THE EFFECT OF MOISTURE STRESS ON PLANT - AVAILABLE SOIL PHOSPHORUS

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We, the undersigned members of the Committee appointed by you to examine the thesis submitted by Mr. Sidney Stuart Blair, B.S.A., in partial fulfillment of the requirements for the degree of Master of Science, beg to report that we consider the thesis satisfactory both in form and content.

Subject: The Effect of Moisture Stress on Plant Available - Soil Phosphorus

We also report that Mr. Blair has successfully passed an oral examination on the general field of the subject of the thesis.

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INTRODUCTION

In spite of the large amount of research on soil-plant-water systems during the past decade, little information is available on the influence of soil moisture or plant water stress on soil and fertilizer phosphorus availability. This is, in part, because much of the data from research dealing with the relationship between plant growth, soil moisture, and phosphorus availability have been inconclusive or even contradictory.

In the western great plains area of North America and particularly throughout most of the agricultural area of Saskatchewan, soil moisture stress probably limits growth more than any other single factor. Equally significant, from the wealth of phosphate fertilizer trials, is the observation that crop response to phosphate fertilizers is proportionately larger during dry than wet seasons. This suggests that the effective availability of soil phosphorus may decrease as soil moisture stress increases. It is not known definitely whether soil moisture stress changes the chemical availability of the soil phosphorus or results in a change of the rooting habit of the plant such that the plant is unable to fully exploit the total soil volume.

The investigations reported in this manuscript have been designed to determine the effect of soil moisture tension and phosphorus concentration in the soil on phosphorus uptake by wheat.

LITERATURE REVIEW

The absorption of phosphorus by plants involves four principal steps, which may be represented in the following manner:

$$P(soil) \rightleftharpoons P(soil\ solution) \rightleftharpoons P(vicinity\ of\ root) P \rightleftharpoons (root) \rightleftharpoons P(in\ plant)$$

dissolution of solid phase P	transportation of P to the root site	absorption of P	translocation of P in plant

The moisture content of the soil may influence each of these steps and thus, influence the uptake of soil phosphorus by the plant root system. Pertinent research carried out on each of these steps is discussed in the following four sections.

Since the uptake of phosphorus from the soil is also related to total plant weight, a final section on the influence of soil moisture stress on plant growth *per se* is included.

The Effect of Soil Moisture Stress on the Release of Solid Phase Phosphorus into the Soil Solution: As the moisture content of the soil decreases from field capacity to the permanent wilting percentage, the thickness of the moisture films surrounding the soil particles decreases,and the intensity with which the water is retained increases. Water remaining in the soil below the wilting percentage becomes "bound water" which has a much lower di-electric constant than that of normal water. The low di-electric constant indicates a greatly reduced polarity, and therefore, its solvent power and dissociating action on salts and other substances must be considerably less than that of 'free' water. This implies that, with a diminishing thickness of moisture films, a corresponding decrease in the proportion of water in the film with normal solvent properties takes place. The actual quantity of available plant nutrients in a given soil must also decrease significantly; this is particularly important for anions such as phosphate which can only be absorbed by the plant roots from the soil solution.(3)

In an experiment designed to measure the dissolution of ions in the soil at moisture contents ranging from field capacity to 500 percent water, Reitemeier (43) found that the phosphate concentration increased slightly in all soils with increasing moisture content. He attributed this increase to ion exchange and to the solution of solid phosphate compounds by the additional amounts of water.

A leaching apparatus to determine the rate at which phosphorus is released into the soil solution was designed by Fried et al (15). The soil was leached rapidly with distilled water until the amount of phosphorus in the leachate became constant. This was considered to be the rate of formation of soil solution phosphorus at that leaching rate. Then, the rate of absorption by barley roots was determined by measuring the amount of phosphorus absorbed, as a function of time, from solutions that did not change in concentration during the course of the experiment. Their data indicated that the minimal rate of formation of soil-solution phosphorus from a clay loam soil was 13 lb./ac./hr. Phosphorus uptake by plants determined on a similar basis was estimated to be only 0.025 lb./ac./hr. These rate measurements point out that the amount of phosphorus renewal in the soil solution by dissolution of solid phase phosphorus is rapid in comparison with the rate of absorption by plants. Therefore, under ideal moisture conditions, the rate of phosphorus uptake by plants appears to be governed by the concentration of phosphorus in solution in contact with the root and not the rate of dissolution of solid phase phosphorus.

Brown (5) reported data which showed the effect of soil moisture upon cation exchange in soils through the moisture range from saturation to permanent wilting percentage. His results indicated that the amounts of cations exchanged from the soil to a cation exchange membrane increased sharply as the soil moisture content increased. The texture of the soil determined the tension range at which the greatest increase in exchange occurred. Anion exchange reactions are of equivalent importance as far as soil phosphorus uptake is concerned, since the plant depends on an anion exchange reaction between the root's absorbing site and the soil solution in order to absorb phosphorus. (10)

Another factor to consider is the effect of the moisture content of the soil on isotopic exchange reactions between the soil and fertilizer phosphorus. Such an exchange, if irreversible, may influence the validity of data obtained where tagged phosphorus fertilizers are used. Brown (5) has stated that ionization and transport of ions through the soil is dependent on the thickness and continuity of water films within the pore system of the soil. Thus, the rate and extent of exchange would be controlled by the status of moisture films. When the entire pore system is filled with water (at saturation), the thickness and continuity of water films will be almost identical to that of the total pore space. Under such conditions, the soil and fertilizer would be able to maintain an efficient exchange. As the moisture content of the soil approaches the wilting percentage, the water films exist primarily as thin isolated wedges. The movement of phosphate through the soil under such conditions would be slow since only a small portion of the pore system would be effective in permitting the diffusion of phosphate ions through the soil. Under these conditions, isotopic exchange could be reduced due to lack of continuous water films.

The relative amount of phosphorus fixed by a given soil may also be dependent on the soil moisture content. Richards and Wadleigh (45) state that soil moisture depletion is conducive to the fixation of available soil phosphorus. This could explain in part the relatively low phosphate content of plants grown under an inadequate soil moisture supply.

Soil moisture content also has an important bearing on the decomposition and mineralization of the organic constituents of the soil. Richards and Wadleigh (45) have stated that microbial activity increases with increasing moisture content up to the aeration porosity limit. Thus, it would appear, that to whatever extent the mineral nutrition of plants is dependent upon the activity of soil microorganisms, the soil moisture level could have an indirect effect on phosphorus availability through its influence on soil microbes.

Thus, at high moisture stresses (low moisture contents), the amount of soil phosphorus entering the soil solution system may be lowered by: 1) a decrease in the dissolution of solid phase phosphorus or conversely by an increase in the fixation of available soil phosphorus, 2) decrease in isotopic exchange between the soil and fertilizer phosphorus, and 3) a decrease in the microbial breakdown of organic phosphorus compounds.

<u>The Effect of Soil Moisture Stress on the Movement of Phosphate Ions to the Root Surface</u>: Fried et al (15) have indicate that the soil mass may not be effective in supplying phosphorus to plants, since the effective soil volume may only be the region in the immediate vicinity of the roots. They stated that in cases where there is intensive removal of phosphorus from the effective soil volume by plant roots, the rate of phosphorus uptake by the plant would be determined by the changing phosphorus content in the soil solution. Thus, the total uptake may be better characterized

by an ability to maintain the phosphorus concentration at the roots surface under intensive removal than by original high soil phosphorus concentrations. The concentration of phosphorus in the soil solution at the absorbing site would then be dependent on the rate of release of phosphorus to the soil solution and the translocation of the dissolved solute to the absorbing site.

The two principle mechanisms of solute transfer in the soil are diffusion, and transportation in the moving liquid phase. This movement may be modified by chemical processes such as ionic exchange and the formation of precipitates or by absorption by plant roots. The rate of water movement in the soil falls rapidly as the moisture content falls below field capacity (7). When the liquid phase is motionless or when the motion is extremely slow, any movement of phosphorus to the roots must be due to diffusion.

The rate of anion diffusion in three soils of different texture, varying in moisture tension from 1/3 to 15 atmospheres, was studied using the chloride ion by Porter et al (42). They found that, as moisture tension increased, the moisture films surrounding the particles decreased, diffusion path length increased, and the absorption of anions by clay particles increased. These factors effectively combined to reduce the rate of ion transfer to the root surface. In research conducted by Danielson and Russell (8), an increase in Rb 86 uptake at higher moisture levels was attributed to the presence of thicker moisture films through which the ions could diffuse. Olsen et al (38) arrived at a similar conclusion when assessing the possible reasons for a reduced uptake of phosphorus by corn seedlings grown on soils of increasing moisture tension. They concluded that at high moisture tension there is a reduction in phosphorus diffusion to the root's surface which markedly reduces the uptake of phosphorus.

Barber (1) stated that transportation of the phosphate ion in the moving liquid phase is also important. His concept of ion movement proposed that water taken up by the plant causes a mass flow of ions to the roots surface. If the concentration of an ion is such that mass flow transports more phosphorus to the root interface than is absorbed, the ion accumulates at the root solution interface. If the concentration of an ion is so low that mass flow does not bring as much to the root surface as the root absorbs, then additional quantities of the ion must reach the root by diffusion, and hence, ion diffusion becomes the determining factor in supplying the plant root. He concluded that the process that has the greatest effect on the availability of a particular nutrient depends on: 1) the concentration of the nutrients in the water which moves toward the plant root as a result of water uptake by the plant root, 2) on the moisture content of the soil which dictates the flow rate of this water, and 3) on the rate of uptake of nutrients by the plant root.

Day and Forsythe (9), from investigations dealing with the movement of $CaCl_2$ through exchange resins, suggested that ions released from the solid phase are picked up by the moving stream and then carried through the porous system along paths that are essentially continuations of those previously followed by the ions diverted from the stream by exchange. The authors believed that the direction and rates of movement of ions, during periods when they are not constrained by chemical forces, are prescribed by the true hydrodynamic flow patterns frequently employed in soil moisture movement studies. In conclusion, they stated that the diffusion of ions must be regarded as an independent mechanism that will be superimposed on the hydrodynamic mechanism, and that the fluid transfer of water resulting from unsaturated flow overwhelms the diffusion of ions under a concentration gradient. A similar effect for saturated flow, where water movement is sufficiently large, was pointed out by Shaperio et al (50) who designed a precise experiment to determine the effect of soil moisture movement and phosphorus diffusion on plant growth and composition. They diluted a given weight of soil with sand, thus increasing the length of the diffusion path and the mean distance between soil particles and the root surfaces. If increased path length had no effect on the phosphorus supply to the root surface, yield and phosphorus content would be constant with increased sand dilutions; however, if increased diffusion path reduced the yield and phosphorus content, recirculation of the soil solution would eliminate this effect. They found that dilution with sand had no effect on the phosphorus content of the soil solution. Yield of phosphorus and percent phosphorus in the tissues, remained approximately constant up to 1:1.1 sand dilutions but decreased at greater dilutions in both recirculated and non-circulated systems. Recirculation increased the yield and percent phosphorus - the increase being attributed partly to the sampling of a larger volume of soil for the replenishment of the soil solution. This indicated that the diffusion process alone was unable to renew the phosphorus at the root surface as fast as the observed uptake rate. Soil water movement transports phosphorus ions to the root surface. This water movement controls the soil volume contributing to the phosphate replenishment. In conclusion, they stated that water movement accounts for a much greater transfer of phosphorus to the root surface than diffusion.

This evidence is further supported by data presented by Gardiner and Mayhugh (18). In a review of their paper, Shaperio stated that the soil water diffusivity varies with the soil moisture content, becoming larger as the soil becomes more moist. The moisture gradient, which develops in the soil near the root surface during active absorption of water by the root, causes a movement of soil moisture from the bulk soil to the layer near the root surface. Depending on the initial soil moisture content, the soil water diffusitivity is 10 to 10,000 times greater than the diffusion coefficient for the phosphorus ion in free solution.

Well established plant roots also affect the flow and distribution of water, and hence available phosphorus in the soil. A high moisture tension in the soil, in the immediate vicinity of the plant root, sets up a tension gradient that tends to move water toward the root. This tendency for water to move to plant roots in response to tension gradients is of considerable importance for plants with large well developed root systems, where a small distance of movement over a considerable combined length of root system, would account for an appreciable volume of water and dissolved phosphorus being brought into contact with the root.

Thus, the moisture content of the soil has been shown to control the movement of phosphorus to the root's absorping site, since both mass flow and diffusion may decrease as the soil moisture stress increases.

<u>The Effect of Soil Moisture Stress on Phosphorus Absorption by Roots</u>: A plant root absorbs ions from the immediate vicinity of the root's surface. For many plants, the absorp-

tion occurs along the root from a few millimeters back of the tip to the point where the root becomes suberized.

It is generally agreed among plant physiologists that a plant excretes an anion in exchange for one it absorbs. Russell (46) has pointed out that absorption involves an expenditure of energy, the source of which is presumably carbohydrates that are oxidized in the absorbing cells.

Pierre and Parker (41) have stated that plants cannot absorb phosphorus directly from the solid phase nor can they absorb soil organic phosphorus present in the solution phase. This is verified by Black (3) who asserted that plant available phosphorus must be in the ortho form in the soil solution before it can be absorbed by plant roots. Further research by Hagen and Hopkins (22), indicated that HPO_4- and $H_2PO_4^{=}$ were the main phosphate ions absorbed by excised barley roots.

Phosphorus uptake by plants grown in the soil is affected by both soil and plant characteristics. Duncan and Ohlrogge (11) related the variables determining phosphorus uptake by plants in a very general equation which stated that uptake was a function of the root surface, concentration of phosphorus in the soil solution, and the condition of the plant due to its past history. Fried et al (15) have shown that the uptake of phosphorus from a soil system is a consequence of a series of consecutive reactions —plant uptake being limited by the slowest reaction in the series.

(1) Soil Reaction-: P soil $\rightleftharpoons$ P solution

(2) Plant Reaction-: P solution $\rightleftharpoons$ P inside plant

According to these authors, the rate of phosphorus release by the soil is at least 250 times as great as the rate of plant uptake. They stated that the uptake of phosphorus by plants from a soil system may reflect not only the phosphate status of the soil but also other factors that influence the rate of plant uptake of phosphorus. For example, the kinetics of phosphate absorption by excised barley roots was studied by Hagen and Hopkins (22) who concluded that the concentration of the hydroxyl ion influenced plant uptake of phosphate by competitively inhibiting absorption of both $HPO_4^{=}$ and $H_2PO_4^{-}$.

Grunes et al (21) derived a mathematical expression of factors affecting absorption of soil and fertilizer phosphorus by plants. The following equation expressed the total phosphorus absorbed by plants: $Pt = Ps\ (Rs) + Pf\ (Rf)$ where Pt = total phosphorus absorbed; Ps = soil phosphorus absorbed by unit root absorbing area; Pf = fertilizer phosphorus absorbed by unit root absorbing area; Rs = active root absorbing area in vicinity of soil source; Rf = active root absorbing area in vicinity of phosphorus fertilizer source. Thus, the soil factors essential for normal root growth will also affect the absorption of phosphorus and other nutrients by plants. These factors include: 1) a favourable soil reaction 2) placement and nature of added soil nutrients (fertilizers) 3) favourable moisture conditions 4) adequate oxygen 5) suitable temperature 6) friability or looseness of the soil so that the roots are not restricted in their free growth and development.

The relationship between phosphorus absorption and the soil moisture content is very complex. Hagen et al (24) reviewed an investigation by Hawthorne (25) who listed nine papers which reported that phosphorus uptake is unaffected by the soil moisture content within the available range, twelve papers reporting that phosphorus uptake was decreased by increasing moisture stress and some papers reporting that phosphorus uptake is increased by decreased soil moisture contents.

Jenne et al (29) found that phosphorus percentages in the entire plant and in the various plant parts were not influenced materially by soil moisture stress. Spratt (52) concluded that moisture stress did not appreciably alter the percent total phosphorus until the permanent wilting point was reached. His results indicated that fertilizer phosphorus as a percent of total phosphorus in the grain increased appreciably with increasing soil moisture stress. A corresponding decrease in soil phosphorus as a percent of total phosphorus took place with increasing moisture tension. In a similar type of study designed to test the effect of soil water stress on phosphorus absorption by wheat plants, Fawcett and Quirk (12) concluded that the total phosphorus content of roots and tops showed definite decreases with increasing water stress.

Mederski and Wilson (35) devised a split root technique in which the top portions of the roots of corn plants developed in a sand culture and the remaining portion of the root system developed in soil adjusted to seven known moisture contents from field capacity to the wilting percentage. Thus, plants could be grown without addition of water to the soil and with only a small loss of original soil water content over a 25 day growing period. This minimized the effect of an internal water deficit developing in the plant and also minimized the magnitude of localized soil moisture changes in immediate proximity to the roots. They observed that under conditions of low humidity phosphorus uptake (expressed as percentage P in the tissue) increased linearly as the moisture content of the soil increased. Under high humidity conditions the differences in percent phosphorus in the plant tissue were not statistically significant. Smirnov (52) also used a split root technique, placing one strand into moist soil or water and the other in soil of various moisture contents which contained phosphorus-32. He found that, when the moisture content of the fertilized soil fell below 50 percent of the moisture capacity, uptake of soil phosphorus and particularly P32 decreased sharply. When it was 20-25 percent of the moisture capacity, root growth was impaired and the movement of phosphorus from the root to the shoot was retarded. Uptake of P32 from the soil at the wilting point was negligible when the moisture content of the soil containing the other root strand was less than 40-50 percent of the moisture capacity.

Data included in a paper by Brown et al (6) indicated that increasing the soil moisture from the wilting percentage to saturation resulted in a linear increase in the uptakes of nitrogen, potassium, phosphorus and calcium. When this was correlated with the transpirational loss by plants, the authors concluded that nutrient uptake and transpiration increased simultaneously over the range from wilting percent to saturation. Root growth also increased as the moisture content of the soil increased; however, Brown felt that this was not sufficient to entirely explain the large increase in ion absorption.

Olsen et al (38) determined phosphorus uptake by corn seedlings placed in soils at three phosphorus levels and at five moisture tensions from 1/3 to 9 bars. The absorption of phosphorus by corn seedlings, during a 24 hour period decreased significantly as the moisture tension was increased from 1/3 to 1 bar, from 1 to 3 bars, and from 3 to 9 bars. Phosphorus uptake followed a curve that closely resembled the moisture desorption curves for the soils. Thus, a linear relationship between phosphorus uptake and moisture content was found for a given soil. The authors also believe that there is a moisture tension-phosphorus concentration interaction. This effect is most pronounced at high levels of phosphorus where phosphorus uptake decreased from 23 mg/g to 8 mg/g as the moisture tension increased from 1/3 to 9 bars. In the low level treatments, phosphorus uptake decreased from 3.4 mg/g to 1.4 mg/g with increasing moisture tension. This agrees with the findings of Jordan et al (30) who concluded that as soil moisture tension increased phosphorus uptake by potatoes from soil and fertilizer sources decreased.

Danielson and Russell (8) investigated the uptake of Rb86 by corn seedlings from soil and osmotic solutions under various levels of moisture stress and oxygen tension. Their data indicated that moisture stress appeared to have no direct influence on the absorption of Rb86 by corn seedlings because osmotic pressure did not significantly affect Rb86 accumulation. However, Rb86 accumulation decreased rapidly with increasing soil moisture tension.

The authors stated that the thickness of the moisture films connecting the soil particles controlled the rubidium concentration at the root surface, and thus the rate of ion diffusion from the soil to the root would decrease as the film thickness decreased. Reduced water intake by the roots would also presumably reduce the movement of water and nutrients to the absorbing surface thereby reducing the amount of ions in the proximity of the root.

After examination of the evidence obtained in the above experiments it is apparent that nutrient absorption is strongly influenced by the moisture condition of the soil. In general, the absorption of phosphorus, as well as other nutrients, has been found to increase with increasing soil moisture content.

The Effect of Soil Moisture Stress on Phosphorus Transfer in the Plant: The behavior of water in the plant portion of the system has been studied extensively. The same underlying physical principles which govern soil water behavior also determine the properties and processes of water in the plant.

According to Russell (48), water movement in plants generally occurs through tissues that are water saturated. He asserted that the physical dimensions and macroscopic permeability of the water transmitting media are believed to respond to changes in the moisture content and water potential because of volume changes in the cells and tissues which occur in elastic, non-lignified plant parts. Such behavior is in contrast to the effects of changes in water content and water potential on the water transmission properties in soils where bulk volume changes are usually less pronounced, and variations in macroscopic permeability arise primarily because of changes in the volume function of the liquid phase. He concluded that it is unlikely that the water transmitting characteristics of plants will be so highly dependent on the water potential of the system as is the case in soils.

It is well established that the rate at which ions are absorbed by the roots of intact plants, and the subsequent transfer to their leaves may be considerably affected by the rate of transpiration. The main view, currently held by plant physiologists regarding the mechanism whereby transpiration can affect the overall process by which ions pass upwards through intact plants is that the transfer of ions across the root to the vascular stele is an active process dependent on metabolically produced energy, and that the effect of transpiration is to accelerate the movement of ions in water after they have been released to the vascular stream. In some cases, however, ions have been shown to move passively in water from the outer surface of the root upward to the shoot. This evidence is based on the fact that in many cases the rate of absorption correlates with the rate of transpiration. In a recent review of this subject, Russell and Barber (49) concluded that the transfer of ions from the root surface to the conducting xylem depends on the expenditure of energy, and that at some point in the process of ion transfer, accelerated absorption may take place by increasing the rate of transpiration.

Fried et al (16) discussed the various mechanisms of nutrient transfer across the root from the epidermis to the xylem, and concluded that the mechanism of nutrient transfer is an active one. This stipulates that ion absorption should not be dependent on transpiration. The authors outlined the overall process in the following manner:

$$Rb + R \overset{(1)}{\rightleftharpoons} RbR \rightleftharpoons Rb \text{ (actively accumulated + R in root)}$$

$$RbR \overset{(2)}{\rightleftharpoons} Rb \text{ (actively secreted into xylem)} \xrightarrow[(3)]{\text{transpiration}} Rb \text{ in shoots.}$$

Rb represents a Rubidium ion and R a metabolically produced carrier. Thus, the relative rates of the various reactions would determine the influence of translocation on nutrient absorption. That is, if reaction (2) was rapid in comparison with reaction (3), transpiration would influence absorption however, if reaction (2) was relatively slow, transpiration would not influence absorption. Fried concluded that transpiration would then have the greatest effect on absorption when ion concentration at the root surface was high and consequently reaction (2) was fast.

Wright and Barton (59) placed sunflowers in a solution culture to which P32 was added. The environmental factors, light and humidity, were varied to produce different rates of transpiration. Their investigation indicated that there is a definite relationship between the rate of transpiration and the absorption of P32 and its subsequent translocation to the leaves and stems. They concluded that as the amount of water transpired by a plant increased, the quantity of P32 in the leaves also increased. Similar results were reported by Mederski and Wilson (35) whose data showed that at low humidities, where transpiration was considerable, there was a close correlation between ion uptake and soil moisture; however, at high humidites, where there was a greatly reduced transpiration rate, the influence of soil moisture on the level of phosphorus accumulation was eliminated. Brown et al (6) obtained conclusive evidence which showed that the transpirational loss of water and the absorption of phosphorus increased simultaneously with increasing moisture content over the available moisture range. Beyond this however, transpirational losses continued to increase while the uptake of phosphorus decreased.

Thus, one can conclude that the absorption and subsequent translocation of phosphorus ions increases as the transpiration rate increases due to increasing soil moisture content. However, the effect of soil moisture on phosphate movement in the plant appears to be much less consistent than that observed for either nitrogen or potassium. It is possible that phosphate ion concentration at the absorbing surface of the root conditions the effect of translocation of phosphorus uptake, the effect being greatest where ion concentration at the root surface is high.

The Influence of Soil Moisture Stress on Plant Growth: Water is essential for plant growth. It is needed in much larger quantities than any other nutrient to carry out its role in morphological and physiological plant processes. Kramer (31) outlined the general function of water in plants, including: 1) water is an important constituent of the protoplasm; 2) water is an essential reagent in the photosynthetic process; 3) water is the solvent in which salts and gases enter plants, and in which solutes move from cell to cell and tissue to tissue in the plants; 4) water is essential to maintain sufficient turgidity for growth of cells and maintenance of the form and position of leaves, new shoots, and other slightly lignified structures.

The outstanding characteristic of water is its continuous one-way flow from the soil, through the roots, up the stems, and into the leaf's surface where it is evaporated mainly inside the stomata, through which it diffuses into the air. Usually less than 5 percent of the water absorbed is required in the essential functions, the rest being lost by transpiration.

Plant response to soil moisture, in the available range from field capacity to permanent wilting point, has been intensively studied by soil scientists and plant physiologists. Investigators have approached the problem in two manners; (1) long term experiments where the plant dries the soil to a predetermined moisture level before water is added to bring the soil volume to field capacity, (2) short term experiments in which plants are grown in the soil at previously established moisture contents for a length of time such that no appreciable change in soil moisture content takes place.

Russell, (47) in review, stated that no general agreement as to the nature of the response has been arrived at. One school of thought maintained that moisture is equally available to plant growth over the entire moisture range from field capacity to permanent wilting point while the other group of investigators endorsed the concept that plant growth showed differential response to soil moisture over the major part of the plant growth range.

Veihmeyer and Hendrickson (58), in reviewing the literature dealing with the relationship between soil moisture and plant growth up to 1950 concluded that plants can grow well throughout a wide range of soil moisture and that soil moisture is equally available for plant growth from field capacity to permanent wilting percent. They based their conclusions on the assumption that the increase in energy required by plant roots to remove a unit mass of water from the soil, when soil moisture is reduced from field capacity to permanent wilting percentage, is unimportant when the system as a whole is considered. In the following years, new methods have been devised which have enabled investigators to determine the overall effect of soil moisture content on plant growth more precisely.

There is some evidence linking plant response to soil moisture regimes with the phosphorus status of the soil. Mack and Barber (32) grew millet on soils adjusted to 40, 65 and 100 percent of field capacity. Dry matter production and phosphorus uptake increased significantly with increasing levels of soil moisture when fertilizer phosphorus was added to the soil. However, moisture content had little or no effect on plant growth and phosphorus uptake when no fertilizer phosphorus was added.

A comprehensive study, to determine the effects of soil moisture content on plant growth, was conducted in controlled environmental conditions and in field plots by Hagen et al (23). They reported the following relationships between plant growth or functioning and soil moisture stress. Respiration rate, dry matter production, and photosynthesis were not affected appreciably until the moisture content in the entire root zone approached the permanent wilting percent. Green weight production and shoot elongation were reduced significantly when the soil moisture fell into the lower half of the available range. Chemical composition, flower formation, and seed production were also influenced by moisture conditions in the available range. In conclusion, they reported that increasing soil moisture stress does not have a uniform effect upon the various aspects of plant growth and function. Some plant responses are relatively insensitive to increasing moisture stress over the available range while others are distinctly affected.

Mederski and Wilson (35) obtained experimental evidence which pointed out that the weight of plant tops and roots increased linearly with increasing soil moisture and that raising the humidity to 98 percent did not eliminate the influence of soil moisture. Spratt's (53) data also indicated that there is a significant increase in both forage and grain yield as the moisture content of the soil increases from permanent wilting to field capacity.

Hutcheon and Rennie (28) concluded that a single period of stress at any stage of crop growth, even though followed by favorable moisture conditions for the remainder of the growth period, would produce a marked decrease on the yield and composition of grain.

Gingrich and Russell (20) compared growth responses of corn roots to seven soil moisture tensions (1/3-12 atm) and osmotic stresses, each in combination with five oxygen concentrations, by growing small seedlings for 24 hours at 25° C in soil and osmotic pressure media. From their investigation, they concluded that radical elongation, increase in dry weight and the hydration of excised seedlings decreased rapidly with increasing soil moisture tension or osmotic stress through the range from 1/3 to 12 atm. Soil moisture-response curves were curvilinear. In comparison, the osmotic stress-plant response curves were linear; thus, prompting the authors to conclude, that factors other than straight physio-chemical effects of stress were operative. In earlier work, Gingrich and Russell (19) had concluded that the measured growth properties were much more sensitive to changes in moisture tension in the range between 1 and 3 atm. than for any other range when oxygen was not limiting.

In order to determine the effect of soil moisture content on root growth and water uptake, Peters (40) planted corn seedlings in sand-clay mixtures designed so that he could vary the moisture content while holding moisture tension constant, or vary moisture tension while the moisture content was constant. He assumed that there was a close relationship between root elongation and water uptake. His results indicated that the elongation of corn roots was a function of soil moisture tension - the shape of the curves conforming in general to the shape of the moisture characteristic curves. This suggested that the elongation of plant roots was merely a reflection of tension upon plant tissue. However, elongation was also found to be a function of soil moisture content since at a given tension elongation was a linear function of soil moisture content. Peters concluded that the reduction in growth, water uptake, and tissue hydration of corn roots under systems of moisture tension can be partially attributed to some function of soil moisture content and soil moisture flow.

Investigations conducted by Olsen et al (38) also pointed out that the dry weight of roots decreased as the moisture tension increased. They attributed this largely to a reduction in the number of root hairs present at higher moisture tensions. They asserted that factors, which affect the physiology of the actively absorbing root have to be considered as well as the factors which control the moisture and ion transmission properties of the soil when assessing the possible reasons why ion accumulation and water absorption by plants is decreased when soil moisture tension is increased.

Hunter and Kelley (26) studied the extension of plant roots into dry soil. Their data positively showed that the roots of corn were able to elongate into dry soil and build up the moisture content of that soil; however, no evidence was obtained for the absorption of nutrients from a dry soil.

Taylor (56,57) developed an equation for integrating the soil moisture tension in the root zone of growing crops. In applying this equation to crops grown in a rotation under different moisture conditions, he concluded that the hypothesis that soil moisture is equally available to plants throughout the entire growth range from field capacity to permanent wilting point is untenable.

In summary, Stanhill (55) recently reviewed 80 papers in which soil moisture regime was defined as an irrigation treatment in which the soil was allowed to dry until a definite measured point is reached within the available moisture range before sufficient water is added to restore the entire root zone to field capacity. In 83 percent of these experiments, plant growth positively responded to differences in the amount of available water depleted before the soil was rewet to field capacity.

Even though some disagreement does exist as to the effect of soil moisture on plant growth, it is generally concluded that soil moisture positively influenced top and root growth in the available range.

MATERIALS AND METHODS

Preparation of Soil Containing the Various Levels of Residual Soil P_2O_5: The Ap horizon of a Melfort clay loam soil from the Birch Hills district, was used in the two growth chamber experiments. This soil had a pH of 6.9, a conductivity of 1.6 mmhos per cm, and traces of sulfate and chloride ions. Lime carbonates were absent. The soluble phosphorus content, as measured by the carbonated water extraction method, was 29.1 ppm. phosphorus.

Three levels of residual soil phosphorus, 0,150, and 300 lb. of P_2O_5 per acre were prepared. The required amount of ammonium phosphate, calculated on the basis of 4000 g. of oven dry soil per crock was weighed. The fertilizer was then added to approximately 200 g. of soil. The soil plus the phosphate was tabled back and forth on an oil cloth until well mixed. Then, approximately 1000 g. of soil were spread out on the oil cloth and the soil-phosphorus mixture sprinkled over it. This was tabled again, and the process repeated until the entire 4000 g. of soil had been mixed thoroughly with the added phosphate. Ammonium nitrate was added to the soil to equalize the difference in nitrogen content that the soil treatments had received from the ammonium phosphate. When the twenty-five crocks of soil required for each phosphorus level had been prepared in this manner, they were emptied, thoroughly mixed together with a shovel, and then, the specified amount (4000 g.

on an oven dry basis) reweighed into each crock. This latter mixing helped to insure that all treatments were as uniform as possible.

A preliminary growth experiment was conducted in order to hasten the equilibrium of the added phosphorus with the soil system. The crocks were seeded to wheat and placed in the greenhouse. The soil was then watered to field capacity (40 percent) and the moisture content allowed to drop to 22 percent (permanent wilting percentage = 20) before rewetting. The wetting and drying of the soil in this manner increased the equilibrium process of the added ammonium di-hydrogen phosphate. After an eight week growth period, the crop was removed and discarded. The soil from each phosphorus level treatment was passed through a one-quarter inch screen, bulked together, and air dried. Twenty crocks for each soil phosphorus level were tared and 4000 g. of oven dry soil placed in them to be used in the first growth chamber experiment.

Prior to the second experiment, the soil from crocks which had the same level of residual soil phosphorus ~~was~~ were bulked together, air dried, and mixed thoroughly prior to repotting for the second growth chamber experiment.

<u>Preparation and Placement of the Radioactive Fertilizer Source</u>: The radioactive isotope of phosphorus (P32) was obtained from the Commercial Products Division, Atomic Energy of Canada Ltd., as carrier free-ortho-phosphoric acid in dilute HCl. The

radioactive solution was made up to 100 ml. and an aliquot, containing a known amount of activity, was then added to a calculated amount of $NH_4H_2PO_4$. This was diluted to 500 ml. and allowed to equilibrate. Five ml. of this solution, added to 4000 g. of oven dry soil, contained the equivalent of 50 lb. of P_2O_5 per acre. The specific activity of the tagged phosphate fertilizer used for the first and second growth chamber experiments was 1106 and 1200 μC. P32 per g. of P31 respectively. Two hundred ml. of the solution were saved for use as a standard to determine the amount of fertilizer phosphorus in the plant tissue.

Two methods of applying the fertilizer phosphorus to the soil were employed: 1) banding the fertilizer with the seed, and 2) mixing the fertilizer throughout the entire soil volume. In the banded treatment, the five ml. of fertilizer solution were uniformly distributed in short bands with the seed. In the mixed treatment, the five ml. of fertilizer solution were added dropwise to, and thoroughly mixed with, about 500 g. of soil. The remaining portion of the soil was mixed with the fertilized soil, as previously described for the non-active residual treatments.

Soil Moisture Stress Application: In order to give the plants in all treatments a chance to develop an adequate rooting system, the plants were grown for three weeks at a low moisture stress (40-32 percent moisture). After this time, the moisture stress treatments were initiated. In the low stress treatment, the moisture content of the soil was not allowed to fall below 32 percent throughout the remainder of the experiment. However, in the high stress treatments, the plants were allowed to dry the soil to 22 percent moisture which is just slightly above the permanent wilting percentage. Water was added to bring the moisture content of the soil back to field capacity as soon as the moisture content of the soil reached the lower limit. The amount of water used by the plants in each crock was recorded so that total water consumption per crock could be determined.

Summary of Treatments: In the first growth chamber experiment, two plants in each crock were grown to maturity, (104 days). The treatments included: 1) three levels of residual soil phosphorus: 0,150 and 300 lb. of equilibrated P_2O_5 per acre, 2) two methods of placing the tagged fertilizer phosphorus: banded with the seed and mixed into the soil, and 3) two moisture regimes: 40-32 percent and 40-22 percent moisture. Each treatment was replicated five times for a total of sixty crocks.

Identical treatments were used in the second experiment but techniques differed somewhat; four plants were grown in each crock instead of two; only four replicates were used; and the crop was harvested 52 days after seeding. At the same time, a third experiment was conducted using the smaller crocks containing 2000 g. of soil to determine the effect of soil moisture stress on soil phosphorus uptake from a reduced volume of soil. Two levels of soil phosphorus - 0 and 300 lb. P_2O_5 per acre, two methods of placement - banded and mixed and two moisture levels, 40-32 and 40-22 were used. The treatments were duplicated for a total of sixteen crocks.

Environmental Conditions in the Growth Chamber: All the experiments were conducted under controlled environmental conditions in a growth chamber. The temperature was set at 60 ± 2^{o}F. for the first three weeks and then raised to 70 ± 2^{o}F. for the duration of the experiment.

The relative humidity during the November to February period in which the first experiment was conducted averaged approximately 45 percent. This is much lower than the 65 percent relative humidity recorded during the second experiment which was conducted during the summer months.

A light period of 18 hours and a dark period of six hours was used throughout both growth chamber experiments. The average light intensity was 1500 foot candles in the centre of the table and about 1300 at the outer edges. Guard rows were placed at the ends of the growth chamber tables.

Nitrogen as NH_4NO_3 was applied in the watering solution used to bring the moisture content of the soil back to field capacity. This solution was such that one liter would apply 10 lb. of nitrogen per acre to the soil.

Harvest of Dry Matter: The forage and the grain from growth chamber experiment one and the forage from growth chamber experiment two were cut, dried at 55°C in a forced air oven, weighed, and then ground to less than 1 mm with a C. and N. Junior Laboratory Mill.

Root weights were determined from two crocks in each treatment from the second growth chamber experiment. The roots were removed by thoroughly soaking the soil in a three percent solution of hydrogen peroxide. Water was then used to wash the soil from the root mass. Roots were placed in a three percent solution of hydrogen peroxide and soaked for two hours to remove adhering soil particles. After this, they were placed on paper towels, dried at 130°F and weighed.

Phosphorus Analysis of Grain and Forage: A quantitative determination of fertilizer phosphorus was made using the briquet method (34). Four gram samples of the ground grain or forage were compressed in a circular die by a carver press for five minutes at 16,000 lb. pressure per square inch. The pellet was then counted using a Geiger-Muller, type D-37, detector tube attached to a Nuclear Chicago, Model 1814 scaler.

A primary standard, standard "A", was prepared to determine the amount of fertilizer phosphorus in the sample. This was accomplished by adding a calculated amount of radio-active fertilizer solution to an accurately weighed sample of grain or forage containing about 200 ml. of water. This 'slurry' was mixed thoroughly, dried at 55° C, ground as finely as possible, and pressed into pellet form.

The decay standard, standard "B", was prepared by compressing a four gram sample of boric acid, which contained enough of the original P32 solution to give a suitable count.

The mg. of fertilizer phosphorus per gram of plant material were then calculated from the formula:

$$\text{mg. fertilizer P/g} = \frac{\text{cor. count of unknown x wt. of fertilizer P in Std. "A"}}{\text{cor. count Std. "A" X } \dfrac{\text{Cor.count Std. "B" (start)}}{\text{Cor.count Std. "B" (present)}}}$$

A method outlined by Brenner (4) and modified by Nyborg (36) was followed for the wet ashing of the grain and forage samples for total phosphorus determination. The meta-vanadate yellow method of color development as outlined by Barton (2) and described by Penner (39) was used to determine the total phosphorus content in the wet ashed solutions.

The "A" Value: The "A" value, which is a measure of the amount of soil phosphorus available for plant growth, is a characteristic of a particular soil under a given set of environmental conditions. Fried and Dean (13,14) conducted a great deal of research on "A" value techniques which has ultimately led to its widespread acceptance. In simplified form their equation for deriving the "A" value may be stated as follows:

$$\text{"A"-value (lb.}P_2O_5\text{/ac.)} = \frac{\text{Soil P in plant}}{\text{Fertilizer P in plant}} \text{ X rate of fertilization (lb.}P_2O_5\text{/ac.)}$$

RESULTS AND DISCUSSION

Characterization of the Moisture Tension Curve

The pF moisture content curve for the Melfort clay loam soil used in the growth chamber experiments is shown in Figure 1. This was determined using the pressure plate-membrane apparatus. The 0.2 bar moisture content of approximately 36 percent suggests that the upper limit used in the pot experiments, 40 percent, is in error. However the latter value was determined experimentally in the greenhouse by adding sufficient water to air dry soil contained in a one gallon crock to wet the soil to approximately 5 inches. The crock was then covered to prevent evaporation, and 48 hours later, sampled to determine the moisture content in the 0 - 5 inch depth.

Measurement of Soluble Soil Phosphorus Using Various Extractants

The soluble or available phosphorus levels established in the Melfort soil were measured using a 1:10 soil:water ratio, carbonated water (33) and sodium bi-carbonate (37). Representative samples were analyzed from each residual phosphate treatment prior to the two growth chamber experiments. In addition, a more detailed sampling and analysis of each treatment was conducted at the termination of the experiments.

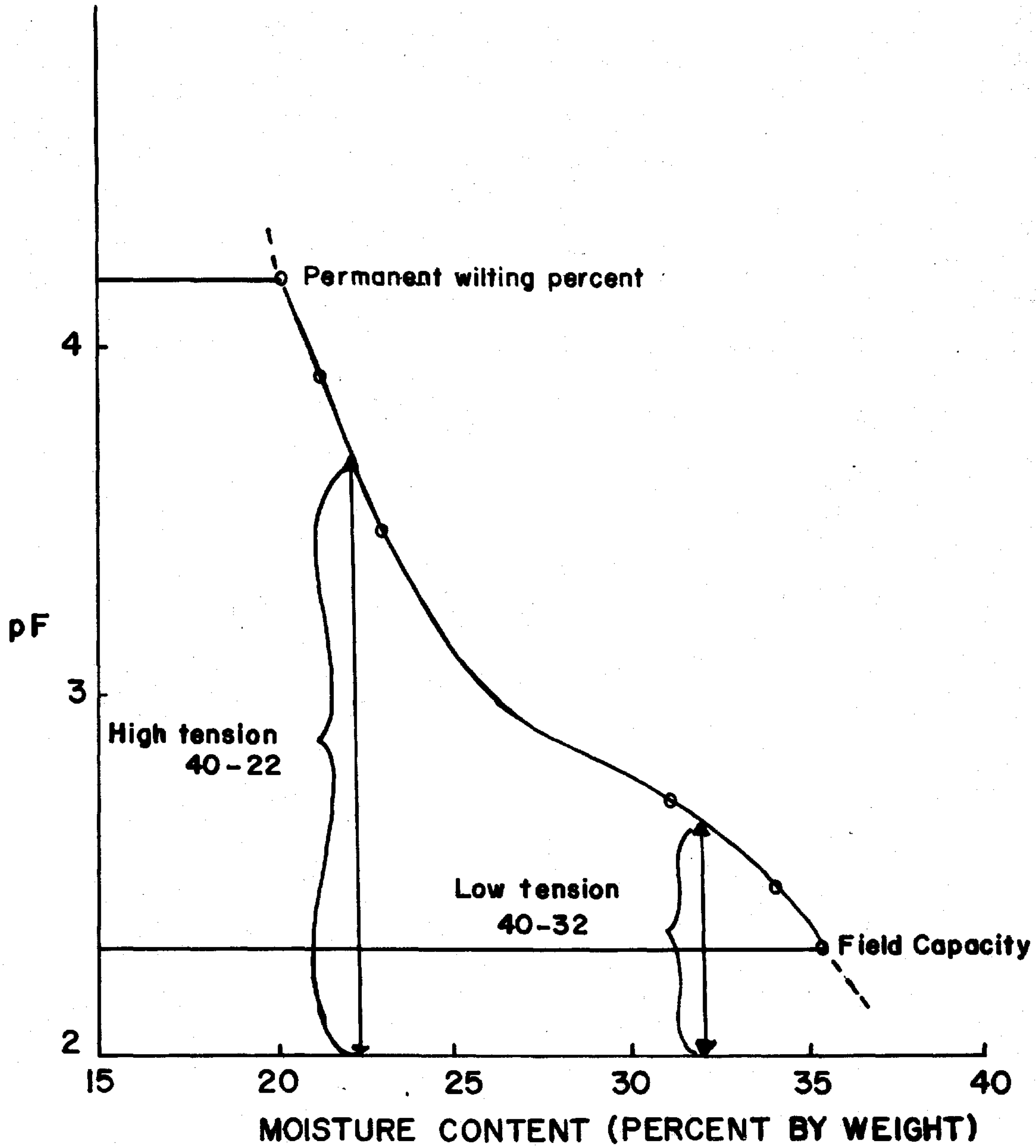

Figure 1. The pF moisture content curve for the Melfort clay loam soil

The various levels of phosphate were established on the premise that the influence of a soil moisture stress on plant available-soil phosphorus reported by Hutcheon and Rennie (28) should be lessened as the soluble-phosphorus content of the soil increased. This is possible providing that the measured decrease in the available soil phosphorus was mainly due to decreased rooting volume and not due to a significant net drop in soluble phosphorus in the soil-root volume (due to decreased 'mass flow', diffusion, or accelerated 'fixation').

Verification of the establishment of increasing levels of soluble phosphorus is clearly evident in the data given in Table 1. However the data also indicates that there was a consistent decrease in the amount of extractable phosphorus recorded between the start and finish of the first experiment; this trend is also evident in the data given for the second experiment. The decrease could be due to plant removal, or reflect a trend toward decreased extractable phosphorus resulting from a gradual fixation of added phosphorus; the latter is unlikely, firstly, since the soil was alternately wetted and dried for two months prior to the growth experiment, and secondly, since the trend toward decreased extractable phosphorus with time is also evident in the zero-residual-phosphorus treatment.

The data obtained where a more detailed sampling was conducted after both experiments clearly show a higher level of extractable phosphorus for the high stress as compared to the low stress treatments (Table 2). Since plant weight for the latter treatment (see Table 4) was significantly greater, it may be concluded that the consistent differences that were recorded between the two moisture stress treatments at all levels of residual phosphorus are due to differences in plant removal.

An attempt was made to calculate the net amount of phosphorus removal from the soil (plant removal - tagged fertilizer additions) and compare this with changes in available soil phosphorus measured by the three procedures. These data are summarized on the basis of residual phosphorus levels and moisture regimes (Table 3). In general the net removal of phosphorus by the plants is reflected in a decrease in the amount of soluble phosphorus extracted from the soil. Thus, it would appear that the residual phosphorus was probably in equilibrium with the soil system at the start of the first growth chamber experiment.

The significance of the various extractants in detecting phosphorus removal by the plant is illustrated in Figure 2. While the net removal of phosphorus from the soil was linearly related to the soluble or available phosphorus concentration in the soil as measured by water soluble and sodium bi-carbonate extractable phosphorus, there was little relationship between carbonated water extractable phosphorus and the net removal of phosphorus from the soil.

Table 1. Level of Soluble Phosphorus (ppm.) Before and After Each Growth Chamber Experiment

Residual - P Level	Water Soluble (1)	(2)	(3)	(4)	Carbonated Water (1)	(2)	(3)	(4)	Sodium Bi-Carbonate (1)	(2)	(3)	(4)
0	0.57	0.53	0.49	0.49	29.1	21.7	21.2	17.8	15.1	16.3	12.1	13.8
150	1.30	0.99	1.05	0.91	35.7	31.7	30.4	23.7	24.8	22.7	20.7	19.9
300	3.53	1.90	1.73	1.43	50.6	42.4	43.5	35.2	39.5	31.0	29.5	25.8

(1) Soil sampled before first experiment

(2) Soil sampled after first experiment

(3) Soil sampled before second experiment

(4) Soil sampled after second experiment

Table 2. The Level of Soluble Phosphorus (ppm.) in Each Treatment After Each Growth Chamber Experiment

Residual P Level	Fertilizer Placement	Moisture Regime	Water Soluble (1)	Water Soluble (2)	Carbonated Water (1)	Carbonated Water (2)	Sodium Bi-Carbonate (1)	Sodium Bi-Carbonate (2)
0	Banded	32	0.47	0.46	19.8	15.8	15.5	11.9
0	Banded	22	0.57	0.51	22.3	19.4	17.5	14.3
0	Mixed	32	0.46	0.40	20.5	17.1	15.5	13.9
0	Mixed	22	0.62	0.57	24.2	19.1	16.7	15.1
150	Banded	32	0.84	0.76	30.1	22.0	23.1	19.2
150	Banded	22	1.09	0.96	34.0	24.6	23.3	20.1
150	Mixed	32	0.93	0.84	29.6	23.0	21.7	19.4
150	Mixed	22	1.11	1.09	33.2	25.2	22.7	21.0
300	Banded	32	1.73	1.41	39.5	34.0	29.9	24.8
300	Banded	22	2.04	1.71	45.2	34.6	31.2	26.1
300	Mixed	32	1.70	1.67	41.5	34.4	30.8	25.0
300	Mixed	22	2.13	1.92	45.4	38.0	32.0	27.2

(1) Soil sampled after first growth chamber experiment

(2) Soil sampled after second growth chamber experiment

Table 3. The Influence of Residual Soil Phosphorus and Moisture Regime on Phosphate Balance (ppm)

a) Residual Phosphorus Levels:

	0	150	300
Total crop removal	28.1	31.1	36.9
Tagged fert. addition	21.8	21.8	21.8
Net P - removal from soil	6.3	9.3	15.1
Decrease in soluble soil phosphorus			
H_2O	0.08	0.39	2.10
H_2CO_3	11.3	12.0	15.4
$NaHCO_3$	2.0	4.9	10.1

b) Moisture Regime:

	First Experiment		Second Experiment	
moisture regime(H_2O)	40-32	40-22	40-32	40-22
Total crop removal	23.0	18.3	13.1	9.6
Tagged fert. addition	10.9	10.9	10.9	10.9
Net P removal from soil	12.1	7.4	2.2	-1.3
Decrease in soluble soil phosphorus				
H_2O	0.78	0.54	0.17	-0.04
H_2CO_3	8.3	4.3	7.2	4.9
$NaHCO_3$	3.7	2.6	1.8	0.2

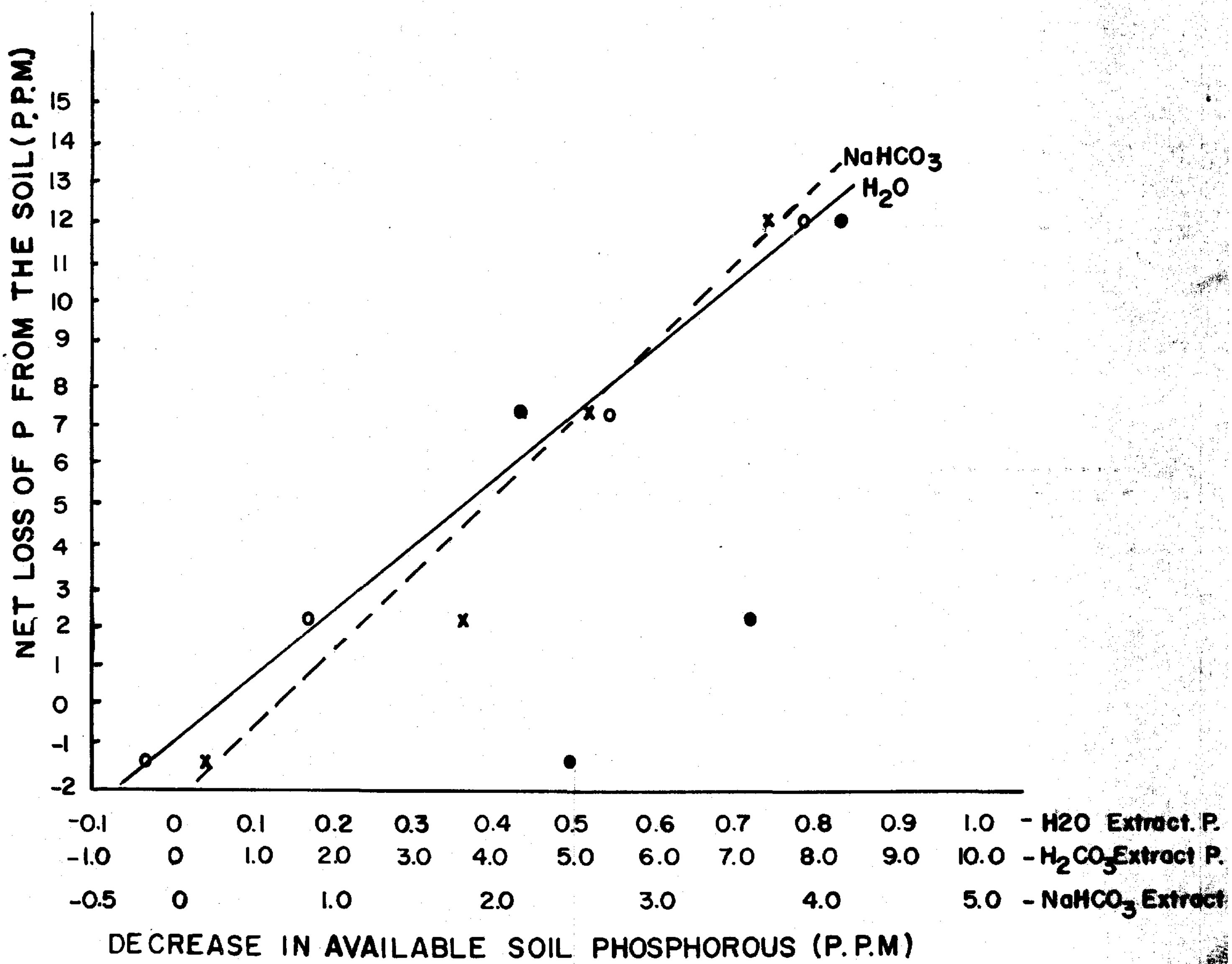

Figure 2. The relationship between uptake of soil phosphorus by the plant and the decrease in the available phosphorus content of the soil

Dry Matter Yields

The effect of soil moisture stress on dry matter yields: The grain plus forage yield in the first growth chamber experiment was significantly decreased by increasing the soil moisture tension in all except the 150-banded-treatment (Table 4.) Since the yield of grain was only slightly affected by increased moisture tension, the changes in total yield largely reflect a decrease in foliage yield. The trend towards decreased grain yields with increased moisture stress evident in the zero residual phosphorus level was not evident in the data obtained from the 150 or 300 lb. residual phosphorus levels where the reverse occurred, with the high stress treatments outyielding the low stress treatments. The mean yields given in Table 5 (a) confirm the above comments in that total plant weight was significantly decreased while the average grain yield was not affected by an increased moisture stress.

A possible explanation for this unusual phenomenon of moisture stress increasing rather than decreasing the yield of grain is as follows. Plants grown under favourable moisture conditions produced an average of 22.5 heads with an average yield of 8.52 g. per crock (0.38 g. per head). Only 17.6 heads were recorded for the high moisture stress treatments, but the average yield per head was 0.50 g. In effect, a significant proportion of the tillers from grain grown under low stress did not produce a seed. Shaw (51) suggested

Table 4. The Influence of Moisture Stress on Dry Matter Yields

Residual - P Level lb. P_2O_5/a.	Placement $NH_4H_2PO_4$	%moisture Low Limit	DRY MATTER YIELD (g./pot) Expt. 1 Total Yield	Grain	Expt. 2 Forage	Root	Forage*
0	banded	32	24.71	9.74	16.99	3.07	10.71
0	banded	22	18.85	8.50	11.87	1.81	9.75
0	mixed	32	25.05	9.54	13.44	2.14	10.08
0	mixed	22	19.52	8.51	10.85	1.99	7.45
150	banded	32	23.25	7.62	17.13	3.26	-
150	banded	22	20.69	8.64	13.64	2.36	-
150	mixed	32	24.61	8.35	16.35	2.71	-
150	mixed	22	19.15	8.53	13.45	2.21	-
300	banded	32	27.50	7.58	16.65	3.46	10.36
300	banded	22	23.95	9.38	13.73	2.27	9.34
300	mixed	32	26.92	8.27	16.56	2.93	10.38
300	mixed	22	22.56	8.75	13.15	2.21	9.25
		L.S.D.	3.36	1.74	1.71	0.50	2.56

* Grain grown in 2000 g. crock

Table 5. The Mean Effects of Soil Moisture Regimes, Residual Soil-Phosphorus Level, and Fertilizer Placement on Dry Matter Yield (Grams Per Pot)

(a) Soil moisture regime

Moisture Regime	Growth chamber expt.(1)		Growth chamber expt.(2)		
	Gr. & For.	Grain	Forage	Roots	Forage *
40-32	25.33	8.52	16.19	2.95	10.38
40-22	20.73	8.72	12.78	2.14	9.10
L.S.D.	1.37	0.71	0.70	0.20	1.28

(b) Residual soil phosphorus level

Residual-P Level	Growth chamber expt.(1)		Growth chamber expt.(2)		
	Gr. & For.	Grain	Forage	Roots	Forage*
0	21.94	9.07	13.29	2.29	9.50
150	21.92	8.28	15.14	2.64	-
300	25.23	8.50	15.02	2.71	9.98
L.S.D.	1.68	0.87	0.86	0.25	1.81

(c) Placement of fertilizer phosphorus

Fertilizer Placement	Growth chamber expt.(1)		Growth chamber expt.(2)		
	Gr. & For.	Grain	Forage	Roots	Forage*
Banded	23.16	8.58	15.00	2.73	10.19
Mixed	22.90	8.66	13.97	2.37	9.29
L.S.D.	1.37	0.71	0.70	0.20	1.28

Forage* - Plants grown in 2000 grams of soil

that when other growth factors are not limiting, high levels of soil phosphorus have been shown to stimulate tillering in wheat plants. In this instance, as the number of tillers increased, the incidence of sterile spikelets also increased. He also pointed out that the yield of plants grown under ideal moisture conditions and high phosphorus levels was probably limited by the photosynthetic capacity of their leaves. Thus, the plants were unable to produce sufficient carbohydrates to fill the large number of spikes that were produced. Under these conditions, carbohydrates could be transported to areas of new shoot (tiller) development rather than to the head where they could have been utilized in the seed development process. This is further supported by the statistical analysis in that the "F" test for grain yield was significant for the moisture content - residual phosphorus level interaction, but it was not significant for moisture level alone.

The crop grown in the second experiment was harvested just prior to the heading stage. The significant reductions in forage yield due to moisture stress recorded for all treatments were similar to those recorded for the first experiment. The average 21 percent decrease in forage yield was accompanied by a 36 percent decrease in yield of roots due to increased moisture stress. The significance of this marked drop in weight of roots, due to an increase in soil moisture stress will be discussed in a later section of this manuscript.

The influence of increased soil moisture stress on forage yields of wheat grown in the small crocks was not as large as those grown in the gallon crocks. An average decrease in yield of 12 percent was recorded. In only one instance, the zero residual phosphorus-mixed placement, was the yield decrease significant.

The effect of residual soil phosphorus level on dry matter yield: The influence of the residual phosphorus treatments on the yield of forage and grain are perhaps most readily seen from the mean data presented in Table 5(b). The residual phosphorus level did not significantly alter the yield of grain, and only when the residual soil phosphorus level was increased to 300 lb. P_2O_5 per acre, was there a significant increase in total plant weight obtained in the first growth chamber experiment. The 150 lb. P_2O_5 residual phosphorus level in the second growth chamber experiment resulted in maximum yields of forage and roots. In the analysis of variance on the root weight data, the "F" test showed that there was a significant phosphorus level - moisture content interaction, thus indicating that the influence of residual phosphorus level on root weight varied depending on the moisture stress. The relative reduction in root weight due to increased moisture stress was more marked at low than at high levels of soluble soil phosphorus (Table 4).

The effect of fertilizer placement on dry matter yield: The average yield of forage or grain was not affected by the fertilizer placement in the first experiment. In the second, short term experiment, the banded treatments outyielded the mixed ammonium phosphate treatments (Table 5(c). However, from the individual treatment data given in Table 4 it is apparent that the differences between the banded and mixed placement decreased as the level of residual phosphorus increased.

Placing the fertilizer in a band with the seed resulted in significant increases in weight of roots (as compared to the mixed placement) where the plants were grown under a low moisture stress (Table 4) for all levels of residual phosphorus. Again, this stimulatory effect on root growth decreased as the level of soluble phosphorus in the soil increased. In contrast, root weights were practically identical for banded and mixed treatments where the plants were grown under a high soil moisture stress.

The effect of soil volume on yield: A preliminary investigation was carried out in conjunction with the second growth chamber experiment to determine whether the use of half gallon crocks, containing approximately 2000 g. of soil could be used in place of the larger crocks in experiments of this type. Reducing the amount of soil in which the plants were grown from 4000 g. to 2000 g. reduced the average yield per crock (calculated from the data given in Table 4) from 14.2 to 9.7 g. Where direct comparisons are possible (the 150 lb. P_2O_5 per acre residual phosphorus level treatment was not included in the small pot experiment), high soil moisture tension decreased yields 13.8 and 22.1 percent for crops grown in the small and large crocks respectively. Mixing the tagged fertilizer through the soil resulted in a 7.5 and 8.8 percent yield decrease as compared to the banded treatment for the respective yields of the small and large crocks. These data, in general, favour the use of large crocks - this observation being somewhat surprising since it would be expected that availability of plant nutrients and water would be more restricted in the crop that was grown in the 2000 as compared to the 4000 g. of soil.

Available Soil Phosphorus ('A' Value)

The effect of soil moisture stress on the availability of soil phosphorus: Where the tagged phosphate fertilizer standard is banded with the seed, Rennie and Spratt (44) have shown that fixation and isotopic exchange reactions are negligible. Any increase or decrease in the fixation capacity of the soil due to soil moisture stress should not influence the availability of the tagged fertilizer standard, thus insuring that the 'A' value data obtained reflect differing levels of available soil phosphorus and not a change in the fertilizer standard.

The following discussion is based in the first instance on the 'A' value data given in Table 6 for the first growth chamber experiment. Where the tagged phosphate fertilizer was banded with the seed, a significant reduction in the 'A' value due to increased moisture stress was recorded for the zero residual phosphorus level treatment only. When the soluble phosphorus content of the soil solution was increased, the A-values recorded remained remarkably constant for both moisture regimes. These data suggest that the lower the soluble phosphorus content of the soil, the greater will be the influence of soil moisture stress on plant available phosphorus. This is confirmed in part by comparing these data with those found by Rennie and Spratt (44) who worked with an Oxbow loam soil which had a soluble phosphorus content comparable to that of the zero residual phosphorus treatment. These authors reported a drop in the 'A' values from 61 to 41 and 61 to 25 for soil moisture regimes of 27 to 17 and 27 to 9 percent moisture respectively.

Increasing the soluble phosphorus content of the soil apparently overcame the adverse effect of an increased soil moisture stress on plant available phosphorus in treatments in which the tagged fertilizer was banded with the seed. Many authors have suggested that decreased mass flow and diffusion of phosphorus into the soil solution-root volume occurs as the moisture content in the soil falls. These data support the theory that the decrease in plant available phosphorus due to a moisture stress, which occurred only at

Table 6. The Influence of Moisture Stress on 'A' Values

Residual-P Level (lb./a.P_2O_5	Placement $NH_4H_2PO_4$	%moisture Low stress	A-VALUE (pounds per ac P_2O_5) Gr.chamber 1 Grain	Gr.chamber 1 Forage	Gr. chamber 2 Forage*
0	banded	32	104.8	109.7	109.7
0	banded	22	79.0	94.1	78.2
0	mixed	32	229.2	302.5	262.6
0	mixed	22	202.5	291.5	243.7
150	banded	32	129.3	151.1	-
150	banded	22	138.1	131.1	-
150	mixed	32	350.6	403.2	-
150	mixed	22	305.4	381.2	-
300	banded	32	205.1	204.0	206.2
300	banded	22	201.7	199.7	186.8
300	mixed	32	463.8	529.5	472.7
300	mixed	22	427.2	507.4	439.6
	L.S.D.		20.9	13.4	31.1

* Grain grown in 2000 gm crock

a relatively low level of soluble phosphorus is primarily due to a restriction in the rooting volume. It is highly feasible that the effect on plant available phosphorus of a decrease in rooting volume (this is varified in root weights outlined in Tables 4 and 5) should be overcome by increasing the solution concentration of phosphorus in the soil.

In direct contrast to the data obtained where the tagged fertilizer standard was banded, a decrease in available soil phosphorus due to increased moisture stress was measured using the mixed fertilizer placement at all levels of soluble phosphorus in the soil. Assuming that fixation reactions and isotopic exchange reactions were similar for the various levels of soluble phosphorus in the soil, and for the two soil moisture stress treatments, it could be concluded that the availability of the soil phosphorus decreased at all residual phosphorus levels as the soil moisture stress increased. Several workers (42,43) have shown that the release of solid phase phosphorus into the soil solution and the transfer of this phosphorus to the root absorbing site are both decreased as the soil moisture tension increases. Therefore, these factors would reduce soil phosphorus uptake and hence would result in lower 'A' values than those recorded under optimum moisture conditions.

Thus, assuming similar fixation and isotopic exchange reactions for the two moisture regimes and three phosphorus levels, it is concluded that the availability of soil phosphorus was regulated by the moisture content of the soil, which ultimately determines the amount of root extension and the amount of phosphorus moving in the soil solution to the root's absorbing site. This conclusion is based on evidence indicated: (1) in the banded treatments, where reduced 'A' values in the low phosphorus level treatment (under increased moisture stress conditions) were attributed to a decrease in root proliferation through the soil, and (2) in the mixed treatments where reduced 'A' values were attributed to decreased soil phosphorus uptake due to a reduction in the availability of the soil phosphorus to the plant (under increased moisture stress).

The 'A' value data obtained from the short term second growth chamber experiment, in general, substantiates the conclusions drawn above, with the exception that the magnitude of the 'A' value data is somewhat higher. Again, where 2000 g. instead of 4000 g. of soil was used almost identical 'A' value data were obtained as that recorded for the experiment grown to maturity. The higher L.S.D. value obtained for the experiment grown in half gallon crocks does not necessarily suggest that these data were more variable. Each treatment was replicated only twice, and thus, the degree of freedom for error was approximately half those for the other experiments.

The effect of residual soil phosphorus level and fertilizer placement on the availability of soil phosphorus: The significant increase in 'A' values with increasing levels of residual phosphorus indicate that the availability of the soil phosphorus increased with increasing levels of residual soil phosphorus thus complementing the extractable phosphorus data discussed earlier.

It is interesting to note that the relative change in 'A' values due to residual phosphorus levels was approximately the same for both the banded and mixed placements; this suggests that irreversible isotopic exchange in the mixed treatment was not very important.

'A' values for the mixed placement are approximately double those of the banded placement for all levels of residual phosphorus. This is in due part to the more favourable positional availability of the banded fertilizer standard and also due to the decrease in the availability of the fertilizer standard when mixed throughout the soil (54).

Fertilizer Phosphorus Uptake

The uptake of fertilizer phosphorus by the plant is a function of the availability of the soil phosphorus and the total weight of plant material produced. The influence of this latter variable can be eliminated where the data are expressed as mg. of P per g. plant material. Thus, any variations in the data given in Table 7 can be attributed to differences in the available soil phosphorus. Where the tagged fertilizer standard was banded with the seed, a significant increase in the fertilizer phosphorus content of the grain occurred due to a decrease in soil moisture tension for the zero-residual phosphorus level. The increased soil moisture stress did not affect the fertilizer phosphorus content of the grain for those treatments where the soluble phosphorus content of the soil solution was increased. Thus, these data confirm the conclusions drawn earlier from the 'A' value data. It is of interest to note that where the tagged fertilizer standard was mixed with the soil, the fertilizer phosphorus content of the grain, at any one residual phosphorus level was statistically identical for both moisture regimes. This would suggest that the chemical availability of the soil phosphorus was unaffected by soil moisture stress, or if fixation did occur, the decrease in available soil phosphorus was accompanied by an equal decrease in the availability of the tagged fertilizer standard. This latter explanation is probably the more plausible one since the 'A' value data recorded for the mixed treatments did suggest a decrease in plant available soil phosphorus as the soil moisture stress increased.

The individual soil phosphorus and total phosphorus uptake data as well as the percentage utilization of the

Table 7. The Influence of Soil Moisture Stress on Fertilizer Phosphorus Uptake (mg P/g. plant material)

Residual P Level (lb./a.P_2O_5)	Placement $NH_4H_2PO_4$	% Moisture Lower Limit	FERTILIZER P UPTAKE (mg./gm.) Trial 1 Grain	Trial 2 Forage	Forage*
0	banded	32	1.75	0.94	0.84
0	banded	22	1.99	0.96	0.75
0	mixed	32	0.98	0.43	0.40
0	mixed	22	1.08	0.40	0.37
150	banded	32	1.57	0.80	-
150	banded	22	1.47	0.80	-
150	mixed	32	0.71	0.32	-
150	mixed	22	0.73	0.33	-
300	banded	32	1.09	0.72	0.67
300	banded	22	1.10	0.68	0.63
300	mixed	32	0.55	0.31	0.32
300	mixed	22	0.56	0.30	0.29
	L.S.D.		0.10	0.04	0.09

* Grain grown in 2000 gm. crock

applied fertilizer and fertilizer phosphorus expressed as a percent of total phosphorus are included in the appendix. These, in general, merely tend to confirm the conclusions drawn either from 'A' value or fertilizer phosphorus uptake data.

The Relationship between Yield of Phosphorus and Root Weights

The yield of phosphorus in mg. per pot (shown in the appendix, Table 10) was reduced by 20.7 and 27.2 percent, respectively, when the moisture stress in growth chamber experiments one and two was increased. The marked decrease in phosphorus yield under conditions of increased soil moisture stress is due to a reduction in dry matter yield (Table 4) as well as a reduction in the total phosphorus content of the grain (Table 13 appendix).

The relationship between yield of phosphorus and root weight per crock in growth chamber experiment two is illustrated graphically in Figure 3. The r-value of 0.91, which was highly significant shows that there is a significant correlation between these two factors. These data conclusively indicate that factors which affect the growth and development of the rooting system of the plant also affect the total uptake of phosphorus by the plant.

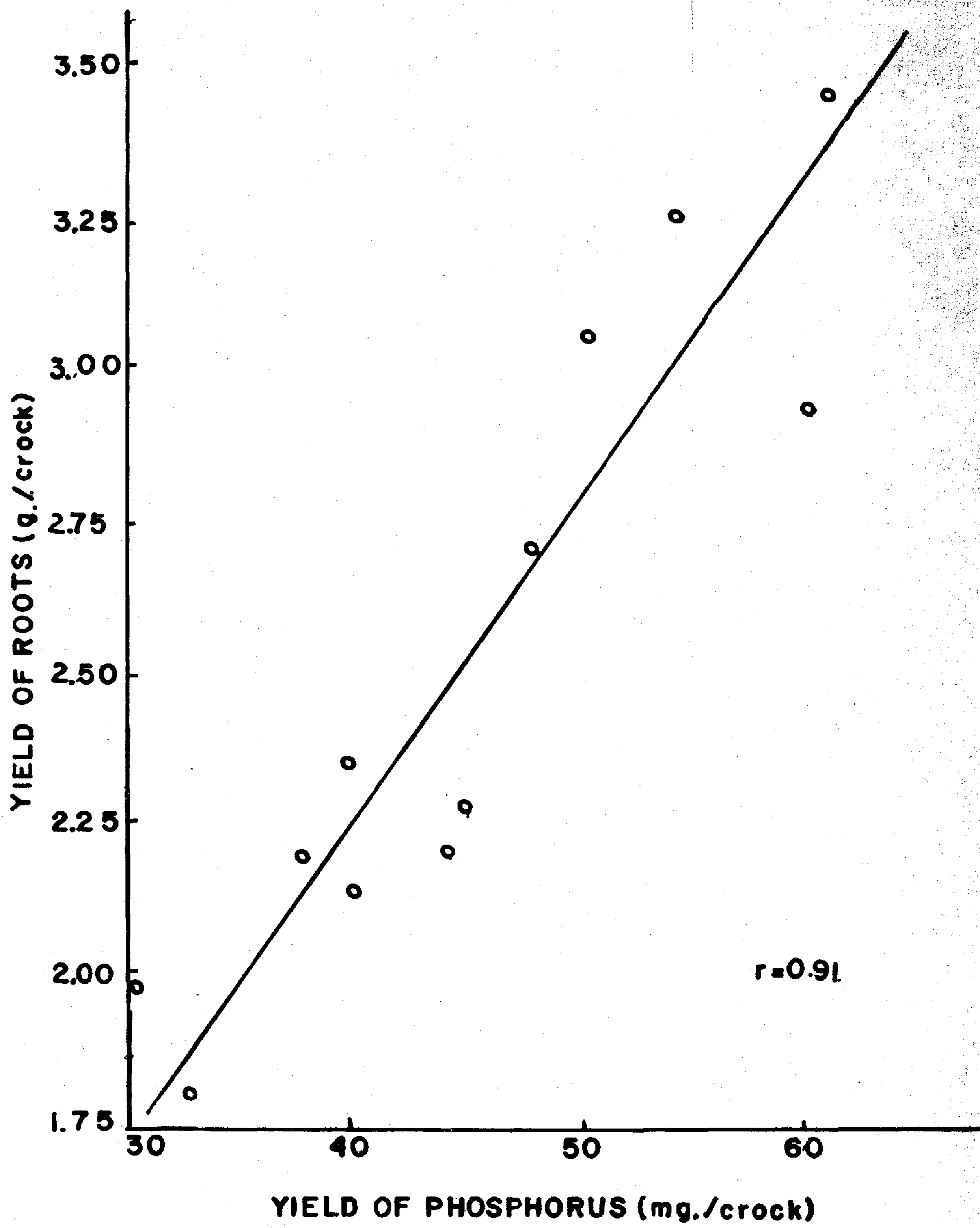

Figure 3. The relationship between root yield and phosphorus uptake

SUMMARY AND CONCLUSIONS

The purpose of this investigation was to determine whether the decrease in plant available-soil phosphorus that occurs under conditions of increased moisture tension was primarily due to a change in the chemical availability of the soil phosphorus, or due to a change in the rooting habit such that the plant is unable to fully expropriate the total soil volume, or due to a combination of both factors.

Two experiments were conducted in controlled conditions in the growth chamber using Thatcher wheat. In the first instance the plants were harvested at maturity, and in the second, at the end of six weeks. The crop was grown on a clay loam soil containing three levels of equilibrated residual soil phosphorus. Tagged fertilizer phosphorus was placed in bands with the seed and mixed throughout the entire soil volume. Moisture stress treatments were initiated when the plants had reached the three week stage.

Three extraction methods were used to characterize the residual phosphorus content of the soil before and after each growth chamber experiment. From this data, it was evident that a low, an intermediate, and a high level of residual phosphorus had been established, and that the soil-phosphorus system had reached equilibrium before the start of the first growth chamber experiment. The amount of extractable phosphorus present in the soil used in the low moisture stress treatment was consistently less than that recorded for the high moisture stress treatment. This was attributed to increased plant removal of phosphorus in the low moisture stress regime.

Forage yield and root weight were significantly decreased by increasing the moisture stress; however, moisture stress did not affect the yield of grain. Placing the fertilizer source in bands, as compared to mixing it through the entire soil volume, increased forage and root yields in the crop harvested after six weeks. Fertilizer placement had no effect on either grain or forage yield in the crop grown to maturity. When the residual phosphorus level of the soil was raised from zero to 150 lb. of P_2O_5 per acre, root and top growth were stimulated in the short term experiment. No yield increase was recorded when the residual phosphorus level was raised to 300 lb. of P_2O_5 per acre. Grain yields were not affected by the residual phosphorus level of the soil.

Under conditions of increased moisture tension, the plant available-soil phosphorus ('A' value) decreased significantly in the banded treatments only at the low level of residual soil phosphorus. This was attributed to a significant decrease in root weight and consequently exploitation of the soil in the high moisture stress treatment. The significant decrease in the measured rooting volume, appeared to have been overcome at higher soluble phosphorus levels by an increase in the solution concentration of phosphorus in the soil. However, in the mixed treatments, the 'A' values decreased significantly with increasing moisture stress at all levels of residual soil phosphorus. Since the measured root weight was not markedly affected by moisture tension (especially in the lower levels of residual soil phosphorus), a decrease in the availability of the soil-phosphorus must have taken place.

Placement of the fertilizer source in short bands in close proximity with the seed significantly increased fertilizer phosphorus uptake, as compared with the mixed placement where isotopic exchange and fixation by the soil significantly reduced its availability to the plant. Increasing the level of residual soil phosphorus decreased fertilizer phosphorus uptake in all treatments. This reflected an increase in the availability of the soil phosphorus rather than a decrease in fertilizer phosphorus availability.

It was shown that there was a highly significant correlation between the measured root yield and the total phosphorus yield per crock. Since the moisture content of the soil decidedly affected root weight in the low, soluble phosphorus level-banded treatment, it has been concluded that moisture stress decreased the availability of soil phosphorus to plants by limiting further development of the root system. However, in the mixed treatments, where the root system was not as well developed as in the banded treatments, and was not as significantly restricted by moisture stress, the phosphorus transmitting characteristics of the soil largely controlled the availability of the soil phosphorus.

This research indicates that there is a need for a more precise characterization of the plant's root system when assessing the mechanism by which plant available-soil phosphorus is decreased by a measured moisture stress.

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APPENDIX

Table 8. The Mean Effects of Soil Moisture Regimes, Residual Soil-Phosphorus Level, and Fertilizer Placement on Fertilizer Phosphorus Uptake (mg.P/g. plant material)

(a) Soil Moisture Regime

Moisture Regime	Growth chamber expt. (1) Grain	Growth chamber expt.(2) Forage	Forage*
40-32	1.12	0.59	0.56
40-22	1.16	0.57	0.50
L.S.D.	0.04	0.02	0.06

(b) Residual Soil Phosphorus Level

Residual-P Level	Growth chamber expt. (1) Grain	Growth chamber expt.(2) Forage	Forage*
0	1.45	0.68	0.58
150	1.13	0.56	-
300	0.83	0.50	0.48
L.S.D.	0.05	0.02	0.07

(c) Placement of fertilizer phosphorus

Fertilizer Placement	Growth chamber expt. (1) Grain	Growth chamber expt.(2) Forage	Forage *
Banded	1.50	0.81	0.72
Mixed	0.77	0.35	0.34
L.S.D.	0.04	0.02	0.06

Forage* - Plants grown in 2000 grams of soil

Table 9. The Percent Utilization of Fertilizer Phosphorus and Fertilizer Phosphorus as a Percent of Total P in Growth Chamber Experiments (1) and (2)

	% Utilization of Fert.P Growth Ch.(1)	(2)	Fertilizer P as a % of Total P Growth Ch. (1)	(2)
0-32-B	66.9	36.2	33.4	31.3
0-22-B	53.4	26.3	38.8	34.8
0-32-M	35.4	13.0	17.9	14.8
0-22-M	29.1	9.9	19.8	14.6
150-32-B	54.0	31.1	28.1	24.9
150-22-B	46.6	24.9	26.7	27.7
150-32-M	25.8	12.1	12.5	11.0
150-22-M	21.8	10.0	14.1	11.6
300-32-B	47.7	27.5	20.6	19.7
300-22-B	40.7	20.5	20.0	20.0
300-32-M	22.4	11.9	9.7	8.6
300-22-M	20.5	8.9	10.5	8.8
Moisture				
32	42.0	22.0	20.4	18.4
22	35.4	16.8	21.7	19.6
Residual P-level				
0	46.2	21.4	27.5	63.9
150	37.1	19.5	20.4	18.8
300	32.8	17.2	15.2	14.3
Placement				
Banded	51.6	27.8	27.9	26.4
Mixed	25.8	11.0	14.1	11.6

Table 10. Phosphorus Yield (mg./pot)

Treatment	Growth chamber expt. 1			Growth chamber expt. 2		
	Total-P	Fert. P	Soil-P	Total-P	Fert. P	Soil-P
0-B-32	87.0	29.1	57.9	50.6	15.9	34.8
0-B-22	59.8	23.2	36.6	32.8	11.4	21.4
0-M-32	86.0	15.4	70.6	40.3	5.7	34.5
0-M-22	63.6	12.6	51.8	30.2	4.3	25.9
150-B-32	83.7	23.5	60.1	54.6	13.6	41.1
150-B-22	76.1	20.3	55.8	39.3	10.9	28.5
150-M-32	90.0	11.2	78.7	48.1	5.3	42.7
150-M-22	67.4	9.5	58.3	37.8	4.4	33.4
300-B-32	105.4	20.7	84.8	61.1	12.0	49.0
300-B-22	88.2	17.7	70.5	44.9	9.0	35.9
300-M-32	100.1	9.8	90.4	60.3	5.2	55.1
300-M-22	84.9	8.9	75.9	44.3	3.9	40.4

Table 11. The Influence of Moisture Stress on Soil Phosphorus Uptake (mg.P/gm plant material)

Residual-P Level (lb./a.P_2O_5)	Placement $NH_4H_2PO_4$	% Moisture Lower Limit	SOIL P UPTAKE (mg./gm.) Trial 1 Grain	Trial 2 Forage	Forage*
0	banded	32	3.69	2.05	1.84
0	banded	22	3.13	1.80	1.14
0	mixed	32	4.50	2.56	2.09
0	mixed	22	4.40	2.45	1.81
150	banded	32	4.13	2.40	-
150	banded	22	4.05	2.09	-
150	mixed	32	5.00	2.61	-
150	mixed	22	4.46	2.48	-
300	banded	32	4.47	2.94	2.77
300	banded	22	4.38	2.61	2.31
300	mixed	32	5.08	3.33	3.03
300	mixed	22	4.79	3.07	2.50
	L.S.D.		0.22	0.16	0.16

* Grain grown in 2000 gm. crock

Table 12. The Mean Effects of Soil Moisture Regimes, Residual Soil-Phosphorus Level, and Fertilizer Placement on Soil Phosphorus Uptake (mg.P/gm. plant material)

(a) Soil Moisture Regime

Moisture Regime	Growth chamber expt. (1) Grain	Growth chamber expt. (2) Forage	Forage*
40 - 32	4.48	2.65	2.23
40 - 22	4.20	2.41	1.94
L.S.D.	0.09	0.07	0.08

(b) Residual Soil Phosphorus Level

Residual-P Level	Growth chamber expt. (1) Grain	Growth chamber expt. (2) Forage	Forage*
0	3.93	2.20	1.72
150	4.41	2.39	-
300	3.68	2.99	2.68
L.S.D.	0.11	0.08	0.12

(c) Placement of Fertilizer Phosphorus

Fertilizer Placement	Growth chamber expt. (1) Grain	Growth chamber expt. (2) Forage	Forage*
Banded	3.98	2.31	2.02
Mixed	4.70	2.74	2.36
L.S.D.	0.09	0.07	0.08

Forage* - Plants grown in 2000 grams of soil

Table 13. The Influence of Moisture Stress on Total Phosphorus Uptake (mg.P/gm. plant material)

Residual-P Level (lb./a.P_2O_5)	Placement $NH_4H_2PO_4$	% Moisture Lower Limit	PERCENT TOTAL P (mg.P/gm.) Trial 1 Grain	Trial 1 Forage	Trial 2 Forage	Trial 2 Forage*
0	banded	32	5.44	2.16	2.98	2.68
0	banded	22	5.12	1.41	2.76	1.88
0	mixed	32	5.48	1.47	2.99	2.48
0	mixed	22	5.48	1.47	2.85	2.18
150	banded	32	5.75	2.56	3.19	-
150	banded	22	5.53	2.25	2.88	-
150	mixed	32	5.71	2.64	2.94	-
150	mixed	22	5.19	2.15	2.81	-
300	banded	32	5.56	3.18	3.67	3.44
300	banded	22	5.48	2.59	3.27	2.94
300	mixed	32	5.62	3.02	3.64	3.35
300	mixed	22	5.36	2.68	3.37	2.79
	L.S.D.		0.22	0.28	0.19	0.52

Forage* - Plants grown in 2000 gm. crock

Table 14. The Mean Effects of Soil Moisture Regimes, Residual Soil-Phosphorus Level and Fertilizer Placement on Total Phosphorus Uptake (mg.P/gm.plant material)

(a) Soil moisture regime

Moisture Regime	Growth chamber expt. (1) Grain	Forage	Growth chamber expt. (2) Forage	Forage*
40 - 32	5.59	2.62	3.23	2.99
40 - 22	5.36	2.09	2.98	2.45
L. S. D.	0.09	0.11	0.08	0.26

(b) Residual soil phosphorus level

Residual-P Level	Growth chamber expt. (1) Grain	Forage	Growth chamber expt. (2) Forage	Forage*
0	5.38	1.80	2.88	2.13
150	5.54	2.40	2.95	-
300	5.51	2.87	3.49	3.13
L.S.D.	0.11	0.14	0.10	0.37

(c) Placement of fertilizer phosphorus

Fertilizer Placement	Growth chamber expt. (1) Grain	Forage	Growth chamber expt. (2) Forage	Forage*
Banded	5.48	2.36	3.12	2.73
Mixed	5.47	2.35	3.09	2.70
L.S.D.	0.09	0.11	0.08	0.26

Forage* - Plants grown in 2000 grams of soil