-04	.601E-04	.599E-04	.622E-04	.588E-04	.261E-04	.886E-05
-2.89	-2.84	-2.74	-2.55	-2.25	-1.89	-1.51	-.942	-.754
.830E-07	.112E-06	.115E-06	.115E-06	.113E-06	.896E-07	.500E-07	.169E-07	.386E-08
-.830E-07	.432E-04	.584E-04	.599E-04	.597E-04	.468E-04	.261E-04	.886E-05	

TIME IS : 240.0 HOURS		10.0 DAYS		CUMULATIVE ROOT EXTRACTION.		METERS VS. DEPTH	
IFUN = 3				RUN = 240.			
.0125	1	.				.10935E-02	
.0375	1		.			.13745E-02	
.0625	1		.			.14655E-02	
.0875	1		.			.15459E-02	
.1125	1		.			.17550E-02	
.1375	1		.			.17462E-02	
.1625	1		.			.12376E-02	
.1875	1	.				.54884E-03	
.2125	1	.				.16098E-03	
.2375	1	.				.31154E-04	

TIME IS : 240.0 HOURS	10.0 DAYS	TOTAL WATER POTENTIAL AS A	FUNCTION OF DEPTH
IFUN = 4	RUN = 240.		
.0125 1			.28990E+01
.0375 1			.28779E+01
.0625 1			.28021E+01
.0875 1			.26352E+01
.1125 1			.23662E+01
.1375 1			.20248E+01
.1625 1			.16775E+01
.1875 1			.13808E+01
.2125 1			.11550E+01
.2375 1			.99133E+00



PARTIAL ROOT LENGTH, METERS/SQ. METER IN EACH LAYER

TIME IS : 240.0 HOURS
IFUN = 6 RUN = 240.

- .36751E+04
- .49660E+04
- .50982E+04
- .50784E+04
- .52739E+04
- .49818E+04
- .39648E+04
- .22112E+04
- .75020E+03
- .17085E+03

[illegible]

J	I	POTH	POTCR	RSLL	RSRT	RTEX	SUMR	TRANSP	DIFF	DIF	COUNT
1	10	-.991	-2.40	.110E+11	.414E+11	.269E-10	.123E-10	.688E-09	.641E-09	-.960	1.00
2	9	-1.15	-2.40	.360E+10	.944E+10	.956E-10	.263E-09	.688E-09	.545E-09	-.817	1.00
3	8	-1.37	-2.40	.179E+10	.321E+10	.205E-09	.328E-09	.688E-09	.340E-09	-.509	1.00
4	7	-1.66	-2.40	.148E+10	.179E+10	.175E-09	.953E-09	.688E-09	.115E-09	-.172	1.00
5	6	-2.00	-2.40	.170E+10	.143E+10	.127E-09	.680E-09	.688E-09	-.125E-10	.187E-01	1.00
6	5	-2.34	-2.40	.219E+10	.135E+10	.987E-09	.697E-09	.688E-09	-.288E-10	.431E-01	1.00
7	4	-2.62	-2.40	.283E+10	.140E+10	0.	.697E-09	.688E-09	-.288E-10	.431E-01	1.00
8	3	-2.79	-2.40	.322E+10	.139E+10	0.	.697E-09	.688E-09	-.288E-10	.431E-01	1.00
9	2	-2.87	-2.40	.354E+10	.143E+10	0.	.697E-09	.688E-09	-.288E-10	.431E-01	1.00
10	1	-2.90	-2.40	.495E+10	.194E+10	0.	.697E-09	.688E-09	-.288E-10	.431E-01	1.00

TIME	SUMR	TRANSP	DIFF	DIF	POTCR	COUNT
868E+06	.697E-09	.668E-09	-.288E-10	.431E-01	-2.40	1.00

1	10	- .991	- 2.39	.110E+11	.414E+11	.267E-10	.668E-09	.641E-09	2.00
2	8	- 1.15	- 2.39	.380E+10	.944E+10	.122E-09	.668E-09	.546E-09	2.00
3	8	- 1.37	- 2.39	.179E+10	.321E+10	.203E-09	.668E-09	.514	2.00
4	7	- 1.66	- 2.39	.179E+10	.178E+10	.323E-09	.668E-09	.343E-09	2.00
5	6	- 2.00	- 2.39	.170E+10	.143E+10	.547E-09	.668E-09	.121E-09	2.00
6	5	- 2.34	- 2.39	.219E+10	.135E+10	.671E-09	.668E-09	.293E-11	2.00
7	4	- 2.62	- 2.39	.283E+10	.140E+10	.684E-09	.668E-09	.163E-10	2.00
8	3	- 2.79	- 2.39	.322E+10	.139E+10	.684E-09	.668E-09	.163E-10	2.00
9	2	- 2.87	- 2.39	.354E+10	.143E+10	.684E-09	.668E-09	.163E-10	2.00
10	1	- 2.90	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
11	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
12	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
13	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
14	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
15	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
16	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
17	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
18	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
19	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
20	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
21	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
22	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
23	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
24	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
25	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
26	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
27	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
28	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
29	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
30	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
31	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
32	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
33	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
34	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
35	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
36	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
37	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	2.00
38	0	- 2.91	- 2.39	.495E+10	.194E+10	.684E-09	.668E-09	.163E-10	

TIME	SUMR	TRANSP	DIFF	DIF	POTCR	COUNT
868E+06	.684E-09	.668E-09	-.163E-10	.245E-01	-2.39	2.00

1	10	- .991	- 2.38	.110E+11	.414E+11	.286E-10	.268E-10	.668E-09	.641E-09	- .960	3.00
2	9	- 1.35	- 2.38	.360E+10	.944E+10	.944E-10	.121E-09	.668E-09	.547E-09	- .819	3.00
3	8	- 1.17	- 2.38	.179E+10	.321E+10	.202E-09	.323E-09	.668E-09	.345E-09	- .517	3.00
4	7	- 1.66	- 2.38	.148E+10	.179E+10	.124E-09	.543E-09	.668E-09	.124E-09	- .186	3.00
5	6	- 2.00	- 2.38	.170E+10	.143E+10	.246E-11	.665E-09	.668E-09	.246E-11	- .368E-02	3.00
6	5	- 2.34	- 2.38	.219E+10	.135E+10	.118E-10	.677E-09	.668E-09	- 9.79E-11	- .139E-01	3.00

7	4	-2.62	-2.38	.283E+10	.140E+10	0.	.677E-09	.668E-09	-.929E-11	.139E-01	3.00
8	3	-2.79	-2.38	.322E+10	.139E+10	0.	.677E-09	.668E-09	-.929E-11	.139E-01	3.00
9	2	-2.87	-2.38	.354E+10	.143E+10	0.	.677E-09	.668E-09	-.929E-11	.139E-01	3.00
10	1	-2.90	-2.38	.495E+10	.194E+10	0.	.677E-09	.668E-09	-.929E-11	.139E-01	3.00

TIME	SUMR	TRANSP	DIFF	DIF	POTCR	COUNT
.868E+06	.677E-09	.668E-09	-.929E-11	.139E-01	-2.38	3.00

TIME	SUMR	CLOCK	HOURC	SUMR	TRANSP	DIF	POTCR	SOLCHO	CUMREM
.8676E+06	1.000	241.0	.6731E-09	.6678E-09	.7932E-02	-2.381	.1597E-01	.1177E-01	

J	I	POTH	POTCR	RSSL	RSRT	RTEX	SUMR	TRANSP	DIFF	COUNT
1	1	-2.89	-2.38	.494E+10	.194E+10	0.	0.	.670E-09	.670E-09	1.00
2	2	-2.86	-2.38	.352E+10	.143E+10	0.	0.	.670E-09	.670E-09	1.00
3	3	-2.77	-2.38	.319E+10	.139E+10	0.	0.	.670E-09	.670E-09	1.00
4	4	-2.60	-2.38	.279E+10	.140E+10	0.	0.	.670E-09	.670E-09	1.00
5	5	-2.32	-2.38	.215E+10	.135E+10	.176E-10	.176E-10	.670E-09	.652E-09	1.00
6	6	-1.98	-2.38	.167E+10	.142E+10	.129E-09	.146E-09	.670E-09	.523E-09	1.00
7	7	-1.65	-2.38	.145E+10	.179E+10	.225E-09	.371E-09	.670E-09	.298E-09	1.00
8	8	-1.37	-2.38	.177E+10	.320E+10	.942E-10	.575E-09	.670E-09	.942E-10	1.00
9	9	-1.15	-2.38	.356E+10	.940E+10	.949E-10	.670E-09	.670E-09	-.686E-12	1.00
10	10	-.990	-2.38	.110E+11	.411E+11	.287E-10	.697E-09	.670E-09	-.274E-10	1.00

TIME	SUMR	TRANSP	DIFF	DIF	POTCR	COUNT
.871E+06	.697E-09	.670E-09	-.274E-10	.410E-01	-2.38	1.00

1	1	-2.89	-2.37	.494E+10	.194E+10	0.	0.	.670E-09	.670E-09	2.00
2	2	-2.86	-2.37	.352E+10	.143E+10	0.	0.	.670E-09	.670E-09	2.00
3	3	-2.77	-2.37	.319E+10	.139E+10	0.	0.	.670E-09	.670E-09	2.00
4	4	-2.60	-2.37	.279E+10	.140E+10	0.	0.	.670E-09	.670E-09	2.00
5	5	-2.32	-2.37	.215E+10	.135E+10	.148E-10	.148E-10	.670E-09	.555E-09	2.00
6	6	-1.98	-2.37	.167E+10	.142E+10	.125E-09	.140E-09	.670E-09	.529E-09	2.00
7	7	-1.65	-2.37	.145E+10	.179E+10	.222E-09	.362E-09	.670E-09	.307E-09	2.00
8	8	-1.37	-2.37	.177E+10	.320E+10	.105E-09	.564E-09	.670E-09	.105E-09	2.00
9	9	-1.15	-2.37	.356E+10	.940E+10	.110E-10	.659E-09	.670E-09	.110E-10	2.00
10	10	-.990	-2.37	.110E+11	.411E+11	.265E-10	.685E-09	.670E-09	-.156E-10	2.00

TIME	SUMR	TRANSP	DIFF	DIF	POTCR	COUNT
.871E+06	.685E-09	.670E-09	-.156E-10	.232E-01	-2.37	2.00

1	1	-2.89	-2.37	.494E+10	.194E+10	0.	0.	.670E-09	.670E-09	3.00
2	2	-2.86	-2.37	.352E+10	.143E+10	0.	0.	.670E-09	.670E-09	3.00
3	3	-2.77	-2.37	.319E+10	.139E+10	0.	0.	.670E-09	.670E-09	3.00
4	4	-2.60	-2.37	.279E+10	.140E+10	0.	0.	.670E-09	.670E-09	3.00
5	5	-2.32	-2.37	.215E+10	.135E+10	.132E-10	.132E-10	.670E-09	.533E-09	3.00
6	6	-1.98	-2.37	.167E+10	.142E+10	.124E-09	.137E-09	.670E-09	.533E-09	3.00
7	7	-1.65	-2.37	.145E+10	.179E+10	.221E-09	.357E-09	.670E-09	.312E-09	3.00
8	8	-1.37	-2.37	.177E+10	.320E+10	.111E-09	.558E-09	.670E-09	.111E-09	3.00
9	9	-1.15	-2.37	.356E+10	.940E+10	.176E-10	.652E-09	.670E-09	.176E-10	3.00
10	10	-.990	-2.37	.110E+11	.411E+11	.264E-10	.678E-09	.670E-09	-.886E-11	3.00

TIME	SUMR	TRANSP	DIFF	DIF	POTCR	COUNT
.871E+06	.678E-09	.670E-09	-.886E-11	.132E-01	-2.37	3.00

TIME	.8712E+06	CLOCK	2.000	HOURC	242.0	SUMR	.6746E-09	TRANSP	.6695E-09	DIF	.7546E-02	POTCR	-2.362	SOLCHQ	.1536E-01	CUMREM	.1177E-01
TIME	.8748E+06	CLOCK	3.000	HOURC	243.0	SUMR	.6761E-09	TRANSP	.6711E-09	DIF	.7434E-02	POTCR	-2.344	SOLCHQ	.1477E-01	CUMREM	.1178E-01
	.8856E+06	6.000	246.0		.6800E-09		.6755E-09		.6685E-02		-2.295			.1306E-01		.1178E-01	
	.8964E+06	9.000	249.0		.5240E-07		.6289E-07		.6299E-02		-26.95			.1663E-01		.1202E-01	
	.9072E+06	12.00	252.0		.6202E-07		.6206E-07		.9020E-02		-33.14			.2226E-01		.1264E-01	
	.9180E+06	15.00	255.0		.4691E-07		.6498E-07		.9231E-02		-27.07			.2553E-01		.1328E-01	
	.9288E+06	18.00	258.0		.2005E-07		.6330E-09		.30.67		-2.000			.2360E-01		.1365E-01	
	.9396E+06	21.00	261.0		.7157E-09		.7101E-09		.8004E-02		-2.624			.2011E-01		.1373E-01	
	.9504E+06	0.	264.0		.7217E-09		.7166E-09		.7172E-02		-2.546			.1760E-01		.1373E-01	
	.9612E+06	3.000	267.0		.7284E-09		.7215E-09		.6863E-01		-2.483			.1562E-01		.1374E-01	
	.9720E+06	6.000	270.0		.7327E-09		.7256E-09		.9651E-02		-2.430			.1381E-01		.1375E-01	
	.9828E+06	9.000	273.0		.6379E-07		.6438E-07		.9115E-02		-32.89			.1737E-01		.1405E-01	
	.9936E+06	12.00	276.0		.7208E-07		.7274E-07		.9049E-02		-39.38			.2247E-01		.1480E-01	
	.1004E+07	15.00	279.0		.5499E-07		.5449E-07		.9132E-02		-32.94			.2531E-01		.1553E-01	
	.1015E+07	18.00	282.0		.2445E-07		.6485E-09		.36.70		-2.000			.2336E-01		.1597E-01	
	.1026E+07	21.00	285.0		.7612E-09		.7545E-09		.8962E-02		-2.859			.1990E-01		.1607E-01	
	.1037E+07	0.	288.0		.7664E-09		.7603E-09		.7920E-02		-2.756			.1739E-01		.1607E-01	
	.1048E+07	3.000	291.0		.7701E-09		.7648E-09		.6864E-02		-2.671			.1542E-01		.1608E-01	
	.1059E+07	6.000	294.0		.7761E-09		.7687E-09		.9641E-02		-2.601			.1362E-01		.1609E-01	
	.1080E+07	9.000	297.0		.6711E-07		.6772E-07		.9128E-02		-35.94			.1732E-01		.1642E-01	
	.1091E+07	12.00	300.0		.7427E-07		.7495E-07		.9150E-02		-42.50			.2232E-01		.1719E-01	
	.1102E+07	15.00	303.0		.5697E-07		.5644E-07		.9376E-02		-35.94			.2507E-01		.1795E-01	
	.1112E+07	18.00	306.0		.2592E-07		.6670E-09		.37.85		-2.000			.2315E-01		.1841E-01	
	.1123E+07	21.00	309.0		.8006E-09		.7931E-09		.9460E-02		-3.031			.1971E-01		.1851E-01	
	.1134E+07	0.	312.0		.8047E-09		.7984E-09		.7829E-02		-2.913			.1721E-01		.1852E-01	
	.1145E+07	3.000	315.0		.8105E-09		.8025E-09		.9950E-02		-2.822			.1523E-01		.1853E-01	
	.1156E+07	6.000	318.0		.8133E-09		.8080E-09		.9014E-02		-2.743			.1344E-01		.1853E-01	
	.1167E+07	9.000	321.0		.7441E-07		.7511E-07		.9262E-02		-41.24			.1701E-01		.1892E-01	
	.1177E+07	12.00	324.0		.8004E-07		.8083E-07		.9862E-02		-48.18			.2142E-01		.1977E-01	
	.1188E+07	15.00	327.0		.6113E-07		.6056E-07		.9459E-02		-41.00			.2370E-01		.2058E-01	
	.1199E+07	18.00	330.0		.2912E-07		.6625E-09		.42.95		-2.000			.2188E-01		.2108E-01	
	.1210E+07	21.00	333.0		.8331E-09		.8250E-09		.9846E-02		-3.247			.1861E-01		.2119E-01	
	.1220E+07	0.	336.0		.8368E-09		.8298E-09		.8398E-02		-3.096			.1622E-01		.2120E-01	
	.1231E+07	3.000	339.0		.8396E-09		.8336E-09		.7145E-02		-2.975			.1435E-01		.2121E-01	
	.1242E+07	6.000	342.0		.8445E-09		.8389E-09		.9157E-02		-2.878			.1263E-01		.2122E-01	
	.1253E+07	9.000	345.0		.3945E-07		.3980E-07		.9007E-02		-24.15			.1761E-01		.2139E-01	
	.1264E+07	12.00	348.0		.4813E-07		.4857E-07		.9055E-02		-29.61			.2553E-01		.2187E-01	
	.1274E+07	15.00	351.0		.3611E-07		.3576E-07		.9743E-02		-23.89			.3039E-01		.2236E-01	
	.1285E+07	18.00	354.0		.1510E-07		.7882E-09		.18.21		-2.000			.2824E-01		.2265E-01	
	.1296E+07	21.00	357.0		.8697E-09		.8626E-09		.8169E-02		-2.994			.2401E-01		.2271E-01	
	.1307E+07	0.	360.0		.8784E-09		.8681E-09		.9637E-02		-2.880			.2097E-01		.2272E-01	

91.8 169. 198. 205. 206. 211. 178. 121. 59.9 22.1 130E+07

.360E-12 .341E-04 .626E-04 .736E-04 .781E-04 .784E-04 .787E-04 .662E-04 .451E-04 .224E-04

-5.45 -5.42 -5.27 -4.86 -4.18 -3.32 -2.45 -1.74 -1.23 -.884

.105E-06 .193E-06 .227E-06 .235E-06 .242E-06 .236E-06 .204E-06 .139E-06 .687E-07 .253E-07
 -.105E-06 .339E-04 .624E-04 .734E-04 .759E-04 .782E-04 .785E-04 .661E-04 .450E-04 .223E-04

TIME IS : 360.0 HOURS		15.0 DAYS	CUMULATIVE ROOT EXTRACTION.		METERS VS. DEPTH
IFUN = 3		RUN =	360.		
.0125	1	.			.15192E-02
.0375	1	.			.20551E-02
.0625	1	.			.23875E-02
.0875	1	.			.25999E-02
.1125	1	.			.30766E-02
.1375	1	.			.33937E-02
.1625	1	.			.30971E-02
.1875	1	.			.19538E-02
.2125	1	.			.79255E-03
.2375	1	.			.29945E-03

TIME IS : 360.0 HOURS	15.0 DAYS	TOTAL WATER POTENTIAL AS A	FUNCTION OF DEPTH
IFUN = 4	RUN = 360.		
.0125	1		.54600E+01
.0375	1		.54574E+01
.0625	1		.53336E+01
.0875	1		.49448E+01
.1125	1		.42887E+01
.1375	1		.34539E+01
.1625	1		.26092E+01
.1875	1		.19235E+01
.2125	1		.14400E+01
.2375	1		.11219E+01

TIME IS : 360.0 HOURS		15.0 DAYS		VERTICAL WATER FLUX RATE.		POSITIVE DOWN	
IFUN = 5		RUN = 360.					
.0125	1					.00000E+00	
.0375	1					-.72547E-11	
.0625	1					-.35265E-09	
.0875	1					-.12302E-08	
.1125	1					-.25938E-08	
.1375	1					-.47377E-08	
.1625	1					-.78616E-08	
.1875	1					-.11344E-07	
.2125	1					-.14383E-07	
.2375	1					-.16431E-07	

TIME IS : 360.0 HOURS
IFUN = 6

15.0 DAYS

RUN - 360.

• .36734E+04
• .67478E+04
• .79348E+04
• .81982E+04
• .84330E+04
• .82423E+04
• .71099E+04
• .48345E+04
• .23979E+04
• .88229E+03

[illegible]

J	I	POTH	POTCR	RSSL	RSRT	RTEX	SUMR	TRANSP	DIFF	DIF	COUNT
1	10	-1.12	-2.88	.275E+10	.804E+10	.163E-09	.163E-09	.870E-09	.706E-09	-.812	1.00
2	9	-1.43	-2.88	.173E+10	.296E+10	.310E-09	.473E-09	.870E-09	.396E-09	-.456	1.00
3	8	-1.90	-2.88	.151E+10	.147E+10	.670E-10	.803E-09	.870E-09	.670E-10	-.770E-01	1.00
4	7	-2.57	-2.88	.185E+10	.100E+10	.109E-09	.912E-09	.870E-09	-.421E-10	.484E-01	1.00
5	6	-3.40	-2.88	.275E+10	.863E+09	0.	.912E-09	.870E-09	-.421E-10	.484E-01	1.00
6	5	-4.25	-2.88	.413E+10	.843E+09	0.	.912E-09	.870E-09	-.421E-10	.484E-01	1.00
7	4	-4.91	-2.88	.565E+10	.867E+09	0.	.912E-09	.870E-09	-.421E-10	.484E-01	1.00
8	3	-5.31	-2.88	.683E+10	.896E+09	0.	.912E-09	.870E-09	-.421E-10	.484E-01	1.00
9	2	-5.45	-2.88	.851E+10	.105E+10	0.	.912E-09	.870E-09	-.421E-10	.484E-01	1.00
10	1	-5.46	-2.88	.158E+11	.194E+10	0.	.912E-09	.870E-09	-.421E-10	.484E-01	1.00

TIME	SUMR	TRANSP	DIFF	DIF	POTCR	COUNT
130E+07	.912E-09	.870E-09	-.421E-10	.484E-01	-2.88	1.00

1	10	-1.12	-2.87	.275E+10	.804E+10	.162E-09	.870E-09	.707E-09	- .814	2.00
2	1	-1.43	-2.87	.172E+10	.296E+10	.307E-09	.870E-09	.750E-10	- .481	2.00
3	8	1.90	-2.87	.151E+10	.794E+10	.759E-10	.870E-09	.490E-09	- .873E-01	2.00
4	7	-2.57	-2.87	.185E+10	.100E+10	.104E-09	.870E-09	.870E-09	- .335E-01	2.00
5	6	-3.40	-2.87	.275E+10	.863E+09	0.	.898E-09	.282E-10	- .375E-01	2.00
6	5	-4.25	-2.87	.413E+10	.843E+09	0.	.958E-09	.282E-10	- .375E-01	2.00
7	4	-.91	-2.87	.965E+10	.867E+09	0.	.898E-09	.282E-10	- .375E-01	2.00
8	3	-5.31	-2.87	.683E+10	.896E+09	0.	.898E-09	.282E-10	- .375E-01	2.00
9	2	-5.45	-2.87	.851E+10	.109E+10	0.	.898E-09	.282E-10	- .375E-01	2.00
10	1	-5.46	-2.87	.158E+11	.194E+10	0.	.898E-09	.282E-10	- .375E-01	2.00

TIME	SUMR	TRANSP	DIFF	DIF	POTCR	COUNT
130E+07	.898E-09	.870E-09	-.282E-10	.325E-01	-2.87	2.00

1	-1.12	-2.86	.275E+10	.804E+10	.161E-09	.870E-09	.708E-09	- .815	3.00
2	-1.43	-2.86	.172E+10	.296E+10	.305E-09	.870E-09	.403E-09	- .464	3.00
3	1.90	-2.86	.151E+10	.177E+10	.819E-10	.870E-09	.870E-09	- .942E-01	3.00
4	-2.57	-2.86	.185E+10	.100E+10	.101E-09	.889E-09	.870E-09	- .190E-10	3.00
5	-3.40	-2.86	.275E+09	.863E+09	0.	.889E-09	.870E-09	- .190E-10	3.00
6	-4.25	-2.86	.413E+10	.843E+09	0.	.889E-09	.870E-09	- .190E-10	3.00

7	4	-4.91	-2.86	.565E+10	.867E+09	0.	.889E-09	.870E-09	-.190E-10	.219E-01	3.00
8	3	-5.31	-2.86	.683E+10	.896E+09	0.	.889E-09	.870E-09	-.190E-10	.219E-01	3.00
9	2	-5.45	-2.86	.851E+10	.105E+10	0.	.889E-09	.870E-09	-.190E-10	.219E-01	3.00
10	1	-5.46	-2.86	.158E+11	.194E+10	0.	.889E-09	.870E-09	-.190E-10	.219E-01	3.00
TIME	SUMR	TRANS	DIFF	DIF	POTCR	COUNT					
.130E+07	.889E-09	.870E-09	-.190E-10	.219E-01	-2.86	3.00					
TIME	SUMR	CLOCK	HOURLC	SUMR	TRANS	DIF	POTCR	SOLCHO	CUMREM		
.130E+07	.889E-09	1.000	361.0	.8782E-09	.8695E-09	.9940E-02	-2.846	.2013E-01	.2272E-01		
J	I	POTH	POTCR	RSSL	RSRT	RTEX	SUMR	DIFF	DIF	COUNT	
1	1	-5.46	-2.85	.158E+11	.194E+10	0.	0.	.871E-09	-1.00	1.00	
2	2	-5.44	-2.85	.848E+10	.105E+10	0.	0.	.871E-09	-1.00	1.00	
3	3	-5.29	-2.85	.677E+10	.895E+09	0.	0.	.871E-09	-1.00	1.00	
4	4	-4.88	-2.85	.557E+10	.866E+09	0.	0.	.871E-09	-1.00	1.00	
5	5	-4.20	-2.85	.404E+10	.842E+09	0.	0.	.871E-09	-1.00	1.00	
6	6	-3.35	-2.85	.268E+10	.862E+09	0.	0.	.871E-09	-1.00	1.00	
7	7	-2.53	-2.85	.180E+10	.998E+09	.113E-09	.113E-09	.758E-09	-.870	1.00	
8	8	-1.88	-2.85	.148E+10	.147E+10	.329E-09	.442E-09	.429E-09	-.493	1.00	
9	9	-1.42	-2.85	.169E+10	.295E+10	.121E-09	.750E-09	.121E-09	-.139	1.00	
10	10	-1.11	-2.85	.272E+10	.801E+10	.162E-09	.911E-09	-.405E-10	.464E-01	1.00	
TIME	SUMR	TRANS	DIFF	DIF	POTCR	COUNT					
.130E+07	.911E-09	.871E-09	-.405E-10	.464E-01	-2.85	1.00					
1	1	-5.46	-2.83	.158E+11	.194E+10	0.	0.	.871E-09	-1.00	2.00	
2	2	-5.44	-2.83	.848E+10	.105E+10	0.	0.	.871E-09	-1.00	2.00	
3	3	-5.29	-2.83	.677E+10	.895E+09	0.	0.	.871E-09	-1.00	2.00	
4	4	-4.88	-2.83	.557E+10	.866E+09	0.	0.	.871E-09	-1.00	2.00	
5	5	-4.20	-2.83	.404E+10	.842E+09	0.	0.	.871E-09	-1.00	2.00	
6	6	-3.35	-2.83	.268E+10	.862E+09	0.	0.	.871E-09	-1.00	2.00	
7	7	-2.53	-2.83	.180E+10	.998E+09	.108E-09	.108E-09	.871E-09	-1.00	2.00	
8	8	-1.88	-2.83	.148E+10	.147E+10	.324E-09	.433E-09	.763E-09	-.876	2.00	
9	9	-1.42	-2.83	.169E+10	.295E+10	.133E-09	.738E-09	.438E-09	-.503	2.00	
10	10	-1.11	-2.83	.272E+10	.801E+10	.160E-09	.898E-09	.133E-09	-.153	2.00	
TIME	SUMR	TRANS	DIFF	DIF	POTCR	COUNT					
.130E+07	.898E-09	.871E-09	-.272E-10	.312E-01	-2.83	2.00					
1	1	-5.46	-2.82	.158E+11	.194E+10	0.	0.	.871E-09	-1.00	3.00	
2	2	-5.44	-2.82	.848E+10	.105E+10	0.	0.	.871E-09	-1.00	3.00	
3	3	-5.29	-2.82	.677E+10	.895E+09	0.	0.	.871E-09	-1.00	3.00	
4	4	-4.88	-2.82	.557E+10	.866E+09	0.	0.	.871E-09	-1.00	3.00	
5	5	-4.20	-2.82	.404E+10	.842E+09	0.	0.	.871E-09	-1.00	3.00	
6	6	-3.35	-2.82	.268E+10	.862E+09	0.	0.	.871E-09	-1.00	3.00	
7	7	-2.53	-2.82	.180E+10	.998E+09	.105E-09	.105E-09	.766E-09	-.879	3.00	
8	8	-1.88	-2.82	.148E+10	.147E+10	.321E-09	.427E-09	.444E-09	-.510	3.00	
9	9	-1.42	-2.82	.169E+10	.295E+10	.141E-09	.730E-09	.141E-09	-.162	3.00	
10	10	-1.11	-2.82	.272E+10	.801E+10	.160E-09	.889E-09	-.183E-10	.210E-01	3.00	
TIME	SUMR	TRANS	DIFF	DIF	POTCR	COUNT					
.130E+07	.889E-09	.871E-09	-.183E-10	.210E-01	-2.82	3.00					

TIME	CLOCK	HOURC	SUMR	TRANS	DIF	POTCR	SOLCHO	CUMREM
.1303E+07	2.000	362.0	.8792E-09	.8709E-09	.9537E-02	-2.814	.1934E-01	.2272E-01
TIME	CLOCK	HOURC	SUMR	TRANS	DIF	POTCR	SOLCHO	CUMREM
.1307E+07	3.000	363.0	.8803E-09	.8721E-09	.9336E-02	-2.783	.1859E-01	.2272E-01
.1318E+07	6.000	366.0	.8839E-09	.8756E-09	.8286E-02	-2.699	.1639E-01	.2273E-01
.1328E+07	9.000	369.0	.8846E-07	.6525E-07	-.9340E-02	-34.07	.2060E-01	.2304E-01
.1339E+07	12.00	372.0	.7232E-07	.7299E-07	-.9138E-02	-40.60	.2651E-01	.2379E-01
.1350E+07	15.00	375.0	.5504E-07	.5453E-07	.9302E-02	-34.27	.2972E-01	.2453E-01
.1361E+07	18.00	378.0	.2461E-07	.7832E-09	31.24	-2.000	.2738E-01	.2477E-01
.1372E+07	21.00	381.0	.9027E-09	.8947E-09	.8966E-02	-3.168	.2328E-01	.2507E-01
.1382E+07	0.	384.0	.9059E-09	.8996E-09	.7012E-02	-3.019	.2031E-01	.2508E-01
.1393E+07	3.000	387.0	.9123E-09	.9033E-09	.9925E-02	-2.900	.1797E-01	.2509E-01
.1404E+07	6.000	390.0	.9145E-09	.9065E-09	.8817E-02	-2.797	.1583E-01	.2510E-01
.1415E+07	9.000	393.0	.7248E-07	.7316E-07	-.9302E-02	-38.11	.2000E-01	.2546E-01
.1426E+07	12.00	396.0	.7865E-07	.7938E-07	-.9300E-02	-44.83	.2543E-01	.2639E-01
.1436E+07	15.00	399.0	.6024E-07	.5969E-07	.9223E-02	-38.48	.2823E-01	.2709E-01
.1447E+07	18.00	402.0	.2755E-07	.7592E-09	35.55	-2.000	.2608E-01	.2757E-01
.1458E+07	21.00	405.0	.9259E-09	.9210E-09	.9633E-02	-3.298	.2213E-01	.2768E-01
.1469E+07	0.	408.0	.9328E-09	.9254E-09	.8049E-02	-3.137	.1928E-01	.2769E-01
.1480E+07	3.000	411.0	.9377E-09	.9287E-09	.9692E-02	-3.013	.1703E-01	.2770E-01
.1490E+07	6.000	414.0	.9396E-09	.9315E-09	.8689E-02	-2.906	.1498E-01	.2771E-01
.1501E+07	9.000	417.0	.5903E-07	.5959E-07	-.9318E-02	-32.25	.1986E-01	.2799E-01
.1512E+07	12.00	420.0	.6701E-07	.6768E-07	-.9933E-02	-38.45	.2683E-01	.2868E-01
.1523E+07	15.00	423.0	.5086E-07	.5040E-07	.9518E-02	-32.27	.3082E-01	.2937E-01
.1534E+07	18.00	426.0	.2241E-07	.8201E-09	26.32	-2.000	.2850E-01	.2977E-01
.1545E+07	21.00	429.0	.9554E-09	.9467E-09	.9124E-02	-3.208	.2420E-01	.2986E-01
.1555E+07	0.	432.0	.9580E-09	.9510E-09	.7265E-02	-3.053	.2108E-01	.2987E-01
.1566E+07	3.000	435.0	.9631E-09	.9543E-09	.9237E-02	-2.931	.1863E-01	.2988E-01
.1577E+07	6.000	438.0	.9649E-09	.9570E-09	.8192E-02	-2.825	.1639E-01	.2989E-01
.1588E+07	9.000	441.0	.6385E-07	.6445E-07	-.9252E-02	-33.07	.2120E-01	.3019E-01
.1598E+07	12.00	444.0	.7180E-07	.7245E-07	-.9037E-02	-39.49	.2803E-01	.3094E-01
.1609E+07	15.00	447.0	.5432E-07	.5381E-07	.9381E-02	-33.35	.3182E-01	.3167E-01
.1620E+07	18.00	450.0	.2407E-07	.8329E-09	27.89	-2.000	.2934E-01	.3210E-01
.1631E+07	21.00	453.0	.9782E-09	.9697E-09	.8811E-02	-3.220	.2490E-01	.3220E-01
.1642E+07	0.	456.0	.9835E-09	.9738E-09	.9964E-02	-3.056	.2168E-01	.3221E-01
.1652E+07	3.000	459.0	.9858E-09	.9769E-09	.9114E-02	-2.921	.1916E-01	.3222E-01
.1663E+07	6.000	462.0	.9874E-09	.9795E-09	.8064E-02	-2.807	.1684E-01	.3223E-01
.1674E+07	9.000	465.0	.4227E-07	.4276E-07	-.9423E-02	-22.31	.2243E-01	.3241E-01
.1685E+07	12.00	468.0	.5224E-07	.5273E-07	-.9235E-02	-27.63	.3172E-01	.3293E-01
.1696E+07	15.00	471.0	.3880E-07	.3846E-07	.8950E-02	-22.46	.3728E-01	.3346E-01
.1706E+07	18.00	474.0	.1595E-07	.9143E-09	16.44	-2.000	.3443E-01	.3376E-01
.1717E+07	21.00	477.0	.1002E-08	.9850E-09	.7158E-02	-2.951	.2921E-01	.3383E-01
.1728E+07	0.	480.0	.1008E-08	.9869E-09	.8612E-02	-2.821	.2547E-01	.3384E-01

TIME
.173E+07ROOT LENGTH, M/SO.M. BY LAYER
204. 270. 306. 305. 275. 207. 122. 56.2

91.8 204. 270. 306. 305. 275. 207. 122. 56.2

.804E-13 .286E-04 .637E-04 .843E-04 .921E-04 .958E-04 .955E-04 .864E-04 .651E-04 .384E-04

ROOT GROWTH RATE

-7.37 -7.31 -7.08 -6.51 -5.56 -4.39 -3.18 -2.17 -1.46 -.994

MATIC POTENTIALS

.125E-06 .277E-06 .367E-06 .400E-06 .416E-06 .414E-06 .374E-06 .281E-06 .166E-06 .763E-07

ROOT DEATH RATE

-.125E-06 .284E-04 .633E-04 .839E-04 .917E-04 .954E-04 .951E-04 .861E-04 .649E-04 .383E-04

NET GROWTH

TIME IS : 480.0 HOURS		20.0 DAYS		RUN = 480.		CUMULATIVE ROOT EXTRACTION.	METERS VS. DEPTH
IFUN = 3							
.0125	1						.17107E-02
.0375	1						.23934E-02
.0625	1						.29481E-02
.0875	1						.33028E-02
.1125	1						.40392E-02
.1375	1						.47882E-02
.1625	1						.50127E-02
.1875	1						.41327E-02
.2125	1						.21847E-02
.2375	1						.10323E-02

TIME IS : 480.0 HOURS		20.0 DAYS	TOTAL WATER POTENTIAL AS A	FUNCTION OF DEPTH
IFUN = 4		RUN =	480.	
.0125	1			.73780E+01
.0375	1			.73463E+01
.0625	1			.71452E+01
.0875	1			.65937E+01
.1125	1			.56725E+01
.1375	1			.45248E+01
.1625	1			.33423E+01
.1875	1			.23587E+01
.2125	1			.16714E+01
.2375	1			.12315E+01

TIME IS :	480.0 HOURS	20.0 DAYS	VERTICAL WATER FLUX RATE,	POSITIVE DOWN
IFUN =	5	RUN =	480.	
.0125	1			.0000E+00
.0375	1			-.4961E-10
.0625	1			-.3261E-09
.0875	1			-.1002E-08
.1125	1			-.2123E-08
.1375	1			-.3870E-08
.1625	1			-.6797E-08
.1875	1			-.1076E-07
.2125	1			-.1481E-07
.2375	1			-.1816E-07

PARTIAL ROOT LENGTH, METERS/SQ. METER IN EACH LAYER

TIME IS :	480.0 HOURS	20.0 DAYS	RUN =	480.						
IFUN =	6									
	.0125	1		.36714E+04						
	.0375	1		.81605E+04						
	.0625	1		.10803E+05						
	.0875	1		.11786E+05						
	.1125	1		.12245E+05						
	.1375	1		.12183E+05						
	.1625	1		.11004E+05						
	.1875	1		.82851E+04						
	.2125	1		.48859E+04						
	.2375	1		.22476E+04						
480.	-7.38	-7.15	-6.59	-5.67	-4.52	-3.34	-2.36	-1.67	-1.23	
480.	.496E-10	.276E-09	.676E-09	.112E-08	.175E-08	.292E-08	.397E-08	.385E-08	.315E-08	.206E-08
.173E+07	O.	-8.14	-2.82	.255E-01	.281	.397E-01	.322E-01	O.	O.	
480.	.220E-06	.925E-07	.116E-08	.886E+10	.659E+09	.418E-10	.929E-07	.650E-03	.289E-05	
480.	O.	17.2								

GLOSSARY OF MODEL VARIABLES

NAME	DESCRIPTION	UNIT
A(3,3)	Matrices derived by Richardson(1981)+ to describe the interaction between daily maximum and minimum temperatures and solar radiations in the continental U.S.	
AA	Coefficient for sigmoid root generation curve	
ABS	Absolute value FORTRAN function	
AFGEN	Table function generator subroutine	
AGFAC	Aging factor parameter controlling leaf aging	
AGING	Relative aging factor modifying shoot death rate	d d ⁻¹
ALOG	Natural log FORTRAN function	
AMAX1	Maximum FORTRAN library function for real numbers	
AMIN1	Minimum FORTRAN library function for real numbers	
AMOD	Modulo FORTRAN function for real numbers	
AR	Amplitude of annual curves of daily solar radiation	Ly d ⁻¹ *
ARS	Axial (xylem) resistance to water flow through roots	s
ATN	Amplitude of annual curves of daily minimum temp.	oF
ATX	Amplitude of annual curves of daily maximum temp.	oF
AVCOND	Average conductivity between two soil compartments	m s ⁻¹
AVPET	Average potential evapotranspiration measured daily	
B(3,3)	The same as A(3,3)	
BB	Coefficient for sigmoid root generation curve	
BD	Soil bulk density	Mg m ⁻³
BGNDAY	Julian day at the beginning of the simulation run	
BIRTH	Root birth rate (formation within the same layer)	m s ⁻¹
BR	Birth rate parameter	
BRMIN	Minimum soil water potential for root birth	m
CAPRIS	Cumulative capillary rise (past the 8th soil layer)	m
CC	Coefficient of mechanical impedance function	
CEVAP	Cumulative evaporation from soil surface	m
CF	Correction factor for iteration loop	
CLOCK	Clock time	
COND	Soil hydraulic conductivity	m s ⁻¹
CONVRT	Relative growth efficiency (kg respired/kg biomass)	kg kg ⁻¹
COS	FORTRAN function for cosine	
COUNT	Counter for the leaf water potential iteration loop	
CRMI	Critical mechanical impedance	m
CRTEX	Cumulative root extraction	m
CRTMRS	Cumulative root maintenance respiration	kg m ⁻²
CSTMRS	Cumulative shoot maintenance respiration	kg m ⁻²
CUMPET	Cumulative potential evapotranspiration	
CUMREM	Cumulative root water removal from all soil layers	m

CUMTRN	Cumulative transpiration	m
DATA	FORTTRAN system data input	
DAY	Cumulative days of simulation time	d
DD	The same as CC	
DELAY	Delay time (half time for computing POTCRD)	s
DELT	Integration time step	s
DEPTH	Depth to midpoint of soil layers, from soil surface	m
DIF	Difference between total root extraction and transpiration	m s^{-1}
DIFF	Relative difference between total root extraction and transpiration	
DIST	Distance of flow between two adjacent soil layers	m
DR	Leaf abaxial diffusive resistance	s m^{-1}
DR	Function to adjust AR for julian day in SOLSIM	
DRAIN	Cumulative internal drainage (past the 8th soil layer)	m
DRAING	Instantaneous drainage rate (past bottom of 8th layer)	m s^{-1}
DT	Function to adjust ATX, ATN for julian day in SOLSIM	
DTBL	Table of shoot death versus leaf area index	
DTHBGN	Relative shoot death rate	$\text{kg kg}^{-1} \text{s}^{-1}$
DTHFAC	Relative root death rate	$\text{kg kg}^{-1} \text{s}^{-1}$
DTRDEM	Minimum value of daily transpiration demand	m d^{-1}
ERROR	Maximum allowable error in iteration loop	
EVAP	Evaporation from soil surface	m s^{-1}
EXP	FORTTRAN function for exponentiation	
EXTENS	Extension rate for root growth into the next soil layer	m s^{-1}
EXTMIN	Minimum soil water potential for root extension into the next soil layer	m
EXTNRT	Extension rate parameter for root growth into the next soil layer	
FA	Soil air filled porosity	$\text{m}^3 \text{m}^{-3}$
FINTIM	Total duration of simulation run	s
FLPFLP	Flipflop control statement for iteration loop	
FLW	Water flux density past the bottom of each soil layer	m s^{-1}
FLOW8N	Capillary rise past the 8th layer(negative upward)	m s^{-1}
FLOW8P	Internal drainage past the 8th layer(negative upward)	m s^{-1}
FRAC	Fraction of carbohydrates remaining in the shoot	kg kg^{-1}
FRACTB	Table function for carbohydrate partitioning based upon canopy water potential	
GEN3	Temperature generating function	
GROFAC	Relative consumption rate of carbohydrate reserves	$\text{kg kg}^{-1} \text{s}^{-1}$
GROWTH	Total plant growth (root and shoot)	$\text{kg m}^{-2} \text{s}^{-1}$
HOURC	hours of simulation time	h
I	Index of soil layer (integer number)	
IB	Vertical axis for graphic output of soil profile	
ICHO	Initial mass of carbohydrates	kg m^{-2}
IFLAG	Flag set	
IFUN	Flag controlling the vertical gradient plots	
IL	Scale for vertical gradient plotting	

IPER	Initial percentage of soluble carbohydrates	
IPOTM	Initial soil matric potential head	m
IYEAR	Calendar year	
IPRTL	Initial partial root length(length per each layer)	m m ⁻²
IROOT	Initial root mass per unit land area	kg m ⁻²
IRTL	Initial total root length per unit land area	m m ⁻²
ISHOOT	Initial shoot mass per unit land area	kg m ⁻²
ITHETA	Initial volumetric water content of the soil	m ³ m ⁻³
IVOLW	Initial volume of water in each layer	m ³ m ⁻²
IX	Index for vertical plotting	
J	Index of soil layers (integer number)	
JD	Integer value of JDAY	
JDAY	Julian day	
K	Horizontal index of soil layer for vertical plotting	
LAI	Leaf area index (leaf area per unit land area)	m ² m ⁻²
LAIFAC	Leaf area index factor for partitioning water loss between plant and soil	
LAITBL	Table function relating LAI and water loss between plant and soil	
LEAFTH	Leaf thickness (leaf area per unit shoot mass)	m ² kg ⁻¹
LINE	Vertical plotting variable	
LOCALE	Location #, a flag to read new data for new location	
LNGFAC	Length factor of the roots (length per unit mass)	m kg ⁻¹
MAXFOT	Maximum photosynthetic rate	kg m ⁻² s ⁻¹
MAXPOT	Maximum canopy water potential allowed	m
MAXRAD	Maximum light flux density (for one day)	W m ⁻²
MI	Mechanical impedance in each soil layer	m
MIFAC	Mechanical impedance factor	
MIDIF	Difference between instantaneous MI and critical MI	m
MNMIFC	Minimum value of MIFAC	
MOD	Integer remainder FORTRAN function	
MPANEV	Measured daily pan evaporation	m s ⁻¹
MPOT	Matric potential of the soil in each layer	cm
MSDPEV	Measured daily pan evaporation	inch d ⁻¹
NETGRO	Net change in root length per layer(growth-death)	m s ⁻¹
NFLW	Net water flow into each soil layer (Darcian only)	m s ⁻¹
NJ	Total number of layers comprising the soil profile	
NJJ	NJ + 1	
NITTTL	Total number of iterations	
NIPIL	Number of iterations per inner loop	
NIPOL	Number of iterations per outer loop	
OUTF	Time interval for outputting vertical gradient plots	s
PCP	Measured daily precipitation values	inch ₁
PET	Potential evapotranspiration	m s ⁻¹
PHOTSN	Photosynthetic rate (net carbon fixation)	kg m ⁻² s ⁻¹
PHTCAR	Photosynthetic carbon conversion factor	
PI	Circumference of a circle divided by its diameter	

POCR	Water potential of plant	m
POTCRD	Delayed plant water potential, allowing time for growth recovery after stress	m
POTCRE	Effective plant water potential, stopping instantly but recovering slowly	m
POTH	Hydraulic potential head in each soil layer	m
POTM	Matric potential of the soil in each layer	m
POTRT	Water potential of the roots	m
PRDEL	Time interval for outputting results	s
PRTL	Partial root length	m m ⁻²
PTOTL	Total soil water potential (grav. + osm. + matric)	m
RADN	Radiation intensity	W m ⁻²
RANGE	Range between average and minimum or maximum temp.	oC
REFT	Reference or average temperature	oC
RESL	Reserve level of carbohydrates in the plant	
RESP	Total respiration of both root and shoot system	kg m ⁻² s ⁻¹
RESPRT	Total root respiration	kg m ⁻² s ⁻¹
RESPSH	Total shoot respiration	kg m ⁻² s ⁻¹
ROOTDY	Root death rate	kg m ⁻² s ⁻¹
ROOTW	Total mass of living roots	kg m ⁻²
RM(N)	Mean annual daily solar radiation for dry(N=1) and wet (N=2) days	Ly d ⁻¹
RRL	Relative root length per layer	m m ⁻²
RRS	Radial resistance to root water uptake (tissue permeability)	s
RSPFAC	Relative shoot maintenance respiration rate	kg kg ⁻¹ s ⁻¹
RSRT	Root system resistance to water flow, total per layer	s
RSSL	Soil resistance to water flow, total per layer	s
RTDTH	Root death rate per layer	m s ⁻¹
RTEX	Root water extraction rate from each layer	m s ⁻¹
RTGRES	Root growth respiration rate	kg m ⁻² s ⁻¹
RTGRO	Root growth rate per soil layer	m s ⁻¹
RTMRES	Root maintenance respiration rate	kg m ⁻² s ⁻¹
RUN	Real number counting number of passes through update	
RUNS	Integer number of "RUN"	
SATCON	Saturated conductivity of soil	m s ⁻¹
SCALE	Scale factor for vertical gradient plots	
SHGRES	Shoot growth respiration rate	kg m ⁻² s ⁻¹
SHMRES	Shoot maintenance respiration rate	kg m ⁻² s ⁻¹
SHOOTD	Shoot death rate	kg m ⁻² s ⁻¹
SHOOTW	Mass of living shoot tissues	kg m ⁻²
SIN	FORTTRAN function for sine	
SLEVAP	Soil evaporation rate	m s ⁻¹
SMAX	Maximum scale factor for vertical gradient plots	
SMIN	Minimum scale factor for vertical gradient plots	
SOLI	Solar radiation intensity	Ly d ⁻¹
SOLCHO	Soluble carbohydrate reserves(Starch) in plant	kg m ⁻²
SOLSIM	Solar radiation simulator subroutine	
SRBAR	Solar radiation mean for a given julian day (see eqns. 4a or 4b of Richardson, 1981)	Ly d ⁻¹
SRL1	Lag 1 serial correlation coeff. for solar radiation (see eqn. 5 of Richardson, 1981)	

SRSD1	Standard deviation of daily solar radiations (see eqns. 4a or 4b of Richardson, 1981)	Ly d^{-1}
STEMP	Temperature of the soil	$^{\circ}\text{C}$
SUMR	Sum of water removal by roots in all layers	m
SUMRD	Estimated root death rate for the whole plant	$\text{m m}^{-2} \text{ s}^{-1}$
SUMRG	Estimated root growth rate for the whole plant	$\text{m m}^{-2} \text{ s}^{-1}$
TCOM	Thickness of a soil layer	m
TEMP	Temperature	$^{\circ}\text{C}$
THETA	Volumetric water content of each soil layer	$\text{m}^3 \text{ m}^{-3}$
THETST	Saturated volumetric water content	$\text{m}^3 \text{ m}^{-3}$
TMAX	Maximum daily temperature	$^{\circ}\text{C}$
TMIN	Minimum daily temperature	$^{\circ}\text{C}$
TMPFCR	Temperature factor for roots, biological Q10-value	
TMPFCS	Temperature factor for shoot, biological Q10-value	
TN	Minimum daily temperature	$^{\circ}\text{F}$
TNBAR	Mean minimum temperature for a given julian day (see eqns. 4a or 4b of Richardson, 1981)	$^{\circ}\text{F}$
TNL1	Residual series of daily minimum temperature (see eqns. 4a or 4b of Richardson, 1981)	$^{\circ}\text{F}$
TNM	Mean annual daily minimum temperature	$^{\circ}\text{F}$
TX	Maximum daily temperature	$^{\circ}\text{F}$
TXBAR	Mean maximum temperature for a given julian day (see eqns. 4a or 4b of Richardson, 1981)	$^{\circ}\text{F}$
TXL1	Residual series of daily maximum temperature (see eqns. 4a or 4b of Richardson, 1981)	$^{\circ}\text{F}$
TXM(N)	Mean annual daily maximum temperature for dry (N=1) and wet (N=2) days	$^{\circ}\text{F}$
TOPGRO	Total growth rate of the shoot system	$\text{kg m}^{-2} \text{ s}^{-1}$
TOTRG	Total growth rate of the root system	$\text{kg m}^{-2} \text{ s}^{-1}$
TRANSP	Transpiration rate	m s^{-1}
TRNTBL		
UARS	Unit axial resistance (along the xylem)	s
URRS	Unit radial resistance per unit root surface	$\text{s} . \text{m}$
VOLW	Volume of water in each soil compartment	$\text{m}^3 \text{ m}^{-2}$
W	Water potential difference for extension of new roots into second soil compartment	m
WATRST	Water stress factor for plant tissue	
X	Water potential difference for new roots branching	m
XX	Water potential difference for new roots extension	m
Y	Index for vertical gradient plotting	
YY	Index for vertical gradient plotting	

+ Richardson, C.W., 1981. Stochastic simulation of daily precipitation, temperature, and solar radiation. Water Reso. Res. 17:182-190.

* For 12 hours daylight, 1 Langley/day $\approx$ 1 W/m^2

A P P E N D I X I I

OTHER DATA

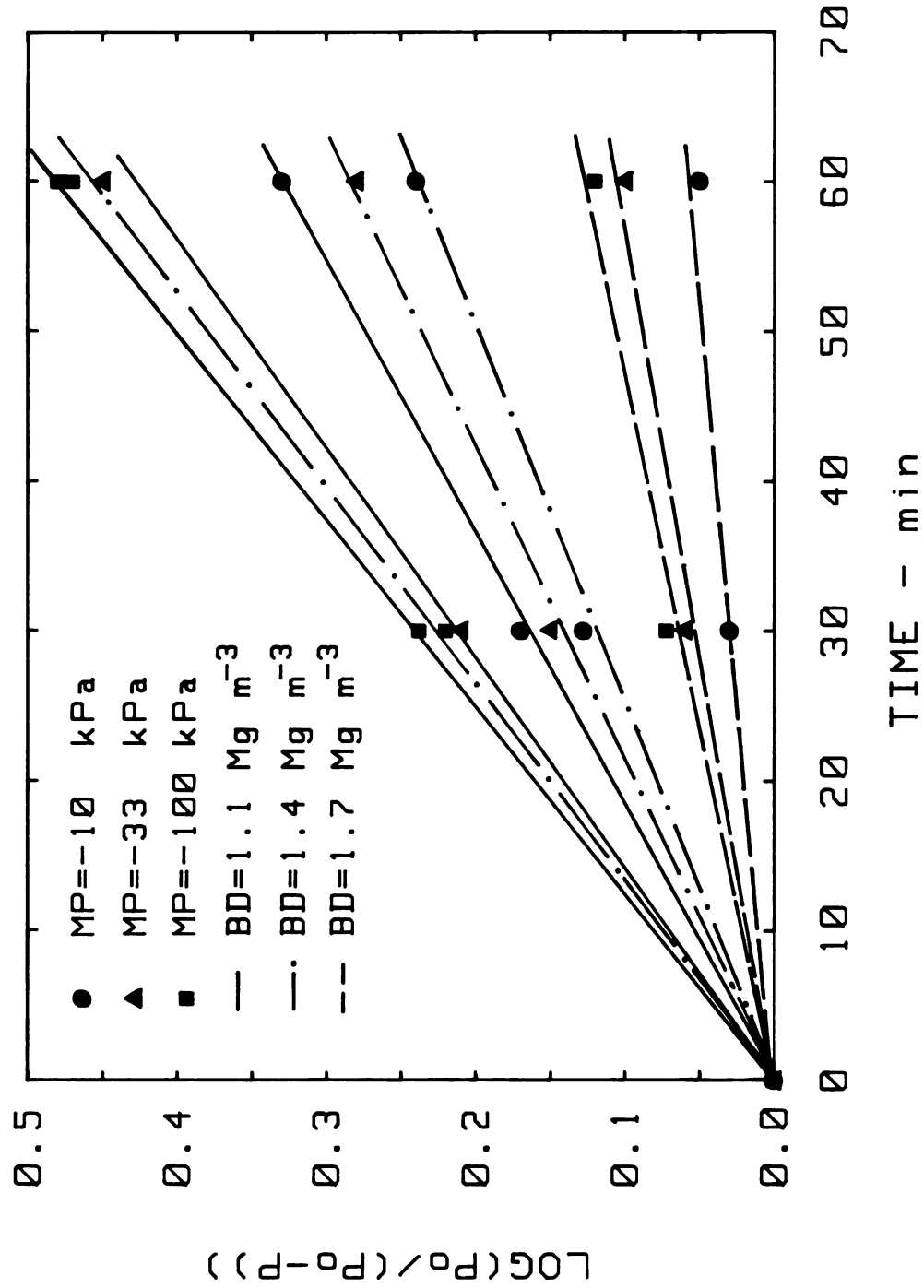


Figure 1. Changes in partial pressure of O_2 inside a diffusion chamber in which diffusion pathway is either free air or soil porosity. The chamber is filled with N_2 at time zero. P and P_0 are O_2 partial pressures when diffusion pathway is the soil or free air, respectively. Soil is Charity clay at three different bulk densities (BD), and at three different matric potentials (MP).

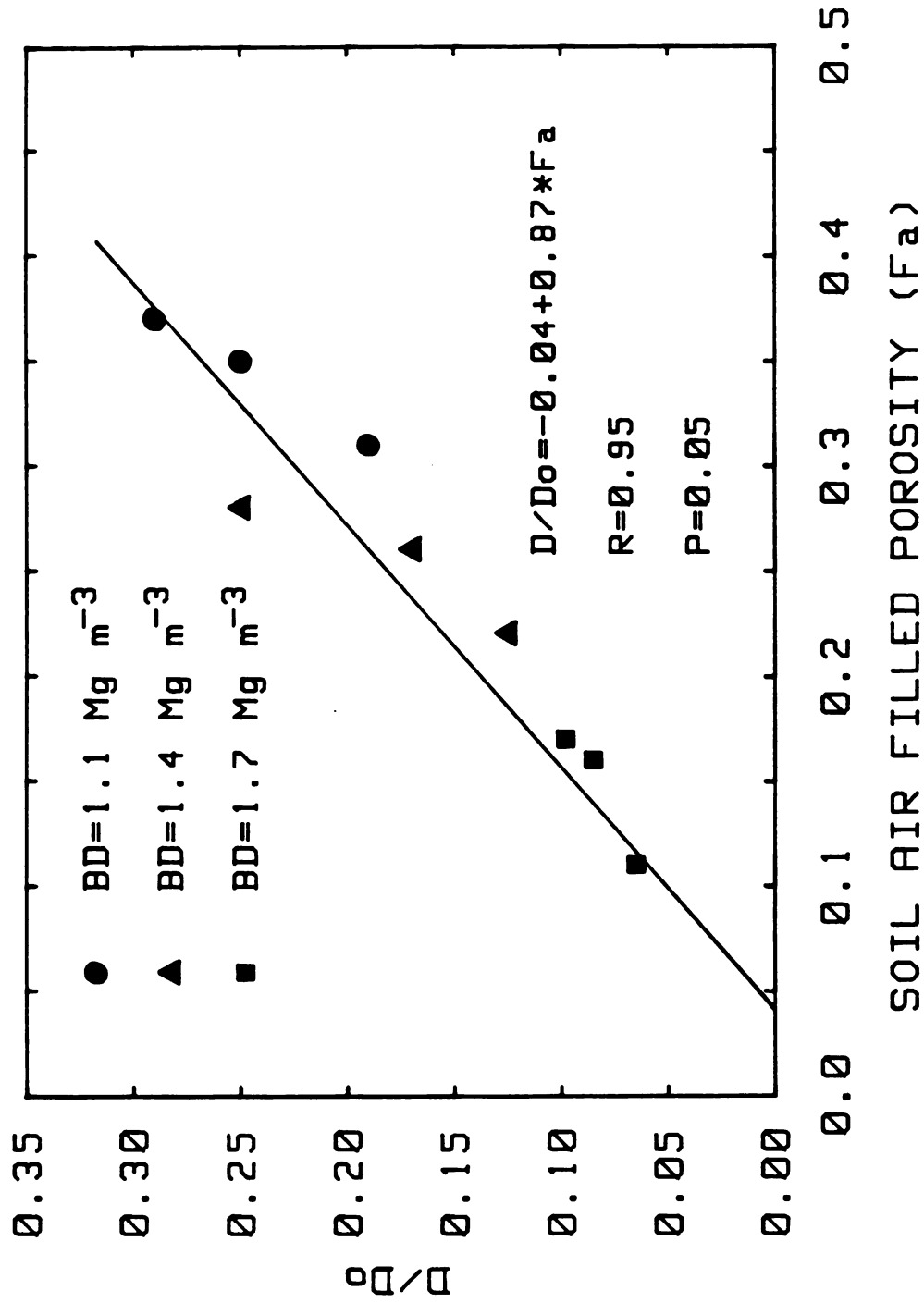


Figure 2. Diffusion impedance of Charity clay soil as a function of soil air filled porosity. D is diffusion coefficient of O_2 in the soil, D_0 is diffusion coefficient of O_2 in the air, and BD is the soil bulk density.

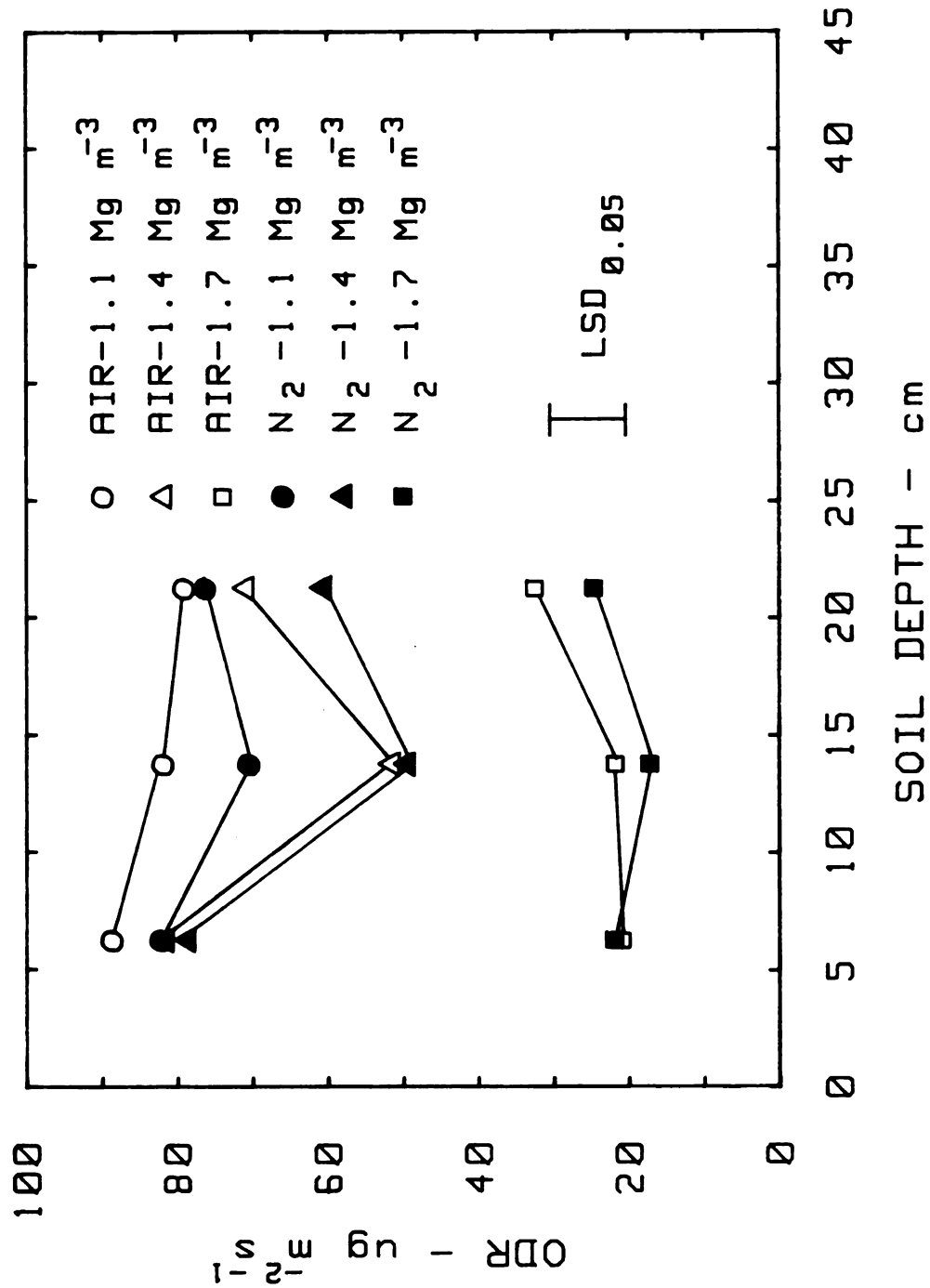


Figure 3. Spatial variations of oxygen diffusion rate in a Charity clay soil in the presence of growing roots, at 10 days after planting.

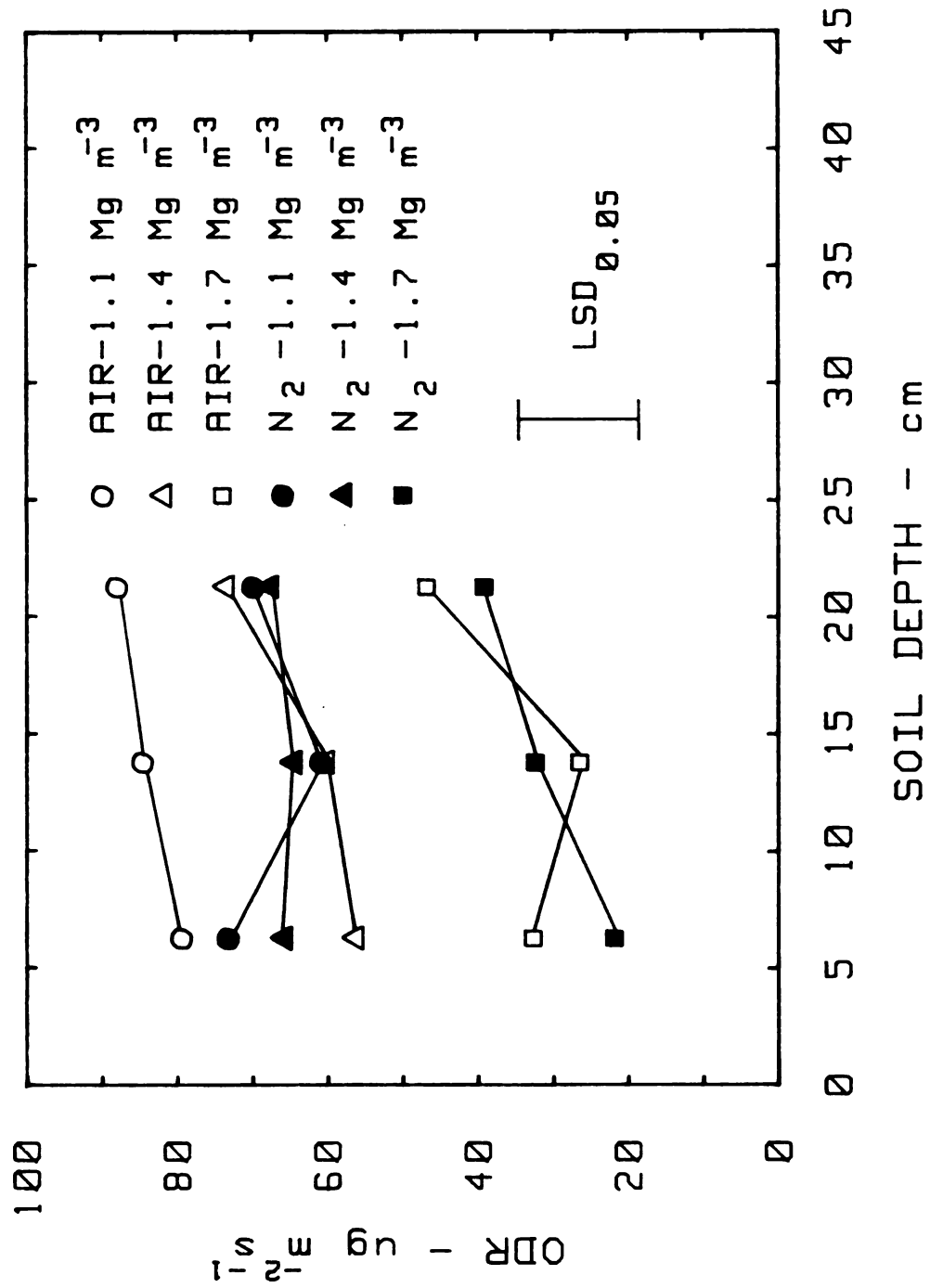


Figure 4. Spatial variations of oxygen diffusion rate in a Charity clay soil in the presence of growing roots, at 20 days after planting.

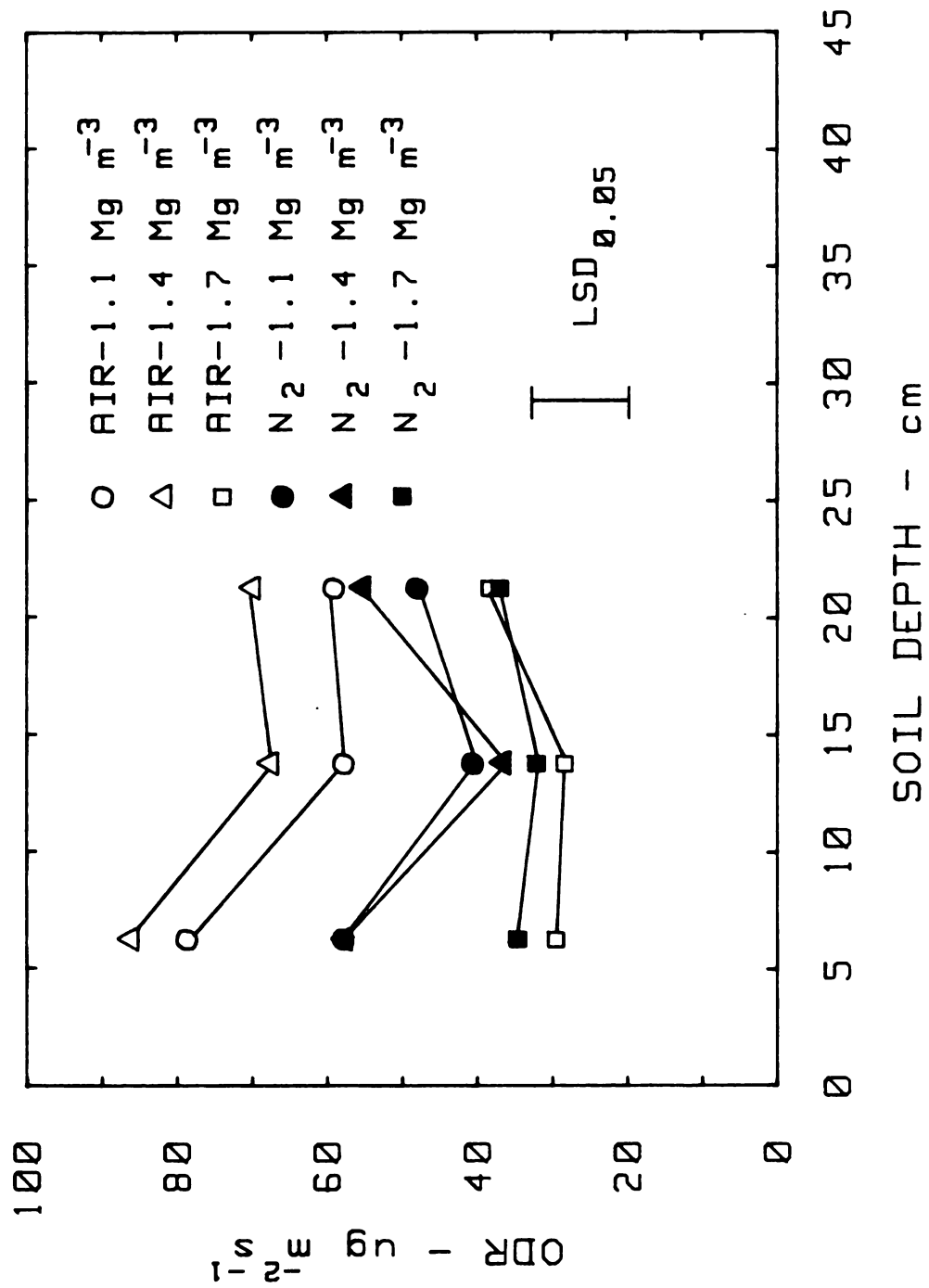


Figure 5. Spatial variations of oxygen diffusion rate in a Charity clay soil in the presence of growing roots, at 30 days after planting.

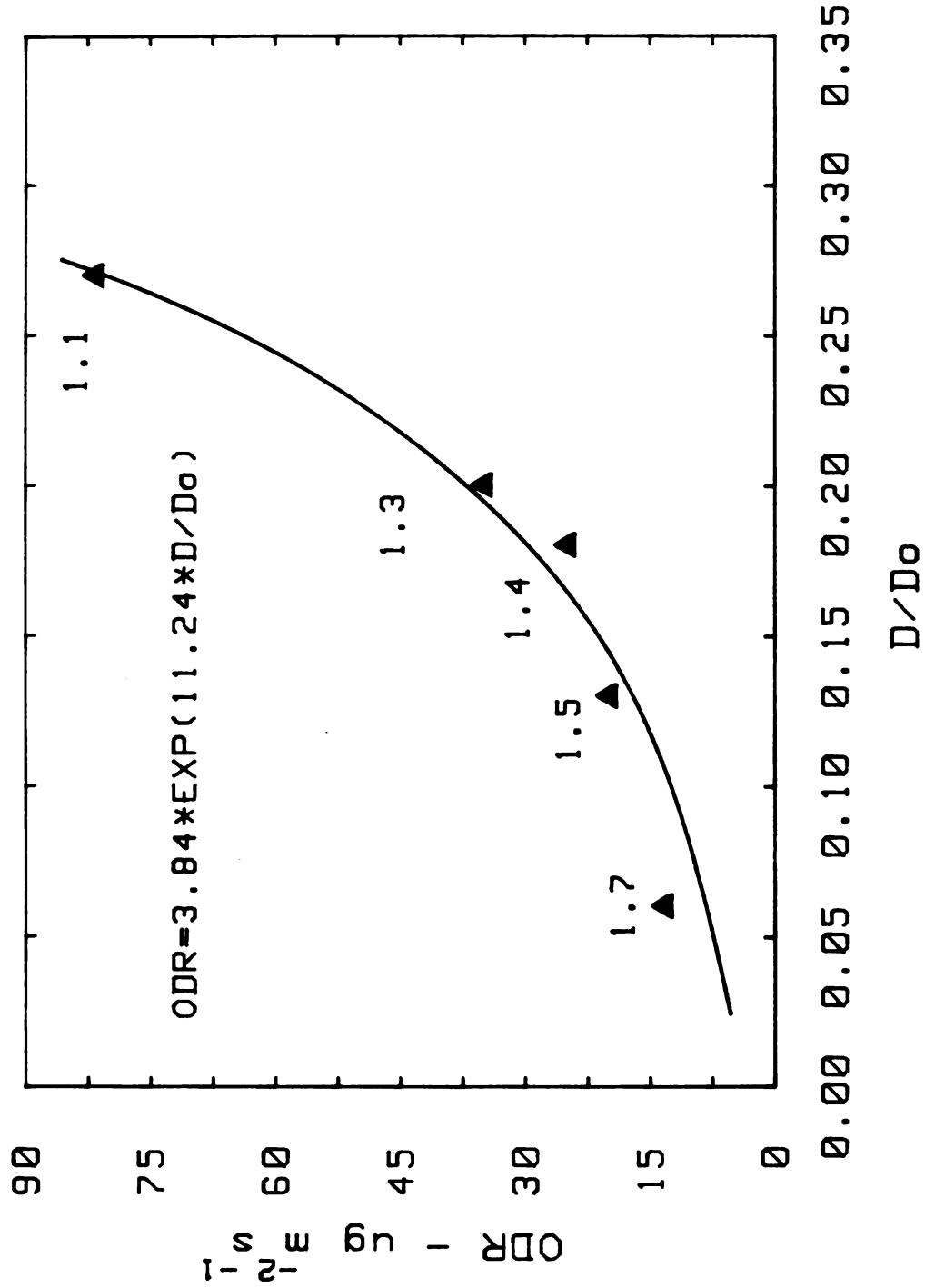


Figure 6. Relationship between oxygen diffusion rate, D/D_o , and soil bulk density in a Charity clay soil. 1.1 to 1.7 are soil bulk densities in Mg m^{-3} . The soil was at -6 kPa matric potential at equilibrium.

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