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Growth, carbon partitioning, water and ion uptake by the root systems of phaseolus seedlings subjected to soil mechanical impedance and water deficit stresses.

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GROWTH, CARBON PARTITIONING, WATER AND ION UPTAKE BY THE ROOT SYSTEMS OF PHASEOLUS SEEDLINGS SUBJECTED TO SOIL MECHANICAL IMPEDANCE AND WATER DEFICIT STRESSES

By BIHU HUANG

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ABSTRACT

GROWTH, CARBON PARTITIONING, WATER AND ION UPTAKE BY THE ROOT SYSTEMS OF PHASEOLUS SEEDLINGS SUBJECTED TO SOIL MECHANICAL IMPEDANCE AND WATER DEFICIT STRESSES

By

Bihu Huang

Soil mechanical impedance and water deficit are known to affect root growth and decrease plant yield. Little is known about the interactive effects of soil compaction and water deficit on the growth of roots and numerous root activities associated with growth, such as the carbon requirements and uptake of water and ions by roots subjected to mechanical impedance and water deficit stresses. This study, using the soil core seedling test method described by Asady et al. (1985), was designed to determine the separate and combined effects of compaction and water deficit on the growth of dry edible bean (<u>Phaseolus vulgaris</u>, L. variety Seafarer) roots and their associated uptake of H_2O , N, P and K, as well as the translocation of the photoassimilates. Three bulk densities (1.1, 1.4 and 1.7 Mg m^{-3}) and two water treatments (control and water deficit) were established in two greenhouse experiments. Data collected 14 days after planting indicated that soil compaction and water deficit decreased root penetration ratios (RPR), root

lengths, and leaf areas. The efficiency of water absorption increased with greater bulk density and was decreased by water deficits. Consequently, less carbon was fixed and a greater proportion of transported carbon was lost by stressed roots. The absorption of N, P and K decreased with the thickening of roots in soils having greater bulk densities. As a result of these stresses, total biomass accumulation decreased by almost 50% below the nonstressed plants.

These data suggest that soil compaction and water stresses, which are applied at the seedling stage, greatly reduce the competition of plants and their growth may be retarded throughout the life of the plant.

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INTRODUCTION

Soil is the natural matrix for plant root growth and is the primary natural resource of agriculture. The basic functions of the soil are designed to produce green plants upon which human beings depend. Water and nutrients which are absorbed from soil by the plant roots are among several basic compounds for plant growth. Plant roots also provide mechanical support to the plant. Therefore, a good soil condition for plant growth should include adequate aeration, optimum temperature, mechanical support and enough water and nutrients.

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 process causes soil particles to be in closer contact with each other, decreasing pore diameters and reducing total soil porosity. These adverse physical conditions reduce soil water permeability and aeration, and increase soil evaporation.

The reduction of total porosity increases soil mechanical resistance which affects seed gemination, seedling growth and emergence, and root development. A compacted soil pan within the top 20 cm limits root development and reduces the nutrient absorption areas which reduces shoot growth and yields.

The absorption and utilization of water directly or indirectly affects every aspect of plant growth. Since water used by crop plants is absorbed

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through roots, the establishment and continued growth of an extensive, functioning root system is of primary importance to plant establishment, survival, and growth (Kramer et al. 1990). The movement of water into plants largely depends on root distribution in the soil, both radially and longitudinally. Hurd (1976) emphasized the importance of root depth, increased branching and root diameter as beneficial factors for improving plant tolerance to soil water stresses Moreover, water uptake by the root system is the primary factor for determining the water status of the shoot. Water deficits in leaves will delay the transfer of assimilates from the photosynthetic tissue into the conducting tissue. Along with cell elongation, photosynthesis, translocation of sugars, and growth have been implicated to be among the first processes to be affected by water stress (Wardlaw 1967).

Both soil compaction and soil water deficits are barriers to root growth. Plants with deeper and diffuse root systems appear to have greater potentials for absorbing water and nutrients because they increase the contact volume with soil thereby increasing their absorption areas for water and nutrients. In contrast, a small root system reduces the capacity for roots to achieve their maximum function. As the consequence of this, plant growth is reduced and yields will be lowered.

Many reports have summarized the effects of compaction and water deficit on plant growth. Little is known about the interactions between soil water and soil compaction. The main objectives of this study were:

- 1. To determine the effects of mechanical impedance and water stress on root morphology and growth.
- 2. To determine carbon fixation and distribution responses to mechanical and water deficit stresses.

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3. To correlate the absorption efficiencies of water and ions to soil mechanical and water deficit stresses.

CHAPTER 1

Literature Review

Of the two environments for the plant growth, the soil is more complicated than the atmosphere (Russell 1977). Between the two parts of the plant, the root and shoot, the root, which grows invisibly in the soil, seems more complex than the shoot. Any of the chemical, physical and biological stresses in the environment of the soil will inhibit root growth and plant productivity. Soil compaction and water deficit are two major adverse environmental conditions which reduce the growth and dynamics of root systems.

Soil Compaction

Soil compaction causes changes in the chemical, physical and biological conditions of the soil. Combinations of changes in those properties cause reductions in the yields of many crops. These reductions in yields were due to losses of root function (Cannell and Jackson, 1981), increased root disease (Burke et al, 1980; Allmaras et al, 1988) and excessive allocations of photoassimilated plant carbon to the root system of stressed plants (Smucker, 1984) as well as their interactive effects.

Roots and soil mechanical resistance

Soil mechanical impedance inhibits root elongation and penetration altering root morphology and causing the roots to become thicker and more branched. The processes involved in root elongation reflect cell division and elongation and the response of cells to their environments. Cells of the root are in mechanical equilibrium such that their internal and external mechanical stresses balance. Dexter (1987) fit root growth data into a model and found that root elongation rates decreased linearly with increasing mechanical stresses which were applied externally to the root. He also indicated that external mechanical stress results from the resistance to root elongation by the surrounding soil. Camp and Lund (1964) reported the effect of soil compaction on cotton root anatomy. They found that cells of roots grown in loose soil elongated longitudinally, whereas cells of roots grown in compacted soil failed to elongate and expanded radially, causing the roots to thicken. Prihar et al (1971) observed that, in the compacted soil, there is greater production of sclerified cells in the cortical and vascular tissues. They considered this to be a response to the external forces and this response to the deformation of the interior cells. More regular layers of cortical cells developed in the loose soil than in the uncultivated soil. This indicates that compaction hinders the multiplication of cortical cells.

Baligar et al (1975) studied the soybean root anatomy as influenced by soil bulk density. They increased bulk density from 1.65 Mg m⁻³ to 1.95 Mg m⁻³ and found that it altered root anatomy. In the high density soil layers a larger percentage of root volume was occupied by cell wall material, and the transverse sections of the roots had a wavy outline with ruptured epidermal cells. The vascular cylinder became more oval with a gradual increase in both casparian thickening in the endodermis and wall thickening in the xylem vessels.

Mechanical stress greatly limits root penetration. As soils are compacted, the particles become closer and the average pore diameter is reduced. When growing roots encounter soil pores which are smaller than their diameters, continuing extension is possible only if the roots are able to exert sufficient pressure to expand the soil pores or to reduce in diameter thus, passing through existing pores (Russell 1977). Wiersum (1957) proved that roots were not only unable to decrease their diameter to enter pores, but also usually increased their diameters when their elongation was restricted by external pressure. Soil that had a resistance to a metal penetrometer of 2-3 MPa would resist radial expansion of the root cavity with a pressure of 0.30-0.4 MPa. For bean roots, this condition was found to cause a 75% reduction in the rate of root elongation (Taylor and Burnett 1964, Mazurak and Pohlman 1968, Farrell and Greacen 1966, and Greacen et al 1968). Tackett and Pearson (1964) studied the interaction between soil compaction and soil oxygen content in cotton seedling root penetration into a sandy clay loam subsoil. They found that a high soil bulk density restricted root penetration regardless of the oxygen content. At low bulk densities root penetration was hampered at oxygen concentrations of 5% or below, but penetration was still considerably higher than in the highly compacted samples with high soil oxygen content. Root penetration apparently was more limited by mechanical impedance than by poor aeration in the sand soil used in that study. Hopkins and Patrick (1969) also showed the same result that little or no penetration occurred at the highest compaction levels or at the lowest oxygen content.

Roots and soil aeration

Poor productivity of the crop stand, which was accompanied by more or less severely damaged root systems, in many cases, seems to be caused by poor aeration. Gill and Miller (1957) reported that normal root growth was adversely affected by reduction of the oxygen concentration of soil air to 10%. Where the roots were not subjected to a mechanical barrier, growth continued at concentrations as low as 1% of oxygen. Wiersma and Mortland (1963) showed that oxygen can be a limiting factor in the growth of sugarbeets which may be corrected by the use of calcium peroxide. According to Lemon and Erickson (1952) active root surfaces are covered with a water film and since oxygen diffusion is only slightly soluble in water, the oxygen diffusion rate in soil is the important factor and not the absolute percent of oxygen. Stolzy et al. (1961) reported that root growth was reduced at oxygen diffusion rates below 23×10^{-8} g cm⁻² min⁻¹.

Soil compaction usually reduces the volume of air-filled pores and the total porosity which reduces aeration and prohibits the diffusion of oxygen. Bertrand and Kohnke (1957) observed that oxygen diffusion was slower in dense than in loose subsoils and a high moisture content intensified the restricting effects. Restricted root growth by a dense subsoil was partly the result of the subsoil acting as a mechanical barrier and partly due to the lack of oxygen. Scott and Erickson (1964) conducted a greenhouse experiment to determine the effects of soil oxygen on root development when plants were grown with soil layers of bulk density 1.90 Mg m⁻³ at 4 inches below the surface. They found that fibrous roots branching from the tap root were greater in amount in the dense layer where calcium peroxide was used as a source of oxygen. Tomato and sugarbeet roots responded similarly to the peroxide in the dense layer. Schumacher and Smucker (1979) showed that oxygen uptake rate by dry bean roots were independent of solution flow rates > 6.0 mL min⁻¹ when inlet pO_2 of the nutrient solution was 0.21 atm. They also suggested that a greater oxygen supply may be required at the root surface to prevent anoxia when roots are mechanically impeded. Asady and Smucker (1989) showed that oxygen diffusion rates of the soil were below the critical level at a bulk density of 1.7 Mg m⁻³ during the vegetative growth stages of dry edible beans

Roots, temperature and disease

Soil temperature is one of the limiting factors for root growth. Stafford and McMichael (1989) reported that primary root length, number of laterals and lateral root length of guar were greatest at 30-35C. Branching intensity of was greatest at 35C. Primary root length was significantly correlated with number of laterals and lateral root length in all three seed sources which were used in their experiment. Since soil compaction causes changes in soil thermal conditions, the interaction effects of compaction and temperature is an important study objective. Burke (1965) and Burke and Nelson (1965) have shown that loose soil and temperatures favorable for rapid plant growth tend to counteract root rot diseases. Soil temperature lower than the optimum for plant growth aggravate root rot (Burke 1964, Burke 1965). Burke et al (1980) showed that bean roots penetrated compact (1.5 Mg m^{-3}) Fusarium- fumigated soil more readily when soil temperatures during the night and day were 21 and 27 C, respectively, than when they were 16 and 21 C. Root penetration of compacted soils was greater at a constant soil temperature of 21 than at 16 C, with plant tops exposed to either 21 or 27 C. Soil temperature affected root growth much less in loose (1.2 Mg m⁻³) soil than in compact (1.5 Mg m^{-3}) soil.

Soil compaction has also been reported to reduce yield by increasing the incidence of root diseases (Gray and Pope 1986). Field experiments were conducted for two years on a Drummer silty clay loam soil to determine if soybean (<u>Glycine max</u> (L.) Merr.) stand establishment and <u>Phytophthora</u> root rot incidence were influenced by soil compaction. They found that the number of plants killed by the fungus was significantly increased by soil compaction for "Corsoy" (susceptible to Phytophthora megasperma

Drechs.f.sp. glycinea, Kuan and Erwin) in both years. The yield of Corsoy was lowered significantly in the compacted plots. The yields of Corsoy and Corsoy 79 were also significantly different on the compacted plots. Fulton et al. (1961) reported the incidence of <u>Phytophthora</u> root rot of soybean increased in fine textured soils subjected to concentrated implement traffic. They demonstrated that under greenhouse conditions a high incidence of <u>Phytophthora</u> occurred when the infested soil was compacted. Burke, and Nelson (1965) and Miller and Burke (1974) reported that soil compaction increased the severity of <u>Fusarium</u> root rot of beans (<u>Phaseolus vulgaris</u> L.), caused by <u>Fusarium solani</u> (Mart.) Appel and Wr. f. sp phaseoli (Burk.) Snyd. and Hans.

Roots and nutrients

Russell et al. (1975) showed that when soil conditions were uniformly favorable for plant growth, root growth was sufficient to supply the mineral requirements of the plant, but when mechanical impedance interfered, root growth and shoot yield were decreased. On soils of low fertility, even a slight decrease in root growth adversely affected plant growth (Parish, 1971). Phillips and Kirkham (1962) found that increasing soil bulk density resulted in coarser corn (Zea mays, L.) roots and decreased P and K uptake. If roots fail to supply adequate nutrients and moisture to the plants, growth will be reduced, and eventually photosynthesis will decrease (Trouse, 1971). Hallmark and Barber (1981) reported that increasing soil bulk density reduced root growth, shoot growth, and nutrient composition of shoots but increased net nutrient influx. The detrimental effect of increasing soil bulk density on shoot growth and nutrient status of soybean plants may have been caused by decreased root growth, coarser roots , and lower root surface area per unit of shoot. Wiersum (1979) showed that shallow rooting can restrict the uptake of a number of mineral nutrients. Barraclough and Weir (1987) reported that early shoot growth and N content were substantially reduced by subsoil pans because of the inaccessibility of mineral N in the subsoil to the mechanically impedanced root system. Garcia et al (1988) reported that nitrogen placement had a greater impact on N uptake when compaction zones were present than when they were not present.

Soil compaction and photosynthesis

Compacted soil has been shown to reduce growth of many plant species (Zimmerman and Kardos, 1961; Rosenberg, 1964; Taylor and Bruce 1968; Trouse 1971). Akiyama and Kubo (1978) showed that photosynthesis of <u>Sasa nipponica</u> and <u>Zoysia japonica</u> decreased when they were grown in compacted soil and the decreases were greater in S. <u>nipponica</u>. Tu and Tan (1987) investigated the effect of soil compaction on photosynthesis and plant growth. They found that there was a highly significant reduction in root biomass, shoot growth and total leaf area of plants grown in compacted soil. Soil compaction also significantly reduced photosynthetic rate and increased root rot severity resulting in reduced growth.

Water Stress

Root growth and water availability

A good root system is important for drought resistance. Elkins et al. (1977) reported that rooting depth improved drought-tolerance for the sandy soils of Alabama. They found that if the roots of crops, such as cotton, corn or soybeans, are confined to the top 15 cm of the soil profile, then the crop will become water-stressed after only 3 days without rain. However, if the

roots can penetrate to 100 cm, then the crop will not become water stressed until after 20 days without rain. Roots which grow down through a seed-bed and encounter a strong, untilled subsoil beneath, may be unable to penetrate the subsoil and may be deflected horizontally. They will continue to grow horizontally along the top of the subsoil until either the seed-bed dries out and roots wilt and cease elongation, or until they find some path of low resistance down through the subsoil via a fissure or biopore. Kramer and Spomer (1990) reported that roots experiencing a single water deficit of short duration (0-20 min.) exhibited a nearly linear proportional response of growth rate (0 to 1.6 mm hr⁻¹) to tissue water potentials over the range from -1 to -10 MPa. Expansion ceased at -10MPa, defining this as the root's wilting point.

Water stress and disease

Ayres (1982) grew barley in soil columns which were inoculated with powdery mildew (<u>Erysiphe graminis</u> f.sp. hordei Marchal) when two leaves had fully expanded. Half the plants were not watered after inoculation so that they suffered water deficits at gradients of bulk soil water potential of between 0.6 and 1.8 MPa developed between the uppermost (0 to 12.5 cm deep) and lowest (37.5 to 50.0 cm deep) regions of the profile. He found that infection reduced the amount of ¹⁴C fixed in watered and drought stressed plants, but only in drought stressed plants did infection reduce the percentage of total assimilates that were translocated to roots. Water deficits stimulated root growth, particularly in healthy plants, making the differences in root growth greater between healthy and infected plants subjected to drought. Reductions in root growth caused by infection were most marked in the upper drier regions of the soil profile, while reductions in translocation were most marked in the middle regions. The reduction in shoot growth caused by infection was similar in watered and drought stressed plants. The percentage of total assimilates that were translocated out of healthy third leaves was not affected by infection of the 2 lower leaves, but was reduced by water deficit. Infection increased translocation into first and second leaves at the expense of the remainder of the shoot, especially in droughted stressed plants.

Plant growth and photosynthesis

Low soil moisture increases internal plant water deficits and detrimentally influences growth and yield through a number of physiological processes, including carbon exchange rate and translocation of assimilates. (Mederski et al., 1973; Wardlaw, 1969). Silvius et al. (1977) reported that drought decreased carbon dioxide exchange rate and altered assimilate distribution, producing growth modifications that favor efficient use of the limited supply of fixed carbon. They found that at leaf water potentials of -1.5to -2.0 MPa, soybean plants displayed alterations in ¹⁴C distribution among plant parts corresponding to alterations in dry weight distribution. Compared to well-watered plants, relatively more ¹⁴C was found in the root of water stressed plants before the pod-filling stage. Finn and Brun (1979) reported that ¹⁴C assimilation and specific nodule activity decreased and stomatal resistance increased with increasing water deficit. Sung and Krieg (1979) reported that photosynthetic rates were reduced as midday leaf water potentials declined from -1.4 to -2.7 MPa in cotton and sorghum. They suggested that photosynthetic rates were reduced with increasing water deficits prior to any significant changes in translocation rates suggesting that photosynthesis is the more sensitive of the two processes. Wardlaw (1967) indicated that the effect of water deficit on the translocation process is related to the availability of photosynthate more so than by a direct effect on the mechanisms of the translocation processes. In soybean, it has been found that net photosynthesis is decreased by about 60% when the water leaf water potential falls between -300 to -2000 KPa and is reduced by 80% at -4000 KPa (Boyer 1970).

In conclusion, a great amount of work has already been completed which reveals that soil compaction and water deficits alter soil temperature, water, nutrient availability and other soil processes resulting in reduced uptake of water and ions by stressed roots. Reduced availability of photosynthates and reduced biomass caused by the root disease responses to compaction and water deficit add to these problems. This study was focused on the combination effects of these two stresses on the root growth and the consequents of those stresses.

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CHAPTER 2

Carbon Partitioning in the Shoots and Roots of <u>Phaseolus</u> Seedlings Subjected to Soil Mechanical and Water Deficit Stresses

ABSTRACT

The carbon requirements by roots subjected to soil compaction and water deficit are essentially unknown. This study was conducted in the greenhouse and consisted of experimentally compacted soils having bulk densities of 1.1 and 1.7 Mg m⁻³ for each water treatment (water control and water deficit). Data collected 14 days after planting indicated that the dry biomass of plants decreased with increased bulk density and greater water deficit. The amount of ¹⁴C in plants decreased with increased bulk density and with greater water deficit. The translocation of ¹⁴C was restricted by water deficit but increased by compaction. Plants on the noncompacted and non-drought stressed treatment, 97% of fixed ¹⁴C was found in plants, and only 3% leaked to soil. In contrast up to 9% of ¹⁴C was lost to the soil by plants subjected to compaction and/or drought stresses.

INTRODUCTION

It is generally believed that soil environmental stresses influence the loss of plant carbon resulting in reduced yields by stressed plants (McCree, 1982, Smucker, 1984). 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. Soil compaction usually changes the existing balance between the liquid, gas, and solid phases of the soil volume resulting in greater bulk densities and reductions in soil porosity (Hillel 1982). Root growth is greatly reduced by these changes (Russell, 1977). Soil drought is another stress affecting plant yield. Many plant physiological processes would be delayed or stopped if plants were restricted by water deficiency (Salisbury, et al, 1978). Low soil moisture content increases internal plant water deficits and detrimentally influences growth and yield through a number of lowered physiological processes, including carbon exchange rate and translocation of assimilates (Mederski et al., 1973, Wardlaw, 1969). Sung and Krieg (1979) reported that photosynthetic rates were reduced by greater water deficits prior to any significant changes in the translocation rates, suggesting that photosynthesis is the more sensitive of the two processes. Whereas the effect of water stress on the translocation process was related to the availability of photosynthates, more so than by a direct effect on the mechanisms of the translocation processes (Wardlaw, 1967). Silvius et al. (1977) reported that compared to wellwatered plants, relatively more ¹⁴C was found in the root of water stressed plants before pod-filling stage.

Asady et al. (1985) reported that container experiments can be used to measure the influence of soil bulk densities on the growth of roots. This method has been used to demonstrate that root penetration ratios and root lengths decline linearly with decreasing air filled porosity (Asady et al., 1985). His study focused on the impedance effects of soil mechanical properties on root growth. Reduced root growth lowered the yields of plants, primarily because more carbon appeared to be lost, thereby reducing the accumulation of photosynthates by plants subjected to soil compaction stresses. The main objective of this study was to quantify the allocation of photoassimilates within plants and soils which were subjected to compaction and water deficit.

Materials and Methods

This study was conducted in the greenhouse using the soil core seedling test described by Asady et. al. (1985). Three polyvinyl chloride (PVC) cores with a diameter of 7.6 cm and wall thickness of 0.64 cm were used for the layered soil assembly (Fig. 1). Heights of the top, middle and bottom layers were 2.5, 2.5 and 7.6 cm, respectively. Each core was filled with a clay soil, (illitic, calcareous, mesic, Aeric Haplaquept) containing 53% clay and having a consistency ranging from very plastic, when wet, to very hard when dry. Soils were sieved to a range of 1.0 to 2.0 mm aggregates, and compacted into a middle layer at a gravimetric soil moisture content of 18%. Compression of soil to a desired bulk density of either 1.1 or 1.7 Mg m^{-3} was achieved by pressing a specific quantity of soil into each layer by a hydraulic press as described by Asady et al. (1985). The bulk density of top and bottom layers was 1.1 Mg m^{-3} . The three layers were wrapped with 5cm wide plastic-impregnated duct tape, saturated for 24 hours, and drained. Dry edible bean seeds (var. Seafarer) were surface sterilized with 0.1% hyperchlorite solution and germinated in the dark on wet paper towels at 25C for three days. Two seedlings were transplanted to each core, and covered with soil. The core assembly was placed on 48x48 cm tension tables (Hillel, 1980) which were established on the greenhouse bench. Each consisted of a fine mesh screen and blotting paper saturated for 24 hours and deleted of all the air bubbles. The tension tables were equipped with a Marionette burette reservoir which supplied water to the soil from 40 cm below the tension table by matric sorption. The tension tables were covered with a white plastic film having water tight ports for the individual soil cores which prevented water loss by surface evaporation. Plants were irrigated with tap water. Plant nutrition was maintained by the natural soil fertility.



Fig. 1. Three layer soil core assembly where chambers A and C contain control soils and B contains the soils compacted to bulk densities of 1.4 and 1.7 Mg m⁻³ at a gravimetric soil moisture content of 18%.

This study included two water treatments: 1) control, which was continuously irrigated by the tension table, and 2) short term water deficits, developed by removing the cores from the tension table on the fourth and seventh days after planting and re-establishing contact with the tension table after 60 hours. Cores of water deficit treatments were temporarily resaturated before returning them to the tension tables and equilibrated to a matric potential 0f 40 cm. Each treatment was replicated four times.

Plants were pulse-labeled with ${}^{14}CO_2$ on the fourteenth day. The soil surface was enclosed by a layer of parafilm sealed with transparent cellulose tape around the plant stems. Each soil core was enclosed by a gas-tight polyethylene plastic bag chamber. A small vial was attached to the middle of the inside of the labeling chamber. The radioactive label was introduced by injecting 0.5 ml HCl into the reaction vial followed by injecting 30ul of NaH¹⁴CO₃. The injection holes in the plastic bag were sealed with transparent tape immediately following injection. Ten minutes after injecting the ¹⁴C-label, 0.2 ml 1N NaHCO₃ was injected into the reaction vial to remove any trapped ${}^{14}CO_2$. Concentrations of CO_2 surrounding the plant during the three hours labeling period were monitored by injecting 0.5 ml gas samples into an infra red gas spectrophotometer (Beckman model 865, Beckman Industries, Fullerton, CA). Remaining ¹⁴CO₂ was removed from the fixation tent by vacuum extraction and trapped by scrubbing through 8 ml of 1N KOH. Plants were harvested at the surface of the soil and leaf area was measured by leaf area meter (Li-3000 Protable Area Meter, Licor, 4421 Superior Street P.O. Box 4425, Lincoln, Nebraska). The soil was cut into the original three layers and the ${}^{14}CO_2$ contents of each layer was vacuumed to remove respired ¹⁴CO₂ and trapped in 8 ml of 1N KOH. Root penetration ratios (RPR) were determined by dividing the number of roots which exited the middle core by the number which penetrated the top of the middle core as outlined by Asady et al (1985). Subsamples of soil were frozen at -20 C and stored for further evaluation. Roots were removed from the soil by washing with the hydropneumatic elutriation system (Smucker, et al, 1982). Roots were frozen and stored at -20C. The plant shoots were also frozen at -20C and held until further processing. All the frozen plant materials were freeze-dried. Leaf, stem, root and moisture soil samples were combusted using an oxygen saturated oxidizer (Biologocal Oxidizer-OX400, R.J. Harvey Instrument Corporation, Nillsdale.N.J.) at a temperature of 680 C (Catalyst) and 900 C (Combustion zone) for 2 to 3 minutes. The ${}^{14}CO_2$ produced by this oxidation process was trapped by a 2:1 solution of Carb-Sorb II (Packard Instrument Company, INC. 2200 Warrenville RD, Downers Grove.Illinois 60515) and Safety-Solve (Research Products International Crop. 410 N. Business Center Dr., Mount Prospect, IL 60056) and ¹⁴Cisotope activities were determined by a scintillation counter (TRI-CARB, model 1500) for 5 minutes.

RESULTS AND DISCUSSION

The total root length was significantly decreased when bulk densities increased from 1.1 to 1.7 Mg m⁻³. Water deficit further decreased the root length. Therefore, the greatest total root lengths were found in nonstressed plants whereas the smallest root length appeared in plants which were stressed by both soil compaction and water deficit (Table 1). The data shows that greater soil density decreased total root lengths by 56% while soil water deficit decreased total root growth by 52%. Combinations of water deficit and soil density decreased total root growth by 59%.

Root penetration ratios (RPR) were significantly reduced by compaction and water deficit. The root penetration ratio in nonstressed control plants (of the water control with a bulk density of 1.1 Mg m⁻³) was 7 to 12 times greater than the stressed plants. More roots accumulated in the top and middle portions of the 3 layered containers when the middle layer was compacted to 1.7 Mg m⁻³. Hence, the relative root lengths in the bottom layers of the treatments having compacted layers were reduced because fewer roots were able to penetrate through the more compacted middle layer (Table 1).

In addition to root length, root dry weight, leaf dry weight and stem dry weight were also significantly decreased by compaction and water deficit (Table 2). The greatest dry weights taken from each of these parameters were always collected from nonstressed plants (Table 2). Both drought and compaction reduced plant dry weights. Leaf area was reduced when bulk density increased from 1.1 to 1.7 Mg m⁻³ for both water treatments. The greatest leaf area (220.2 cm²/plant) was obtained from nonstressed plants (Table 2).

Water	B.D.	Total root	Relative root length		ve root length RPR	
		length	Тор	Middle	Bottom	
	Mg m ⁻³	cm			%	
Control	1.1	2793	14.56	22.50	62.93	64.75
	1.7	1237	31.43	38.10	30.48	5.50
Stress	1.1	1345	20.53	32.68	46.78	8.75
	1.7	1140	34.75	36.35	28.80	6.00
LSD _{0.05}		430	11.04	n.s.	20.14	13.12

Table 1	I. Root length,	root pene	etration ratio,	, and leaf a	area
	respons	es to soil	compaction a	and water	deficit.

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Table 2. Dry bean shoot and root dry weight responses to
soil compaction and water deficit stresses.

Water	B.D.	Leaf area	Leaf dry weight	Stem dry weight	Root dry weight
	Mg m ⁻³	cm ²		g	
Control	1.1	220.2	0.52	0.47	0.36
	1.7	131.1	0.32	0.17	0.25
_					
Stress	1.1	175.8	0.40	0.21	0.24
	1.7	141.5	0.34	0.19	0.23
LSD _{0.05}		35.3	0.07	0.22	0.08

All the parameters discussed above could be used to indicate plant growth responses to soil density and or drought stresses. The total dry matter of the 14 days-old seedlings decreased with increased bulk density and water deficit. There was no effect of compaction on the accumulation of dry matter when plants were under water deficit. This indicated that water is a more restricting stress for biomass accumulation than soil density. Even at the low bulk density, the total dry matter remained very low when soil water was deficient (Fig. 2).

The limitations of soil mechanical impedance and water deficits on plant growth and reduced biomass were also demonstrated by the transport of ¹⁴C-label through the plant and soil continuum. This approach, therefore, appears to be another method for quantifying plant tolerance to drought and mechanical impedance.

Labeled ¹⁴CO₂ was added to the dry beans to determine the distribution of recently fixed plant carbon as well as its transport rates (Table 3). The fixation of ¹⁴C-label decreased with water deficit. The greatest recovery rate (92%) was found in the water control having low bulk density. Recovery of ¹⁴CO₂-label was reduced to 40-45% by the compaction treatments during the 3 hours labeling period (Fig. 3). The reduced recovery of ¹⁴CO₂ by compaction stressed plants resulted in lower fixation of the ¹⁴C by these plants.

This study demonstrated that the ¹⁴C distribution in the plants and soil was influenced by both soil mechanical impedance and drought. Data in Table 3 indicated that higher percentages of ¹⁴C remained in the leaves of drought stressed plants than in the nonstressed plants, suggesting that water deficits restricted carbon transport beyond the site of photosynthesis. Greater



Fig. 2. Whole plant biomass of 14 days—old dry bean seedlings subjected to soil mechanical impedance and water deficit.



Fig. 3. 14C—label fixation of 14 days old dry bean seedlings subjected to soil mechanical impedance and water deficit.

Table 3. Relative distribution in plant and soil of ¹⁴ C -label				
in each experimental unit 3 hours after pulse labeling				
Phaseolus dry beans 14 days after transplanting.				

B.D.	Leaf	Stem	Root	Soil
Mg m ⁻³		% reco	vered ———	
1.1	47.29	32.37	17.76	2.59
1.7	29.14	34.95	26.63	9.28
11	77 87	11.07	7 65	3 47
1.7	46.17	25.21	21.02	7.6 1
<u> </u>	38.21	n.s.	13.15	6.92
	B.D. Mg m ⁻³ 1.1 1.7 1.1 1.7	B.D. Leaf Mg m ⁻³ 1.1 47.29 1.7 29.14 1.1 77.82 1.7 46.17 38.21	B.D. Leaf Stem Mg m ⁻³ — % record 1.1 47.29 32.37 1.7 29.14 34.95 1.1 77.82 11.07 1.7 46.17 25.21 38.21 n.s.	B.D. Leaf Stem Root Mg m ⁻³ — % recovered — 1.1 47.29 32.37 17.76 1.7 29.14 34.95 26.63 1.1 77.82 11.07 7.65 1.7 46.17 25.21 21.02 38.21 n.s. 13.15

bulk densities tended to reduced the accumulation of ¹⁴C - label in the leaves for both water treatments. Therefore, the highest percentage of ${}^{14}C$ in the leaf was found in the water deficit with low bulk density. While the lowest percentage was found in the water control with high bulk density (Table 3). No statistically significant deferences were observed for the percentages of ¹⁴C-label in the stems among the bulk densities and water treatments, although there was a tendency for stems of drought stressed plants to contain lower quantities of labeled carbon, relative to the quantities in the leaves. It appeared that when the leaf contained a lower percentage of ¹⁴C, then the stem had higher percentage of ${}^{14}C$. These data also show that greater bulk densities enhanced the movement of photoassimilates from the leaves and throughout the plant and into the soil, as a lower percentage of ¹⁴C-label remained in the leaves of plants with the greater bulk density. Nevertheless, the ¹⁴C-labeled materials in the roots and soils were significantly greater at the higher bulk density. The percentage of ¹⁴C lost by roots appeared to be affected less by water deficit than by soil bulk densities. This may have occurred because roots grown in the compacted soils needed more energy which resulted from greater respiration rates to overcome this resistance. The greater diameter and branching of roots subjected to mechanically impeding soils may have contributed to the greater carbon losses by bean plants (Schumacher and Smucker 1981). Consequently, a greater percentage of ¹⁴C accumulated in roots stressed by higher bulk densities, and a greater percentage of ¹⁴C leaked into the soil (Table 3). In this study, relative percentages of ¹⁴C lost to the soil were observed to increase nearly 3 times from B.D. 1.1 to 1.7 Mg m⁻³ under the water control. Although the nearly 2 fold greater losses of the ¹⁴C-label by roots in greater bulk density under drought stress were not statistically significant, 7.6% losses would greatly modify both the plant and rhizosphere activities. In summary, the reduced fixation of ${}^{14}CO_2$ and increased loss of ${}^{14}C$ into the soil were observed for the stressed plants. Therefore, less biomass accumulated during the 14 days of growth.

SUMMARY AND CONCLUSIONS

Water deficit and soil compaction stresses reduced root growth. Consequently, RPR, biomass, root length and leaf area decreased. These differences among the distribution patterns of labeled ¹⁴C within different plant parts and the soil were the direct result of soil compaction and water deficit environments. The reduced plant biomass probably resulted from the reduced CO₂ fixation and the increased loss of plant carbon compounds. Further experiments are needed to correlate the losses of plant carbon compounds with the increases in the number of branches and greater diameters of roots responding to the mechanical impedance and water deficit stresses

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CHAPTER 3

Water and Ion Absorption Efficiencies by the Roots of Dry Bean Seedlings Subjected to Soil Mechanical Impedance and Water Deficit Stresses.

ABSTRACT

Little is known about the interactive effects of soil compaction and water deficit on the uptake of water and ions by plant root systems. This study was designed to determine the separate and combined effects of compaction and drought stress on the growth of dry bean roots and their associated uptake of H2O, N, P and K. Three bulk densities $(1.1, 1.4 \text{ and } 1.7 \text{ Mg m}^{-3})$ and two water treatments (control and water deficit) were established during this 14 day experiment. Water deficit increased leaf thickness and soil compaction increased root diameter. Both compaction and drought reduced plant dry matter production. N, P and K absorption efficiencies decreased with the thickening of roots in soils having greater bulk densities under water control treatments. Only potassium absorption efficiency decreased by greater bulk density under water deficit treatments. Water absorption efficiency increased with greater bulk density and was decreased by water deficit. Lower transpiration ratios were correlated to higher yields under water deficit conditions, whereas lower transpiration occurred in the larger root systems which developed in noncompacted or less compacted soils.

INTRODUCTION

A significant amount of work has been reported which reveals the effects of compaction on plant root anatomy and growth (Prihar, et al., 1971) and Baligar, et al., 1975). They reported that root elongation was inhibited resulting in greater radial expansion and thicker roots when soils were in high bulk density. Additional studies have shown that compaction reduces the growth and yield of plants (Zimmerman and Kardos, 1961, Trouse, 1971, Burke et al. 1972, Miller and Burke 1974). Wiersum (1979) reported that shallow rooting restricts the uptake of mineral nutrients. Nutrient uptake by roots has also been reported to be decreased when subjected to soil compaction (Russell et al. 1975, Trouse 1971, and Wiersum 1979). Increasing soil bulk density resulted in decreased uptake of P and K by corn (Phillips and Kirkham, 1962). The placement of nitrogen fertilizer had a greater impact on N uptake when compaction zones were present than when they were not present (Garcia et al, 1988). This study was designed to evaluate the growth of roots and their ion and water absorption efficiencies by stressed roots subjected to soil compaction and water deficit.

MATERIALS AND METHODS

The soil core seedling test, described by Asady et al. (1985) was used in these experiments which were conducted in the greenhouse. Charity clay (illitic, calcareous, mesic, Aeric Haplaquept) soil was sieved to a range of 1.0-2.0 mm aggregates and was compacted into the middle layer (2.5 cm high) of a three core assembly to bulk densities (B.D.) of 1.1, 1.4 and 1.7 Mg m⁻³ at a gravimetric soil moisture content of 18%. The top soil layer (2.5 cm) and bottom soil layer (7.5 cm) were filled with soil to a bulk density of 1.1 Mg m⁻³. The three layers were wrapped with 5 cm wide plastic impregnated duct tape, saturated for 24 hours, and drained. Dry edible bean seeds were surface sterilized with 0.1% hyperchlorite solution and germinated on wet paper towels in the dark, at 25 C, for three days. Three seedlings were transplanted to each core. The surface soil of the core assembly and core container were covered with polyethylene film to prevent water loss by evaporation. This experiment included two water treatments: 1) control, which was maintained by adding water daily, according to the water lost during the previous day, as determined by weighing, and 2) water deficits, which were developed by not irrigating for 14 days. Plant nutrition was maintained by the natural soil fertility. Plants were harvested 14 days after transplanting by cuting them at the surface of the soil and leaf areas were measured by a leaf area meter (Li-3000 Protable Area Meter, Licor, 4421 Superior Street P.O. Box 4425, Lincoln, Nebraska). Roots were removed from the soil by washing manually to retain the intact root system for further analyses. Root length and diameter were determined by computer image processing (Smucker, et al. 1987). Plant tissue (leaves, stems and roots) was dried, weighed and digested before determining the N, P and K contents by the modified method of Parkinson (1975). Nitrogen, phosphorus and potassium absorption efficiencies were calculated based on the total nutrients which accumulated in the roots and shoots during the 14 day experiment and divided by the harvest root weight, length and surface area. Water absorption efficiencies were calculated based on water lost during the last 24 hour period before harvest. Analysis of variance with completely random block design were performed to determine if the treatments were significantly different from each other. Four replications for each treatment are applied to the analysis of N, P and K , and eight replications for each treatment are applied to the analysis of other parameters.

RESULTS AND DISCUSSION

Plant tissue dry weights decreased with increasing bulk density and developing water deficits (Table 1). Compaction (1.7 Mg m^{-3}) significantly decreased the dry weight of leaves, stems and roots when water was not limited. Water deficit decreased dry weights of leaves, stems and roots at bulk densities 1.1 and 1.4 Mg m⁻³. There were nonsignificant decreases between the water control and water deficit at a bulk density of 1.7 Mg m⁻³. This implies that soil compaction decreased dry weight only when soil water conditions were favorable. The production of dry matter seemed more sensitive to water deficit than to mechanical impedance. Once the plants were stressed by a water deficit, the effect of compaction on the plant growth seemed to have less influence on dry weight accumulations.

Leaf areas were significantly decreased by greater bulk density and water deficits (Table 2). Soil compaction caused leaf areas to be significantly smaller only at the greatest level (1.7 Mg m⁻³) of compaction, whereas drought stress decreased leaf areas at all three of the compaction levels. Therefore, it can be seen that the combined influences of compaction and drought reduced leaf area by 49% as compared to the control plants (243.5 cm).

Specific transpiration rates were significantly greater for all the bulk density treatments of the well-watered treatment. The highest bulk density appeared to increase the specific transpiration by plants of drought stress treatments (Table 2). This indicated that the compaction -mediated increases of specific transpiration rates were a function of the water deficit. In comparison to total plant dry weight, which decreased with increasing bulk density (Table 1), specific transpiration rates increased with greater bulk

Water	B.D.	Leaves	Stems	Roots
	Mg m ⁻³		g	
Control	1.1	0.287	0.272	0.126
	1.4	0.266	0.255	0.121
	1.7	0.217	0.174	0.103
Stress	1.1	0.213	0.185	0.101
	1.4	0.198	0.193	0.104
	1.7	0.178	0.131	0.098
LSD _{0.05}		0.045	0.045	0.001

Table 1. Plant tissue dry weight responses to soil mechanical impedanceand water stresses at 14 days after transplanting.

Table 2.	Leaf area and specific transpiration responses to soil
	mechanical impedance and water deficit at 14 days
	after transplanting.

Water	B.D.	Leaf area	Specific transpiration ratio
	Mg m ⁻³	cm ²	mg/cm ²
Control	1.1	243.5	96.71
	1.4	225.5	91.88
	1.7	173.2	107.40
Stress	1.1	143.6	38.27
	1.4	138.8	49.29
	1.7	125.1	72.28
LSD _{0.05}		30.9	27.87

densities (Table 2). This suggests that transpiration may be correlated with yield, because lower transpiration is important for a higher yield when water is limited (Heen, 1980). In this study, lower transpiration ratios correlated to higher total plant dry weight when soil water was deficient $(R^2=0.921)$. Heen (1980) also reported that plants with lower transpiration rates usually occurred in those with good root adaptation. In this study, the plants with larger root systems also had a lower transpiration under water deficit condition (Table 2 and Table 6, $R^2=0.999$).

There were no significant effects of soil bulk density on leaf density, but leaf densities were significantly greater on plants subjected to a water deficit suggesting that water deficits had a greater influence on leaf thickness than soil compaction (Table 3). In contrast, root densities increased with greater soil bulk density, but did not change significantly between water treatments suggesting that soil compaction influenced the thickness of roots more than soil water deficits (Table 4).

Table 5 compares the percentage distribution of root lengths having different diameters. The data shows that the percentage of root length with diameters ranging from 0.1 -0.4 mm decreased with greater bulk density when water was not limiting. Water deficit significantly decreased the percentage of roots at this diameter at bulk densities of 1.1 and 1.4 Mg m⁻³. The percentage of root lengths with diameters of 0.5-0.8 mm increased with greater bulk density. Water deficits caused a significantly greater percentage of roots, in the medium diameter class ranging from 0.5-0.8 mm for all three bulk densities. Greater percentages of large roots, 0.9-1.0 mm, increased with greater bulk density and were decreased by water deficit (Table 5). In summary, a greater percentage of larger roots were recovered from soil

Water	B.D.	Leaf densit	у
		Fresh weight	Dry weight
	Mg m ⁻³	mg/c	m ²
Control	1.1	13.31	1.183
	1.4	13.58	1.178
	1.7	13.99	1.253
Stress	1.1	14.69	1.484
	1.4	14.67	1.424
	1.7	14.22	1.421
LSD _{0.05}		0.84	0.111

Table 3.	Leaf density of 14 days-old dry bean seedlings subjected
	to soil mechanical impedance and water deficit.

Table 4.	Root density of 14 days-old dry bean seedlings subjected
	to soil mechanical impedance and water deficit.

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Water	B.D.	Root d	ensity
	-	Fresh weight	Dry weight ¥
	Mg m ⁻³	m	ng/cm root
Control	1.1	2.921	0.106
	1.4	4.349	0.156
	1.7	3.955	0.160
Stress	1.1	2.105	0.093
	1.4	3.010	0.131
	1.7	3.617	0.145
LSD _{0.05}	5	0.951	0.032

treatments at the highest bulk density. This is additional evidence which demonstrates that mechanical impedance causes roots to become thicker. Water deficit increased the percentage of roots with larger diameters probably because the mechanical impedance increased during drying, reducing root penetration in the drought stressed soil.

Total root growth significantly decreased in soils packed to a bulk density of 1.7 Mg m⁻³, and dramatically decreased with water deficits (Table 6). The data showed a 30% reduction of root length when bulk density was increased from 1.1 to 1.7 Mg m⁻³ under the water control. Water deficits decreased total root length 23% and 24% at bulk densities 1.1 and 1.7 Mg m⁻³, respectively, but water deficit did not further reduce root length at the high bulk densities of 1.7 Mg m⁻³. This indicated that the effects of water deficit on root elongation depended on the compaction levels. Once the mechanical impedance became great enough to inhibit root elongation, the effect of water deficit on root elongation became less important. Tables 1 and 6 suggest that soil compacted to a bulk density of 1.7 Mg m⁻³ reduced plant growth similar to the drought stresses regardless of the level of soil compaction. Carbon allocation to the shoots decreased with greater bulk density and drought stress, so water deficit and greater bulk density (1.7 Mg m^{-3}) significantly decreased shoot to roots ratio (Table 6 and Huang and Smucker, 1990).

Root surface areas having diameters ranging from 0.1-1.0 mm decreased with increasing bulk density and water deficit (Table 7). The root surface areas decreased 27% and 18% for water control and water deficit, respectively, when bulk densities were increased from 1.1 to 1.7 Mg m⁻³. Water deficit decreased the root surface area 18% and 20% at bulk density

water dencit.				
Water	B.D.			
		0.1 - 0.4 mm	0.5 - 0.8 mm	0.9 - 1.0 mm
	Mg m ⁻³		%	
Control	1.1	88.0	10.9	1.1
	1.4	87.1	11.5	1.4
	1.7	85.5	12.8	1.7
Stress	1.1	84.7	14.5	0.9
	1.4	84.1	14.4	1.2
	1.7	84.2	14.1	1.8
LSD _{0.05}	~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~	2.1	1.5	0.4

Table 5. Distribution of root lengths within three diameter classes for dry edible beans subjected to soil mechanical impedance and water deficit.

Table 6.	Root lengths and shoot to root ratios of 14 days old dry
	bean seedlings subjected to soil mechanical impedance
	and water deficit.

Water	B.D.	Total root length	Shoot/root ratio
	Mg m ⁻³	cm	Dry weight
Control	1.1	902.5	4.44
	1.4	887.8	4.31
	1.7	627.0	3.92
Stress	1.1	690.4	3.96
	1.4	671.9	3.72
	1.7	567.9	3.14
LSD _{0.05}	5	115.2	0.482

1.1 and 1.4 Mg m⁻³, respectively. Water deficit decreased root surface areas by 7% at the highest bulk density of 1.7 Mg m⁻³, which was not significant. It appears that the augmented responses of the root surface areas were sensitive to both mechanical impedance and water deficit. The decreased root surface areas of the thicker roots probably resulted in their lower capacities to absorb water and ions. In this study, the total water, and the total N, P and K absorbed by plant roots during the 14 days decreased with lower root surface areas, which occurred at the greatest soil compaction level and water deficit (Table 8). The decreased total consumption of water and nutrients resulted in a reduction in the production of dry matter (Table 1).

Although there was less root growth by Phaseolus plants subjected to mechanical impedance and water deficits, the average ion absorption efficiencies by stressed roots were calculated for the duration of the experiment. N, P and K ions absorption efficiencies were calculated based on the total nutrients which accumulated in the shoots and roots during the 14 day experiment divided by total root surface areas which had accumulated by harvest. Consequently this experiment was not designed to measure specific ion absorption efficiency. N, P and K ion absorption efficiencies decreased with greater bulk density when soil water was sufficient (Table 9). There was a tendency for greater absorption of N and P by roots when plants were subjected to a water deficit. There was a tendency for P absorption efficiency (PAE) to decrease as bulk densities increased for both water treatments (Table 9). It seemed that there were no combined effects of both compaction and water stress on the PAE. The greatest compaction (1.7 Mg m^{-3}) decreased K absorption efficiency (KAE) for both water treatments. However, KAE did not respond to water deficit (Table 9).

Water	B.D.	Root surface area 0.1 - 0.4 mm 0.5 - 0.8 mm 0.9 - 1.0 mm 0.1 - 1.0 mm			
	Mg m ⁻³		C1	m ²	
Control	1.1	133.8	40.12	5.75	179.7
	1.4	130.0	41.67	7.34	179.1
	1.7	90.9	32.79	6.67	130.3
Stress	1.1	102.4	40.84	3.38	146.6
	1.4	98.2	40.58	4.52	143.3
	1.7	81.9	32.69	5.80	120.5
LSD _{0.05}		16.8	7.99	1.83	24.2

 Table 7.
 Root surface area sizes of 14 days-old dry bean seedlings subjected to soil mechanical impedance and water deficit.

Table 8. Total water, N, P, and K in plant shoots and root after 14 days of exposure to soil mechanical impedance and water deficit.

Water	B.D.	Total water consumption	Nitrogen	Phosphorus	Potassium
	Mg m ⁻³	g		mg	
Control	1.1	215.6	45.64	6.59	55.56
	1.4	208.3	44.50	6.16	51.51
	1.7	149.1	36.27	5.58	40.34
Stress	1.1	128.7	36.59	5.81	42.27
	1.4	126.5	34.09	5.49	39.81
	1.7	94.5	32.00	4.63	28.41
LSD _{0.05}		19.4	13.88	1.15	10.00

Bulk density did not affect water absorption efficiency (WAE) based on root surface area or root length when the water in the soil was optimum, but soils that were highly compacted, significantly decreased water absorption efficiency when soil water was limited (Table 10). As expected a water deficit significantly decreased the absorption efficiency of water by the root systems in all three levels of compaction. This indicated that compaction did not affect the capability of roots to absorb water when water was not limiting root growth, but compaction appeared to adversely influence water absorption when water was deficient in the soil (Table 10).

Table 11 presents the water use efficiency (WUE) responses to soil compaction and drought stresses. Shoot WUE was significantly increased by water deficit with no influence by bulk density within each water treatment. Whereas root WUE was significantly increased by both compaction and water deficits. Water use efficiencies, based on whole plant fresh and dry weights were primarily increased by water deficit. Bulk densities of 1.7 Mg m⁻³ appears to increase the WUE on a whole plant fresh weight basis (Table 11).

Water	B.D.	Nitrogen	Phosphorus	Potassium
	Mg m ⁻³	mg i	n whole plant/dm ² r	oot
Control	1.1	12.84	1.84	15.46
	1.4	11.90	1.64	13.78
	1.7	10.14	1.56	11.26
Stress	1.1	12.48	1.98	14.53
	1.4	13.14	2.11	15.31
	1.7	12.05	1.75	10.70
LSD _{0.05}		1.82	0.33	2.43

Table 9. N, P, and K ion absorption efficiencies by14 days-olddry bean seedlings subjected to soil mechanicalimpedance and water deficit.

Table 10.	Water absorption efficiency (WAE) for the 14th day
	dry bean seedlings subjected to soil mechanical
	impedance and water deficit.

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Water	B.D.	Water absorption efficiency			
	Mg m ⁻³	mg H ₂ O/cm ² root	mg H ₂ O/cm root — per day —	g H ₂ O/g root	
Control	1.1	124	24.8	187.0	
	1.4	119	23.8	177.4	
	1.7	147	28.8	176.0	
Stress	1.1	37	8.0	54.2	
	1.4	48	10.2	66.0	
	1.7	77	16.4	95.3	
LSD _{0.05}		32	7.3	46.1	

Water	B.D.		WUE			
		<u></u>		Whole plant		
		Shoot	Root	Fresh wt	Dry wt	
	Mg m	3	g/kg H			
Control	1.1	2.63	0.59	45.05	3.22	
	1.4	2.49	0.58	44.04	3.07	
	1.7	2.63	0.69	47.48	3.32	
Stress	1.1	3.08	0.79	50.36	3.87	
	1.4	3.06	0.82	50.55	3.88	
	1.7	3.25	1.04	61.66	4.29	
LSD _{0.05}		0.39	0.10	6.11	0.45	

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Table 11. Water use efficiency (WUE) of dry bean plant responses to soil mechanical impedance and water deficit.

SUMMARY AND CONCLUSIONS

Compaction and water deficit caused a reduction of dry matter, root length and root surface area. Leaf density was influenced more by water deficit than by soil compaction. While root density was influenced more by soil compaction than by water deficit. The absorption efficiencies of N and P ions decreased with greater bulk densities only when soil water was sufficient. The absorption efficiency of K was decreased by greater bulk density for both water control and water deficit. Water deficit decreased water absorption efficiency for all three levels of bulk densities, and greater bulk densities increased water absorption efficiency when soil water was limited. Water use efficiencies were significantly increased by water deficit, and there was a tendency for further increase of WUE with greater bulk densities.

The study of ion and water absorption efficiencies by the stressed seedling roots has a importance for the future life of the crops. The seedling stage is the beginning of the developmental stage of growth which will have a sequential influence on the final yield. And also, the results of that compaction increased WAE and WUE when soil water was limited give us a information how to use water wisely in those areas where water is in short supply. This study was designed to determine the specific water absorption efficiency, but did not provide adequate data for determining the specific ion absorption efficiency at day 14. Another experiment utilizing multiple harvests and the use of ion isotopes would be required for measuring ion absorption efficiencies by plants subjected to greater drought and compaction stresses.

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CHAPTER 4

SUMMARY AND CONCLUSIONS

Short term experiments were designed to determine the separate and combined effects of soil compaction and water deficit on the root growth of dry edible bean seedlings and the associated uptake of water and ions as well as the relative distribution of photosynthates in the plants and soil.

Leaf area, shoot and root dry weight, root length and root penetration ratio, as the parameters to indicate the growth of plants, were significantly decreased by greater bulk densities and water deficits. The leaf area of the stressed plants decreased about 50% below the nonstressed plants. The ${}^{14}CO_2$ fixation rates decreased primarily because of the smaller leaf areas. Nearly 92% of the ${}^{14}C$ -label was recovered following the 3 hours of pulse labeling for nonstressed plants having leaf areas of 220 cm². Whereas 74%, 47% and 41% were recovered from the stressed plants with the leaf areas of 176, 141 and 131 cm², respectively. Consequently, plant biomass decreased with less fixation and the greater losses by the stressed plants..

Leaf and root densities collected 14 days after transplanting showed that leaf density increased with the development of water deficit, whereas, root density increased with greater bulk densities. This suggested that water deficit had a greater influence on leaf thickness and compaction had a greater influence on the thickness of roots than did water deficits. A larger percentage of roots with bigger diameters in the 0.9-1.0 mm size were found in the greater bulk density treatments which is additional evidence that demonstrates mechanical impedance causes roots to become thicker. Root surface areas also decreased with increasing bulk density and water deficit. The decreased root surface area probably resulted in a lower capacity for uptake of water and ions.

The investigation of total water and ions absorbed during the 14 day experiment showed that total absorption decreased with decreasing root surface areas. After 14 days of drought, the water absorption efficiency (WAE) was decreased by water deficits. When water was not limiting plant growth, soil compaction had little influence on WAE. Greater soil bulk densities seemed to improve WAE when soil water contents were deficient. Ion absorption efficiencies were adversely influenced by the greater bulk density. K ion absorption seemed to be influenced more than N and P, by the soil bulk density and drought stresses.

In conclusion, soil mechanical impedance and soil water deficit stresses altered the root morphology resulting in a series of changes in their functions. The decreased total root length and surface area resulted in a lower capacity for root absorption of ions and water which caused a decrease in plant biomass. Additionally, a greater percentage of the limited amount of photoassimulates were lost to the soil by stressed seedlings. As plant and soil biological systems mature, however, this dynamic and interactive systems becoming more complex. Generally, environmental stresses inhibit root system development and alter the root morphology resulting in root disfunction. Plant growth studies under controlled conditions such as the soil core seedling test, can produce relative results and their interpretations can be extended beyond the seedling stage to other temporal and spatial contexts. Since the continuous growth at all developmental stages has a big influence on final yield, plants stressed at the seedling stage will affect their future growth resulting in a lower tolerance of environmental stresses throughout their life.

Although the studies reported here have shown that water and mechanical impedance stresses adversely influence plant morphology, carbon fixation and retention, as well as ions and water absorption, additional studies are needed to elucidate specific changes in root branching and root thickness correlate to the assimilation and loss of carbon.

