Soybean top and root response to static and fluctuating water table situations

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Soybean top and root response to static and fluctuating water table situations

by

Craig Dean Stanley

A Dissertation Submitted to the Graduate Faculty in Partial Fulfillment of The Requirements for the Degree of DOCTOR OF PHILOSOPHY

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INTRODUCTION

Knowledge and understanding of below ground-plant response to differing environmental conditions is becoming increasingly important to the complete understanding of how and why plants respond the way they do to different environmental stimuli. More often than not, above ground plant response is caused directly by the response of below ground plant components to varying environmental conditions.

Moisture status of the soil is of utmost importance in affecting soil environmental conditions. Whether limited or excessive, the amount of water present can be related directly to plant response and indirectly through its effect on other soil characteristics and processes.

Excessive soil moisture can occur from a number of situations but one common cause is a high water table. This condition greatly affects root growth and development if it is present during the growing season. Presence of the water table and its effects on other soil constituents and processes can also dramatically change the soil environment. The resulting changes in the soil environment can profoundly affect growth and development of plant roots and, often a development of the plant tops. These responses depend on extent and duration of the water table and, possibly on the plant developmental stage.
Major objectives of this study were to characterize and describe root and top response of soybeans to several different water table situations, both static and fluctuating. Attempts were made to explain why and when such responses occurred. Investigations of limiting soil characteristics vital to root growth were made and attempts were made to describe at what level they became limiting.

Another main objective was to determine the length of time that a soybean plant can tolerate a temporary water table before some effect on top and root growth is observed. Using this result, the possibility of a growth stage tolerance or adjustment factor for root response to temporary water table situations was investigated.
LITERATURE REVIEW

Plant response to water stress conditions is commonly thought of as a response to deficient soil moisture situations. Also of importance, however, is the response by plants to water stress conditions brought about by excess moisture. When this situation occurs, and anaerobic conditions develop, dramatic changes in the soil environment can take place which cause definite effects on the growth of the plants.

Several different aspects of this condition must be discussed in order to understand the possible factors contributing to plant growth responses. Development of anaerobic conditions, whether in bulk soil or in localized areas of the soil, and the soil physical and chemical processes that are affected, are important in understanding the soil contribution to plant response to anaerobic conditions. The plant, itself, and changes that occur morphologically and physically as a result of the particular soil environment and how they will affect production are extremely important. Also, interactions between plant and soil must be considered to give a complete overview of the situation arising as a result of high soil moisture conditions causing anaerobic conditions to occur.
Anaerobic Conditions

Anaerobic conditions are defined as those which occur in absence of oxygen. Often, in the soil, this condition results from high soil moisture situations such as waterlogging or high water table situations. Russell (1977) points out, however, that anaerobic conditions can occur in local areas in the soil, anywhere oxygen diffusion into the area is less than that which is needed to carry out the normal respiratory processes of organisms living in the soil. Russell indicates that extreme differences in oxygen concentration can occur between short distances in the soil due to the different soil pore sizes. When this situation occurs, both aerobic and anaerobic conditions can exist in close proximity. Russell states that when this happens, root growth may be affected by the diffusible products of soil reaction caused by the anaerobic conditions even though the roots themselves are in aerobic environments and that these substances which occur in only anaerobic environments may exist, also, in the aerobic portions of the soil.

Anaerobic conditions can develop in a number of ways. Immediate development can occur with the occurrence of high water table or waterlogging situations due to the filling with water of the previously air-filled pores. Anaerobic conditions can develop slowly when diffusion of oxygen into
an area is restricted and depletion occurs by respiration of local organisms within the area.

Soil Factors Affecting Aeration

Many soil factors affect aeration of the soil. The available pore space is one of the most important. Oxygen diffusion can be greatly affected by the soil characteristic. Because of the extremely large difference in diffusion rate between gaseous and liquid-phase oxygen (10,000 to 1) once water blocks the air channels connecting the pore spaces and the oxygen must diffuse through water, anaerobic conditions can develop (Allen, 1976).

Another factor is the compaction level or the bulk density of the soil. When layers of soil differ in compaction, localized areas of anaerobic conditions can result because the air passages between pore spaces can be blocked more easily.

Soil texture becomes important in restricting aeration when the percentage of clay particles is very high. Very small pore spaces are usually prevalent in these soils making them slow to aerate once moisture has entered the pores.

The stability and size of aggregates can influence soil aeration. If an aggregate is large and very stable, localized zones of anaerobic conditions can exist within because of restricted oxygen diffusion between external and internal
Chemical and Biological Changes in the Soil as a Result of Anaerobic Conditions

Changes which occur in the soil under anaerobic conditions caused by excessive soil water can have definite effects on top and root growth of plants. The effect of the high soil water conditions on nutrient availability and losses, toxic substances produced, and microbial activity can dictate how well a plant will respond to indirect effects of the anaerobic situation.

Studied of some great length is the loss of nitrogen which can occur in soils with high soil moisture. Losses can occur by leaching or denitrification involving the reduction of nitrate to atmospheric nitrogen with nitrite and nitrous oxide as intermediate products. Burford and Millington (1968) showed that the amount of nitrous oxide present in the soil was a valid indicator that denitrification was occurring and that this process takes place only in an anaerobic environment. Nitrous oxide was detected in greatest quantities in soils of high soil moisture. Cady and Bartholomew (1961) showed that as oxygen concentration decreased in the soil, denitrification increases. When oxygen was present, nitrous oxide was not reduced to atmospheric nitrogen, but that this reduction occurred quickly in anaerobic soils. Arnold (1954) provided
evidence that nitrogen oxide occurred rapidly as the soil approached saturation rapidly and that at low soil moistures low amounts of nitrous oxide were evolved. Dowdell and Smith (1974) supported Arnold by showing that the level of nitrous oxide is inversely related to the oxygen content of the soil and correlated with the nitrate and nitrite content of the soil water.

The different types of soil under anaerobic conditions, also, can have an affect on the denitrification process. Cooper and Smith (1963) showed that for anaerobic soils the rate of denitrification can be affected by soil pH. In acid soils, the initial reduction of nitrate to nitrite is the rate limiting step, while in alkali soils the reduction of nitrite to nitrous oxide determines the rate. In all cases, the conversion of nitrous oxide to atmospheric nitrogen was rapid.

Other nutrients essential to plant growth can have their availability changed as a result of very high soil moisture conditions. Devitt and Francis (1972) demonstrated that waterlogging caused the concentrations of P, Fe, Mn, and Cu to increase while causing the concentrations of N, Ca, K, Na, and Mg to decrease. They showed, however, that these changes were not reflected in plant nutrient uptakes. Williams and Simpson (1965), working on pasture soils, observed that short
periods of waterlogging lowered the availability of phosphorous due to the conversion of phosphate to non-available forms during anaerobic conditions. The phosphate sorption capacity of the soil increased upon waterlogging but decreased after the soil was air-dried. Grable (1966) stated that flooding can increase the availability of many nutrients but with temporary high water table conditions, it is difficult to assess the effect on nutrient availability. It is in situations such as these that localized zones of anaerobic conditions may remain so that nutrient availability of the soil as affected by temporary water tables as a whole would be difficult to characterize. Jones et al. (1971) indicated that waterlogging can decrease sulfur availability to the plant. However, upon plant analysis, no significant increases in sulfur uptake were detected.

Other chemical changes which can affect plant growth dramatically can occur in the soil as a result of high soil water and resultant anaerobic conditions. These involve the production of toxic substances. The synthesis of various organic acids, hydrocarbon gases, and other inhibitors of plant growth may occur only when the conditions are anaerobic and the proper substrates are present.

McCalla and Norstadt (1974) showed that plant residues often provide the necessary substrates for toxic organic acids.
to be synthesized by various micro-organisms. Many phenolic acids, which are toxic to plants, occur in many crop residues. They showed that weathering of the residues can decrease the potential toxicity but when residues were incorporated and influenced by high soil moisture conditions, production of toxic acids increased greatly. Stevenson (1967) found that wet organic soils produce large quantities of aliphatic acids. These acids have been shown to inhibit root growth. Acetic acid was found to be the most abundant volatile fatty acid present, but butyric formic, and propionic acids, also, could be present in toxic quantities if proper substrates were available. Wang et al. (1967) showed agreement by detecting acetic and propionic acids, among others, being formed in waterlogged soils. He, also, found that the presence of these acids had significant effects on decreasing root growth as well as top growth. Addition of organic matter increased organic acid formation since the needed substrate was added.

Toussoun et al. (1968) showed that a soil moisture content above 30% was required for phytotoxic substance production when plant residues were incorporated. They, also, found that once the conditions were right, toxicity could be detected 7 to 10 days after the residue was incorporated and reached a maximum of three weeks after incorporation. Many ether-soluble acids were found, with benzoic and phenylactic acids
being the most prevalent. Results were consistent for many types of residue including barley, cotton, cowpea, and soybean residue.

Another type of toxic substance which can be produced when anaerobic conditions exist is the production of hydrocarbon gases. Of major concern here is the production of ethylene. Ethylene has been shown to have definite effects on the growth of plants which will be discussed later. The formation of ethylene in the soil occurs at faster rates when anaerobic conditions exist. Smith and Dowdell (1974) extensively studied ethylene production in the soil and found a clear relationship between soil moisture and ethylene production. When soil moisture was high, the amount of ethylene produced was high and reductions of oxygen contents were rapid. Another important factor in the production of ethylene was soil temperature. Ethylene production increased twenty-fold when temperature was raised from 4° to 11°C. Overall, Smith and Dowdell concluded that the effect of soil moisture content on air-filled pore spaces, temperature, oxygen concentration depression, and the availability of the necessary substrates for microbial activity influenced the amount of ethylene produced from a particular soil. They found that, in light textured soils which are unusually wet, concentrations of ethylene likely will be produced which are high enough to inhibit root growth.
Smith and Restall (1971) found that ethylene seemed to be produced by enzymatic activity rather than chemical activity, in both sterile and non-sterile soils. Concentrations of up to 20 ppm were found after ten days of incubation at 20°C. Total evolution correlated well with percent organic matter and was affected by wetting and drying of the soil and root activity. Burford (1976), using a cow manure slurry incorporated into soil, showed that large amounts of ethylene, ethane, and propane evolved after a short incubation period. He postulated that addition of the organic substrates along with the restricted soil aeration caused the hydrocarbon gas production that followed. Lynch (1972) found that glucose and methionone were probably the most important substances needed for ethylene production. These two substances occur in quantity upon decomposition of fresh organic matter. This may prove to be important in understanding the role of ethylene affecting plant growth during transient anaerobic conditions, where root damage and decomposition itself may provide sufficient substrate material during transient anaerobic conditions for further inhibition of growth.

Microbial action is involved in the production of ethylene. Dasilva et al. (1973) showed that certain species of bacteria, fungi, and actinomycetes are capable of producing ethylene. This fact suggests that both eucaryotic and
procaryotic forms of microbes can synthesize ethylene. Lynch (1975) found that mainly fungi rather than bacteria played the major role in microbial production of ethylene, although some anaerobic bacteria did produce the substance. Earlier, Lynch (1972) found that yeasts also were very influential in ethylene production.

Carbon dioxide in sufficient quantities has detrimental effects on root growth, but is often considered relatively unimportant when compared to other toxic material in the soil. Williamson (1970) concluded that the lack of oxygen, not the abundance of carbon dioxide, in the soil atmosphere has the greatest influence on root growth inhibition. In high soil moisture situations, carbon dioxide concentrations often increase and oxygen concentrations decrease. This is because of carbon dioxide's greater water solubility than oxygen which allows it to diffuse more readily in solution. Oxygen is used up by plant and microbial respiration, while carbon dioxide is produced and accumulates. Smith and Robertson (1971) studied different combinations of carbon dioxide and ethylene and concluded that carbon dioxide had no appreciable effect on ethylene production or upon ethylene's effect on root growth up to the point where the concentration of carbon dioxide itself inhibited root growth. So no interrelationship between the two gases is seen.
The reduction-oxidation potential (redox potential) is of major importance in affecting soil chemical processes. Allen (1976) states that oxygen in the soil usually sets the level of the redox potential. As oxygen is depleted by roots and soil microorganisms after a soil becomes waterlogged the redox potential drops quite low, depending on the pH of the soil. For a soil with a pH of 7.0, redox potential changes can range from +400 millivolts for aerobic conditions to -150 millivolts for extreme anaerobic conditions. After most of the oxygen has become depleted, nitrates in the soil become the source of oxygen for oxidation. This reaction as discussed earlier, results in the evolution of atmospheric nitrogen. If anaerobic conditions continue, manganese and iron are reduced and finally sulfate is reduced to hydrogen sulfide gas which is highly toxic to plants.

Microbial activity changes as anaerobic conditions develop. The roles microbial populations play in production of organic acids and hydrocarbon gases in the soil already have been discussed. Allen (1976) stated that microbial populations and activity follow redox potential and aeration changes. When the redox potential continues to drop, bacteria involved in iron and sulfur reduction become more active.
Plant Response to Anaerobic Conditions Caused by High Soil Water Content

Many studies have been conducted to find how and why plants respond the way that they do when grown under high soil water conditions. The anaerobic conditions that accompany high soil water content can have immediate effects on the physical state of a plant. Russell (1977) characterized plant morphological response by noting that often the effects can be visible in a matter of a few hours. Wilting may occur with some downward curving of petioles and stems. Chlorosis and early senescence of leaves may occur while root growth becomes very restricted. Eventual death of the plant occurs if the condition is severe and continues for a long enough period.

Jackson and Campbell (1976) demonstrated leaf epinasty with tomatoes under waterlogged conditions. Kramer (1951), studying plant-water relations under flooded conditions, observed a reduction in transpiration and in root water uptake. Some wilting occurred of the above ground portion of the plant. Changes in the root systems also occurred. In some species, adventitious root development increased and where this occurred rapidly, the plant was damaged less. Bryant (1934) observed that barley primary roots developed longer and that fewer secondary roots were present in aerated than in non-aerated soil. Also, he found that roots were 15%
greater in diameter in non-aerated than in aerated soil while roots were four times longer in aerated soil than in non-aerated soil. Grable (1966) noted that anaerobic conditions tended to suppress the growth of root hairs. He suggested that this suppression may cause a decrease in nutrient uptake by roots.

Different degrees of high soil moisture can cause differences in response by plants. Minessy et al. (1970), using different water table heights on fruit trees, found that the higher the water table, the less the leaf area that developed on the trees and the lower the yields. Analysis of nutrient content in leaves and roots showed differences that were related to water table height. Rogers (1974) used different rates of irrigation to alfalfa and obtained differing anaerobic conditions. He found that no yield difference could be detected between high and low soil water level treatments until after the first harvest. After that harvest, the high treatment lowered yield by reducing growth and this effect continued for six months after the watering treatments were stopped. Root rot was very prevalent in the high water level treatment and almost non-existent in the low. An effect on root distribution was observed, also, with most of the roots in the high water level treatment occurring in the top 60 cm of the soil profile.
Follet et al. (1974) grew corn on soil with different water table heights and concluded that maximum shoot growth occurred at their intermediate water table heights near 200 centimeters. Chaudhary et al. (1975) also grew corn under differing water table heights and concluded that a height of 120 centimeters was considered optimal for corn growth. They found, however, that this height depended on the type of growing season, wet or dry. During dry years, 60 to 90 cm water tables were considered optimal. Hiler et al. (1971) detected drastic reductions in growth of sorghum growing in shallow water table affected soils (30 - 60 cm) as opposed to soils with deeper water tables (90 - 120 cm). Williamson and Krig (1970) concluded that the response of plants to differing water table heights depended upon the type of crop, the type of soil, and the watering procedure for the crop. From the Chaudhary et al. (1975) studies, the list must also include the type of growing season.

Several plant processes are changed as the plant becomes influenced by anaerobic conditions caused by high soil moisture. Van't Woudt and Hagen (1957) stated that transpiration tends to increase immediately after waterlogging. The increase lasts for about a day and is followed by a sharp decline. Depending on the species, a recovery sometimes is detected even though flooding continues. This recovery generally is
related to the ability of the plants to develop adventitious roots. Van't Woudt and Hagen (1957) indicated that photosynthesis tends to follow the same pattern as transpiration. Stewart et al. (1969) grew bermudagrass under different water table heights, measured evapotranspiration, and found that evapotranspiration increased with cover for 63 and 100 cm water table depths, but decreased with shallower water tables. Actual evaporation from the soil surface increased for the 25 cm water table treatment, which indicates substantial decreases in transpiration for that treatment. Gales (1976) reported that waterlogged conditions decreased transpiration as well as leaf water potentials when compared to non-waterlogged treatments.

Some effects on root water and ion uptake have also been observed. Drew and Trought (1977) showed that waterlogged conditions inhibited ion uptake by wheat. Transport of mobile nutrients like nitrogen and phosphate from older leaves also occurred, causing a yellowing condition. Devitt and Francis (1972), however, found no differences in plant uptake of nutrients for subterranean clover growing in waterlogged soil as opposed to non-waterlogged soil. Minessy et al. (1970), also, showed no effect of waterlogging on mineral content in leaves or roots, thus root nutrient uptake probably was not affected by waterlogging.
Kramer and Jackson (1954) grew tobacco under flooded conditions and detected wilting of the plants. This wilting was attributed to a sudden decrease in root permeability and thus in water uptake. They hypothesized that microorganisms were decaying dying roots under the anaerobic conditions and plugging the xylem vessels.

Most of the evidence presented thus far has dealt mainly with observed response to general anaerobic conditions without explaining why the response occurred. Excellent work by Huck (1970), using soybeans and cotton, demonstrated root response to oxygen deficient soil air. Anaerobic conditions were established by replacing the original soil air with oxygen-free air therefore eliminating any soil moisture interactions. He found that within two to three minutes, root cell division and elongation halted when the oxygen-free soil air environment was established. Immediate recovery was observed if the oxygen was allowed back into the soil if only a short time period had elapsed. However, if oxygen was excluded beyond five hours for soybeans and three hours for cotton, root growth did not recover and root tips darkened and eventually died. If oxygen remained present after this had occurred, adventitious roots developed. Roots require oxygen for growth and it appears that lack of oxygen is the primary and most direct factor that causes root growth inhibition. All other factors which cause inhibited root
and top growth due to anaerobiosis seem indirect. Factors such as toxic material formation, soil chemical reactions, and soil physical changes are often triggered by the high moisture conditions as well as anaerobic conditions.

Grable (1966) suggested that long term detrimental effects of oxygen deficiency in soil on plant root systems are due to the degree of anaerobic respiration which occurs. This fermentation process produces only a fraction of the energy normally produced by aerobic respiration, thus growth is inhibited. Grable (1966) stated that short term injury can not be blamed on this lack of respiratory energy because a certain length of time is required for this energy depletion to occur. He postulated that short term injury could be linked to the formation of toxic compounds, such as ethanol, within the plant and that these toxic compounds occurred because of lack of oxygen to the root.

Lemon and Wiegand (1962) studied the oxygen requirement for plant respiration and stated four conclusions which came from their studies. First, the rate of oxygen uptake by roots varies with genetic background and age of tissue. This variation may be a factor in determination of the effects of oxygen deficient conditions on different species at different stages of growth. Second, when oxygen is plentiful in the soil atmosphere, the supply of other necessary compounds
determines the reaction rate for respiration. Third, when the concentration of oxygen at the root surface is below critical levels, the diffusion process controls the rate of oxygen uptake by the roots. Fourth, critical oxygen concentrations at root surface are dependent upon the radius of the root and the diffusion coefficient of oxygen within the root. One can see from their work that the response of plants to low oxygen levels in the soil would change constantly as root system changes occur.

One important point stated by Lemon and Wiegand was that oxygen diffusion rates in the soil control root oxygen uptake at low oxygen levels. Letey et al. (1965) conducted extensive work relating oxygen diffusion rates to root and top growth. They established a relationship between oxygen diffusion rate (ODR) and root growth but not between ODR and top growth because of the variation of the oxygen diffusion rates with position in the soil and time. They concluded that, in general, root growth became limiting at rates of 10 x 10^{-8} g cm^{-2} min^{-1}. Maximum growth rates were observed at oxygen diffusion rates of 40 x 10^{-8} g cm^{-2} min^{-1}. Corn was able to grow in conditions lower in oxygen than plants such as cotton, bluegrass, or sunflowers. Tolerance to low oxygen conditions may be related to the ability of the plant to transport oxygen absorbed by top portion of plants to the
roots so that the requirement for externally supplied oxygen from the soil is lower.

Williamson (1964), using corn, sorghum, and soybeans, concluded that the volume of soil in which the roots were growing possibly had an effect on the oxygen diffusion rates that were required for growth. He suggested that for restricted soil volumes, a high rate of oxygen diffusion would be necessary to supply the required oxygen to the roots. In an unrestricted soil volume, however, the root system would be distributed over a large volume of soil, so that, logically, a lower rate of oxygen diffusion should supply adequate amounts of oxygen to the roots. He, also, found that corn and sorghum yields were at maximums at the same oxygen diffusion rates, although sorghum was hurt less (yield-wise) at lower rates. Follett et al. (1974) found that oxygen diffusion rates of $26 \times 10^{-8} \text{g cm}^{-2}\text{min}^{-1}$ limited corn root growth.

Cline and Erickson (1959), using very shallow water tables, showed that pea growth was related very well to the oxygen diffusion rates found in the later growth stages, but not during early growth. They attributed their response to possible different oxygen sensitivities at different growth stages, particularly late stages.

Thus far, all citings that involve oxygen diffusion rates have used the platinum microelectrode method of
measurement. This method estimates oxygen diffusion to root surfaces by measuring electrical oxygen current flow between a platinum and a reference electrode. Current is proportional to the rate of oxygen reduced at the platinum electrode, so the oxygen diffusion rate can be calculated from the measured electric current. Many factors can affect the technique and, therefore, one must be careful when analyzing results. Birkle et al. (1964) presented an excellent review on the factors which affect ODR measurements.

The physical presence of water in high soil moisture situations, also, can have a direct detrimental effect on root growth. Roots can become watersoaked and internal root air spaces can become filled with water. As a result, internal root aeration rates become drastically reduced. This condition can cause reduction in root water uptake as observed by Glinka and Reinhold (1962).

Plant hormonal activities may change upon imposition of anaerobic and high soil moisture conditions. Phillips (1964a) suggested that the root system may serve as the center for the oxidative inactivation of excess shoot-synthesized auxin and thereby regulates shoot auxin levels. He showed that some early effects of flooding on plants were elevated shoot auxin levels and a blockage in the formation of non-auxin shoot growth hormone by roots. This effect could cause plant growth to be greatly changed because of excess auxin
In another study, Phillips (1964b), found that auxin levels in shoots increased substantially when waterlogged for fourteen days but then auxin levels dropped to the control levels. He postulated that the rise in auxin concentrations in shoots was due to the cessation of auxin movement to the roots, or to the inhibition of oxidation of shoot synthesized auxin in root tissue. This occurred as a result of the reduced movement of auxin from shoot to root. A rise in root levels of auxin were, also, observed and he suggested that this was possibly a result of an accumulation of root-synthesized auxin, or the inhibition of the oxidation of shoot-synthesized auxin in the roots, or a combination of both.

Gibberellic acid levels and transport also may be affected by waterlogged conditions. Reid et al. (1969) showed that tomato plants grown in a waterlogged soil exhibited reduced gibberellic acid transport from the roots to shoot through the xylem. This reduced transport resulted in inhibited stem growth above. Reid and Crozier (1971) detected an accumulation of gibberellic acid in shoots after three to four days of flooding. They suggested that this accumulation was due to the plant's ability to form adventitious roots after the flooding and that these roots were supplying the gibberellic acid to the shoots. Some applied gibberellic acid was
used at different stages of flooding and it was observed that, when applied at early flooding, the gibberellic acid caused a stimulation of growth, but when applied at late flooding, no stimulation of growth was found. They concluded, therefore, that at late stages of flooding, factors other than reduced gibberellic acid transport were inhibiting growth.

Ethylene, as mentioned earlier, is a hormone which seems to become present in substantial quantities when anaerobic conditions exist. Much work has related ethylene levels in the soil and plant to plant and root responses. Smith and Jackson (1974) discuss evidence concerning root response to high levels of ethylene. Inhibition of root elongation, and promotion of root primordia and of root hairs are some of the apparent ethylene effects.

Ethylene accumulates in both top and root portions of the plant when grown in a waterlogged soil. Kawase (1976) observed five-fold increases of ethylene concentrations for sunflowers when waterlogged conditions were established. When the water was removed, the concentrations decreased. He postulated that ethylene accumulation may occur because its escape is blocked by the physical presence of water. Kawase (1972), also, observed increases of ethylene concentrations in submerged horticultural plants.
Jackson and Campbell (1975) found that waterlogging caused leaves and shoots of tomato plants to contain high concentrations of ethylene and that these concentrations were instrumental in causing epinastic growth of petioles. They also found that the waterlogged soil itself developed high concentrations of ethylene, probably formed by microbial action. Ethylene movements within the plant were measured using $^{14}$C-labelled ethylene. The measurements showed that ethylene can move quickly from roots to shoots and that the movement probably occurs in a manner other than the transpirational stream. They also observed that adventitious root development seemed to be promoted by ethylene.

Crossett and Campbell (1975), working with barley, concluded that both shoot and root growth were reduced by ethylene present in soil air. They observed that seminal root extension became inhibited, while lateral root growth was stimulated by ethylene. Ethylene did not seem to affect ion absorption rates, however. If the ethylene was removed from the soil, seminal root growth increased. This increase was greater for short term exposure to ethylene than for long term. Lateral root growth stopped upon ethylene removal. Split-root studies showed only those roots in contact with ethylene in the soil were affected.

El-Belatagy and Hall (1974) worked with both excessive and deficient soil water situations and found that ethylene
concentrations in broadbean plants greatly increased for both situations. They concluded that the increases were a result both of decreased diffusion and increased synthesis of ethylene. This activity was superimposed on normal diurnal fluctuations of internal ethylene concentrations. In addition to reduced growth rates, they found that high concentrations of ethylene were correlated with increased leaf and flower abscission and senescence.

Smith and Russell (1969) used different concentrations of ethylene in the soil air to determine the actual amounts which cause different rates of root elongation. They found that 10 ppm completely inhibited root elongation, 1 ppm inhibited elongation by 50%, and only slight effects were detected at 0.1 ppm. Concentrations of 10 ppm are commonly found in soils in an anaerobic state. Smith and Russell also observed clumps of root hair development at high concentrations of ethylene in the soil. Measurements of oxygen and carbon dioxide tensions in the soil showed that both affected the ethylene influence.

Kawase (1974) grew sunflowers under submerged conditions and found that ethylene concentrations increased in stems and roots. He also observed initiation of hypocotyl hypertrophy and new root formation in the hypocotyl as a result of the flooded conditions. He found a high correlation between the concentration of ethylene present and hypocotyl diameter.
Other correlations were observed between ethylene concentrations and chlorophyll breakdown, epinasty of leaves, and number of roots initiated.

Phytotoxic substances which are produced by soil reactions or microbial actions cause detrimental effects on plant root and top growth. Plants synthesize some phytotoxic substances themselves in response to anaerobic and high soil water conditions. Fulton and Erickson (1964) found that the oxygen diffusion rates below $38 \times 10^{-8} \text{gm cm}^{-2}\text{min}^{-1}$, caused tomatoes to synthesize ethanol. Very small decreases of the oxygen diffusion rates were observed to cause large increases of ethanol to be produced. They also observed that plants in reproductive stages produced more ethanol than plants in non-reproductive growth stages. Crawford (1967) also measured increases in ethanol production by plants growing in anaerobic conditions. He found that species which were less tolerant of the anaerobic conditions produced the highest quantities of ethanol.

In studies where soil profiles were kept partially anaerobic by varying the water table depths, differences in responses occur depending on the type of soil used and the plant species. Hiler et al. (1971) observed large differences in yield of sorghum when differing water table depths were used. Yields were reduced when plants were grown in soil with 30 and 60 centimeter water tables as opposed to 90 and
120 centimeter water tables. Rai et al. (1971) used water table depths of 15, 30, and 45 centimeters from the soil surface and found that alfalfa yields were greatest when the water table was at 45 centimeters. Ralston and Daniel (1972), however, found that similar water tables' depths caused no differences in growth of creeping bentgrass.

Williamson and Willey (1964), using 22, 42, and 75 centimeter water tables, concluded that overdrainage of tall fescue would cause yield reductions if no water was added from the surface. The yields from the 75 centimeter treatment were significantly lower than the other. Root distribution patterns were greatly affected by the presence of the water tables. In the 22 centimeter water table treatment, for example, root development was most extensive in the top 10 centimeters due to aeration problems below.

Williamson (1968) concluded that water table depth was important in determining plant response but that the method of watering also played a role. He used both surface and subsurface watering and found that stringbeans, when growing in a soil with a 15 centimeter depth water table without surface watering, yielded one-half the yields of those plants grown in soils with 60 - 75 centimeter water tables and with supplemental surface watering. When both a 15 centimeter water table and surface watering were used, there was no
yield from the plants. High yields were observed in
the 30 centimeter water table without surface watering treat­
ment.

Letey et al. (1962) stated that differences in plant
response to anaerobic conditions may be observed at different
stages of growth. A growth stage factor may play a role in
determining how a plant responds to anaerobic conditions and
how further development will be affected. A plant may be
more tolerant to low oxygen levels in the soil at certain
growth stages. Cannell et al. (1977) found that pea plants
are more sensitive to waterlogging at late growth stages.
Watson et al. (1976) found that waterlogging at early growth
stages caused greater yield reductions for barley, wheat,
and oats than at later growth stages.

Rai et al. (1971) observed no differences between yields
for alfalfa grown in soil with high and low water tables
when the water tables were established 2 - 4 weeks after the
first harvest. If the water tables were raised just after
harvest, significant decreases in yields were measured for
alfalfa growing in soil with the shallow water table (15
centimeters). Aleksandrova and Skazkin (1964) found that
barley yield was reduced 50 - 70% when flooding occurred at
flowering while reductions of 0 - 50% were observed when the
plants were flooded at heading.
Different degrees of tolerance to anaerobic conditions have been observed among plant species. Different types of plant mechanisms which allow tolerance determine the degree to which plants will withstand anaerobic soils. One such trait is the ability of a plant to develop adventitious roots in soil areas where total anaerobic conditions do not exist. Went (1943) observed that if some portion of a root system is not affected by the anaerobic conditions and if this portion is sufficiently large, it can provide enough water and nutrient uptake to keep the plant growing normally. Kramer (1951) showed that plant species with the ability to develop adventitious roots undergo less damage caused by anaerobic conditions. This rooting ability may be controlled by hormonal changes within the plant caused by the lack of oxygen.

Organic metabolism within plants can be an indicator of tolerance to flooded conditions. Crawford and Tyler (1969) observed that malic acid accumulated in plant species which were flood tolerant and decreased in intolerant species. The significance of these changes is not fully understood, but perhaps plant metabolic changes occur which cause alternative pathways of biochemical reactions within the plant to be followed which, in turn, causes tolerance of the flooded conditions. Tyler and Crawford (1970) also found that levels of shikimic acid were higher in plant roots growing in flooded
conditions than roots growing in aerated soil. Again, they concluded that a possible alternative pathway for metabolism was occurring which resulted in physiological adaption to the anaerobic conditions.

Most plants which are tolerant of high soil moisture conditions have large amounts of aerenchyma tissue which are present in both shoots and roots. These tissue are composed of continuous air spaces which may allow transfer of oxygen absorbed by the shoot to roots, thus, less oxygen is needed from the soil by the roots. Barber et al. (1962) measured internal air spaces in rice and barley roots and found that in rice roots, air space accounted for 5 - 30% of the total internal space. This evidence was related to the degree of tolerance each plant species exhibited for flooded conditions. This comparison showed a possible reason that rice was very much more tolerant than barley. They also detected oxygen movement shoots to roots in both species. Van der Heide et al. (1963) suggested that barley may have some degree of ability to adapt to flooded conditions by developing large intercellular spaces which then allow oxygen transfer from shoots to roots.

Many plants have shown some adaptive ability to tolerate high soil water conditions by exhibiting the ability to change root permeability to water uptake. Glinka and
Reinhold (1962) concluded that this ability prevented water-logging of internal root air spaces and the damage that could result because of it.
PART I. EFFECT OF DIFFERENT LEVELS OF STATIC WATER TABLES ON TOP AND ROOT GROWTH OF SOYBEANS
OBJECTIVES OF STUDY

This study was conducted to observe effects on root and top growth of soybeans (*Glycine max* (L.) Merr.) caused by different static water table situations. Specific objectives of the study were to:

1) describe root growth and distribution patterns for soybeans grown under static water tables of different levels;

2) determine effect on soybean top growth and yield for these different water table situations;

3) describe carbon dioxide, oxygen, and ethylene concentrations in the soil atmosphere at distances away from the free water level throughout the growing season and relate these concentrations to root growth;

4) describe mid-season water use differences as caused by the different water table levels;

5) determine if temperature gradients existed in the soil profile and relate the resultant temperatures to root growth and distribution.
MATERIALS AND METHODS

This study was carried out during the summer of 1976 in an underground root observation laboratory (rhizotron) located five miles southwest of Iowa State University at Ames, Iowa. The rhizotron consists of 50 separate compartments of the dimensions 38 cm x 38 cm x 215 cm deep. Concrete walls provided support for compartment liners. Three walls and the floor of each liner was sheet metal welded together, and the fourth wall was a sheet of 1.25 centimeter acrylic plastic bolted and sealed on to the steel walls. The inside steel walls were coated with fiberglass to prevent oxidation of the steel and any chemical reaction with the soil.

The entire facility consisted of 25 compartments on each side with a one meter walk-way between. The top of each compartment was flush with the soil surface, making the bottom of the facility nearly 225 centimeters below the soil surface.

Each compartment had approximately 5800 cm² of viewing area. The shallowest depth that roots could be observed was 30 centimeters. The acrylic plastic viewing wall of each compartment was scribed in five centimeter depth increments to facilitate root growth measurements.

The rhizotron was constructed in a field location to enable experiments within to grow in a field environment.
while still maintaining a laboratory situation. Figure 1 shows how the rhizotron appeared in the field with surrounding border rows. The row width between compartment rows and border rows was 76 centimeters. The row of soybeans directly over the walk-way was necessary to assure normal growth. The entire rhizotron plot area dimensions were 20.6 x 30 meters.

The soil type of the surrounding area was Nicollet loam (fine-loamy, mixed, mesic Aquic Hapludolls). The soil type used in the rhizotron compartments was Sparta loamy fine sand (sandy, mixed, mesic Entic Hapludolls). Soil of this type was taken from the top 15 centimeters of a soil profile and was screened through 1.25 centimeter mesh to remove debris. No attempt was made to reconstruct the natural soil profile. This soil type was used because of its high hydraulic conductivity which permitted easier maintenance of the water tables. The entire soil profile of each compartment was flooded and then drained before the water table treatments were established. Final bulk densities for the compartment soil columns ranged only from 1.33 g/cm$^3$ to 1.38 g/cm$^3$ indicating a fairly uniform degree of compaction at all depths.

Each compartment was planted with four "Wayne" soybean seeds on May 27, 1976 and was thinned to two plants per
Figure 1. Rhizotron field plot diagram
compartment at seedling stage. This resulted in a planting density of approximately four plants per meter of row. The surrounding border area was planted at a rate of approximately fourteen plants per meter of row. A subsequent experiment showed that different plant populations in the border rows had no effect on the growth of the plants. The border rows were planted in rows of six different cultivars, including "Wayne", because other studies were being conducted in the border areas.

Water tables were established at 75, 105, and 150 centimeter distances below the soil surface. Two replications were used. A fourth treatment had no water table, again with two replications. The water tables were maintained by use of constant head devices. Water from a large reservoir maintained water level in a lower reservoir. Whenever water was used, the compartment water table was lowered and water from the lower reservoir was fed in at the bottom of the compartments through porous tubes embedded in the soil and connected to the acrylic plastic wall. An overflow tube was, also, used to insure that the water table did not rise above the control level during rainstorms.

Root growth was measured three times weekly throughout the growing season. Roots were counted at the visual intersections of roots with the scribed depth lines on the acrylic plastic viewing area. Counts were taken at 15 centimeter
intervals beginning with the 30 centimeter depth level. These counts were taken as a frequency count which could estimate relative amounts of roots at certain depths and could be compared to other depths in the compartment. No actual root lengths were estimated from this procedure because of possible effects of the acrylic plastic surface on root concentration (Taylor and Böhm, 1976). Also, the depths to which the deepest visible root had penetrated at the time of measurement was recorded and used to describe rooting penetration rates.

Stage of growth and plant heights were measured three times weekly throughout the growing season. The stage of growth description developed by Pehr et al. (1971) was used. Plant heights were measured at the uppermost node of the soybean plants.

Water use was measured by recording the amount of water that had to be supplied by the water table reservoir to maintain the water table at the controlled level. Because the upper profile was moist at planting, measurements were unimportant until midseason when virtually all of the water that the plants were using could be estimated from the amount of water that was supplied by the constant head devices. Very little precipitation occurred during the growing season so that error caused by addition of water from above was avoided.
Temperatures at different depths in the soil columns were measured using thermocouples and a potentiometer. The temperatures were measured at 10 centimeter increments above the water table levels. In the no-water-table treatment, the thermocouples were placed at the 45, 70, 100, 125, and 145 centimeter depths.

Oxygen, carbon dioxide, and ethylene components of the soil atmosphere were measured at weekly intervals throughout the growing season. Syringe septa were placed at the same depths as the thermocouples described earlier were. Gas-tight syringes were used, taking two milliliter samples from each depth and then were immediately transferred to a laboratory at Iowa State University. Analysis was carried out by using a gas chromatograph to determine individual gas amounts.
RESULTS AND DISCUSSION

The overall results from the static water table study indicated that the water table treatments used in the study caused small differences between treatments for top growth and developmental response. However, a definite effect on root growth and distribution was observed.

Figure 2 illustrates normal root distribution for "Wayne" soybeans grown in an irrigated rhizotron compartment. After normal progression downward of root penetration in the early season, the roots became relatively evenly distributed between 60 and 195 centimeters below the soil surface for the remainder of the growing season.

Root penetration of the plants in the irrigated treatment are shown in Figure 3. Root penetration rates were somewhat steady until the bottom of the compartments was reached (about 216 centimeters). Average root penetration rates were 4.2 centimeters per day for the irrigated treatment.

Figure 4 illustrates the dramatic effect of a water table on root growth. The figure shows root penetration for the three water table treatments and an indication of the location of the different water tables. Since use of the rhizotron restricts viewing of root growth above 30 centimeters, root penetration observations began rather abruptly whenever the first visible root appeared.
Figure 2. Root distribution pattern progression for irrigated no-water-table treatment throughout the growing season. Roman numerals represent averages of two measurement periods (dates shown in parentheses below)

I (6/20 to 6/24) VI (7/18 to 7/20) XI (8/10 to 8/12)
II (6/27 to 7/01) VII (7/22 to 7/25) XII (8/15 to 8/17)
III (7/05 to 7/06) VIII (7/27 to 7/29) XIII (8/19 to 8/22)
IV (7/08 to 7/11) IX (8/01 to 8/03) XIV (8/24 to 8/26)
V (7/13 to 7/15) X (8/05 to 8/08) XV (8/29 to 8/31)
XVI (9/02 to 9/07)
ROOT INTERSECTION COUNTS

DEPTH IN SOIL PROFILE (cm)

IRRIGATED - NO WATER TABLE TREATMENT
Figure 3. Maximum rooting depth progression for irrigated and non-irrigated no-water-table treatments throughout the growing season.
DAYS FROM PLANTING

MAX ROOTING DEPTHS
NON-WATER TABLE TREATMENTS

AVE MAX ROOTING DEPTH (cm)

- IRRIGATED
- NON-IRRIGATED
Figure 4. Maximum rooting depth progression for high, middle, and low static water table treatments throughout the growing season.
DAYS FROM PLANTING

- HIGH WATER TABLE (75cm)
- MID WATER TABLE (105cm)
- LOW WATER TABLE (150cm)
Considering the low water table treatment (150 centimeters) first, steady root penetration rates occurred early in the growth cycle, ranging from 4.4 to 5.5 centimeters per day (Figure 4). This rate continued until the roots had penetrated to within ten centimeters of the water table level. At this point, root penetration rates greatly slowed to about 0.26 centimeters per day. Eventual penetration of two centimeters into the water table apparently occurred.

Comparison of these root penetration characteristics to those of the no-water-table treatment show little differences up to the point where roots in the low water table treatment penetrate into areas close to the water table level. Root penetration rate differences do exist, however, with the roots in the water table treatment penetrating at a slightly faster rate. The irrigated plants' rates may be slower because of the surface water procedure that supplied moisture to the top soil layers. This may have caused deep root penetration that was related to the plants' need for water uptake from the lower depths to be less since plentiful water was available in the top layers. This seems to be evident in Figure 3 when the comparison of the irrigated treatment to a no-water-table, unirrigated treatment is made. Since water becomes limiting in the upper layers of the soil for the unirrigated treatment because of depletion by the plants, root penetration occurred at a faster rate and to deeper depths because of the plants'
need for water.

The big difference between the root penetration rates of the irrigated versus the low water table treatment is the root response to the presence of the free water in the latter treatment.

Root distribution, also, is affected greatly by the water table's presence. A comparison of the root distribution patterns for the low water table treatment (Figure 5) versus the no-water-table treatment (Figure 2) shows similarities until the presence of the water table began to influence the roots in the low water table treatment. Once downward root penetration had essentially halted, massive numbers of roots (relative to the numbers observed at shallower depths) began to appear at depths 15 to 30 centimeters above the free water level. Little change in root distribution was observed at the upper levels. The evenly distributed pattern of the irrigated treatment does not seem to occur if a strong source of water for root water uptake is present. The effect of the water table seems two-fold. An inhibition effect which prevents deep root penetration below the level to which the water table was established, seems to be coupled with a beneficial effect of providing a source of water for plant growth.

Comparison of the root penetration occurring in the middle water table treatment (105 centimeters) shown in Figure 4, seems to show a somewhat similar response to the low water
Figure 5. Root distribution pattern progression for low static water table level (150 cm) throughout the growing season. Roman numerals represent averages of two measurement periods (dates for each period are shown below)

<table>
<thead>
<tr>
<th>Roman Numeral</th>
<th>Dates</th>
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<tbody>
<tr>
<td>I</td>
<td>6/23 to 6/25</td>
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<td>VIII</td>
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<td>XIII</td>
<td>8/18 to 8/20</td>
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<tr>
<td>XIV</td>
<td>8/23 to 8/25</td>
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<tr>
<td>XV</td>
<td>8/27 to 8/30</td>
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</table>
LOW STATIC WATER TABLE LEVEL (150cm)
table treatment except that the inhibiting effect of the water table occurs sooner. Penetration rates are slower, also, than either those of the low water table or the irrigated treatment. A penetration of about 3.9 centimeters per day occurred until the roots grew to within 20 centimeters of the water table level. Rates for the rest of the season then ranged from 0 to 0.3 centimeters per day.

Again, root distribution patterns were altered from normal by the water table’s presence as shown in Figure 6. Similar root distribution patterns as compared to the irrigated treatment occurred in the early season, but, once again, as the roots grew near the water table level and appreciable downward growth stopped, large numbers of roots appeared in areas just above the free water level. Little change in root numbers was observed at the upper soil levels except at 30 centimeters where new root growth in the late season may have been caused by late summer rains.

Root penetration in the high water table treatment (75 centimeters) was hardly detected before the water table began to influence its rate (Figure 4). When it was measured, the penetration rate was very slow (about 0.6 centimeters per day) until penetration came to within 10 to 15 centimeters of the water table level. Penetration rates of 0 to 0.1 centimeters per day were observed for the remainder of the growth cycle.
Figure 6. Root distribution pattern progression for middle static water table level (105 cm) throughout the growing season. Roman numerals represent averages of two measurement periods (dates for each period are shown below)

I (6/23 to 6/25)   VI (7/16 to 7/19)   XI (8/09 to 8/11)
II (6/28 to 6/30)  VII (7/21 to 7/23)  XII (8/13 to 8/16)
III (7/02 to 7/05) VIII (7/26 to 7/28) XIII (8/18 to 8/20)
IV (7/07 to 7/09)  IX (7/30 to 8/02)   XIV (8/23 to 8/25)
V  (7/12 to 7/14)  X  (8/04 to 8/06)  XV (8/27 to 8/30)
The influence of the high water table causing restricted soil rooting volume for the plant seems very evident from the rooting patterns as shown in Figure 7. Massive root growth occurred in the areas just above the water table level as can be seen by the high root counts observed at the 60 centimeter level. These high numbers may be a result of the restricted volume of soil in which rooting can take place. Root growth that would have occurred at deeper depths, seemed to occur at the deepest depths possible as dictated by the position of the water table. Since water uptake from this area was not limiting, an accumulation of roots occurred.

Obvious differences exist between the three water table treatments for root response. Most obvious is the depth to which roots penetrated in response to the height of their respective water table. The penetration rates, also, differ between treatments. Apparently, the deeper the water table, the faster the penetration rate down to a distance of 15 to 20 centimeters from the water table level. The upper water tables seem to influence root penetration at distances further away from the free water level than does the deep water table, causing slowed penetration rates sooner.

Root distribution patterns are similar between water table treatments in that all showed increased root development at depths near the water table level. Differences exist, however, in the numbers of roots that do appear. In the low
Figure 7. Root distribution pattern progression for high static water table level (75 cm) throughout the growing season. Roman numerals represent averages of two measurement periods (dates for each period are shown below)

I (6/23 to 6/25)  VI (7/16 to 7/19)  XI (8/09 to 8/11)
II (6/28 to 6/30)  VII (7/21 to 7/23)  XII (8/13 to 8/16)
III (7/02 to 7/05)  VIII (7/26 to 7/28)  XIII (8/18 to 8/20)
IV (7/07 to 7/09)  IX (7/30 to 8/02)  XIV (8/23 to 8/25)
V (7/12 to 7/14)  X (8/04 to 8/06)  XV (8/27 to 8/30)
HIGH STATIC WATER TABLE LEVEL (75cm)
water table treatment, high numbers of roots were observed at distances up to 30 centimeters away from the water table level. In the middle water table treatment, high numbers of roots were observed only at distances within 15 centimeters of the free water level and not nearly as high in magnitude as numbers observed in the high water table treatment the same distance away from the water table level. The great numbers of roots observed at the 60 centimeter level in the high water table treatment can be attributed to the increased restriction of soil rooting volume caused by the water table height.

Although differences between treatments in relation to root growth response did exist, the same factor which affected downward root growth probably affected all treatments. Factors such as soil moisture content, aeration, gaseous composition of the soil air, and soil temperature, as well as soil changes which may have caused toxic substance production all must be considered. Probably the most important factor controlling the root response was the soil aeration caused by the high amounts of water present. Roots must have oxygen in order to grow normally. When water fills the soil pore spaces, oxygen is moved out of the soil atmosphere and growth becomes inhibited as what oxygen that remained trapped in the soil becomes depleted. The degree to which this will occur in the soil areas above a water table depends upon the type of soil.
Capillary action of the soil lifts water from the free water level and causes soil water contents to become very high in areas above the water table. This phenomenon would be observed to a greater degree in poorly aggregated soils containing high amounts of clay. This increased amount of water causes more of the pore space to be occupied by water and, thus, less oxygen is available to the roots for continued growth.

Anaerobic conditions can be conducive to ethylene production in the soil. Ethylene has been shown to possess inhibitory effects on root and top growth. To detect oxygen and ethylene concentration changes, as well as carbon dioxide changes, gas samples were taken from the soil of each treatment at various distances above the water tables' levels. Attempts were made to analyze these samples to describe the gases' effects on top and root growth. Many problems were encountered using gas-tight syringes to take the samples. Because samples were taken directly from the soil, soil particles often plugged the needles. Also, since many of the areas sampled were high in soil moisture, water was pulled into the needles. Attempts were made to eliminate these problems by insertion of small plastic tubes at each level from which samples were to be taken. This technique seemed to be somewhat successful until water seeped into the tubes and caused the original water-in-the-syringe problem to reoccur. With all the problems, erratic, low-reliability results were
obtained and the data were not included in the study analysis.

Results from other studies show what might have occurred. Smith and Dowdell (1974) showed clearly that direct relationships exist between high soil moisture contents and the production of ethylene and the depression of oxygen levels in a sandy loam soil. It can be assumed, therefore, that certainly oxygen levels decreased and some probable ethylene production occurred in this study as a result of the water tables' presence. The degree to which these changes affected total plant growth may be different than in some other studies. Jackson and Campbell (1975) showed that ethylene production caused epinastic growth of top plant parts to appear for plants growing in a waterlogged soil. No ill effects were observed for top growth in this study, so if one assumes that some ethylene was produced, it was not present in high enough amounts to affect top growth. However, inhibition of downward root growth was evident and possibly can be attributed, at least in part, to ethylene production.

Lack of oxygen present in the soil atmosphere probably contributed the most to the inhibition of downward root growth. Letey et al. (1962), Williamson (1964), and Lemon and Wiegand (1962) all provide evidence to support this statement. Bryant (1934) and Jackson and Campbell (1975) noted that when conditions become oxygen limiting, some adventitious or
secondary root development occurs. This fact, along with the restriction of soil rooting volume and favorable soil moisture conditions in areas above the water table levels, may explain why large numbers of roots developed in soil areas just above the water tables.

No effects on top growth caused by any water table treatment were observed. Figure 8 illustrates plant height progression for each of the three water table treatments. Data for the irrigated treatment were not included in the figure, but virtually no plant height differences were observed between irrigated and water table treatments. Stage of growth measurements were made and, again, no significant differences were observed. A harvesting error precluded yield measurements.

Water use was measured for each water table treatment during the middle part of the growing season to establish whether or not the water table treatments caused root water uptake to be affected. Water use was estimated from the amount of water supplied daily by each water table reservoir to its respective compartment. Valid estimates could not be made in this manner in the early season because most of the water then being supplied to the plants came from moisture present in the upper layers of the soil. Once this moisture source became effectively depleted, most of the water that was used came from the water tables. Virtually no rainfall occurred
Figure 8. Plant height progression for the three static water table treatments throughout the growing season
during most of the growing season, so no water was added to the soil profile from the top that would cause errors to this method of estimation. Figure 9 shows the water use patterns for the three water table treatments throughout the growing season. Water extraction from the water table takes place first in the high treatment, followed a week later in the middle treatment, and two weeks later in the low treatment.

Amounts of water used varied between treatments until about the 69th day after planting. From this point until the 111th day water uses showed only minor differences between treatments. After the 111th day, late season rainfall probably caused the differences in water uptake measured. Differences in day-to-day amounts used were affected primarily by the daily atmospheric demand for moisture differences. Such small differences in water uptake existed among treatments that no conclusion concerning the water table effects on this plant process can be drawn. Kramer (1951) concluded that one result of anaerobic soil conditions caused by high soil moisture was the reduction of root water uptake. If this reduction did occur in this study, it did so in the same magnitude for all water table levels. Most likely, the water table levels used in this study had little effect on root uptake inhibition, based on the unaffected growth of the top portion of the plants. The inhibition of root water uptake may become more evident, however, with extremely high
Figure 9. Daily water use amounts for each of the three static water table treatments throughout the growing season.
WATER TABLE AT 75cm
WATER TABLE AT 105cm
WATER TABLE AT 150cm

WATER USE (mL)

DAYS FROM PLANTING
water table or flooded conditions.

The use of the rhizotron for this particular study facilitated growth of the soybean plants under laboratory conditions in a field environment. It allowed constant monitoring of both above and below-ground growth parameters without disturbance. The use of this facility, however, created artificial conditions which must be discussed here.

First of all, the compartment size itself may have limited root growth as it would appear in the field because of the confinement of the width of the compartment. However, field studies dealing with confined rooting volumes caused by differing row widths and their effects on root penetration indicate that this may not be as much of a problem as one might suspect. Rooting volumes per plant in the rhizotron are comparable to rooting volumes per plant for plants growing with 40 centimeter row widths. No differences were found between 40 and 100 centimeter row widths in the field for rates of root penetration. (H. M. Taylor, Dept. of Agronomy, ISU, personal communication, 1978)

Another factor which is peculiar to the use of the rhizotron is the lack of temperature stratification with depth in the soil profiles in each compartment. This lack can affect root growth, distribution, and penetration data. Since a walkway exists between the two rows of compartments, the soil in the compartments tend to take on the same temperature as the
air temperature of the walk-way, uniformly throughout the soil columns. In some ways this fact can be used to an advantage. Since temperature is somewhat controlled, one can study other factors which affect growth without temperature interference.

Light must be used to illuminate the walk-way and to take root measurements. With the relatively short periods of time that the lights are on, even if an effect of the light on root growth existed, it probably should not make much of a difference. The light does sometimes promote algae growth, but this was rarely a problem.

The amount of light intercepted by the top portion of the plants probably was greater due to the lower plant population density. This may have caused effects different in magnitude from what would have happened in the field, but, differences between treatments in the rhizotron were compared directly between each other and not compared directly to a field situation.
CONCLUSIONS

This study showed that downward root penetration and distribution with depth was affected by the presence of a static water table. Inhibition of downward growth probably occurred primarily due to a lack of oxygen needed for root growth in soil areas affected by the water tables. Root distribution was altered by the water tables' presence, which caused large amounts of root accumulation in areas just above the free water levels. Little effect on root water uptake was observed among treatments. No effect on the top growth and development was observed for the water table depths used in this study despite the different soil rooting volumes that resulted from the different water table depths.
PART II. EFFECTS OF A TEMPORARY WATER TABLE SITUATION ON STEM GROWTH OF SOYBEANS
OBJECTIVES OF STUDY

This study was conducted to measure the effects of temporary water tables on subsequent stem growth of soybeans during and after the water tables were removed. Specific objectives of this study were as follows:

1) to determine the amount of time after the initiation of a water table before stem growth becomes affected by the presence of the water table;
2) to determine if rapid plant recovery is made after removal of water tables;
3) to determine oxygen diffusion rates of the soil immediately above and below the water table.
MATERIALS AND METHODS

A study was conducted in a growth chamber at Iowa State University during the winter of 1977 to determine shoot and root reactions at various times during imposition and after removal of a temporary water table.

“Wayne” soybean plants were grown in acrylic plastic tubes 7.6 centimeters in diameter and 122 centimeters long, one plant per tube. The tubes were filled with Sparta loamy fine sand (sandy, mixed, mesic Enti Hapludolls), screened through 1.25 centimeter mesh. The tubes were wrapped with aluminum foil to prevent algae growth. The plants were grown in a greenhouse provided with supplemental lighting until the vegetative growth stage reached V8 (Fehr et al., 1971). The plants were then transferred to a growth chamber where the experimental measurements were carried out. The growth chamber lights were operated on a 14-hour daylight period and a 10-hour night period. Temperature was kept at a constant 22°C.

A 50 centimeter water table depth was used in the study. Only two tubes per treatment were used because of limited equipment for stem diameter measurements. Constant head devices as described in Part I were used to maintain the water table at the 50 centimeter depth. Four days after initiation of the water table treatment, one tube was
relieved of the water table while the other continued for four more days. One treatment without an imposed water table was also used.

Stem diameter measurements were taken on each plant continuously throughout the experimental period and stem diameter gains or losses were recorded each day. These measurements were obtained using extremely sensitive linear variable displacement transducers (LVDT). One LVDT was attached to each plant at the stem base using a special supporting apparatus. The method and apparatus used are described by Klepper et al. (1971). The supporting apparatus allowed detection of expansion and contraction of the stem during diurnal periods as well as long term stem diameter expansion. These expansions and contractions were sensed by the LVDT's and amplified electronically and graphically on a strip chart recorder.

Oxygen diffusion rates were measured daily one week prior to the imposition of the water table. The method used is described by Letey and Stolzy (1964) utilizing 22-gauge platinum microelectrodes. Measurements were taken five times during the experiment after the water table had been imposed. Both -0.65 and -0.8 volt potentials were used.
RESULTS AND DISCUSSION

Figure 10 shows accumulative daily gain of stem diameter as a function of time for the two plants affected by the water table and for the no-water-table treatment. Daily gain rates were steady although different from each other prior to the imposition of the water table. Plant #1 (8-day treatment) showed a gain rate of about 0.08 mm/day, while Plant #2 (4-day treatment) showed a gain rate of about 0.04 mm/day. Plant #3 (no-water-table) showed a gain rate of about 0.15 mm/day. These differences may be due to unequal conditions prior to the water table imposition or may be due to differences in stem sizes when the measurements began. Nonetheless, changes in the stem diameters after the water tables were imposed are strikingly similar.

On Plant #1, the water table was imposed on day 7 and continued to day 15. The plant stems continued to increase in diameter for about two days then began levelling off to a gain of 0 to 0.01 mm/day.

On Plant #2, the water table was imposed for 4 days (days 7 through 11) and then was removed. It continued to grow for two days after water table imposition, then growth ceased for one day. The stem diameter then decreased for two days, and finally levelled off at a smaller diameter until the end of the experiment.
Figure 10. Accumulative stem diameter gains for the 4-day water table, 8-day water table, and no-water-table treatments.
The plant which had no water table treatment imposed on it continued at or near a gain rate of 0.15 mm/day for the entire experiment. The fact that stem diameter linearly increased with time during the experiment provides evidence that the water tables affected growth in the other two treatments.

Stem diameter diurnal fluctuations have been shown to be related to changes in the water status of a plant in short term periods, and to changes in growth in gains made over long term periods (Klepper et al., 1971). Since water uptake affects growth directly, any decrease in needed water uptake will affect the growth rate.

In this study, it was shown that stem diameter growth rates decreased markedly when the water table treatment was implemented as opposed to plant reaction to no water table treatment at all. Plant water uptake was probably being inhibited and this, in turn, decreased stem growth rates.

Since much of the root system of the plants was below the water table, it must be assumed that the lack of an adequate amount of oxygen present for normal root functions was caused by the presence of free water in the soil pore spaces. This lack of oxygen, in turn, affected root function, especially water uptake.

Oxygen diffusion rate measurements showed that at and below the water table level, oxygen diffusion was essentially
zero. With increased distances upward from the water table level, oxygen diffusion rates ranged from 6.0 to 19.2 x 10^-8 \text{ gm cm}^{-2} \text{min}^{-1} from 2 to 10 centimeters above the free water level, respectively. Williamson (1964) showed that for soybeans, oxygen diffusion rates below 15 to 20 x 10^-8 \text{gm cm}^{-2} \text{min}^{-1} reduced yields. Several studies have shown that generally oxygen diffusion rates in the range of 20 to 30 x 10^-8 \text{gm cm}^{-2} \text{min}^{-1} and below, limit root growth depending, of course, on the plant species. The oxygen diffusion rates obtained in this study, even at the higher rates, probably had a detrimental effect on normal root activity and subsequent stem growth.

This study showed that imposition of a water table for as few as two days probably caused some effect on root function because stem growth slowed at that time. Oxygen diffusion rates were lower than rates generally accepted as being required for normal root growth and function, at least to 10 centimeters above the water table level. No recovery from the effects of the water table treatment on stem growth was observed when the water table was removed after four days.
PART III. EFFECTS OF TEMPORARY WATER TABLES IMPOSED
AT DIFFERENT GROWTH STAGES ON SUBSEQUENT
ROOT AND TOP GROWTH OF SOYBEANS
OBJECTIVES OF STUDY

This study was conducted to observe and measure effects of temporary water table treatments imposed at different stages of growth on subsequent top and root growth of soybeans. Specific objectives of the study were to:

1) determine top and root growth responses to temporary water tables imposed at different stages of development;

2) determine if, and to what degree, root tolerance of, or inhibition by, the temporary water tables is related to stage of growth, amount of root system affected, and possible soil-plant interactions occurring in response to the water table conditions;

3) determine the ability of plant root systems to recover from adverse conditions caused by the different water table treatments;

4) determine oxygen diffusion rates at which soybean root growth becomes inhibited.
MATERIALS AND METHODS

This study was carried out during the summer of 1977 on a research farm located five miles southwest of Iowa State University at Ames, Iowa. This study once again used the rhizotron which was described in Part I.

The compartments used in this study were filled with Sparta loamy fine sand which was screened through 1.25 cm mesh to remove rocks and other debris. No effort was made to reconstruct any natural soil profile when the soil was screened into the rhizotron compartments.

The soybean cultivar "Wayne" was used to maintain consistency with results of earlier studies. Wayne is a non-determinate soybean of maturity group III. It is a full canopied, wide leaf cultivar, with a fairly flat leaf orientation that causes a relatively closed canopy. Each compartment was planted with four seeds and thinned to two plants at seedling stage.

The experiment consisted of imposition of two different water table levels (45 cm and 90 cm below the soil surface) on compartments which had not been previously affected by a water table during three different stages of growth of the soybeans. The length of time that the water tables were maintained at the desired level was one week. After this period the water was allowed to drain until all water in
the compartment was at negative water potential. Two no-water-table treatments were also used. One was adequately watered frequently throughout the growing season and one was watered only by natural precipitation. Each of the eight treatments had three replications. Thus, 24 compartments were used in the study.

The growth stages (Fehr et al., 1971) at which the water tables were imposed were as follows: 1) pre-flowering vegetative growth stage (V3-V10), 2) post-flowering pre-pod set growth stage with continued vegetative growth and initial reproductive growth (R2), and 3) post-pod set growth stage (R4).

Water tables were established by allowing water to enter through a porous tube connected to the acrylic plastic wall inside the compartment. An indicator tube, connected to another porous tube in the bottom of the compartment, was placed along the side of the compartment so that one could readily determine location of the water level at any particular time.

Water was obtained from a reservoir located outside of the rhizotron. The reservoir was a 250-liter barrel suspended approximately 2.5 meters above ground surface giving a total head of about 4.6 meters. The resultant pressure provided the force to establish the water tables quickly and maintain them easily. Once the desired water level was reached,
water entry was discontinued. The water level indicator tubes also acted as overflow tubes and prevented the water tables from rising above the desired level. Because a sandy soil was used in the study, this method of water table control worked well. More difficulty would probably be met if a finer textured soil was used. Once a water table was established, it was readjusted to the desired level in the morning and in the afternoon.

Plant growth stages and plant heights were measured three times weekly throughout the growing season. Seed yields were measured upon maturity of the plants at the end of the growing season.

Root growth and distribution measurements also were taken three times weekly. Depth to the deepest observable living root material was recorded. Frequency counts at different depths were obtained by counting the root and scribed line intersections as described earlier in the static water table study. These counts were used not to estimate exact root lengths but to indicate relative concentration of roots distributed throughout the compartment. Roots undergo physical changes at which a decision must be made as to whether or not it is a functioning or non-functioning root. A root was considered viable if it still had a white appearance and had maintained direct contact with the soil around it. In other words, if a root became discolored or decreased in
diameter so as to cause a gap between it and the soil, it was not considered viable and, therefore was not counted.

Leaf water potentials were measured at various times during the season to detect any water stress being placed on the plants by the presence or non-presence of the water table treatments. Leaf water potentials were measured with a pressure chamber according to the procedure as described by Klepper and Ceccato (1969). Measurements were made during peak atmospheric demand periods. Samples were taken on fully sun-lit middle leaf of an upper trifoliate. The leaf was placed in the pressure chamber with the petiole exposed through a sealed gasket to the atmosphere. Air pressure was increased within the chambers until plant sap began to extrude from the exposed petiole. At this point, the pressure was held constant and recorded. This pressure was assumed to be the leaf water potential at which water was being retained in the leaf.

Periodic soil moisture measurements were made with a neutron probe to monitor soil water extraction patterns at certain depths with respect to amount of viable roots observed.
RESULTS AND DISCUSSION

Root Development (Pre-flowering Treatment)

Two major growth parameters, average maximum rooting depth and root distribution with depth, were monitored to observe effects on the root systems of the various treatments.

Figure 11 illustrates the effect of the water table treatments on soybean root systems a short time prior to flowering or approximately at the V7 to V8 growth stage. Each datum point represents the average of the three replicates within each treatment. Differences between the high water table treatment (45 centimeters from the soil surface) and the low water table treatment (90 centimeters from the soil surface) are illustrated by separate line graphs. Also, the dates of water table establishment and removal are shown.

The effect of the water table influence on the downward growth of the roots is very pronounced when imposed at this time of the plants' growth cycle. Once the water tables were established, downward growth became greatly slowed and did not resume the previous growth rate until approximately six days after removal of the water table in the case of the high level, and two days after removal for the low level. Although downward root growth rates for the high and low treatments are very similar after the fifty-third day,
Figure 11. Maximum rooting depth progression for the high and low temporary water tables imposed during the pre-flowering period
DAYS FROM PLANTING

MAX ROOTING DEPTH
PRE-FLOWERING TREATMENTS
1977

WATER TABLES ESTABLISHED (6-23-77)
WATER TABLES REMOVED (6-30-77)

AVE MAX ROOTING DEPTH (cm)

HIGH WATER TABLE LEVEL (45cm)
LOW WATER TABLE LEVEL (90cm)
root growth downward for the high treatment constantly lags behind the low treatment in terms of actual depth on a particular day. The differences, however, are not significant enough to establish a water table depth effect on rooting depth for this study.

Since the top portion of the plants are still completely in vegetative growth stages, rapid downward growth of the roots occurs under normal conditions. This is occurring until the high soil moisture caused by the presence of the water table begins. It is at this point that conditions for root growth deteriorate to the point that downward growth stops. Previously discussed studies on the oxygen diffusion rate of Sparta soil at distances near the water table level have shown that most likely the limited oxygen supply is contributing greatly to the inhibition of root growth.

Figure 12 illustrates the downward rooting characteristics for the irrigated and non-irrigated no-water-table treatments. It seems evident that lack of adequate moisture in the upper layers of the soil causes more rapid downward growth because the non-irrigated treatment always has roots deeper than those of the irrigated treatment.

When the pre-flowering water table treatments are compared to the irrigated treatment, downward root growth rates are similar until after the water tables are established.
Figure 12. Maximum rooting depth progression for the irrigated and non-irrigated no-water-table treatments
DAYS FROM PLANTING

MAX ROOTING DEPTHS
NON-WATER TABLE TREATMENTS

AVE MAX ROOTING DEPTH (cm)

- IRRIGATED
- NON-IRRIGATED
After the water tables are removed, downward penetration rates for the water table treatments are about two-thirds of the no-water-table irrigated treatment (about 2.6 cm/day for water table treatments compared to about 4.3 cm/day for the irrigated treatment). It seems that at this particular growth stage, the soybean plant is partially able to overcome the effects of a temporary water table, as far as downward root growth is concerned.

Figures 13 and 14 show the progression of rooting patterns for the entire growing season for the high and low water table level treatments, respectively, imposed during pre-flowering growth stages. As mentioned earlier, root intersection counts were made at 15 centimeter intervals throughout the soil profile beginning with the 30 centimeter level. No estimates of actual rooting length can be made from these counts, although trends showing relative densities of roots at different depths of the soil profile can be utilized. Also, one must remember that because of the nature of the facility used in this experiment, no measurements can be made on roots growing in the top 30 centimeters of the soil profile.

Again, no large differences between the high and low water table levels are evident as far as root distribution patterns. Small differences do occur, however, in relative numbers of roots counted at certain depths during particular time periods, and in the depth to which some roots are observed.
Figure 13. Root distribution pattern progression for the high temporary water table imposed during the pre-flowering treatment period. Roman numerals represent averages of two measurement periods (dates for each period are shown below). Water table was established from 6/23 to 6/30

I (6/20 to 6/24) VI (7/18 to 7/20) XI (8/10 to 8/12)
II (6/27 to 7/01) VII (7/22 to 7/25) XII (8/15 to 8/17)
III (7/05 to 7/06) VIII (7/27 to 7/29) XIII (8/19 to 8/22)
IV (7/08 to 7/11) IX (8/01 to 8/03) XIV (8/24 to 8/26)
V (7/13 to 7/15) X (8/05 to 8/08) XV (8/29 to 8/31)
XVI (9/02 to 9/07)
PRE-FLOWERING TREATMENT - HIGH WATER TABLE LEVEL (45cm)
Figure 14. Root distribution pattern progression for the low temporary water table imposed during the pre-flowering treatment period. Roman numerals represent averages of two measurement periods (dates for each period are shown below). Water table was established from 6/23 to 6/30.

<table>
<thead>
<tr>
<th>Roman Numerals</th>
<th>Dates</th>
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<tbody>
<tr>
<td>I</td>
<td>6/20 to 6/24</td>
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<tr>
<td>II</td>
<td>6/27 to 7/01</td>
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<td>III</td>
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<td>XV</td>
<td>8/29 to 8/31</td>
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<tr>
<td>XVI</td>
<td>9/02 to 9/07</td>
</tr>
</tbody>
</table>
ROOT INTERSECTION COUNTS

DEPTH IN SOIL PROFILE (cm)

PRE-FLOWERING TREATMENT - LOW WATER TABLE LEVEL (90 cm)
The differences that do exist may be a result of the amount of roots that were directly affected by the influences of the two water table levels. The water tables were imposed so early in the growth cycle of the plants that the amount of roots near or under the water table level for either height was small compared to what it would have been in later growth stages. It probably is because of this fact that the plant rooting characteristics are seemingly only temporarily set back for a short period of time and then return to normal growth.

This is especially true in the case of the low water table treatment (90 centimeters). The deepest root observed at the time of water table imposition was at 100 centimeters and very few root intersections were seen at the 90 centimeter level. This meant that very little of the total root system was affected directly by the presence of the water table. The water table did nothing more than increase the soil moisture of the profile to field capacity after it was removed. No discoloration of the soil, or shrinking and browning of the roots was observed. The lack of observation of these characteristics would suggest that no physiological damage to the roots was caused by the influence of the water table.

Figures 15 and 16 show the progression of rooting patterns for the entire growing season for the irrigated and non-irrigated treatments, respectively. The irrigated
Figure 15. Root distribution pattern progression for the irrigated, no-water-table treatment throughout the growing season. Roman numerals represent averages of two measurement periods (dates for each period are shown below)

I (6/20 to 6/24) VI (7/18 to 7/20) XI (8/10 to 8/12)
II (6/27 to 7/01) VII (7/22 to 7/25) XII (8/15 to 8/17)
III (7/05 to 7/06) VIII (7/27 to 7/29) XIII (8/19 to 8/22)
IV (7/08 to 7/11) IX (8/01 to 8/03) XIV (8/24 to 8/26)
V (7/13 to 7/15) X (8/05 to 8/08) XV (8/29 to 8/31)
VI (9/02 to 9/07)
IRRIGATED - NO WATER TABLE TREATMENT
Figure 16. Root distribution pattern progression for the non-irrigated no-water-table treatment throughout the growing season. Roman numerals represent averages of two measurement periods (dates for each period are shown below)

I (6/20 to 6/24)  VI (7/18 to 7/20)  XI (8/10 to 8/12)
II (6/27 to 7/01)  VII (7/22 to 7/25)  XII (8/15 to 8/17)
III (7/05 to 7/06)  VIII (7/27 to 7/29)  XIII (8/19 to 8/22)
IV (7/08 to 7/11)  IX (8/01 to 8/03)  XIV (8/24 to 8/26)
V (7/13 to 7/15)  X (8/05 to 8/08)  XV (8/29 to 8/31)
XVI (9/02 to 9/07)
Non-Irrigated Treatment
treatment's results can be considered as a normal root density pattern. When the water table treatments' results are compared to the irrigated treatment's results, no large differences are evident. Some differences occur because of the immediate effect that the water table has on the roots counted at the lower depths, but these are small. These lack of differences support the contention that a temporary water table of these depths, imposed at this time of the growth cycle of soybeans, has little effect on subsequent root growth after it is removed. Only the delaying of normal downward root penetration while the water table is in place is evident.

Root Development (Post-flowering Treatment)

Effects on subsequent root growth and distribution by a temporary water table imposed during early reproductive stages of growth (approximately R3) were strikingly different from those when the water table was imposed during pre-flowering. Differences existed for both rooting depth characteristics and root distribution patterns.

Figure 17 illustrates rooting depth progression for 45 and 90 centimeter water table levels imposed after flowering had begun. The water tables were established on the sixty-second day after planting and continued for one week. Prior to the water table treatments, normal root penetration was occurring. This is shown by comparing Figure 17 and Figure 12,
Figure 17. Maximum rooting depth progression for the high and low temporary water tables imposed during the post-flowering treatment period.
DAYS FROM PLANTING

MAX ROOTING DEPTH
POST-FLOWERING
1977

WATER TABLES ESTABLISHED (7-14-77)
WATER TABLES REMOVED (7-21-77)

HIGH WATER TABLE LEVEL (45cm)
LOW WATER TABLE LEVEL (90cm)
which shows downward root growth for a normal irrigated situation.

Once the water table levels were established, downward growth halted. Unlike the previously discussed pre-flowering treatment, however, no recovery of downward growth was made after the water table was removed (Figure 17). This was true for both high and low water table treatments although some small differences occurred between treatments. These differences were statistically non-significant using Duncan's multiple range testing technique.

There are three possible explanations for the observed results. First, it is possible that the high soil moisture condition caused production of some toxic compounds which remained in the soil after the water table was removed, thereby causing inhibition of any further root growth. Studies by McCalla and Norstadt (1974), Stevenson (1967), and Wang et al. (1967) provide evidence that organic acids toxic to root growth can arise from microbial decomposition of plant residue in the soil. Ethylene production can occur in anaerobic soils, but usually its effect is eliminated once oxygen re-enters the soil atmosphere. Despite the possibilities of this toxic substance production causing inhibited root growth in the post-flowering treatment, it would, also, have occurred in the pre-flowering treatment. Since downward growth was not inhibited after the removal of the water table in the
pre-flowering treatment, the residual effects of any toxic substances that may have been produced as a result of water table presence, probably did not cause any inhibition of downward growth in the post-flowering treatment, either.

Another possible explanation for the observed results is that permanent injury to the roots occurred in response to the low oxygen and high soil moisture conditions. Since oxygen supply to the roots was limited, root respiration would become limited, causing injury leading to eventual death of the root. Since more roots were below the water table level in the post-flowering treatment than in the pre-flowering treatment, more direct injury to the roots probably would have resulted. As to what may have inhibited regrowth and downward penetration of roots after removal of the water table, toxic substance production caused by root injury may be the explanation. Ethanol production by roots increases during anaerobic conditions resulting in greatly inhibited growth (Crawford, 1967). Again, ethylene production may have occurred by decomposition of the roots themselves. Lynch (1972) concluded that substrates needed for ethylene production, glucose and methionone, arise in significant quantities upon decomposition of fresh organic matter. However, as discussed earlier, once oxygen is introduced back into the soil atmosphere as it would be with water table removal, the effects of ethylene on root growth are most likely eliminated. This
may not be entirely true if ethylene becomes trapped in localized anaerobic areas in the soil. This would not affect the entire root system and its growth, based on work by Crossett and Campbell (1975).

Although not as many roots were below the water table level in the pre-flowering treatment as were in the post-flowering treatment, several roots were, especially in the high water table level (45 centimeters). No inhibition of downward root growth was observed after the water tables were removed, so possibly this explanation is not entirely valid, although permanent injury to the roots seems evident.

The other possible explanation is that the observed response is controlled by the particular growth stage that the plant is at when the water table treatment is imposed. It seems logical that water stress caused by high soil moisture conditions would show greater effects on root development at some stages of growth more than others. This is true for water stress caused by limited soil moisture conditions, so one would expect it would be true, also, for excessive moisture conditions. Possible hormonal changes may be occurring within the plant which may be contributing to the root response. Auxin and gibberellic acid levels have been shown to accumulate in certain plant parts and transport of these hormones within the plant becomes inhibited when plants are grown in anaerobic soil conditions. These possible hormonal
changes may account for greater or lesser tolerance of temporary water table conditions imposed at different stages of growth.

This possible growth stage explanation seems to be supported by the root distribution pattern changes that occurred as a result of the water table treatments. Figures 18 and 19 illustrate the distribution patterns for both high and low water table treatments for different periods during the growing season. The one-week water table treatments were established during period V and released at the end of period VI shown on the figures.

One can see that for both high and low water table levels, almost immediately a definite shift in root distribution occurred after the removal of the water tables. The shift consisted of a gradual decrease, or at least no increase, of viable roots in the lower profile, with massive increases at the shallower depths of the soil profile (30 - 60 centimeters). Some dying of the roots in the areas that were under the water table occurred during the treatment period, but the vast majority of the roots remained in a visibly normal physical state, except for halted downward growth and increased root intersection numbers. When Figures 18 and 19 are compared to the irrigated situation (Figure 15), one can see that relative numbers of roots at lower depths are similar but distribution patterns are completely different.
Figure 18. Root distribution pattern progression for the high temporary water table imposed during the post-flowering treatment period. Roman numerals represent averages of two measurement periods (dates for each period are shown below). Water table was established from 7/14 to 7/21

I (6/20 to 6/24) VI (7/18 to 7/20) XI (8/10 to 8/12)
II (6/27 to 7/01) VII (7/22 to 7/25) XII (8/15 to 8/17)
III (7/05 to 7/06) VIII (7/27 to 7/29) XIII (8/19 to 8/22)
IV (7/08 to 7/11) IX (8/01 to 8/03) XIV (8/24 to 8/26)
V (7/13 to 7/15) X (8/05 to 8/08) XV (8/29 to 8/31)
XVI (9/02 to 9/07)
POST-FLOWERING - HIGH WATER TABLE LEVEL (45cm)
Figure 19. Root distribution pattern progression for the low temporary water table imposed during the post-flowering treatment period. Roman numerals represent averages of two measurement periods (dates for each period are shown below). Water table was established from 7/14 to 7/21

I (6/20 to 6/24)  VI (7/18 to 7/20)  XI (8/10 to 8/12)
II (6/27 to 7/01) VII (7/22 to 7/25) XII (8/15 to 8/17)
III (7/05 to 7/06) VIII (7/27 to 7/29) XIII (8/19 to 8/22)
IV (7/08 to 7/11) IX (8/01 to 8/03) XIV (8/24 to 8/26)
V (7/13 to 7/15) X (8/05 to 8/08) XV (8/29 to 8/31)
VI (7/18 to 7/20)  VII (7/22 to 7/25)  VIII (7/27 to 7/29)  IX (8/01 to 8/03)  X (8/05 to 8/08)  XI (8/10 to 8/12)  XII (8/15 to 8/17)  XIII (8/19 to 8/22)  XIV (8/24 to 8/26)  XV (8/29 to 8/31)  XVI (9/02 to 9/07)
ROOT INTERSECTION COUNTS

DEPTH IN SOIL PROFILE (cm)

POST-FLOWERING - LOW WATER TABLE LEVEL (90cm)
One possible explanation for the massive regrowth of roots in the upper layers when the water tables were released is that conditions suitable for root growth returned in these soil areas first. Once the free water was removed, oxygen was allowed back into the soil pore spaces in the upper profile. These now nearly ideal conditions, both in terms of oxygen and soil moisture, may have been conducive for massive initiation of new roots. Lack of any new root growth in the lower profile also may be a result of the initiation of the many roots above. Once new roots were formed, the majority of photosynthate being produced in the top portion of the plant may have been directed to those areas closest to the top for continued growth and water uptake. Resistance to root water uptake in the upper layers probably would be less because of the adequate soil moisture available there and because new roots probably have higher uptake rates. Also, it would have taken longer for conditions conducive to root growth to improve in the lower soil layers so that roots could continue to grow. This delay may have allowed the energy produced by the top portion of the plant to be directed primarily toward the top portion of the root system.

Another possible explanation for the lack of root growth below where the water table level was previously located is that those roots were permanently damaged by the presence of the water table. Leaf water potential measurements taken
during and after removal of the water tables' presence will be discussed later. These leaf water potential data showed that some stress was placed upon the plants during the water table presence, but stress was relieved after removal. The total lack of downward growth and very sparse regrowth of new roots below, along with visible observations of discoloration of many existing roots, indicates that if the lower roots did "die", a dramatic shift of distribution of roots occurred.

Also, and more importantly, roots that remained above the water table in the high treatment (45 centimeters) were apparently enough to compensate for the loss of the roots below where the water table was located.

Since obvious differences in root reaction to the water table treatments occurred, it may be possible that roots are more sensitive to high soil water conditions during the post-flowering period. Although amounts of the root system below the water table level differed between periods, no discolored roots were observed below either water table level during the pre-flowering period. This seems to indicate that the roots were not damaged greatly, possibly because roots at this growth stage may be more tolerant of the high soil moisture and low oxygen contents.

Many studies which used radioactive tracers of $^{14}$C to detect movement of sugars, amino acids, and minerals within
plants, have shown an increased "pulling power" for these substances occurs toward any flowers that have been initiated. It is not known whether this is a direct sink-source relationship, or if it is caused by some hormonal action. Regardless of the reason, this process, if it occurs, could cause a decrease in the ability of roots to tolerate unfavorable soil conditions.

Root Development (Post-pod Set Treatment)

Several problems were encountered with analyzing the data for the water table treatments imposed after pod set. The main problem, because no water other than negligible natural precipitation had been added to the compartments up to this time, was a possible need for water by the plants interacting with any effects caused by the water table treatments. This problem will be most evident in the later discussion of plant height and yields.

Effects of the water tables on maximum rooting depths is shown in Figure 20. By the time the water tables were imposed, depth of rooting was about stabilized because the roots were nearing the bottom of the compartments (about 216 centimeters). Although all maximum depths were near the bottom, raw data for each of the compartments showed that no more downward growth was observed after the water tables were imposed. It is concluded, therefore, that the effect on down-
Figure 20. Maximum rooting depth progression for the high and low temporary water tables imposed during the post-pod set treatment period.
DAYS FROM PLANTING

MAX ROOTING DEPTH
POST-POD SET TREATMENTS 1977

HIGH WATER TABLE LEVEL (45cm)
LOW WATER TABLE LEVEL (90cm)

WATER TABLES ESTABLISHED (8-9-77)
WATER TABLES REMOVED (8-16-77)
ward growth was similar to that which occurred for the earlier post-flowering treatments, and that explanations for the halted root penetration are also similar.

As mentioned earlier, moisture supply may have been limiting for the post-pod set treatments prior to the establishment of the water tables. The root distribution patterns for the post-pod set treatments are shown in Figures 21 and 22 for the high and low water table levels, respectively. The patterns for both levels are logical for a soil to which no water has been added.

In the early season, the roots are concentrated in upper layers, with root numbers decreasing with depth. As the season progressed, the need for more water became greater and more roots appear in the lower depths where the water is present. This rooting pattern is present when the water tables are imposed during periods XI and XII (Aug. 9 - 16) on each of the figures.

Although the water tables seemed to have an effect on plant rooting depth, virtually no effect on changes in root distribution occurred. This seems to indicate a physiological response by the plant rather than a response that occurred because of soil chemical changes that may have occurred due to the anaerobic conditions. As hypothesized earlier concerning the response of root growth resulting from the post-flowering treatments, the roots below the free water levels may have
Figure 21. Root distribution pattern progression for the high temporary water table imposed during the post-pod set treatment period. Roman numerals represent averages of two measurement periods (dates for each period are shown below). Water table was established from 8/9 to 8/16.

I (6/20 to 6/24)  VI (7/18 to 7/20)  XI (8/10 to 8/12)
II (6/27 to 7/01) VII (7/22 to 7/25) XII (8/15 to 8/17)
III (7/05 to 7/06) VIII (7/27 to 7/29) XIII (8/19 to 8/22)
IV (7/08 to 7/11) IX (8/01 to 8/03) XIV (8/24 to 8/26)
V (7/13 to 7/15)  X (8/05 to 8/08)  XV (8/29 to 8/31)
VI (9/02 to 9/07)
ROOT INTERSECTION COUNTS

POST-POD SET - HIGH TABLE LEVEL (45cm)
Figure 22. Root distribution pattern progression for the low temporary water table imposed during the post-pod set treatment period. Roman numerals represent averages of two measurement periods (dates for each period are shown below). Water table was established from 8/9 to 8/16.

I (6/20 to 6/24)  VI (7/18 to 7/20)  XI (8/10 to 8/12)
II (6/27 to 7/01)  VII (7/22 to 7/25)  XII (8/15 to 8/17)
III (7/05 to 7/06)  VII (7/27 to 7/29)  XIII (8/19 to 8/22)
IV (7/08 to 7/11)  IX (8/01 to 8/03)  XIV (8/24 to 8/26)
V (7/13 to 7/15)  X (8/05 to 8/08)  XV (8/29 to 8/31)
XVI (9/02 to 9/07)
ROOT INTERSECTION COUNTS

DEPTH IN SOIL PROFILE (cm)

POST-POD SET - LOW WATER TABLE TREATMENT
been permanently damaged so as to function ineffectively. But, being later in the growth cycle and with rapid pod fill occurring, there may have been a lack of enough energy being directed downward toward the root system to cause large amounts of root initiation to occur in soil areas above where the free water levels had been. Once again, a growth stage factor may, at least partially, be controlling the root response to these particular water table situations.

Additional Root Observations

A supplemental study was conducted in the rhizotron to determine oxygen diffusion rates which limit soybean root growth, and the effects of a static, long-term water table established after flowering on top and root growth. Oxygen diffusion rates were measured at various distances above a static water table at 105 centimeters below the soil surface in the previously described Sparta fine loamy sand soil. The same water table constant head devices described in Part I were used. These oxygen diffusion rates were measured using 22-gauge platinum microelectrodes, 4 millimeters long, according to the procedure as described by Letey and Stolzy (1964). An applied potential of -0.65 volts was used. Oxygen diffusion rates were measured approximately five minutes after application of the potential.

Oxygen diffusion rates of 15 to 20 \(\times 10^{-8}\) gm cm\(^{-2}\) min\(^{-1}\)
seemed to inhibit soybean root growth. These determinations were hampered by the ability of the plants' roots to adapt to the static water table situations and to play a role in controlling the position of the free water level. The roots grew normally down to within about 20 centimeters of the free water level and then slowed their downward growth considerably. Oxygen diffusion rates were measured at this time (just about flowering) and related to the observed root growth. As the season progressed, more and more roots appeared above where we attempted to maintain the water table level. Presence of these roots caused more and more water usage from the water table. As daily amounts of water consumption rose, root penetration moved downward into the area where the water table was supposed to have been maintained. Both soil moisture contents and oxygen diffusion rates showed that the water level had dropped. The atmospheric demand placed on the plants caused more water to be extracted at faster rates than the water table reservoir could supply. This excessive demand over supply resulted in effective lowering of the water table, and that lowering allowed growth further downward than expected. Microelectrodes had not been installed at depths below the original water table level because it was assumed that these depths would be well below the free water level. The solution to this problem would have been a means of putting a positive
pressure on the water entering the compartment so that the entry rate could be balanced with the extraction rate.

Despite these problems, the values presented earlier seem to be reliable, at least for early season root growth.

The second part of the supplemental study was to observe effects on root growth caused by a static, long term water table established after flowering. This study again involved the use of the rhizotron compartments. Plants grew under normal no-water-table conditions until between the R3 and R4 growth stages. At this point, a free water table surface was established at a depth of 75 centimeters below the soil surface. Root penetration at this time had reached 193 centimeters deep and 85% of all root counts made at that time were below the 75 centimeter level. Root growth and distribution and top measurements were continued for the next six weeks while the water table remained. Two replicates were used.

Response of both top and root growth to this situation were observed. Immediately, downward root growth ceased for the remainder of the season. This cessation agrees with results from the temporary water table study, but, in the present case, very long term detrimental growing conditions must be the reason for inhibited root growth. Also, virtually all increases in root counts below the water table level ceased. Above the water table level, massive regrowth and initiation of new roots occurred.
Water usage was measured to provide one indication of the plants' reaction to the presence of the water table. Since the soil above the water table was dry, most of the water consumed by the plants was assumed to come from the water table and not from storage above it. The water use initially was approximately one-fourth that which was being used in a constant static water table situation. The amount used gradually increased as more became visible above the water table level, but never reached the amount used in the static water table treatments.

This water use reaction seems to indicate that the water table caused a stress in the plants. The stress effectively hindered normal root function (especially root water uptake) for those roots below the free water level. This stress was continued until the plants were able to compensate for the loss of the roots below, by formation of new roots above the water table.

Another observation of the root response to the water table presence was the lack of visual damage to the apparently functionless roots below the free water level. No discoloration was present, nor was any deterioration observed while the water table remained. When the water table was removed, the roots began to deteriorate, and did so quite quickly. It seemed that the water was "preserving" the apparently dead roots until oxygen reentered the soil pore spaces upon
removal of the water table. Decomposition then took place quickly.

Top Growth Results

Imposition of the temporary water tables at different stages of growth seemed to affect plant heights more than stage of development. Figure 23 shows the stage of development progression in terms of days from planting date for both the water table treatments and for the no-water-table treatments. Each water table treatment line shown in Figure 23 is the combination of both water table level treatments for each of the three time periods. Only slight differences occurred between the different water table levels for a given treatment period, so they were combined for each period. Also, only slight differences existed between treatment periods. A maximum time lag of five days does exist for the treatment where the water table was imposed after flowering but before pod set, but this appears to be an insignificant deviation. The differences of growth stage progression between the un-irrigated and irrigated no-water-table treatments (up to a fourteen-day lag of irrigated behind unirrigated) demonstrate that inadequate moisture tends to increase rate of stage development.

The effects of the various treatments on plant heights was more marked than on stage of development. Both the pre- and post-flowering water table treatments developed
Figure 23. Growth stage development (Fehr et al., 1971) for all water table and non-water table treatments. High and low water table levels are averaged together for each water table treatment period.
GROWTH STAGE DEVELOPMENT 1977

- Preflowering
- Post flowering
- Post pod set
- Non-irrigated
- Irrigated

DAYS FROM PLANTING

0 30 40 50 60 70 80 90 100 110 120 130
significant differences between the low and high water table levels. The post-flowering treatment showed little differences between water table levels mainly because the water tables were imposed after height increases had ceased.

The high and low water tables imposed before flowering caused distinct differences in plant heights, but not until after four weeks after the water table treatments were removed (Figure 24). One would expect that if the actual presence of the water table was to affect the growth of the plant, the response would be relatively soon after the water table had been imposed. This response was the case with the growth chamber study described earlier. It seems that the response must depend upon the amount of root system directly affected by the presence of the water table. At the time when the water tables for the pre-flowering period were established, the deepest roots were only 90 to 100 centimeters deep and the majority of the root intersections counted were between the 45 and 75 centimeter depths. However, several studies of soybean root systems have shown that, especially during early vegetative growth, the vast majority of the plant's root system is in the top 30 centimeters of the soil profile, which could not be viewed in the rhizotron compartments. So, at this period of the plant's growth cycle, most of the viable roots probably were not affected directly by the presence of
Figure 24. Plant height progression for the high and low water tables imposed during the pre-flowering treatment period.
PLANT HEIGHTS 1977
PRE-FLOWERING TREATMENT

LOW WATER TABLE LEVEL
HIGH WATER TABLE LEVEL

WATER TABLES REMOVED (6-30-77)
WATER TABLES ESTABLISHED (6-23-77)

PLANT HEIGHT (cm)

DAYS FROM PLANTING
the water table. But the residual effects, mainly increased soil water content, remaining after the water tables were removed, aided the plants later in their growth cycle. As Figure 24 shows, plant height differences did not develop until at later growth stages. The high water table level treatment seemed to benefit the plants more than the low treatment, probably because more water was added to the soil, making more water available to the plants later on.

For the case when the water table was imposed for the period after flowering but before pod set, similar end results occurred, but possibly for different reasons. Plant height differences between the high and low water table level treatments (Figure 25) occur almost immediately after the water tables were established, but large differences did not occur until at later growth stages. Again, the plant height response seems to reflect the amount of water remaining in the soil profile after the water tables were removed. Obviously, the root growth (and probably root function) was affected by the water tables' presence as discussed earlier. The effects caused dramatic changes in downward root growth and distribution patterns. If these roots became permanently damaged, one would expect that the high water table level would have damaged more of the root system, therefore, causing more stress to be placed on the whole plant. One would also expect that
Figure 25. Plant height progression for the high and low water tables imposed during the post-flowering treatment period.
PLANT HEIGHTS 1977
POST-FLOWERING TREATMENT

WATER TABLES REMOVED (7-21-77)
WATER TABLES ESTABLISHED (7-14-77)

LOW WATER TABLE LEVEL
HIGH WATER TABLE LEVEL

PLANT HEIGHT (cm)

DAYS FROM PLANTING
this would be reflected in the top growth performance. Because this did not occur in this study, one can only conclude that the water table levels used were still low enough so that the unaffected roots in the upper soil layers were able to sustain the plant until new root growth was initiated. If this occurred, then again, the high water table treatment would have added more water to the soil profile, making more water available for plant growth. This possibility seems to explain the results shown in Figure 25.

When the plant heights of the pre- and post-flowering water table treatments (Figures 24 and 25) are compared to those of the irrigated no-water-table treatment (Figure 26), insignificant differences are evident prior to the water table imposition. It seems that water availability to the plants was not hindered, at least up to these times, so that any response was probably due to the water tables' influence.

Figure 27 shows the plant heights for the post-pod set treatment period. The water table treatments had little effect on the plant heights because maximum heights were already reached by the time the water tables were established. Final plant heights are lower this treatment period than in the earlier ones mainly because of need for water prior to water table imposition rather than because of the water table imposition. This can be understood by comparing Figure 27 with the
Figure 26. Plant height progression for the irrigated and non-irrigated no-water-table treatments
PLANT HEIGHTS
NON-WATER TABLE TREATMENTS
1977

PLANT HEIGHT (cm)

DAYS FROM PLANTING

IRRIGATED
NON-IRRIGATED
Figure 27. Plant height progression for the high and low water tables imposed during the post-pod set treatment period
PLANT HEIGHTS 1977
POST-POD SET TREATMENT

- WATER TABLES REMOVED
  (8-16-77)

- WATER TABLES ESTABLISHED
  (8-9-77)

HIGH WATER TABLE LEVEL
LOW WATER TABLE LEVEL

PLANT HEIGHT (cm)

DAYS FROM PLANTING
irrigated treatment on Figure 26. Plant heights for the post-pod set treatment level off long before the irrigated treatment's do and at a much shorter height. Insufficient water for growth must be contributing to the shortened plant heights.

Overall results of the plant height data indicate that the water tables had a beneficial, rather than a detrimental, effect on plant heights. A statistical analysis, using Dun­can's multiple range test, showed that final plant heights for the high water tables in both the pre-flowering and post-flowering treatments were significantly different from their respective lower water table levels at the 5% level, but not significantly different from each other. No significant difference was detected between the high and low water table levels for the post-pod set treatment period. All water table treatments for all treatment periods were significantly different from both the irrigated and unirrigated treatments.

Yield Results

The yields for the temporary water table study are presented in Table I. Yields for each of the six plants within each water table or non-water table treatment were averaged and represented in the table. A statistical analysis, using Duncan's multiple range testing procedure, showed no significant differences (p = 0.05) among the pre- and post-flowering
Table I. Mean yields for various water table and non-water table treatments

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Yield (g/plant)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-flowering -- high level</td>
<td>62.9</td>
</tr>
<tr>
<td>Pre-flowering -- low level</td>
<td>50.0</td>
</tr>
<tr>
<td>Post-flowering -- high level</td>
<td>72.5</td>
</tr>
<tr>
<td>Post-flowering -- low level</td>
<td>54.3</td>
</tr>
<tr>
<td>Post-pod set -- high level</td>
<td>42.0</td>
</tr>
<tr>
<td>Post-pod set -- low level</td>
<td>43.2</td>
</tr>
<tr>
<td>Irrigated</td>
<td>69.7</td>
</tr>
<tr>
<td>Non-irrigated</td>
<td>27.5</td>
</tr>
</tbody>
</table>

high level treatments and the irrigated treatment. The three low water table level treatments for each treatment period showed no significant difference \((p = 0.05)\) among each other, although they all were significantly lower than the high water tables applied at the same time. No significant difference \((p = 0.05)\) existed between yields of the high and low water tables for the post-pod set treatment period.

In both the pre- and post-flowering treatments, the high water table level yielded significantly higher than the low water table level. This seems to indicate, as with the plant heights, that a beneficial effect resulted from the higher water table level which was probably caused by the greater amount of water added to the soil column which was available for later plant use. Also, the results from the post-pod set treatment period seem to support the notion
that the moisture situation prior to the establishment of the water table treatments probably was deficient and probably affected the yield results more than the water table treatments.

Leaf Water Potential Results

Leaf water potentials were measured at various times during the growing season for all three periods of water table treatment. The leaf water potentials were determined during the highest atmospheric demand period of the day. These potentials were used to indicate whether or not a water stress had developed in the plants as a result of the water table treatments.

Measurements taken on the pre-flowering treatments during water table imposition period showed a range in leaf water potentials from -12.5 to -13.8 bars (Table II). Irrigated plants showed leaf water potentials ranging from -11.9 to -13.8 bars for the same period. A comparison of water table treatment potentials with the irrigated potentials indicated that no stress was occurring as a result of the presence of the water tables.

These data seem to reflect the amount of root system that was affected by the presence of the water table treatments. Since very little of the root system, proportionately, was below or near the free water level at the time the water tables were established, no stress effect caused by decreased water uptake should occur. Subsequent measurements of leaf
Table II. Leaf water potentials for different water table treatment periods for both high (45 cm) and low (90 cm) water table levels

<table>
<thead>
<tr>
<th>Date</th>
<th>Pre-flowering High (bars)</th>
<th>Pre-flowering Low (bars)</th>
<th>Post-flowering High (bars)</th>
<th>Post-flowering Low (bars)</th>
<th>Post-pod set High (bars)</th>
<th>Post-pod set Low (bars)</th>
<th>Irr. (bars)</th>
</tr>
</thead>
<tbody>
<tr>
<td>6/24</td>
<td>-12.9</td>
<td>-12.7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-11.9</td>
</tr>
<tr>
<td>6/27</td>
<td>-13.8</td>
<td>-12.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-13.8</td>
</tr>
<tr>
<td>7/05</td>
<td>-15.1</td>
<td>-15.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-13.5</td>
</tr>
<tr>
<td>7/19</td>
<td>-14.7</td>
<td>-14.6</td>
<td>-16.3</td>
<td>-15.5</td>
<td></td>
<td></td>
<td>-13.5</td>
</tr>
<tr>
<td>7/22</td>
<td>-15.4</td>
<td>-15.2</td>
<td>-11.8</td>
<td>-12.1</td>
<td></td>
<td></td>
<td>-11.8</td>
</tr>
<tr>
<td>7/25</td>
<td>-14.0</td>
<td>-15.3</td>
<td>-12.6</td>
<td>-11.8</td>
<td></td>
<td></td>
<td>-12.4</td>
</tr>
<tr>
<td>8/02</td>
<td>-13.6</td>
<td>-15.3</td>
<td>-12.8</td>
<td>-13.8</td>
<td></td>
<td></td>
<td>-11.7</td>
</tr>
<tr>
<td>8/11</td>
<td></td>
<td></td>
<td>-10.3</td>
<td>-11.3</td>
<td>-11.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8/18</td>
<td>-13.8</td>
<td>-14.2</td>
<td>-12.3</td>
<td>-12.0</td>
<td>-13.9</td>
<td>-11.3</td>
<td>-12.6</td>
</tr>
</tbody>
</table>

Water potentials during the rest of the season on these same plants showed a gradual lowering of potentials, but none of the plants showed any signs of stress although potentials were consistently lower than the irrigated treatment's.

Some indication of stress was detected for the post-flowering treatment on July 19 (Table II). These leaf water potentials were determined while the water tables were still present. When compared to the irrigated values, a definite stress effect from the water tables' influence seems to have occurred. This effect, however, was short lived as subsequent leaf water potential measurements showed no indication of a stressed condition.

The post-pod set treatment showed no signs of stress.
either during or after removal of the water tables.

In summary, generally no stress situations as indicated by leaf water potentials seemed to develop during the imposition or after removal of the water table treatments, except for the post-flowering treatments. During this period, some stress was detected while the water tables were present, but rapidly recovered in water potential after the removal of the water tables. As discussed earlier, it was hypothesized that possible permanent damage occurred to the root system inundated by the water tables that were applied at post-flowering. The resultant adjustment of the plant to this situation may have caused the lower leaf water potentials. After the plant had adjusted by initiating many new roots in areas above the water table levels, the stress signs disappeared because adequate water uptake seemingly occurred.
CONCLUSIONS

Results from this study where temporary water tables were established at different times during the growth cycle indicate that soybeans seem to change with time in ability to tolerate temporary water table situations. Root response to water tables established at pre-flowering, post-flowering, and post-pod set stages of growth show three different reactions.

Soybean roots during the pre-flowering growth stage apparently were able to continue growth downward shortly after removal of the water table. The plant is completely vegetative at this time so it is conceivable that more photosynthate is directed towards roots than at later growth stages. Also, no apparent functional or physical damage occurred to the roots below the water table levels at this stage indicating a greater tolerance by the roots to the high soil moisture, low oxygen conditions.

During the post-flowering growth stage, the root system had the ability to adjust but not to completely overcome effects of the water tables. Downward root growth ceased soon after the water tables were imposed and massive root growth occurred above the depth to which the water tables had been. Lower roots seemingly were permanently damaged because very little deep regrowth occurred after the water tables were removed. This evidence seems to indicate that
roots may be more sensitive and less tolerant of the high soil water conditions during this particular growth stage. However, the plant's ability to adjust to this situation is strong as evidenced by the massive root initiation that occurred at the shallower depths, and ultimate plant heights and yields. Possibly this characteristic response is due to the fact that the plant is in both vegetative and reproductive growth which may cause, by sink-source relationships of energy allocation by the plant, a drive for continued root growth which is less than that in the vegetative growth stage alone, but more than that for complete reproductive growth.

Soybean root growth response to water tables during the post-pod set growth stage indicated no ability of the plant to overcome the situation, at least in terms of continued root growth. Apparently, all root growth stopped below the level of the water table, and no new growth occurred above that level. The plant was in complete reproductive growth so that possibly most of the photosynthate being produced was being directed into seed formation rather than new root initiation.

Supplemental studies indicate that oxygen amounts present in the soil atmosphere were probably the most limiting factor for normal root growth. Oxygen diffusion rates were found to be limiting at $15$ to $20 \times 10^{-8} \text{gm cm}^{-2} \text{min}^{-1}$. 
Damage to roots caused by temporary water tables seems to occur in two phases. First, while the water table is still present, the damage seems to be more functional damage rather than visually detectable physical damage, although some internal damage may be occurring. Possible internal damage was shown by decreases in water uptake by the plant after the water table was established. Second, once the water table is removed, physical deterioration of the roots that were below the water table level occurs. This visual damage is assumed to be a result of the addition of oxygen into the soil atmosphere facilitating microbial decomposition of the damaged roots.

No detrimental effects caused by the temporary water tables were observed on top growth and stage of development. Effects resulting from the different water table heights for the pre- and post-flowering treatments indicated that the high level caused greater plant heights and yields to occur than the low level. This was attributed to the amount of water that was added to the soil profile by each of the levels after water table removal.
LITERATURE CITED


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