AN ABSTRACT OF THE THESIS OF

David Stuart Stevenson for the Ph.D. in Soils

Date thesis is presented January 8, 1963

Title EFFECTS OF SOIL MOISTURE-TENSION ON RUBIDIUM UPTAKE BY SUNFLOWERS

Redacted for Privacy

Abstract approved ______________________________
(Major professor)

There is considerable evidence that the growth and elongation of plant roots increases linearly or almost linearly with increasing water contents or decreasing moisture-tension of soil. If this is true it is difficult to distinguish the effects of different water contents on absorption phenomena such as water or ion uptake from the effects of the water contents on the root growth itself. Any absorption process which directly correlates with the amount of root growth is subject to misinterpretation as to the ultimate effect of changing water contents on the particular process. One useful alternative is to measure the root growth precisely and account for, through covariance, the differences in root growth as a result of differences in water contents or moisture-tensions in the soil.

Samples of soil at various water contents and containing rubidium ions, were placed around the stems of six-week old sunflower plants and adventitious roots allowed to grow into the soil samples. The period of adventitious root growth was six days. Root growth, water lost from the soil samples, and the rubidium taken up into the above-ground parts of the plants were measured. All experiments were conducted in a controlled-environment growth room.

Root growth was found to be closely related to the initial water contents of the soil samples. The relationship was slightly curvilinear. Water taken up by the adventitious roots was found to be dependent upon the amount of root growth and therefore closely related to the initial water contents. In all cases where the adventitious root systems were exposed to soil that was drier than that containing the main root systems of the plants the amounts of water which moved into the plants appeared to be small, much of the water remained in the adventitious roots themselves. When the water content of the soil for the adventitious roots was at a higher water content than that containing the main root systems, considerably more water appeared to move into the plants through the adventitious root systems.

Rubidium uptake was not consistently affected by the different water contents, nor was the uptake correlated with the amount of root growth. There was, however, at least as much rubidium accumulated in the plants in 28 hours, when the adventitious roots were wetter than the main root systems, as was accumulated in the plants in six days when the adventitious roots were drier than the main root systems. It appears that the transport of water from the roots to the plants may be an important factor in ion accumulation and it may be that the uptake of ions will not correlate with water conditions at the root surface unless and until rapid transport of water takes place.

Since water uptake appears to be closely related to the amount of root growth, the effects of water contents on the absorption process itself must be interpreted with caution or the root growth measured and accounted for. It is not known if the same holds true for ion uptake. In these experiments the rubidium uptake was not closely related to root growth but it is not possible to say if this holds true for ion absorption in general.

EFFECTS OF SOIL MOISTURE-TENSION ON RUBIDIUM UPTAKE BY SUNFLOWERS

by

DAVID STUART STEVENSON

A THESIS

submitted to

OREGON STATE UNIVERSITY

in partial fulfillment of
the requirements for the
degree of

DOCTOR OF PHILOSOPHY

June 1963

APPROVED:

Redacted for Privacy

Assistant Professor of Soils

In Charge of Major

Redacted for Privacy

Head of Department of Soils

Redacted for Privacy

Dean of Graduate School

Date thesis is presented January 8, 1963

Typed by Muriel Davis and Betty Thornton

ACKNOWLEDGMENTS

The author expresses his deepest appreciation to Dr. Larry Boersma for his assistance and council during the period of research and preparation of this thesis. The author is also grateful to Dr. D. D. Evans for his guidance during much of the course of my Doctorate program and for his assistance in the preparation of this manuscript.

Special appreciation is extended to Dr. H. B. Cheney and Dr. D. P. Moore for their council during the course of the research and to Mr. Gene Maas for his help with the chemical analyses.

Very special thanks are due my wife for her enduring patience, devotion and encouragement and indeed for her very tangible assistance, including the preparation of this manuscript.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

EFFECTS OF SOIL MOISTURE-TENSION ON
RUBIDIUM UPTAKE BY SUNFLOWERS

INTRODUCTION

The study reported in this thesis was conceived from the question of what takes place at the interface between the soil and the root surfaces of the plant during active growth. The experimentation was designed to investigate the problem of what the effects of changes in water content of the soil might be on root growth and on the absorption of nutrient elements as well as the water which a plant normally absorbs. As the water content of the soil changes, the effect is not simply a decrease in the amount of water, but there is an accompanying change in the activity of the water, a change which is not proportional to the change in water content. With respect to the root surface, this activity of the water manifests itself in the amount of energy which must be expended in order to move water from the soil into the plant root. As the soil water content declines, the amount of energy required to remove the water increases rapidly. The energy with which the water is held in the soil is expressed in terms of a negative pressure or more commonly soil moisture tension. The common units of tension are atmospheres, bars, pounds per square inch and other pressure units. Soil moisture tension is sometimes defined as the pressure difference across a porous wall or membrane which is in contact with soil of which the water content has reached an equilibrium value with a constant applied pressure[1/].

There is a common belief among soil and plant scientists that absorption phenomena at the root surface and indeed the root growth and perhaps the entire water economy of the plant is governed in part by the soil moisture tension rather than by the actual water content. Such a belief is based on the assumption that reactions at the soil-root interface are similar to the reactions which occur at the interface of the soil and the particular instrument with which the tension is measured. The assumption may or may not be true. To use a common expression "what the root sees" may be quite different from that which is measured by instruments.

The soil moisture tension ranges from very close to zero tension or atmospheric pressure when the soil is saturated with water, to several hundreds of atmospheres when the soil is air dry. However, beyond a tension of approximately 15 atmospheres under normal environmental circumstances most plants cannot obtain water from the soil rapidly enough to maintain turgidity of the leaves and the plant wilts. If this condition is prolonged the plant will die from desication. This level of soil moisture tension is commonly called the permanent wilting point.

1/ Soil moisture tension may be expressed in terms of potential, or the work required to remove a unit mass of water from the soil.

Normally it is not possible to hold the moisture tension constant at a particular value when plants are growing in the soil. It is therefore not possible to study the effects of a given tension or water content upon absorption phenomena at the root surface. Most studies of this kind have been to examine the effects of ranges of moisture tension from close to zero to some given level. This thesis study was designed to examine the effects of moisture tension ranges other than those referred to above. The growth of adventitious roots provided a possible means of imposing soil moisture tensions upon the roots without the necessity of exposing them to very low tensions. If the roots could be induced to grow into soil already established at a particular tension, then as long as these roots absorbed water the tension would rise from that point and should never be lower than the established level. With this technique, there was a good possibility of examining some of the effects of certain narrow ranges of soil-moisture tension.

If root growth were governed by soil moisture tension or the water content, then it would be necessary to account for differences in root growth before deciding what the effects of the moisture conditions might be on nutrient or water absorption by a particular root system. In other words it would be necessary to express the absorption data on the basis of a unit mass or unit length of root. If either or both of these absorption phenomena were not directly related to the amount of root growth, then whatever effects different moisture tensions might have on nutrient or water absorption might be attributed to a tension effect on the absorption itself, assuming that translocation from the root into the plant takes place and is itself not governed by the moisture conditions of the soil.

Knowledge of the effect of soil-water contents or tensions upon root growth and upon absorption by the root is extremely important to an understanding of what takes place at the soil-root interface. About all that is known at the present time is how the plant reacts to moisture changes with only limited knowledge of how the root system reacts even with respect to growth alone. Yet even a few basic leads as to the soil water effect upon reactions concerning the plant roots could be invaluable in understanding what occurs when fertilizers are applied, for example, under dryland conditions as opposed to irrigated conditions. Or, with respect to water relations between plant and soil there could be a better understanding than at present of what is meant by availability of water. Is availability a function of the tension in the soil, or of water content and rate of water movement, or is it simply a function of root growth and activity? The same question applies to the availability of nutrient elements essential for plant growth.

REVIEW OF LITERATURE

The following paragraphs contain a review of literature dealing with the problems of the growth of plant roots as related to soil water content and moisture tension. Included is a brief review of the current, important concepts of the process of ion absorption from soil by plant roots, with a short discussion of what part water may play in the absorption process. Following this is a review of the role which transpiration of water by plants plays in the absorption and translocation of ions into the plants. Finally, there is a review of the studies of the effects of changes in water content and moisture tension in soil systems on the absorption and accumulation of ions in plants.

Soil moisture and root growth

The amount of root growth as related to soil moisture tension has never been satisfactorily measured. There have been numerous attempts to relate root growth to various degrees of dryness or wetness of the soil, or to long and short periods of dryness, or to various kinds of moisture regimes involving different cycles of wetting and drying of the soil. However, it remains virtually impossible to attribute a particular amount of root growth to a particular moisture tension. This is simply because as the root grows and absorbs water the soil moisture tension changes. There must be full recognition of this whenever any interpretations are made of water uptake, nutrient uptake, growth, or any function occuring at the soil-root interface.

With respect to root growth as affected by soil water conditions, Jean and Weaver (10) and Weaver (28) made some rather extensive observations on the root growth of many crop species under dryland and irrigated conditions. Jean and Weaver noted that under some circumstances, a low moisture supply stimulated a greater root development and consequently a greater absorbing surface than was found with a high moisture supply of the irrigated soil (28, p. 64). Most of these instances occurred with young plants, relatively early in the season. There may have been a temperature effect as the irrigated soil probably was the cooler of the two soils. However, in general, as the plants approached maturity there was deeper and more extensive root development under irrigation. There was a tendency for more branching, more lateral roots, and finer roots under dryland conditions than under irrigation.

Bennett and Doss recorded the root weights from a number of grasses and legumes taken from plots irrigated when 80 per cent, 65 per cent, and 30 per cent, respectively, of the available water was lost. They found that except for African alfalfa and red clover, the greatest weight of roots was associated with the lowest moisture regime (1, p. 205). Except for reed canary grass, the greatest depth of root penetration was under the lowest moisture level(1,p.206).There is no explanation for these findings and the results are not what is normally expected or found. Kmoch _et al_. found that wetting the soil to different depths prior to seeding winter wheat in Nebraska produced increased root penetration associated with the increased depth of wetting (15, p. 20, 22). However, the soil water conditions after seeding were so poorly defined that these observations and the weight measurements are most inconclusive.

These few observations serve to emphasize the complexity of the problem. Root growth is a function of many things; the aeration of the soil, the moisture supply, mechanical impedence or lack of it, soil structural barriers, water table, soil temperature, nutrient supply, aerial environment, and growth characteristics of the plant itself. In order to study but one of these factors, the water supply or soil moisture tension as it affects root proliferation and elongation, one must standardize or control all of the other factors. This becomes an enormous problem, particularly in field studies. Yet the amount of root growth is likely to have a profound effect on the results of uptake studies, whether they be water or nutrient absorption studies, and without a knowledge of the magnitude of this effect, interpretation of the results becomes a rather questionable undertaking.

There is, then, but one alternative if one wishes to measure the effect of moisture supply on nutrient uptake and that is to measure the amount of root growth quite precisely and account for the differences in root growth before making any decision about the ultimate effect of soil moisture tension on nutrient absorption.

Ion absorption by plant roots

While it is not the purpose of this treatise to examine or discuss in detail the precise mechanisms of ion uptake or ion absorption by plant roots it is desirable to obtain some recognition of the current concepts of ion absorption from the soil and soil solution. Two processes are proposed, both of which may play some part in the movement of ions from the soil into the plant roots.

The contact exchange theory is described by Jenny (12, p. 115-118) as a mechanism for reactions between absorbents, or solids in general, without the participation of free electrolytes. The theory involves the concept of overlapping oscillation spaces of adsorbed ions. Assuming that two solid particles or a particle and root surface are brought into sufficiently close contact, the oscillation spaces or spheres overlap to the point where the two oscillating ions simply change places. Water, although usually present, plays no essential role in this type of exchange. Cations may be exchanged without an accompanying anion partner or conversely anions may be exchanged without an accompanying cation.

The older, classical solution theory of ion uptake by plants is also described by Jenny (12, p. 109-110). This process involves the release of carbon dioxide from the root, followed by the formation of carbonic acid, diffusion of the carbonic acid to the clay particle surface and exchange of a cation from the clay surface for hydrogen from the acid. This is followed by diffusion of the cation bicarbonate pair back to the root surface where the cation is once more exchanged for hydrogen, this time from the root surface. Alternatively, the cation-anion pair may enter the root together. Obviously, water plays a very essential role in such a process.

Jenny and his associates vigorously defend the concept of contact exchange as a process which plays a major role in ion uptake by plant roots. Jenny and Overstreet (13, p. 257-272), Jenny (12, p. 107-130), and Gonzalez and Jenny (8) discuss the phenomenon at some length and present evidence that the contact exchange does take place. For example, Gonzalez and Jenny showed that alfalfa seedling roots took up strontium much more rapidly when in contact with an Amberplex membrane containing adsorbed strontium than when in the solution at equilibrium with the membrane. It is difficult to understand how it is possible to bring a root into contact with a membrane in a solution without the presence of a water film between the root and the membrane immersed in solution. Walker noted that the work leaves little doubt of the reality of the contact exchange phenomenon (27, p. 328) but he claims that the magnitude of the effect is relatively small. He states that all Jenny and his associates have demonstrated is that cation uptake by contact exchange is much more rapid than uptake from solution in the absence of anions in simplified systems (27, p. 331).

Olsen and Peech on the other hand have shown that the uptake of cations by excised barley roots was the same from a clay suspension as from the corresponding equilibrium dialyzate even though the cation concentration of the suspension greatly exceeded that of the dialyzate (20, p. 258-259). This indicates that contact exchange was of no consequence whatever in the suspension systems. Olsen and Peech give an explanation of equal uptake from suspension and dialyzate by assuming that the part of the total volume of the root cell which is referred to as the free space is accessible to the ambient solution and not to the clay particles and that the ambient solution in the free space constitutes the substrate for cation accumulation (20, p. 260).

Steward and Sutcliffe object to the concept of contact exchange on the basis that the distances involved in the overlapping ion oscillation spaces approach only a few hundred angstroms (26, p. 427). As Olsen and Peech point out, it can be shown that the effective thickness of the overlapping space for a 0.001 M solution of a monovalent cation is only 200 angstroms as compared with the cell wall thickness of at least 2000 angstroms (20, p. 260). They claim that it is improbable that the cell cytoplasm could come close enough to the solid clay particle for exchange to take place.

The foregoing paragraphs are presented to introduce the possible modes of ion uptake by plant roots and to indicate that there is some question as to the relative importance of the contact exchange phenomenon. There is no question that plant roots do take up ions from solution; it is very well known that plants will grow well with their roots immersed in solution without the presence of solid particles of any kind. This says nothing of the precise mechanism by which roots take up ions from solution but the fact remains that they do so very readily. It appears advisable to examine the possibilities of what takes place as the water content of the growth medium changes.

Assuming for the moment that the contact exchange phenomenon plays a significant role in ion uptake, any changes in water content of soil should have no direct effect on the ion absorption itself. However, if a decline in water content (increase in soil-moisture tension) reaches a point where metabolic activity of the root is impaired, there may be some decrease in ion uptake. Or, as the soil dries out, the thickness of water films between root surface and soil particle surface may decrease to the point where added root surfaces are in sufficiently close contact with the solid surface to create additional contact exchange sites. These two effects would tend to offset each other.

There are at least two possible changes which take place with respect to ion uptake from the soil solution as the soil dries out. First, the ionic concentration of the soil solution tends to increase with the result that an increased number of ions appear in the immediate vicinity of the root surface. This presents the probability that ion uptake would be enhanced. Secondly, as the soil dries out the conductance of the water, with its ionic constituents, towards the root surface declines. This would tend to decrease the number of ions approaching the root surface as the root removes both water and ions from the immediate vicinity. Here again, the two effects tend to offset each other.

Over-riding both situations, namely, with respect to contact-exchange and with respect to uptake from solution, are at least two other important considerations. First, as the soil dries out there may be some impairment of the transpiration stream and translocation of ions from the root to other parts of the plant. Secondly, there is the question of how much effect the declining moisture content of the soil has on the actual amount of new root growth. It is appropriate to examine some of the literature pertinent to the possibilities pointed out in the preceding paragraphs.

Transpiration and ion uptake

With experiments on small apple trees in the greenhouse, Schneider and Childers showed that transpiration decreased as the soil dried out. There was, however, no indication at what stage of drying or what water content the decrease began except that it started before the soil had reached the permanent wilting percentage (23, p. 581). Slayter showed decreases in transpiration from both tomato and privet as the moisture stress in the soil increased. In the tomato, a decrease in transpiration and a drop in relative turgidity2/ in the leaves were the first indications of the effect of soil moisture stress. Transpiration had dropped to one-third of the maximum by the time the soil had reached fifteen atmospheres of moisture tension. In the privet, the decrease in transpiration began at about five atmospheres tension without an accompanying drop in relative turgidity (25, p. 325, 327).

West and Perkman recorded the water content of a soil under citrus trees by sampling the soil for a period of time after an irrigation. They also recorded the evaporation of water from a free water surface in an evaporimeter pan over the same period of time. This evaporation was taken as a measure of the transpiration which, according to West and

---

2/ Relative turgidity is the ratio of the amount of water in the leaf to that which the leaf contains when fully turgid.

Perkman, should occur as long as water in the soil was readily available. The water losses from the soil were taken as actual transpiration by the trees. They were able to show that the actual transpiration rate by the trees slowly declined relative to that which they measured by the evaporation pan (29, p. 330, 332). There is some question about the validity of using evaporation from a free water surface as a straightforward measure of transpiration or of using the water losses from the soil as a measure of actual transpiration by the trees. Some evaporation undoubtedly also occurred from the soil, especially when the soil surface was still moist, even though their soil water records were taken below a depth of four inches.

Loustalot, working with pecan seedlings, found both transpiration and photosynthesis to decrease under drought conditions in both sand culture and soil. Most of the reduction occurred as the soil water content was approaching the wilting percentage (16, p. 522, 526, 529). The moisture tensions as the decreases began were not given. Loustalot found a slight reduction in total ash content under drought conditions but attributed this to destruction of young fibrous roots (16, p. 526, 530).

Freeland controlled the transpiration rates of corn and beans by adjusting the relative humidity of the air surrounding the plants. The plants were grown in culture solution. The ranges of transpiration were about 2.5 times from lowest to highest with corn and almost three times from lowest to highest with beans. He obtained an 8 per cent increase in total minerals, a 71 per cent increase in phosphorus and a 35 per cent increase in potassium in the corn plants with the higher transpiration. The comparable increases in the beans were 31 per cent, 23 per cent, 623 per cent, for total minerals, phosphorus, and potassium, respectively, for the higher transpiration rates. Calcium increased 26 per cent in the beans but not at all in the corn (6, p. 373, 374). Growth differences were at a minimum because the experiments were conducted over a period of only 3 or 4 days. The ion uptake was given in grams of each element taken up by the plant and the percentage increases were given as the uptake for the high transpiration over that for the low transpiration. Freeland had noted earlier that the increase of nutrient uptake was not proportional to the increase in transpiration. Increases in transpiration were about 2-4 times the increases in uptake (5, p. 357-360).

Wright showed that phosphorus, potassium, and calcium absorption by bush beans from culture solutions was almost always enhanced by increased transpiration rates (30, p. 173). In these experiments, transpiration was adjusted by raising or lowering the relative humidity.

Mendiola, on the other hand, was unable to find any direct correlation between percentage ash and relative rates of transpiration in tobacco plants (18, p. 654). There is some question, however, as to the interpretation of these experiments because although the plants were more than one month old, there was only slightly more than six grams of fresh weight per plant. In addition, the total amounts of transpired water were extremely small (18, p. 645, 648); in fact, many workers observe more water loss via transpiration in one day than was found for the entire month of these experiments.

Muenscher, in one of the earliest studies of the effect of transpiration on nutrient uptake, found that reducing transpiration by increasing humidity or increasing the concentration of the nutrient solution did not influence total ash very much but that reducing transpiration by shading reduced photosynthesis and brought about a corresponding decrease of total ash (19, p. 321, 322, 324, 328).

Hylmo (9, p. 336-340) in an extensive and well conducted series of experiments found that calcium uptake by peas was related to the rate of transpiration regardless of whether the transpiration was controlled by light intensity, humidity, temperature of the nutrient solution or by complete removal of transpiring organs (9, p. 341). In the latter case, there was still a little Ca uptake and interestingly, the figure for uptake agreed with the theoretical value obtained by extrapolating the regression line of the Ca uptake-transpiration curve back to the ordinate of zero transpiration (9, p. 346). The same positive correlations between Ca uptake and transpiration occurred at each concentration of the nutrient solution. Hylmo found, however, that transpiration decreased with increasing concentration of the culture solution and that Ca uptake increased (9, p. 351).

Hylmo (among others) notes a two-phase nature of ion uptake. When plant roots are brought into contact with the ion solution there is a rapid initial uptake which declines to a steady smaller uptake (9, p. 399). He states that water transport can have an accelerating effect on the movement of ions to the absorbing regions of plant root cells. Hylmo states that from his work there is no absolute demonstration that the transpiration stream directly affects the uptake of ions but says there is a strong indication that the ions are drawn through the root by mass flow in the transpiration stream (9, p. 384, 385).

Wright and Barton measured absorption and distribution of radioactive phosphorus under different transpiration rates induced by changes in light, relative humidity and osmotic pressure of the culture solution. Absorbed p^{32} was recorded on film. The absorbed p^{32} was located in the top leaves in the experiments conducted in the light (high transpiration) and in the lower leaves in the experiments conducted in the dark (low transpiration). The actual amounts of p^{32} under the light and dark conditions were not recorded. Much less p^{32} was absorbed under high humidity than under low humidity and considerably less was absorbed under high osmotic pressure than under low. In the latter case the transpiration rate was only very slightly, and probably not significantly lower under high osmotic pressure than under low (31, p. 387-388). The authors claim that the differences in p^{32} uptake are attributable to differences in transpiration rate but actually only where the transpiration was lowered by high relative humidity is this actually the case. The differences resulting from the light and dark treatments are only differences in location of the p^{32}; the actual amounts are not known. The differences in uptake between the two osmotic pressure treatments cannot be attributed to the negligibly small differences in transpiration rates.

There seems to be general agreement that the transpiration rate does have some relationship with ion uptake, but here again, it is not known if this is a matter of ion uptake or of translocation within the plant. Mostly, the effect of transpiration on ion uptake is thought to be indirect[3/], that is, rather than affecting ion uptake *per se*, transpiration is thought to be simply a manifestation of the activity of the plant. A plant that is actively transpiring is capable of readily taking up ions, while a plant, which for one reason or another is not actively transpiring, may or may not be capable of readily absorbing ions through the root system. If transpiration is retarded by external or environmental influences, such as high relative humidity, a plant will still grow, readily

---

3/ In order to distinguish between direct and indirect, the term direct here would mean that if there was a change in the transpiration rate, this would in some way affect the absorption process itself, as well as influence the translocation following absorption.

absorb ions and apparently function normally, but on the other hand, if transpiration is retarded by lack of water in the soil or by something harmful within the plant, then plant functions, including ion uptake, are also retarded. Yet, there are instances where the percentage of some cations were increased in plants grown under high moisture tensions and instances where there were decreases in percentages of some cations in plants grown under reduced transpiration rates induced by high humidities or reduced light intensity. The former of these seemingly contradictory instances result from the fact that the data reported on a percentage composition basis do not account for differences in the amount of growth and that in almost all instances the total amounts of cations taken up were smaller when transpiration was retarded by high soil moisture tension. In most cases of this kind the tension was not controlled but was simply the tension achieved as the plants removed water from the soil. Tests of this kind must, of necessity, start with low tensions and if the plants are grown for any length of time, they must be intermittently subjected to low tensions which precludes any possibility of interpreting results in terms of a tension-cation uptake relationship. This is because it is impossible to determine what uptake may occur at any particular tension. There are a few recent reports in which the investigators have attempted to control soil moisture tension at some particular level. These reports will be referred to later.

For those cases where the percentage of some of the cations were decreased when transpiration was reduced by high humidity or other environmental influences, there is no alternative but to conclude that there must be some kind of a relationship between transpiration and ion uptake. There is, however, little indication of what the nature of this relationship must be. The decreased uptake with decreased transpiration may occur simultaneously but not necessarily proportionately. In fact, the decrease in transpiration may be 2 to 5 times the corresponding decrease in ion uptake.

There are, then, two rather distinct situations. One in which increases or decreases in ion uptake are associated with increases or decreases in transpiration resulting from changes in the external environment and the other in which the respective increases or decreases in ion uptake result from changes in soil moisture tension. With respect to the former, there appears to be some relationship, albeit an uncertain one as to its nature, and with respect to the latter there is no certainty that there is a relationship, except that as the tension approaches that of the wilting point, transpiration rates decrease.

Soil moisture and ion uptake

Mederski and Wilson utilized a split root technique in which corn plants were grown in sand separated by a wax membrane from soil below.

The roots of the plants penetrated through the membrane and permeated the soil. Water was supplied in the sand layer and the soil below was established at several predetermined water contents or tensions. Very small amounts of water were taken up from the soil by the plants during the 25 days that the experiment was in progress (17, p. 150).

Both root and top growth increased linearly with increased starting water contents in the soil. Under conditions of high humidity only the percent Mg in the tops increased with increased soil water. With lower humidity (higher transpiration) the percentage of P and K in the tops increased with increased soil water (17, p. 151). The author's original hypothesis was that as soil water decreases, ion uptake decreases and growth is impaired. The evidence they present appears to support this thesis at least in a limited way. The fact that root growth was greater at higher moisture contents presents at least the possibility that increased root growth alone, rather than increased uptake per unit of root surface, was responsible for the increased uptake and increased growth. The authors did not relate the actual amounts of water lost from the soil to the uptake of the ions. A revaluation of the data, as far as was possible, seemed to indicate little or no relationship between water taken up from the soil and the percentage of cations in the plants.

Danielson and Russell experimented with corn seedlings in soil at moisture tensions ranging from 1/3 to 12 atmospheres as established by pressure membrane equipment. The experiments lasted only 24 hours. Seedlings were also grown in culture solutions of different osmotic pressures. These cultures were established in perlite, a finely divided porous material. The authors measured the uptake of rubidium isotope under the above conditions (2, p. 3-4). They found that the uptake of Rb^{86} was not affected by the osmotic pressure and concluded that moisture stress had no influence. They did, however, find moisture tension had a marked influence on Rb^{86} uptake by the seedlings, the uptake decreasing as the tension increased. The largest decreases in uptake came between 1/3 and 3 atmospheres. On a water content basis the relationship was linear (2, p. 5). The data are given as relative Rb^{86} uptake per unit dry weight of embryo. The authors assume that the thickness of moisture films control the rubidium concentration at the root surface, stating that the ion diffusion from soil to root would decrease as the film thickness decreased (2, p. 5). Why this should be is difficult to understand, because the distance of diffusion from adjacent soil particles should actually be less. It is more likely that with decreased moisture films, less root surface is in direct contact with water or soil solution.

It is true, as the authors state, that reduced water uptake by roots at higher tensions would likely reduce the movement of water and nutrients to the absorbing surface and reduce the amount of ions in the proximity of the root. On the other hand, the authors found a higher concentration of Rb^{86} in solution extracts from the soil at 12 atmosphere than they did at lower tensions (2, p. 4). This higher concentration should, in part at least, compensate for the reduced amount of solution. Any differences in the amount of root growth by the corn seedlings was not accounted for in these experiments.

Jenne, et al. conducted a field study on irrigated and nonirrigated corn plots. They sampled the corn at various times during the season and analyzed the plant tissue for N, P, K, Ca, and Mg. Relative amounts of dry matter and the above elements were lower under the high moisture stress of the non-irrigated plots (11, p. 72). Percentage composition indicated only small differences. Phosphorus and magnesium decreased slightly while potassium and calcium increased slightly in the dry plots (11, p. 73). These differences in percentage composition are confused with amount of both top and root growth. In field tests of this kind, transpiration rates are an unknown factor, although presumably they would be lower on the non-irrigated corn.

Gates found that the uptake of N and P was reduced in tomato plants during wilting. Uptake resumed when the plants were re-watered. Both nutrients appeared to be translocated from the laminae to the stem during wilting but following re-watering, this trend was reversed. The reduction in nutrient uptake took place at both moderate and severe wilting suggesting that the effect may begin rather early as the moisture supply begins to decrease (7, p. 126, 127-145).

Dean and Gledhill developed a technique of placing a mat of rye plant roots in contact with soil at various moisture tensions and measuring the amount of P^{32} taken up from the soil (3, p. 75-76). They found that in every case there was greater absorption of P^{32} from soil at low tensions than from soil at high tensions. Strangely, in every case water moved from the roots into the soil and increased the soil water content appreciably, evidently dehydrating the roots even at moisture tensions as low as 0.1 atmosphere (3, p. 75-76). Roots which had been preconditioned at 0.1 atmosphere tension took up more P^{32} than roots preconditioned at 15 atmospheres prior to placing the root mat against the soil at various tensions (3, p. 77). The authors indicate that soil water conditions may influence the physiology of the roots or perhaps the nutrient availability in the soil. Moisture stress apparently produces an effect which tends to reduce the absorbing capacity of the roots (3, p. 78).

In a study involving eight species of grasses and legumes on a sandy loam soil, Kilmer _et_ _al_. found that of twelve elements determined in the forage, only phosphorus showed consistent increases with increased water supply (14, p. 284). However, the results were rather inconclusive and the moisture picture and root distributions were not very well defined. Any differences they obtained may be the result of differences in root growth or in root-top ratios. Eaton, in studying water uptake and salt accumulation in sugar beet, barley, sorghum, alfalfa, cotton, and tomato , noted that chlorine in the plant tends to match the chlorine content of the substrate. He noted that other ions vary considerably, some increasing and some decreasing with increased content in the substrate (4, p. 322). Eaton makes the interesting observation that as soil moisture tension increases from 0.1 atmosphere to 16 atmospheres the salt concentration of the soil solution tends to double (4, p. 332). Actually, most of this doubling probably occurs at relatively low tensions as the salt concentration is undoubtedly more directly proportional to the water content of the soil than to the tension. The water content may be halved or more than halved by the time the tension reaches one atmosphere.

What affect the increased concentration of salts as the soil dries out might have on nutrient uptake by roots is rather difficult to say. Certainly, there ought to be an increased number of any one ion species in the immediate vicinity of the absorbing root surface. On the other hand, there will be a tendency for ions to diffuse away from the more concentrated solution near the root towards the less concentrated bulk solution in the soil. This would be opposed to the mass flow of water and ions toward the root as the root absorbs both water and nutrients.

The relative magnitudes of all the opposing forces involved here are not known but the net result is obviously a movement of both water and nutrients toward the root whether by diffusion or mass flow or both. In any case, Shapiro et al. as a result of a study in which they increased the diffusion path by sand dilution of soil, indicated that diffusion alone was insufficient to supply phosphorus to soybean and corn roots in large enough quantities to fulfill the needs of the plants (24, p. 162, 163). They stated that normally water movement overwhelms the diffusion to the point where the latter is insignificant (24, p. 164).

It appears that there are some relationships between ion uptake and transpiration rates, although they are probably indirect. Mass flow of water certainly is a factor, but there seems to be no proportionality between mass flow and ion uptake. There is sufficient evidence to indicate that whenever ion uptake is studied with intact plants, transpiration must be either controlled or itself be measured and evaluated.

As far as soil moisture tension and ion uptake are concerned, there is very little evidence as to the nature of the relationship, indeed there is yet to be resolved a satisfactory technique for the study of the relationship. The initial part of this thesis is the development of a technique which may, at least in part, circumvent the problem of moisture tension control. The problem of top growth increases during experiments may be minimized and the root growth with respect to tension or water content can be measured and ion uptake data evaluated on the basis of unit weight or mass of root. Subsequently the technique can be utilized to study the relationship between soil moisture tension or water content and ion uptake.

SPECIFIC OBJECTIVES

The first objective of this study was to develop a technique of growing adventitious roots into small volumes of soil and over relatively short periods of time, for the study of root growth and cation uptake over several different ranges of soil moisture tension. As was pointed out in the previous section, the problem of obtaining constant moisture tensions, except near the saturation point or zero tension, is an almost insurmountable one in soils. If some way could be found to avoid rewatering at least part of the root system, some of the effects of tension ranges other than zero to some particular tension might be evaluated with respect to growth, ion uptake or water absorption. A system of adventitious roots growing into soil already established at a given tension presents one possible means of making such evaluations. The rewatering of the plants could be done through the main root system.

The second objective was to utilize the adventitious root technique to study the effect of various tension ranges on the growth of roots. Little is known about the effects of low water contents in soils on the growth of roots. The question of how much of the root growth takes place when the soil is moist or the tension low, and how much takes place later when the soil has partially dried out and the tension risen, has not been fully answered.

The third objective was to study the effects of the tension ranges on the uptake of rubidium. Rubidium was chosen simply as an indicator cation, partly because it behaves somewhat like potassium and partly because it is normally present only in trace amounts. In this study it was relatively easy to measure precisely the amount of root growth and to take this growth into account when evaluating the uptake of the cation. The author firmly believes that some evaluation of the root growth in relation to ion uptake is essential before it is possible to properly interpret the effects of moisture tension on ion uptake or on water absorption. In making such an evaluation this question needs to be answered. How much of the effect on ion uptake or water absorption is due to the moisture tension itself, and how much is due to differences in the amounts of root growth because of differences in tension?

MATERIALS AND METHODS

Plant growth conditions

All experiments were conducted in a controlled environment growth room in which light, temperature, and relative humidity were kept constant. The light intensity was approximately 2,000 foot candles 18 inches away from the lights. The lighting system consisted of 48 fluorescent tubes, four feet long, and sixteen 75-watt incandescent lamps. The incandescent lamps are needed to improve light quality for plant growth. The fluorescent tubes are classed as VHO powertubes and were spaced one inch apart edge to edge. Every seventh space was occupied by two incandescent bulbs permitting two bulbs for every six fluorescent tubes. The daylength was set at sixteen hours.

The air in the room was circulated constantly with approximately 10 per cent exchange with outside air for each cycle of the air. The room itself is almost four times the area occupied by the lights under which the plants were grown.

The temperature of the room was maintained at 70 degrees F. with minor fluctuations of plus and minus 1 degree and a day-to-night lowering of about 2 degrees. The relative humidity was reasonably constant, fluctuating slightly between 57 and 60 per cent.

Sunflower, which was chosen as the test plant for all the experiments reported in this thesis, grows well under these conditions without any apparent abnormalities except for some yellowing and eventual withering of the lower pair of leaves. The cause of this defect was not found. The sunflowers reached an average height of 20-24 inches in about six weeks and appeared very healthy and vigorous at all times. The plants were grown from germination to harvest entirely within the growth room. Approximately 100 pounds of nitrogen and 100 pounds of phosphorus per acre on a weight basis, was added to the pots when the seeds were planted, and throughout the growth period the plants were watered two to three times daily.

Soils

Two different soils were used as the growth media. One was a sandy loam soil somewhat like the Newberg series. This soil has a cation exchange capacity of 15.9 milliequivalents per 100 grams of soil. The moisture-tension curve for this soil is shown in Figure 1.

The other soil used was a clay loam of the Chehalis series. This soil has a cation exchange capacity of 29.7 milliequivalents per 100 grams of soil. The moisture-tension curve for this soil is shown in Figure 2.

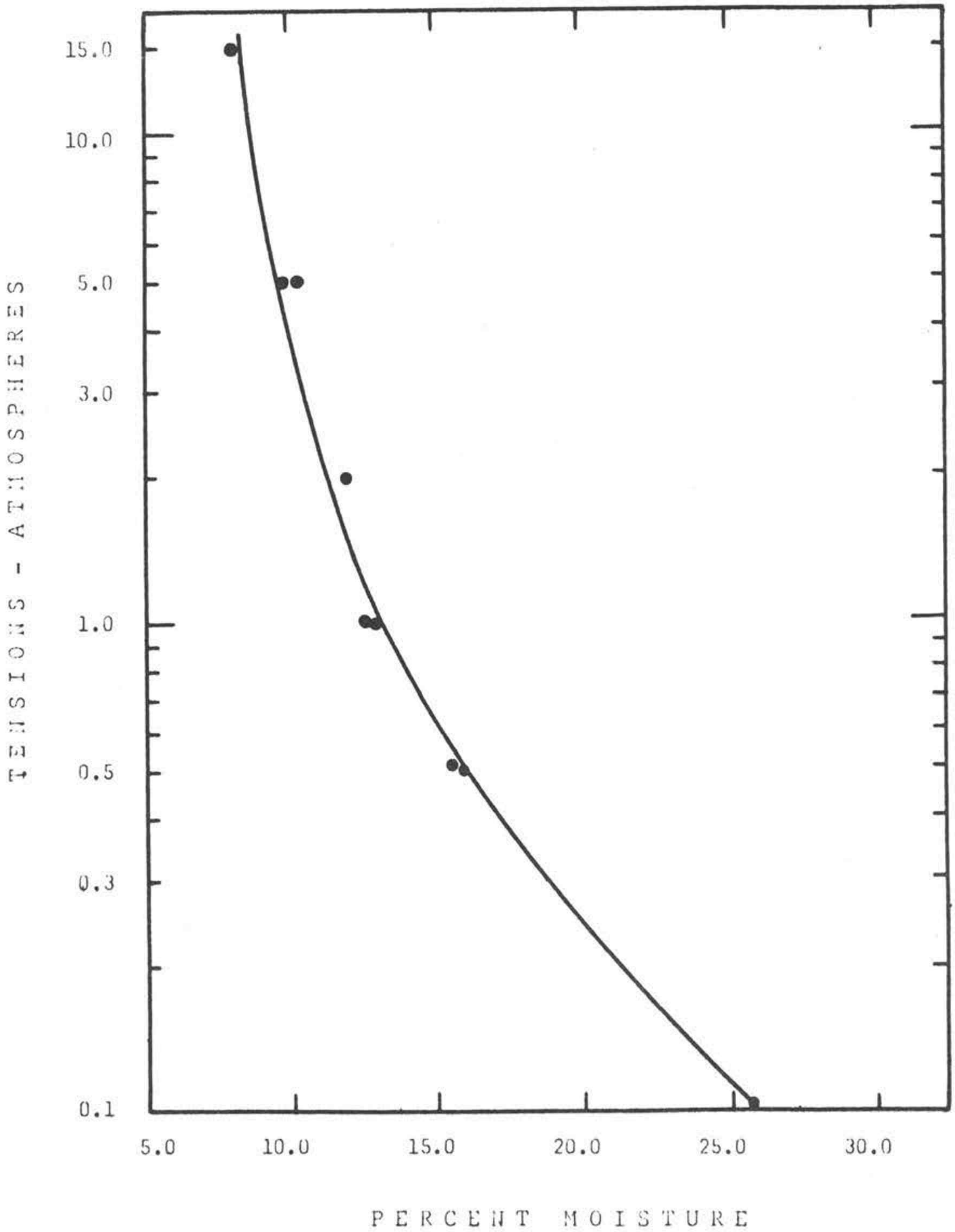

Figure 1. Soil moisture-tension curve for sandy clay loam.

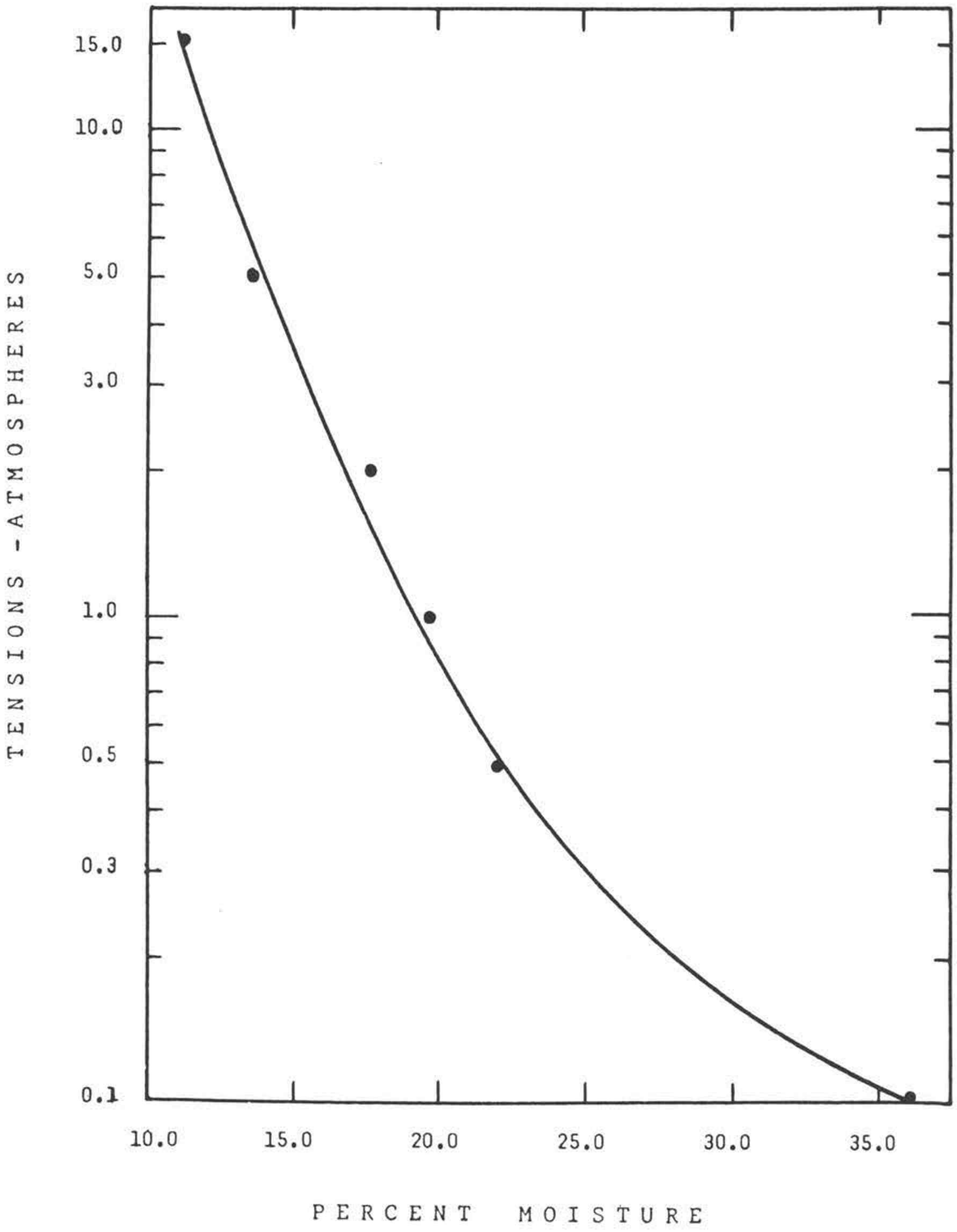

Figure 2. Soil moisture-tension curve for clay loam soil

Both of these soils were collected from the top six inches of the soil profile, screened to remove debris, stones, and large clods, then stored at water contents ranging from 10 to 15 per cent until used.

The amount of soil placed in each pot was in all cases 2,500 grams regardless of the water content at the time. Because of slight differences in water content at different times of planting there were slight differences in the amounts of oven-dry soil in the pots for the different tests. The weight of soil on an oven-dried basis for the sandy loam soil ranged from 2,236 grams to 2,262 grams per pot. For the clay loam soil, the weights of soil on an oven-dried basis ranged from 2,078 grams to 2,189 grams per pot.

At the start of each test period, which will be described later, the water content of the sandy loam soil was established at approximately 25 per cent or a moisture tension of 0.1 atmosphere. The figure 25 per cent is not precise because in order to calculate the amount of water needed to bring the soil to 25 per cent, the weight of the plant had to be estimated. Variations in the actual weights of the plants between pots resulted in some variation in final moisture contents of the pots. At harvest, the plants ranged in weight from 60 to 80 grams fresh material with the result that the moisture percentage in the pots ranged from about 25 to 26 per cent. This variation was considered to be insignificant.

The water content of the clay loam was established at 35 per cent or a moisture tension of 0.1 atmospheres. Here again the plant weights had to be estimated in order to calculate the amount of water needed. In these tests the plant weights ranged from 75 to 120 grams with the result that the moisture percentage in the pots ranged from about 33 to 35 per cent. Again this variation was considered insignificant.

During the test period the pots were watered three to four times daily and at no time was the water content allowed to decrease more than 100 grams. A decrease of 100 grams of water would represent a decline to approximately 21 per cent in the sandy loam soil and to about 30 per cent in the clay loam soil.

Plants

The sunflower was chosen as the test plant for several reasons. The sunflower plant was already known to germinate easily and grow very well in the growth room conditions previously described. The plant would grow to considerable size in a relatively short time and thereby provide sufficient plant material for chemical analysis later. The sunflower provided a strong rigid stem upon which to affix containers of soil for the growth of adventitious roots. Finally, the plant was known to be capable of producing adventitious roots quite readily and quickly in soil placed around the stem at the first or cotyledonary node. Subsequently, as the tests progressed the sunflower proved to be an excellent choice.

Test procedure

Briefly, the technique was to grow the sunflower plants until they reached a height of about 18 to 24 inches, place a known amount of soil containing rubidium (the same soil as that in which the plants were grown) around the stems at the first node, allow the adventitious roots to grow for six days, harvest the plants, and analyze the material for rubidium content. Moisture treatments were imposed upon the soil placed around the stems. The procedure in detail follows.

Some convenient means of placing constant weights and volumes of soil around the stems of the sunflowers had to be found. The container had to be made in such a way that it could be placed around the stem of the plant, filled with soil, then closed and sealed against evaporative losses of moisture.

To fulfill these requirements, containers were constructed from lucite tubing and plastic sheeting. A diagram of the container is shown in Figure 3. For each container, a cylinder 6.7 centimeters long was cut from 5.0 centimeter diameter tubing. A 1.5 centimeter wide slot was cut lengthwise of the tube to permit the cylinder to slip onto the plant stem. A second cylinder, which fitted closely inside the first, was constructed of thin sheet plastic and also had a half-inch wide slot. When

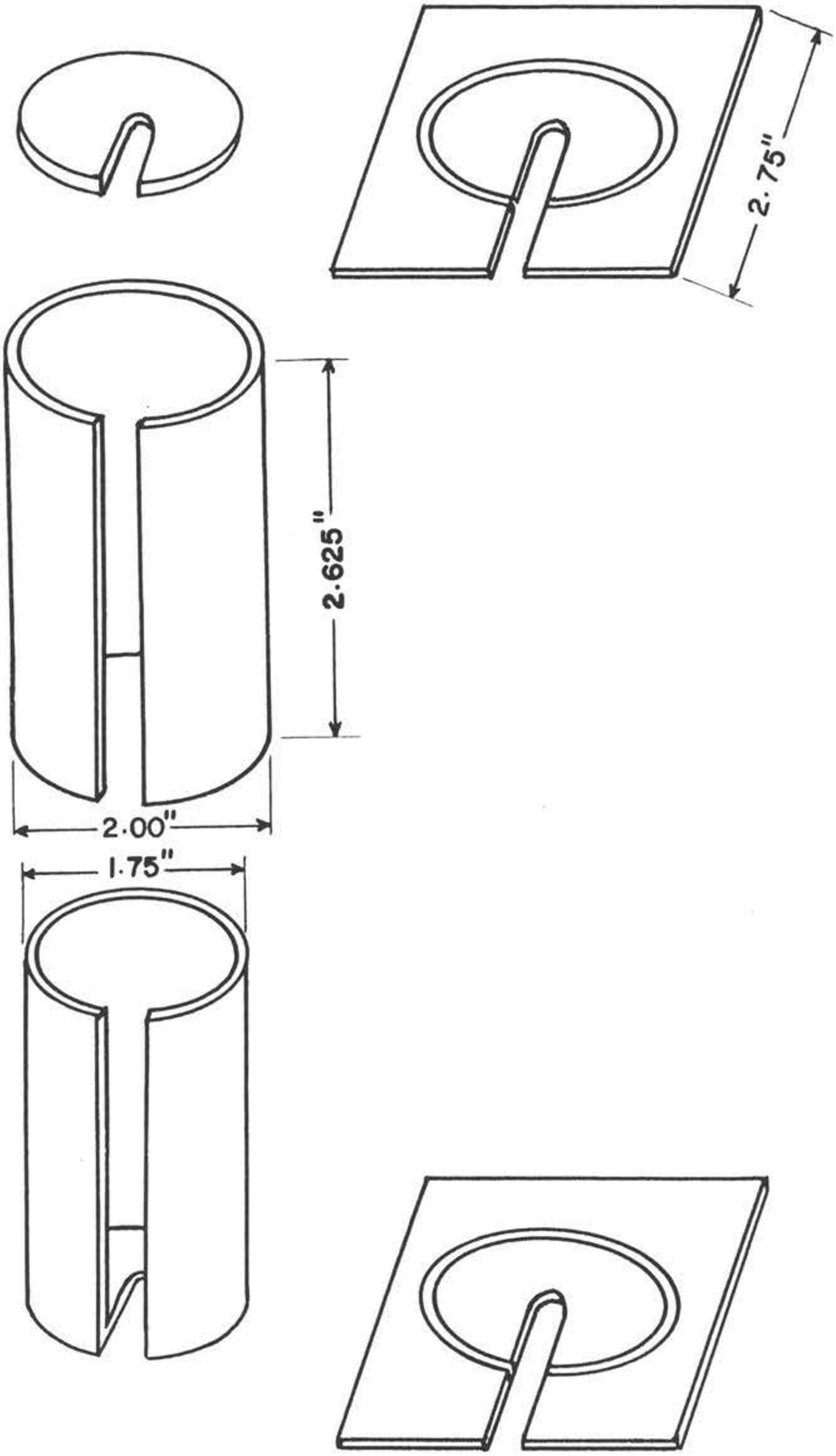

Figure 3. Plastic soil container used in the root growth study

the slots of the two cylinders coincided both cylinders could be slipped over the plant stem. When the inside cylinder was turned relative to the other, the two formed one complete cylinder surrounding the stem. End plates for both the inside and the outside cylinders were constructed of sheet plastic. A 1.5 centimeter hole was drilled in each of these plates, then a slot was cut from the outer edge to the hole in the center. The plates could then be slipped over the stem at both top and bottom of the cylinders. When the inner plates were rotated 180 degrees relative to the outer plates the result was a solid top and bottom to the cylinders with only the holes in the center to accommodate the stem. The whole assembly was held together with rubber bands. The effective volume of the container was approximately 70 cc.

Before these containers were placed around the plant stems a thin layer of non-absorbent cotton was wrapped around the stems at the point where they protruded from the containers at both top and bottom. In the test with sandy loam soil the containers were sealed with melted paraffin soaked into the cotton. The paraffin was placed there by means of an eye dropper. In all the remaining tests except one, the containers were sealed with paraffin and also with petroleum jelly around the edges.

Checks were made on the containers to determine the water losses from the soil inside. These checks were made under conditions identical with those of the various tests with plants except that plastic rods replaced plant stems. Table 1 shows the water losses which took place under the two methods of sealing.

Table 1. Water losses from soil in adventitious root growth containers.

Soil type	Grams of oven-dry soil	Per cent moisture	Sealing method	Grams of water lost in 6 days
Sandy loam	70	13.9	paraffin	2.40
Sandy loam	70	14.0	paraffin	2.20
Clay loam	66.6	20.1	paraffin and petroleum jelly	0.55
Clay loam	66.6	20.1	paraffin and petroleum jelly	0.55

The containers, when placed around the plant stems, held 70 grams of the sandy loam soil and 65 grams of the clay loam soil both on an oven-dried basis. The standard way of packing the soil into the containers was by tamping the soil with a spatula in such a way that the 65 or 70 gram samples just filled the containers. Slight differences in packing may have caused some differences in the amount of adventitious root growth. The soil in the containers settled slightly during the course of each test so that the final volume was probably 65 to 67 cc.

The soil for the containers was prepared in the following manner. Moisture treatments were imposed on the soil by establishing different water contents in separate aliquots of soil prior to placing them in the containers around the plant stems. Some 96 hours prior to the test, the rubidium, in the form of the chloride salt, was added to 600 grams of soil (oven-dried basis) with sufficient water to bring the soil up to the water content for the lowest-moisture treatment. The amounts of rubidium and the water contents are given in Tables 2 and 3. The soil and water containing the rubidium was thoroughly mixed by hand and stored in a tight container for 24 hours. After 24 hours, the 600 grams of soil was divided into three aliquots. One aliquot was stored without alteration in a sealed container. Water was added to the second aliquot to raise the water content to the second treatment level, and similarly, water was added to the third aliquot to raise the water content of the soil to the third treatment level. In both cases, the soil and water were thoroughly mixed by hand and stored in sealed containers. All three aliquots were left in the sealed containers for 72 hours before the soil was placed around the plant stems.

The moisture treatments in terms of both water content and soil moisture tension differed somewhat between the two soil types. There was also some difference in the amounts of water and rubidium added to the clay loam soil as the series of tests progressed. The first two tests, one for the sandy loam soil and the other for the clay loam soil, consisted of three moisture treatments with six replications. Only six plants were under test at a time providing for three treatments and two replicates with one week between each pair of replicates. The plants for each pair of replicates were started precisely one week apart. For these two tests, the rubidium contents of the soils were kept at 5 per cent of the cation exchange capacity in terms of milliequivalents per 100 grams of soil.

In the third test, lithium, at 10 per cent of the cation exchange capacity, replaced rubidium as the cation for measurement. This was done to examine the possibility that lithium might be a more suitable cation than rubidium for chemical analysis of the plant material. This is discussed further in the section on chemical analysis. This test was done on the clay loam soil. There were four replicates for this test and the moisture treatments were the same as in test two. In the fourth test rubidium was again used, but at three times the concentration or at 15 per cent of the cation exchange capacity. Moisture treatments were still the same, but there were only two replicates. For the fifth test both the water contents for treatments and the rubidium contents were increased. There were four replicates in this case.

A sixth test was conducted in a different manner. The soil placed around the plant stems was established at 24.3 per cent water for all the plants, and the adventitious roots were allowed to grow for six days. The containers were sealed only at the bottom and during the six days 1 gram of water was added every two days to the soil at the top of the container. This was to compensate, at least in part, for evaporative losses out through the unsealed cover. On the sixth day rubidium, equivalent to 20 per cent of the cation exchange capacity, was added with sufficient water to raise the water content of the soil in the containers to 40 per cent. The moisture tension in the soil was then below 0.1 atmosphere. At the same time, the soil water content in the pots which contained the main roots of the plants was established at approximately 35 per cent or close to 0.1 atmosphere. The soil in three out of six pots was then covered with vermiculite, to minimize evaporation, and allowed to dry out as the plants extracted water. The remaining three plants were kept watered in the usual manner; that is, the soil was brought back to about 35 per cent periodically during the 28 hours that the test progressed.

The water lost via transpiration from the soil covered by vermiculite was recorded by periodic weighing of the pots, and the total amount of water lost from the uncovered pots was recorded by measuring the amount of water added to them to keep the soil water content close to the 35 per cent level. The test was terminated when the plants, which were allowed to deplete the soil water under the vermiculite, showed wilting of the lower three pairs of leaves on each plant. These plants were under severe moisture stress as compared with those which were kept watered. This experiment consisted of two treatments and three replications.

The purpose of this last test was to determine if there was any effect on rubidium uptake of the high water-stress imposed on the plants themselves while the adventitious roots were exposed to the very low water-stress. In all previous tests, the adventitious roots were under various degrees of water-stress while the plants were not subjected to any large degree of stress.

Table 2 gives, for each test, information such as soil type, age of plants, duration of the tests, rubidium or lithium contents, and the treatment of the main root systems of the plants.

The various moisture treatments for the different tests are given in Table 3. These are the actual water contents as determined by oven-dried samples of the soil at the time it was placed around the plant stems. The tensions are determined from moisture tension curves prepared in the laboratory. The moisture tension curves for the two soils were determined by means of the pressure membrane apparatus as described by Richards (21, p. 451-454) and the porous plate apparatus, also described by Richards (22, p. 105-110). The former is used for high tensions and the latter for lower tensions, below one atmosphere. At high tensions the water is held in the soil as films surrounding the soil particles. For this reason the porosity or structure of the soil is considered to be relatively unimportant and therefore disturbed soil samples are used for

Table 2. General information on the handling of experimental materials, soils, and plants

Test number	Soil type	Age of plants (days)	Duration of test (days)	Rb content of soil around stems (Meq/100gm)	(%C.E.C.)	Treatment of main roots of plants
1	sandy loam	56*	6	0.8	5	watered to 25% #
2	clay loam	42	6	1.5	5	watered to 35% #
3	clay loam	42	6	3.0**	10	watered to 35% #
4	clay loam	42	6	4.5	15	watered to 35% #
5	clay loam	42	6	4.5	15	watered to 35% #
6	clay loam	42	28 hrs.	6.0	20	see text

* The plants were 48 days old for one replicate pair.
** Lithium replaced rubidium.
# Plants were watered daily as described in text.

Table 3. Water contents and moisture tensions of soil placed around the sunflower stems.

Test number	Treatment number	Soil moisture percentage of each replicate pair 1-2	3-4	5-6	Soil moisture tension (atms) of each replicate pair 1-2	3-4	5-6
1	1	12.6	12.9	13.2	1.10	0.99	0.94
	2	15.3	15.7	16.0	0.55	0.49	0.46
	3	18.1	18.9	18.8	0.33	0.29	0.29
2	1	17.8	17.5	18.2	1.40	1.50	1.29
	2	20.8	21.6	21.9	0.65	0.55	0.52
	3	24.9	25.5	25.8	0.30	0.28	0.26
3	1	18.4	17.9		1.20	1.36	
	2	21.6	21.6		0.55	0.55	
	3	25.6	25.6		0.27	0.27	
4	1	17.3			1.62		
	2	21.0			0.62		
	3	24.9			0.32		
5	1	19.3	21.5		0.94	0.56	
	2	24.1	26.0		0.34	0.26	
	3	29.0	31.0		0.18	0.14	

pressure membrane determinations. At the low tensions, porosity is considered to be important and therefore, normally, cores taken from the soil in situ are used for the porous plate determinations. However, since the soil used for these experiments was all in the disturbed condition, the samples for both the pressure membrane and porous plate determinations were disturbed.

The water contents and tensions given in Table 3 are those at the beginning of each test and constitute the treatments imposed upon the soil into which the adventitious roots grew. The roots then, were exposed to these initial water contents which increased as the experiment progressed. The final water contents and tensions when the plants were harvested will be given in the section on results and discussion.

At the end of each individual test the plants were harvested. Each plant was weighed, separated into stem, leaves, and petioles, and the individual parts weighed. The adventitious roots were shaken free of soil, washed clean in tap water, cut from the stem, blotted dry between sheets of filter paper, and weighed immediately. These weights are the only ones recorded for the adventitious roots. The soil which was shaken free of the roots was placed in sample cans, weighed, oven-dried, and reweighed to determine the water content. That portion of the stem which had been surrounded by the soil and on which the roots grew was not included with the rest of the stem to avoid possible direct contamination of rubidium (or lithium) from the soil.

The individual parts, (stem, leaves, and petioles) were oven-dried at 60 degrees centigrade then reweighed to obtain the dry weights of the plants. The stem and leaf samples were then pulverized in a blender and stored for chemical analysis for the rubidium or lithium. The petioles were broken up into small pieces and stored for analysis.

Chemical analysis

One-gram samples of the plant material were digested in 10 cc of nitric acid, heated over a hot plate. Five cc.of perchloric acid were added and the mixture heated until the fuming ceased and the solution cleared. The solution was then filtered hot and the residue and filter paper were washed several times with hot distilled water. The filtrate was made up to 50 cc.and stored for rubidium (or lithium) determination on the flame photometer.

For determination of the rubidium a standard curve of 50, 35, 25, 15, 10, 7, and 4 ppm was established with the flame photometer covering the full scale from 0 to 100 per cent transmittance. This curve is shown in the appendix, Figure 14. Conveniently, this curve is linear and has a slope of exactly one-half.

A check for potassium interference at 50 ppm potassium was made and showed an interference of 2.0 transmittance units of the photometer scale. Unfortunately, for the first test (sandy loam soil) no determinations were made for actual potassium contents of the plants. Checks made later on plants grown on the clay loam soil showed that the actual potassium content ranged from about 200 ppm in the stems to about 600 ppm in the leaves and petioles. Assuming that the plants grown on the sandy loam soil for the first test had about the same range of potassium contents, the interference from potassium may have been considerably greater than had been anticipated. The plant material had been discarded before this could be checked out.

The slit width for the determinations of rubidium on the plants from the first test was relatively wide at 0.14 millimeters and the wave length setting was 780 millimicrons. This slit width adds to the probability of considerable potassium interference. This interference problem will be discussed further in the section on results and discussion. Duplicate photometric readings made on the same solutions from plant materials showed a range of 0.5 to 1.5 transmittance units between the readings.

The same standard curve for rubidium was prepared for each succeeding test. However, the slit width was narrowed to 0.06 millimeters at the expense of some sensitivity, to attempt to remove some of the potassium interference. At the same time, a potassium interference curve was prepared for solutions of 100 to 600 ppm potassium. The interference in terms of transmittance units at the decreased slit width ranged from 0 at 100 ppm to 5 at 600 ppm potassium and was linear. The interference curve is shown in figure 15 in the appendix. The actual potassium contents of the plants were determined and a correction for the potassium in each sample was applied to the rubidium reading for that sample. Tests two through six with the exception of the lithium test were handled the same way.

The amounts of lithium taken up by the adventitious roots proved to be small and there was no way to detect the lithium content because of calcium interference on the flame photometer. Quantitative measurements were not made for lithium, although there appeared to be traces of the lithium in the plant material. Because of this, lithium was not used again.

The samples from the lithium test served as control samples for the rubidium determinations. The lithium line is sufficiently far removed from the rubidium line that any lithium present would not likely interfere. The samples were read in a flame photometer at the settings for rubidium and these readings compared with those for the rubidium samples. This was done to check the possibility of interference besides that from potassium. The results of this check will be presented in the section on results and discussion.

The photometric per cent transmittance readings for rubidium were converted to milligrams of rubidium per gram of dry plant tissue, multiplied by the number of grams of dried tissue per plant part and summed over the parts of each plant, i.e, stem, leaf, and petiole. The latter data should then represent the total amount of rubidium which moved into the plant through the adventitious roots.

RESULTS AND DISCUSSION

Root Growth

The amount of adventitious root growth which occurred throughout all the tests appeared to be somewhat variable and at times seemed to be contingent upon some factors other than the moisture treatments imposed on the soil. The plant itself, the aeration condition of the small growth containers, and the degree of packing of the soil all may have had some influence on the root growth. Any discussion of these factors at this time would, however, be pure speculation.

The root growth data in relation to soil moisture tension in test one for the sandy loam soil are given in Table 4. Columns one and three are the treatments imposed upon the soil before it was placed around the plant stems and are the same values as those given in Table 3 under materials and methods. Column two gives the water content, as determined by the oven drying procedure, of the soil from around the stems when the plants were harvested. Column four gives the corresponding soil moisture tensions taken from the moisture-tension curve for the soil. Comparisons of columns one and two show the ranges of water contents to which the adventitious roots were exposed, and comparisons of columns three and four show the corresponding ranges of moisture tension.

The statistical F test indicates that the differences between the amounts of root growth were not significant even at the 5 percent level. This means that the moisture treatments, either in terms of soil water contents or in terms of soil moisture tension, had no consistent effect upon the growth of adventitious roots. This result is corroborated in Figure 4 which shows a very wide scatter of points representing grams of adventitious root growth as a function of the original soil moisture tension.

Table 4. Adventitious root growth in relation to moisture treatments on sandy loam soil in test 1.

1 Original soil water content (per cent)	2 Final soil water content (per cent)	3 moisture tension (atms.)	4 moisture tension (atms.)		5 Adventitious root growth (grams)
		Moisture Treatment 1			
12.6	9.4	1.10	6.00		0.6220
12.6	9.4	1.10	6.00		0.6210
12.9	10.0	0.99	3.90		0.4438
12.9	9.8	0.99	4.40		0.3413
13.2	9.9	0.94	4.20		0.4206
13.2	10.2	0.94	3.50		0.1351
				Mean	0.4306
		Moisture Treatment 2			
15.3	10.5	0.55	2.90		0.7680
15.3	12.0	0.55	1.20		0.2443
15.7	12.2	0.49	1.28		0.5009
15.7	11.4	0.49	1.78		0.6362
16.0	12.0	0.46	1.38		0.9075
16.0	12.4	0.46	1.20		0.4883
				Mean	0.5909
		Moisture Treatment 3			
18.1	13.1	0.33	0.94		0.8181
18.1	11.7	0.33	1.60		0.2734
18.9	14.8	0.29	0.60		0.3801
18.9	14.9	0.29	0.59		0.3642
18.8	14.9	0.29	0.59		0.3919
18.8	15.0	0.29	0.59		0.1364
				Mean	0.3941

Statistic F for root growth means - 2.274
F required for significance at 5 per cent - 4.103
Degrees of freedom = 2 and 10

The relationship between root growth and the final soil moisture tension is not shown because even if there appeared to be a dependence of root growth upon the final tension, the relationship would be merely an artifact since the final tension would be dependent partly upon original tension as well as partly upon the amount of root growth.

Table 5 gives the adventitious root growth in relation to the soil water contents and tensions of the clay loam soil in test two. For this test, the statistic F for root growth means is highly significant, indicating a strong dependence of root growth upon soil water content and tensions. This is in direct contrast to the results of test one with the sandy loam soil. The curve in Figure 5 verifies the F test and shows the curvilinear nature of the relationship. This curve was calculated by curvilinear regression analysis. As indicated in Figure 5 both regression coefficients, i.e., b1 and b2, are significant at the 5.0 per cent level. However, despite the significance the curve is almost linear. This curve should not be interpreted beyond the limits of the data.

This same relationship is shown in terms of soil moisture tension in Figure 6. The curve in Figure 6 was obtained simply by converting several points from the curve of Figure 5 to the corresponding soil moisture tensions and plotting these points in Figure 6.

Table 6 gives the adventitious root growth in relation to moisture treatments for tests three and four combined. These data are comparable in every way with those in Table 5 as far as soil water conditions are concerned. Analysis of variance was not made on the data in Table 6 but rather the data were combined with those of Table 5 and curvilinear regression analysis was made of the combined data from tests two,

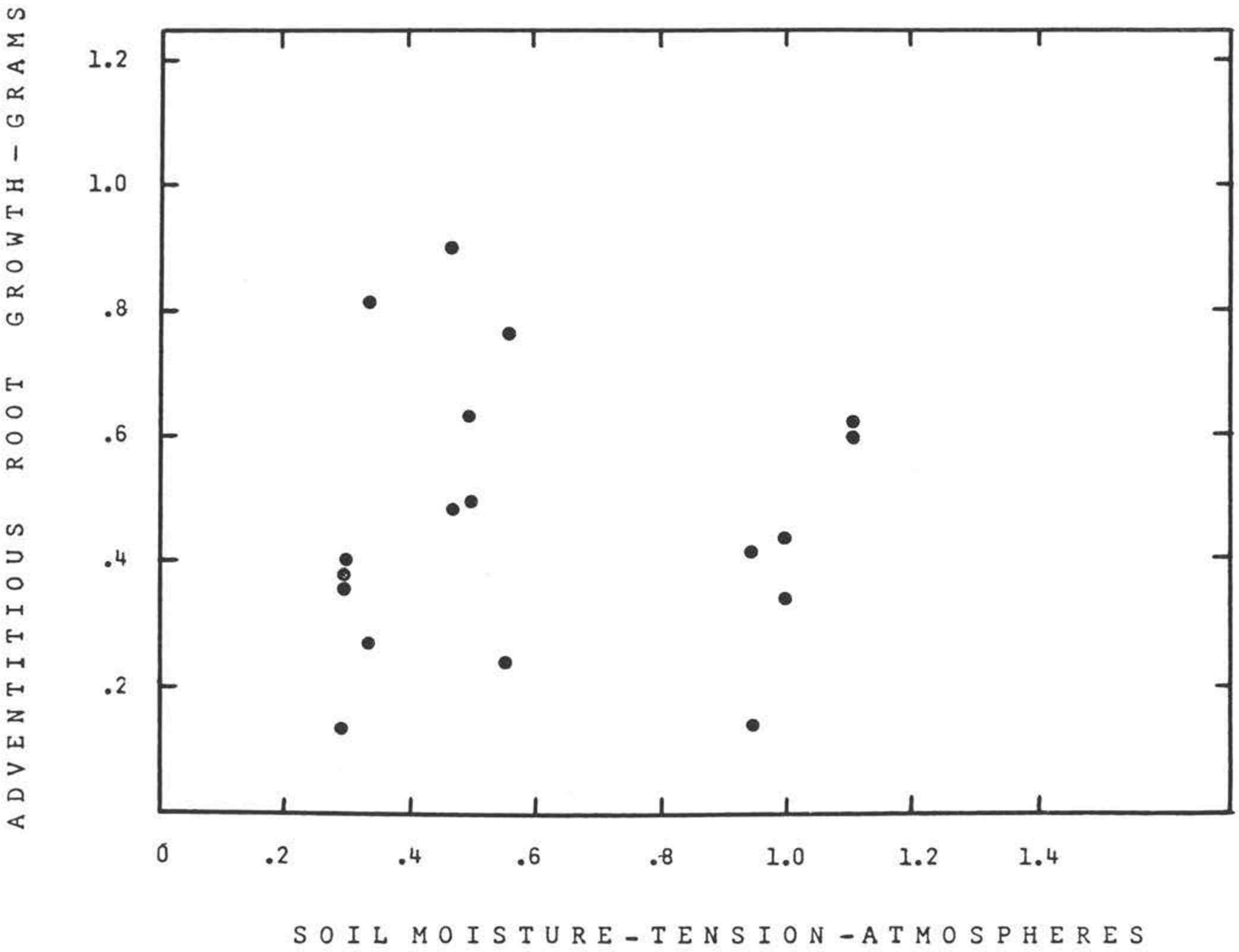

Figure 4. Adventitious root growth related to soil moisture-tension in sandy loam soil.

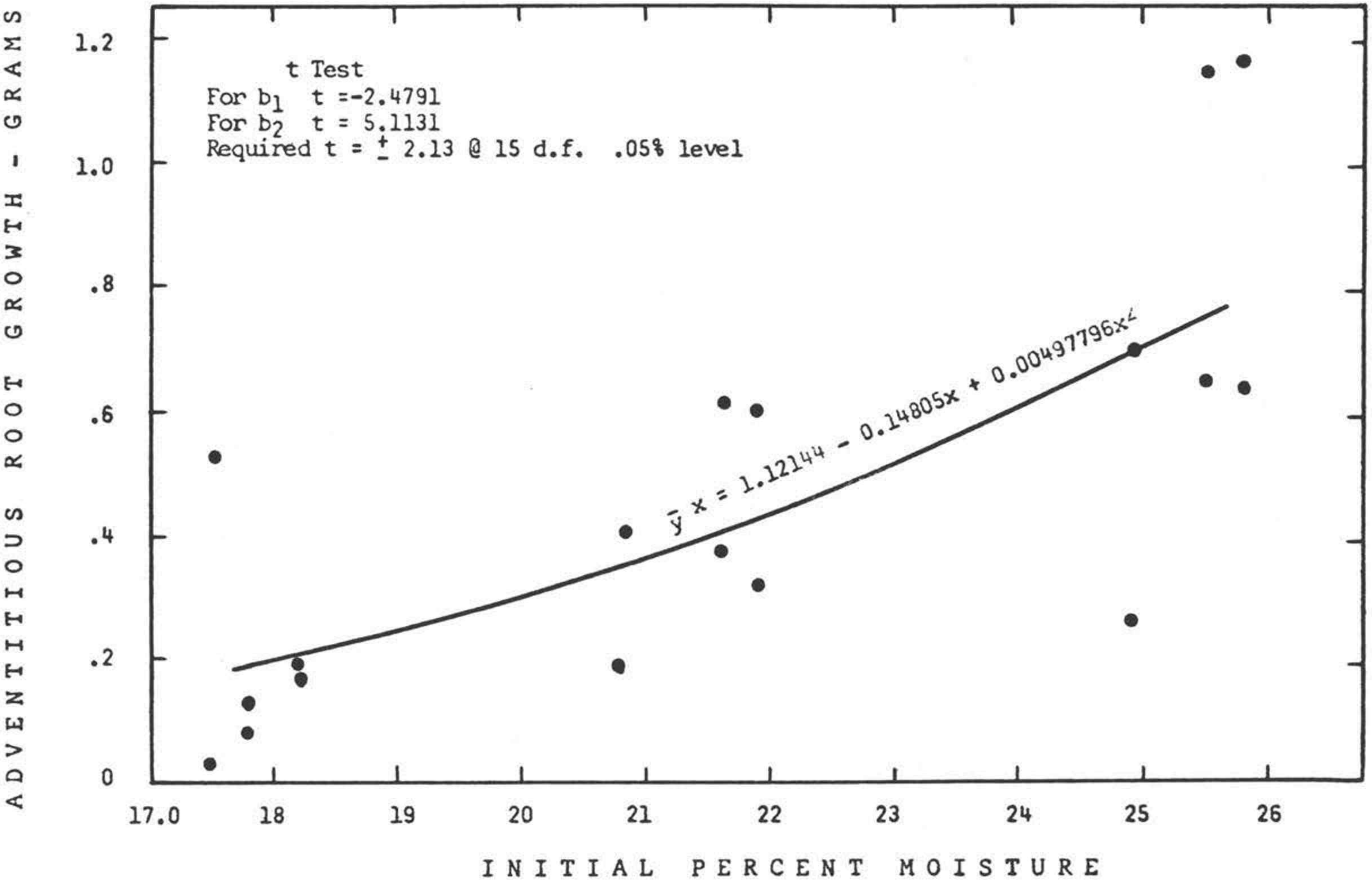

Figure 5. Adventitious root growth as related to initial per cent moisture in clay loam soil.

three, and four. The result of this analysis is shown in Figure 7. Again regression coefficients are highly significant and the F test for regression is also highly significant.

Table 5. Adventitious root growth in relation to moisture treatments on clay loam in test 2.

1 Original soil water content (per cent)	2 Final soil water content (per cent)	3 moisture tension (atms.)	4 moisture tension (atms.)		5 Adventitious root growth (grams)
		Moisture Treatment 1			
17.8	16.5	1.40	2.10		0.1300
17.8	16.5	1.40	2.10		0.0768
17.5	16.2	1.50	2.15		0.0220
17.5	16.0	1.50	2.40		0.5227
18.2	16.5	1.29	2.10		0.1828
18.2	16.8	1.29	1.90		0.1770
				Mean	0.1852
		Moisture Treatment 2			
20.8	19.0	0.65	1.00		0.1856
20.8	17.9	0.65	1.32		0.4039
21.6	18.8	0.55	1.08		0.6170
21.6	19.1	0.55	0.99		0.3760
21.9	19.6	0.52	0.87		0.3280
21.9	18.8	0.52	1.08		0.6084
				Mean	0.4198
		Moisture Treatment 3			
24.9	21.0	0.30	0.62		0.7005
24.9	22.3	0.30	0.48		0.2737
25.5	21.0	0.28	0.62		1.1595
25.5	22.4	0.28	0.47		0.5532
25.8	23.4	0.26	0.39		0.5469
25.8	21.6	0.26	0.55		1.1713
				Mean	0.7342

Statistic F for root growth means 9.104 with 2 and 10 d.f.
F required for significance at 1 per cent = 7.559

The same curve as in Figure 7 showing the relationship between root growth and soil water conditions in terms of tension is given in Figure 8. The greater curvature to the line of regression with tension

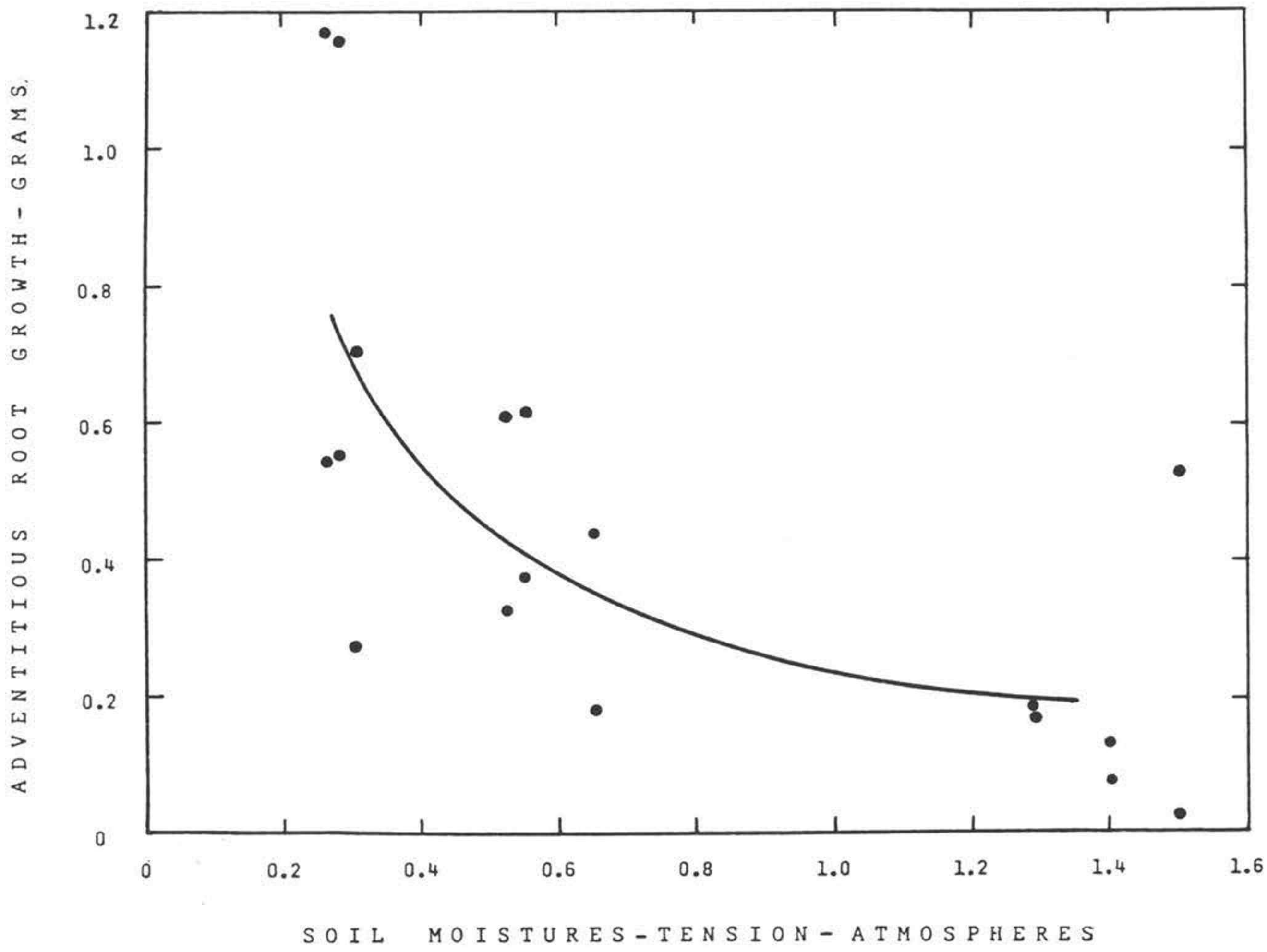

Figure 6. Adventitious root growth as related to soil moisture-tension in clay loam soil.

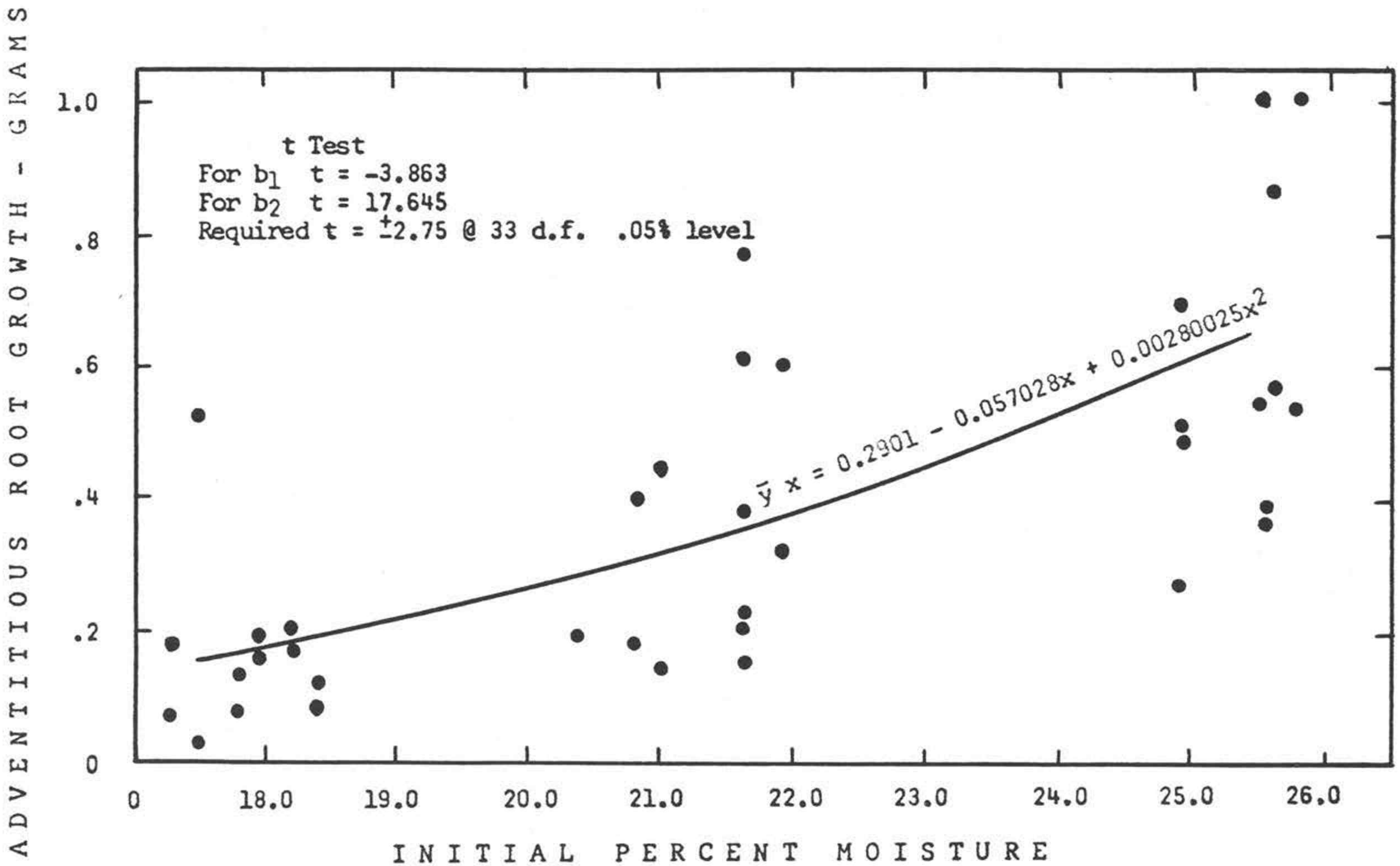

Figure 7. Adventitious root growth as related to initial percent moisture in clay loam soil.

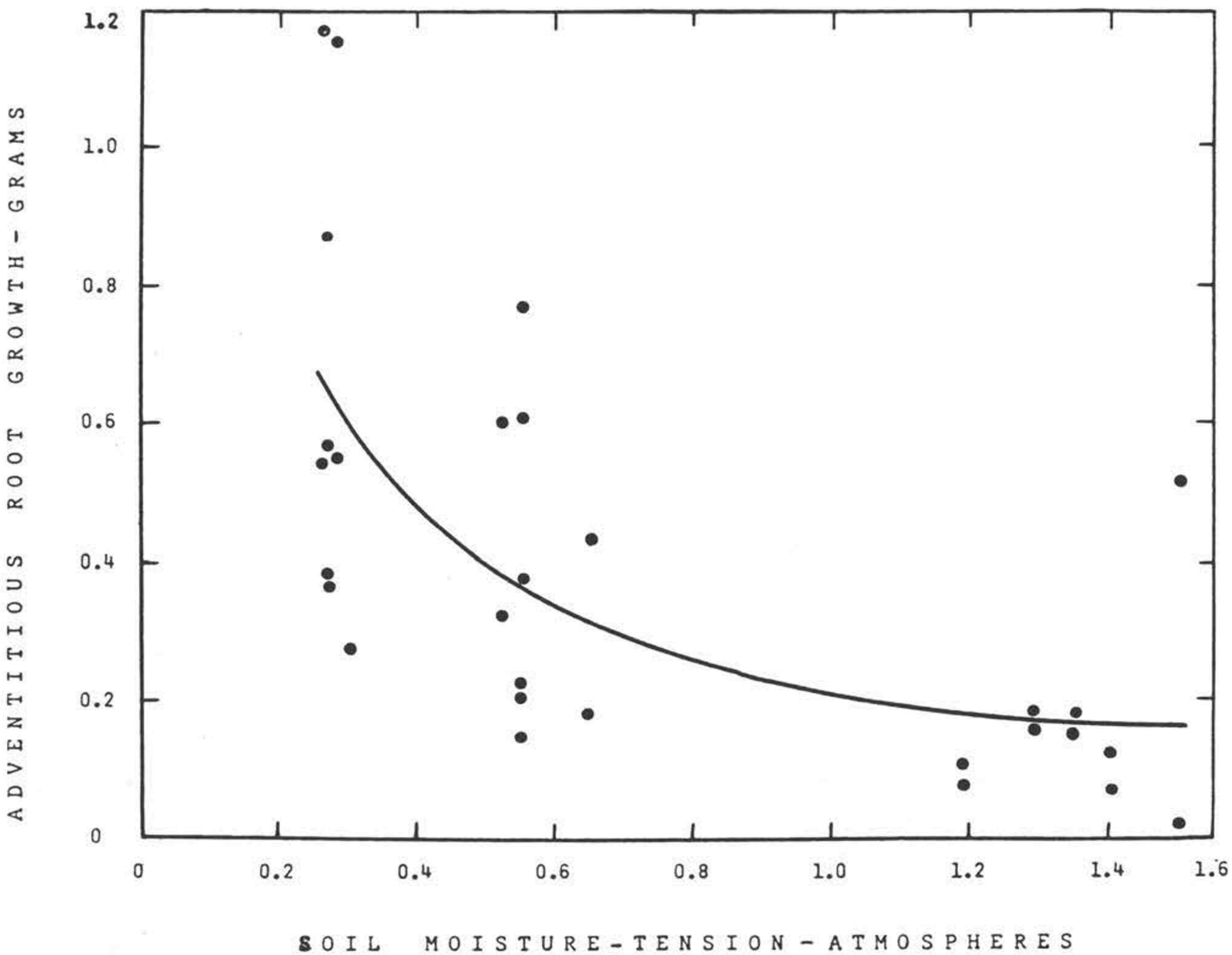

Figure 8. Adventitious root growth as related to soil moisture-tension in clay loam soil

than with water contents results from the exponential relationship between percent moisture and tension (see the moisture tension curve, Figure 2).

The regression line in Figure 7 is closer to being linear than the line in Figure 5 (test two). It should be recalled that Figure 7 includes the data from test two. However, the two lines are almost identical and the confidence intervals for the two equations are similar and simply narrowed for the second equation because of increased degrees of freedom. The two lines can be considered the same and therefore the tests three and four substantiate the results of test two quite well.

There is little doubt of the strong dependence of adventitious root growth in the clay loam soil upon the initial soil water contents at least within the range of water contents in Figures 5 and 7. This, of course, says nothing of what the root growth might be if the soil was rewatered one or more times. However, the results do show, in relative terms, how root growth will react to a particular water content. As the moisture declines and the tension rises, root growth apparently declines almost linearly. The question might be raised that the differences in root growth were the result of differences in root growth initiation rather than lack of growth after the roots had started at the lower water contents. There was considerable variation in the number of roots which started growth but there appeared to be no relationship between the number which started and the initial water contents. Sometimes there were more roots started at the low water than at the higher water contents; sometimes the reverse occurred. The differences observed in all the tests were in the length, thickness, and degree of branching of the roots rather than in their actual number.

Table 6. Adventitious root growth in relation to moisture treatments on clay loam soil in tests 3 and 4.

1 Original soil water content (per cent)	2 Final soil water content (per cent)	3 Original moisture tension (atms.)	4 Final moisture tension (atms.)	5 Adventitious root growth (grams)
		Moisture Treatment 1		
18.4	16.8	1.19	1.85	.1210
18.4	16.9	1.19	1.84	.0800
17.9	16.3	1.35	2.20	.1843
17.9	16.6	1.35	2.00	.1557
17.3*	16.4	1.61	2.15	.0682
17.3*	16.7	1.61	1.95	.1773
			Mean	.1311
		Moisture Treatment 2		
21.6	20.0	0.55	0.78	.2284
21.6	19.8	0.55	0.83	.1506
21.6	19.9	0.55	0.81	.7736
21.6	20.4	0.55	0.72	.2119
21.0*	19.8	0.62	0.84	.1460
21.0*	19.5	0.62	0.88	.4543
			Mean	.3275
		Moisture Treatment 3		
25.6	23.2	0.27	0.41	.5705
25.6	22.9	0.27	0.43	.8722
25.6	23.7	0.27	0.37	.3822
25.6	23.5	0.27	0.83	.3744
24.9*	23.0	0.30	0.42	.4955
24.9*	23.4	0.30	0.39	.5142
			Mean	.5353

* Test 4, remainder test 3.

It is not unreasonable to assume that the growth of the main root system would be affected in much the same way by the water contents as were the adventitious roots. If the assumption is correct, it is quite apparent that the soil water conditions at any particular time can have a profound effect upon the growth of plant roots. As a soil goes through a series of wetting and drying cycles, as in the case under irrigation, root growth may occur as a series of bursts of growth corresponding to the periods of low moisture tensions. Such a situation might easily lead to a misinterpretation of data purporting to relate a particular phenomenon such as water absorption or ion uptake to soil water conditions, providing a correlation exists between the amounts of root growth and the particular phenomenon under study. The amount of water absorption or ion uptake may depend more on the number of times or length of time the soil is moist than upon the moisture content or tension. In other words it may be that when the soil is moist, most of the root growth occurs and concurrently most of the absorption of water and nutrients occurs. Treatments which permit longer periods between rewatering the soil, that is, supposedly drier regimes, may simply result in less time for root growth to occur and consequently less time for absorption to occur. Results which might be interpreted as an effect of lower water contents or higher tensions at the root surface might simply be a result arising from less root growth.

The relationships shown in Figures 5 and 7 agree, in a general way, with the observations of Jean and Weaver (10) and those of Kmoch et al. (15) but do not agree with those of Bennet and Doss (1). These relationships agree quite well with the results of Mederski and Wilson (17) where they found a linear increase in root growth with increasing initial water contents of the soil. The relationships also support the opinion that root growth should be accounted for before relating moisture conditions to absorption at the root surface.

Table 7 gives the adventitious root growth in relation to moisture treatments for test five, the one in which both rubidium content and water content were increased.

It is interesting to note that even though the F test indicates no significance for treatment effects the root growth means lie very close to the curvilinear regression line at 20 percent and 25 per cent moisture in Figures 5 and 7. At the higher level of 30 per cent moisture the root growth did not increase further beyond that at the 25 per cent moisture level.

The adventitious root growth showed a tendency to level off as the soil water increased from the 25 per cent level to the 30 per cent level. This may have been caused by improper packing of the soil in the small containers at the 30 per cent water content. The soil had a strong tendency to form spherical clods at the 30 percent water content, and the final soil structure in the containers was vastly different from that of the soil at the lower water contents. The soil appeared as a number of relatively large balls with large air spaces between them as compared with the compact appearance of the soil at the 20 per cent and 25 per cent water contents. It would be unwise to interpret the absence of further root growth increase at the 30 per cent moisture level as a lack of effect of the additional moisture. The moisture effect was very likely obscured by the very poor packing of the soil.

In the sixth and final test in which the adventitious roots were grown for six days before the rubidium was added, root growth was considerably greater than in all the previous tests on the clay loam soil. Table 8 gives the adventitious root growth which occurred. The root growth containers were not sealed at the top for this experiment.

Table 7. Adventitious root growth in relation to moisture treatments on clay loam in test 5.

1 Original soil water content (per cent)	2 Final soil water content (per cent)	3 Original moisture tention (atms.)	4 Final moisture tension (atms.)		5 Adventitious root growth (grams)
		Moisture Treatment 1			
19.3	17.5	0.94	1.51		0.1692
19.3	17.1	0.94	1.70		0.1770
21.5	18.7	0.56	1.10		0.0786
21.5	18.0	0.56	1.30		0.7070
				Mean	0.2830
		Moisture Treatment 2			
24.1	21.2	0.34	0.60		0.7405
24.1	21.1	0.34	0.61		0.3562
26.0	21.6	0.26	0.55		0.5238
26.0	22.0	0.26	0.50		0.2870
				Mean	0.4769
		Moisture Treatment 3			
29.0	26.5	0.18	0.24		0.1708
29.0	25.7	0.18	0.27		0.2840
31.0	25.7	0.14	0.27		0.5159
31.0	25.6	0.14	0.27		0.6448
				Mean	0.4038

Statistic F for root growth means = .0592 for 2 and 6 d.f.
Required F for 2 and 6 d.f. - 5.143 at 5 percent.

It will be recalled that the rubidium was added with sufficient water to raise the water content to 40.1 per cent on the sixth day and that the experiment lasted for 28 hours more.

It is very apparent that a great deal more root growth occurred under the conditions of this test than under the conditions of the previous tests. The root growth which took place into the soil at 25 percent moisture in the previous tests was anywhere from one-half to one-tenth the amounts in this test. It might be argued that the roots grew for 28 extra hours (two daylight periods and one dark period) and at a very high water content for the period. However, during the first six days of adventitous root growth it was very apparent, through visual observation of roots against the inside walls of the containers, that there was much more extensive root growth than had taken place in previous tests. Even before the rubidium and water was added on the sixth day there was rather massive root growth and branching taking place as compared with the previous experiments.

Table 8. Adventitious root growth which occurred at 25 percent moisture in unsealed containers in eight days.

1	2	3
Plant No.	Initial soil-water content (per cent)	Adventitious root growth (grams)
1	24.3	1.8940
2	24.3	3.8250
3	24.3	0.6613
4	24.3	2.1025
5.	24.3	1.9145
6	24.3	1.1409

The only reasonable explanation for the marked increase in adventitious root growth appears to be the fact that the tops of the small containers were not sealed. The small amounts of water which were added at two-day intervals was probably of little consequence. The freedom for gaseous exchange to take place with outside air may have greatly enhanced the growth of the roots. However, it is entirely possible, if not probable, that the aeration of the sealed containers more nearly approached the normal field conditions than did the aeration of the unsealed containers. The aeration of the unsealed containers may have approached the conditions of only the first few inches of a field soil. This observation is in general accord with the common observation that plants produce the greatest concentration of roots close to the soil surface providing sufficient moisture is present for root growth.

Water Intake by Adventitious Roots

Since it is not possible to separate the amounts of water lost by evaporation from the small containers around the plant stems from the amounts absorbed by the adventitious roots, it is not possible to discuss water absorption *per se* by the roots. The losses by evaporation are likely to be somewhat variable. The relative magnitude of the water losses by evaporation are given in Table 1, but to attempt to apply a constant correction for each plant throughout the tests would be arbitrary and misleading. The following section is presented to show the relative magnitudes of water losses from containers and to show whatever relationships these losses might have with root growth. This is done with the understanding that some losses are by evaporation, some by absorption by the plant, and some by incorporation into the adventitious roots themselves. Whether there was any water movement in the opposite direction, i.e., out of the adventitious roots, at any time is not known. However, since the net effect was always some loss and since generally the losses were greater in magnitude than the purely evaporative losses as given in Table 1, there must have been some net movement of water into the roots either to remain as part of the roots or to move into the plant.

Table 9 gives the water losses from the sandy loam soil around the plant stems during the six-day period of test one. The moisture treatments are those previously described in Table 3.

Table 9. Adventitious root growth and water lost from sandy loam soil.

	Soil moisture treatments					
	1		2		3	
Replicate	Root growth (gms.)	Water lost (gms.)	Root growth (gms.)	Water lost (gms.)	Root growth (gms.)	Water lost (gms.)
1	0.6220	2.24	0.7680	3.36	0.8181	3.50
2	0.6210	2.24	0.2443	2.31	0.2734	4.48
3	0.4438	2.03	0.5009	2.45	0.3807	2.87
4	0.3413	2.17	0.6362	3.01	0.3642	2.80
5	0.4206	2.31	0.9075	2.80	0.3919	3.22
6	0.1351	2.10	0.4883	2.52	0.1364	2.66

These data are plotted in Figure 9 and the line of regression shown. The regression equation is given but the F test for regression indicates no significance. In other words the slope of the regression line is not significantly different from zero. This means that the amount of water lost from the soil around the stems of the plants was quite independent of the amount of root growth. A comparison of the amounts of water lost from the sandy loam soil during the test on the plants (Table 9) with the amounts lost by evaporation when no plants were present (Table 1) indicates that in some cases, virtually all of the water loss could have resulted from evaporation. Therefore, it is unlikely that any dependence of water lost on root growth would appear.

Examination of the data from water lost from the soil around the stems reveals that some of the values are actually less than the amounts lost by evaporation from the containers with only the plastic rods present. Whether the effectiveness of sealing with paraffin alone around the plant stems was highly variable or whether water was being added to the soil through the adventitious roots is not known. There was no observable effect of moisture treatments on water losses.

Table 10 gives the water losses from the clay loam soil around the plant stems for tests two, three, and four. The water loss data from these tests are comparable in every way because the moisture treatments are the same throughout the three tests and therefore the data may be combined. The water losses are plotted against root growth in Figure 10, together with the line for linear regression. The F test indicates that the regression is highly significant. The relative magnitudes of the water losses in Table 1 for the paraffin-petroleum jelly sealing method and of the losses in Table 10 indicate that probably a considerable portion of the water loss was by absorption into the adventitious roots. It should be noted, however, that the greater the amount of root growth the greater will be the amount of water in the roots themselves. Assuming that the roots contained about 90 per cent water, the average amount of water in the roots, over all treatments was about 0.35 grams. The average amount of water lost, over all treatments, was 1.32 grams. Using the evaporation value from Table 1 (0.55 grams.) and adding the amount in the roots, a total of about 0.90 grams of

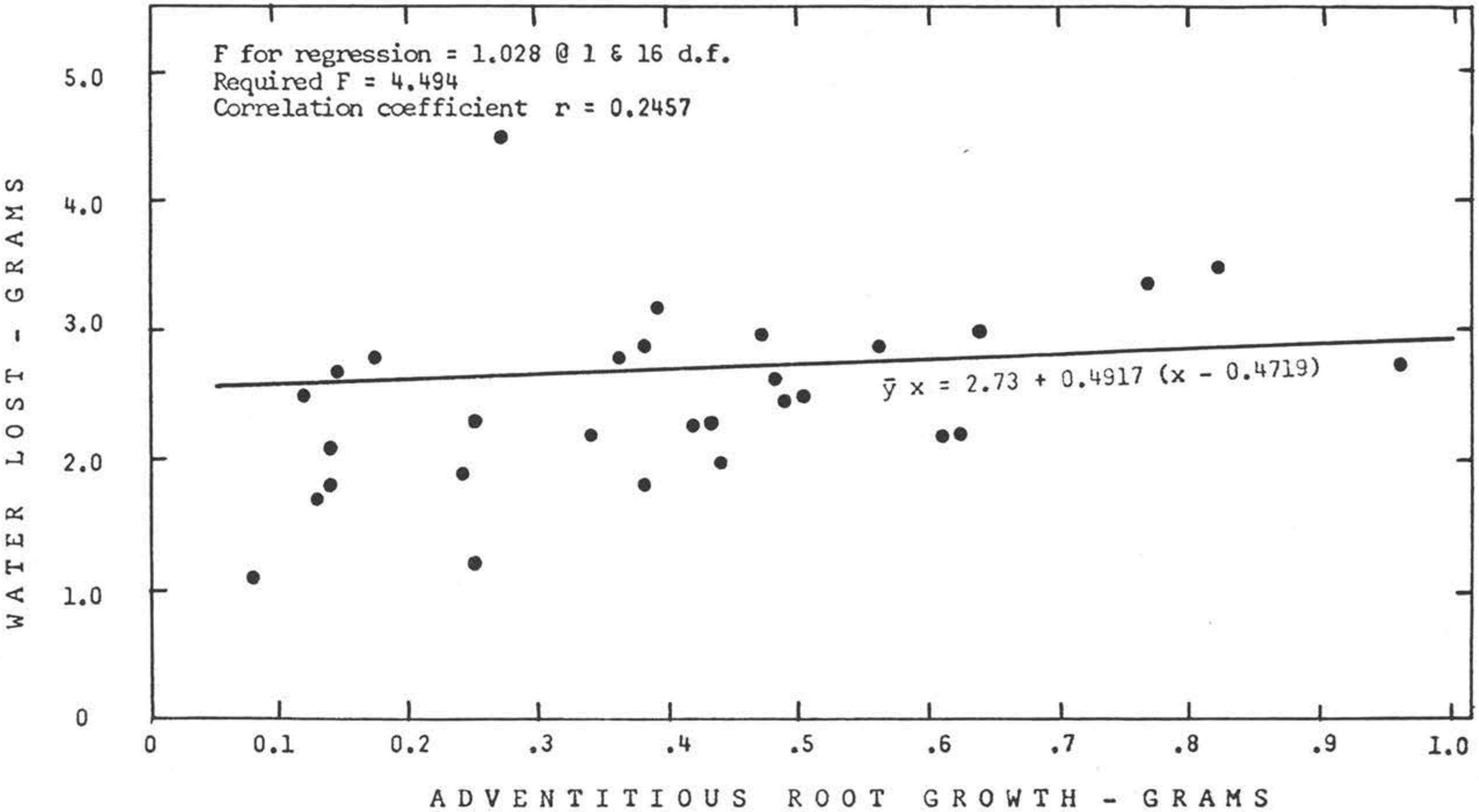

Figure 9. Water lost as related to adventitious root growth in sandy loam soil in small containers. Test 1.

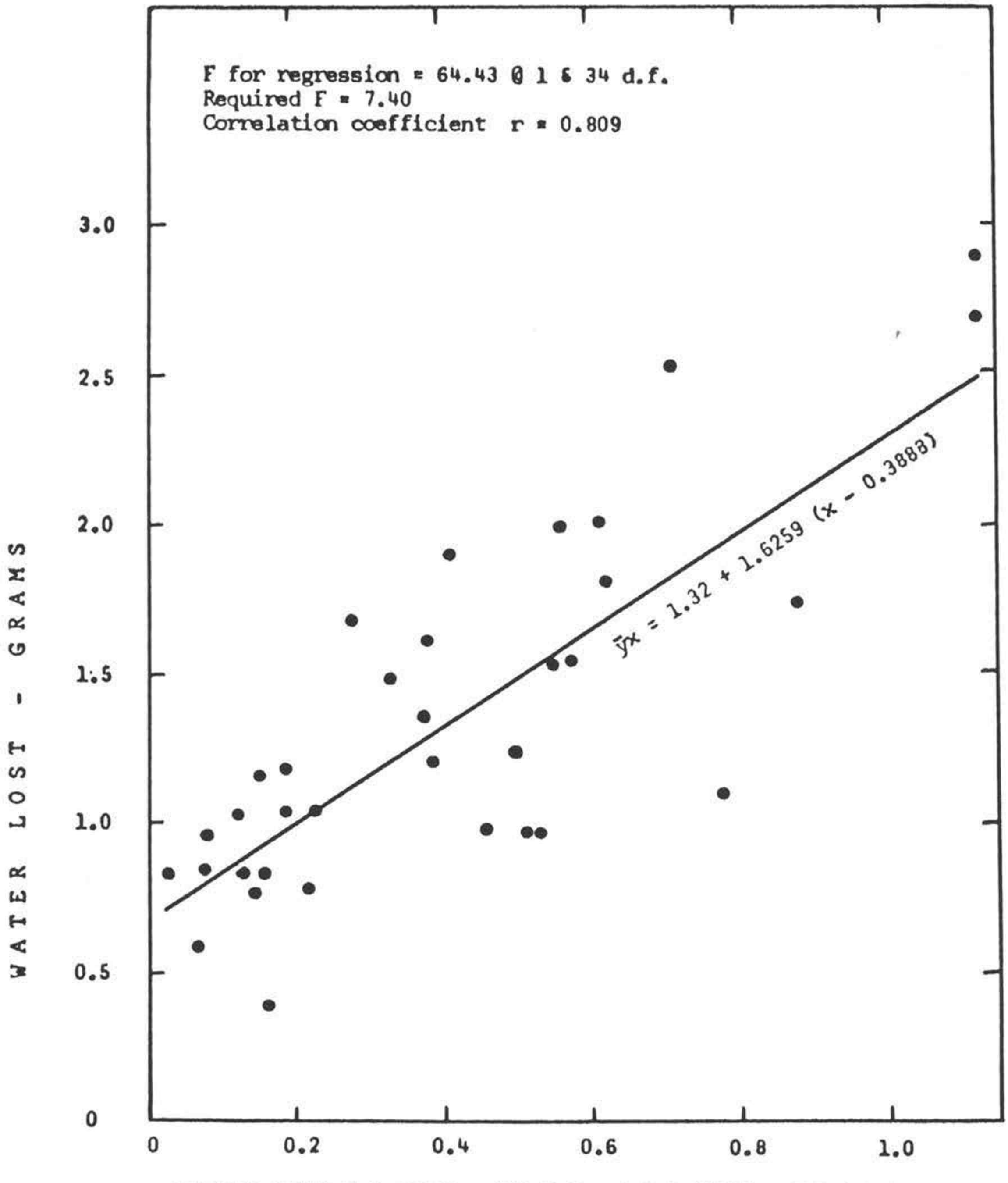

Figure 10. Water lost as related to adventitious root growth in clay loam soil in small containers. Test 2, 3 and 4.

Table 10. Adventitious root growth and water lost from clay loam soil in tests 2, 3, and 4.

		Soil moisture treatments					
		1		2		3	
Test No.	Replicate	Root growth (gms.)	Water lost (gms.)	Root growth (gms.)	Water lost (gms.)	Root growth (gms.)	Water lost (gms.)
2	1	0.1300	0.84	0.1856	1.18	0.7005	2.53
	2	0.0768	0.84	0.4039	1.90	0.2737	1.68
	3	0.0220	0.84	0.6170	1.82	1.1595	2.90
	4	0.5227	0.97	0.3760	1.62	0.5532	2.00
	5	0.1828	1.09	0.3280	1.49	0.5469	1.54
	6	0.1770	0.90	0.6084	2.01	1.1713	2.70
3	1	0.1210	1.03	0.2284	1.04	0.5705	1.55
	2	0.0800	0.96	0.1506	1.17	0.8722	1.74
	3	0.1843	1.03	0.7736	1.10	0.3822	1.32
	4	0.1557	0.84	0.2119	0.78	0.3774	1.35
4	1	0.0682	0.58	0.1460	0.78	0.4955	1.23
	2	0.1773	0.39	0.4543	0.98	0.5142	0.97

water is accounted for, leaving about 0.40 grams or roughly one-third of the water lost which moved into the plants. However, this is only an average estimate and therefore about all that can be said here is that the water losses from the containers was strongly dependent upon the amount of root growth. The ultimate fate of this water is not accurately known. This correlation of water loss and root growth in the clay loam soil is in marked contrast to the lack of such a correlation in the sandy loam soil.

The water losses from the soil in the small containers in test number five were about the same as those in tests two, three and four. Test five was the one in which both water contents and rubidium contents were increased in the soil around the plant stems. The water losses in relation to amounts of root growth fall right in line with the relationship shown in Figure 10. There were no further increases in water losses at the 30 per cent moisture treatment over those at the 20 or 25 percent moisture treatments. The only relationship was again between root growth and water loss and since the root growth did not increase further at the 30 per cent level (as noted in the previous section) neither did the water loss.

The data for water losses from the soil in the small containers for test number six are given in Table 11. This test is the one in which the adventitious roots were first grown for six days at approximately 25 per cent moisture in the soil. The water content was raised to 40 per cent for a further 28 hours and it is the water losses over this short period that are recorded in Table 11. It should be recalled that the adventitious root growth was considerably more extensive and that the covers of the small containers were not sealed.

Table 11. Water losses from clay loam soil at 40 per cent moisture as related to the weights of adventitious roots in test 6.

Plant No.	Adventitious roots (grams)	Water lost from soil in containers (grams)
1	1.8940	5.0
2	3.8250	8.5
3	0.6613	2.8
4	2.1025	4.5
5	1.9145	4.9
6	1.1409	4.2

These data are plotted in Figure 11. Because of the limited data regression analysis was not done on these data. However, it is quite apparent that there were greater losses of water with the larger amounts of roots than with the smaller.

It is noteworthy that the amounts of water lost from the soil in this test are very much higher than in the previous tests with the clay loam soil. These increased losses are in accord with the greatly increased amounts of roots but it is important to note that these losses occurred over a period of only 28 hours as compared with six days in the previous tests. Some of those losses were undoubtedly evaporation but since the soil in each of the containers was at approximately the same initial water content and all of the containers unsealed, such losses should be almost the same from one container as from another. The evaporation over the 28-hour period was probably quite small even though the covers of the containers were unsealed.

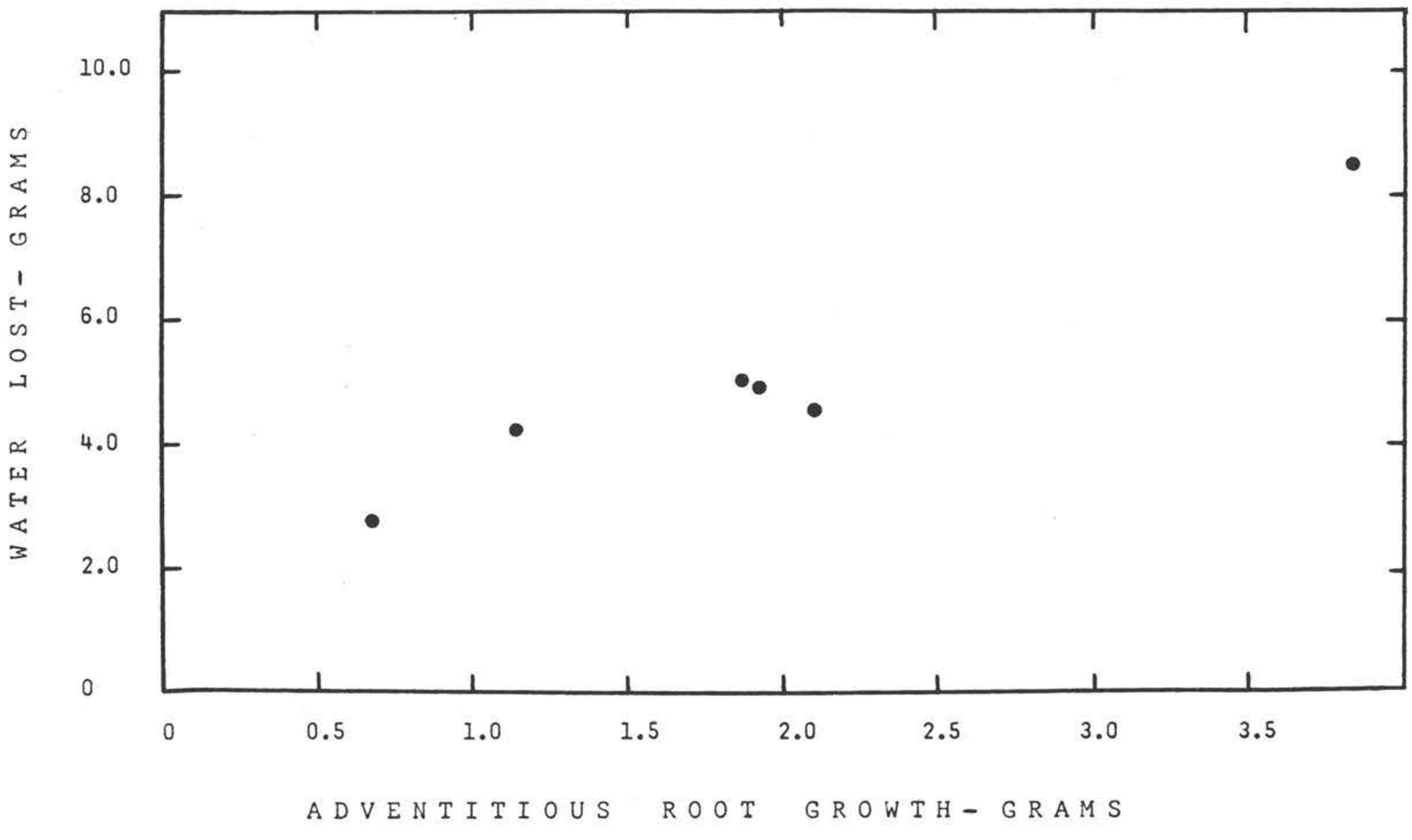

Figure 11. Water lost as related to adventitious root growth in clay loam soil in small containers. Test 6.

Since most of the adventitious root growth had already taken place before the losses were measured, much of the water that was absorbed by the roots must have been translocated into the plant to join the main transpiration stream. The evidence from this particular test, even though somewhat limited, gives reasonable assurance that there is some correlation between the amount of root growth and the amount of water absorbed. Such a correlation may or may not hold over the entire range of moisture from close to zero tension to the 15 atmosphere or wilting tension.

Analysis of variance of the data in Table 11 indicates no effect on water losses from the moisture treatments of the main root systems. It is apparent that the plants which were subjected to severe soil moisture stress did not take up more water from the moist soil occupied by the adventitious roots than did the plants not subjected to stress. The water intake was much more clearly related to the amount of root growth than to the degree of moisture stress imposed upon the plants.

Transpiration by Sunflower

In test number six the transpiration losses were recorded in order to obtain a measure of the magnitude of transpiration losses, it appeared desirable to measure the degree of control which the room conditions had over the constancy of the transpiration rate. The following data are presented for no other purpose.

Table 12 presents the accumulative losses from the three pots covered with vermiculite and the three pots which were rewatered frequently. The former is considered as transpiration, because evaporation through the vermiculite was negligible, and the latter is considered as transpiration plus evaporation (evapotranspiration). The evaporation from each of the uncovered pots would be approximately the same.

These data are plotted in Figure 12. It is quite apparent from the two curves that the evapotranspiration losses occur more rapidly than those of transpiration alone. This is to be expected, of course, but it is noteworthy that the evapotranspiration losses take place at a constant rate during each day. In addition, since the two parts of the curve exclusive of the overnight period are parallel, the rate appears to be constant from day to day. This indicates that the condition of the growth room permitted a relatively constant transpiration rate throughout the test periods.

The transpiration rate of the unwatered plants began to decline at about 10 hours or at a water content of about 23-24 percent. This moisture percentage is well above that at which the sunflowers first showed signs of wilting and even further above the permanent wilting percentage. The transpiration rate did not recover after the overnight period for these plants. This decrease in transpiration rate is apparently the first sign of water stress affecting the plant.

Rubidium Uptake

As has been noted in the section on materials and methods, interference from potassium was a major factor in the determination of rubidium on the flame photometer at the low concentrations in the plant material. In order to circumvent this problem a potassium interference curve was established, and a corrective reading was made for the potassium content of each sample. As a further check on interference from other sources, the control samples without rubidium were read on the photometer and the readings compared with the samples with rubidium present. Figure 13 shows this comparison.

Table 12. Accumulative transpiration and evapotranspiration from vermiculite covered clay loam soil and uncovered clay loam soil.

Number of hours	Transpiration from covered soil (grams)	Evapotranspiration from uncovered soil (grams)
3	167	185
5	295	317
8	481	536
10	570	659
11	602	706
21.5*	688	879
22.5	710	932
23.5	740	998
24.5	762	1064
26.5	804	1201
27.5	822	1270
28.5	835	1340

* Includes overnight period of 8 hours of darkness.

The maximum range of percent transmittance readings for the control samples are shown as the wide bar for each of the stem, leaf and petiole samples with the mean shown as a line across the bar. The maximum range of transmittance readings for the samples containing rubidium are shown as a narrow bar with the mean shown as a line drawn across the bar.

If the difference between the lowest reading for the control

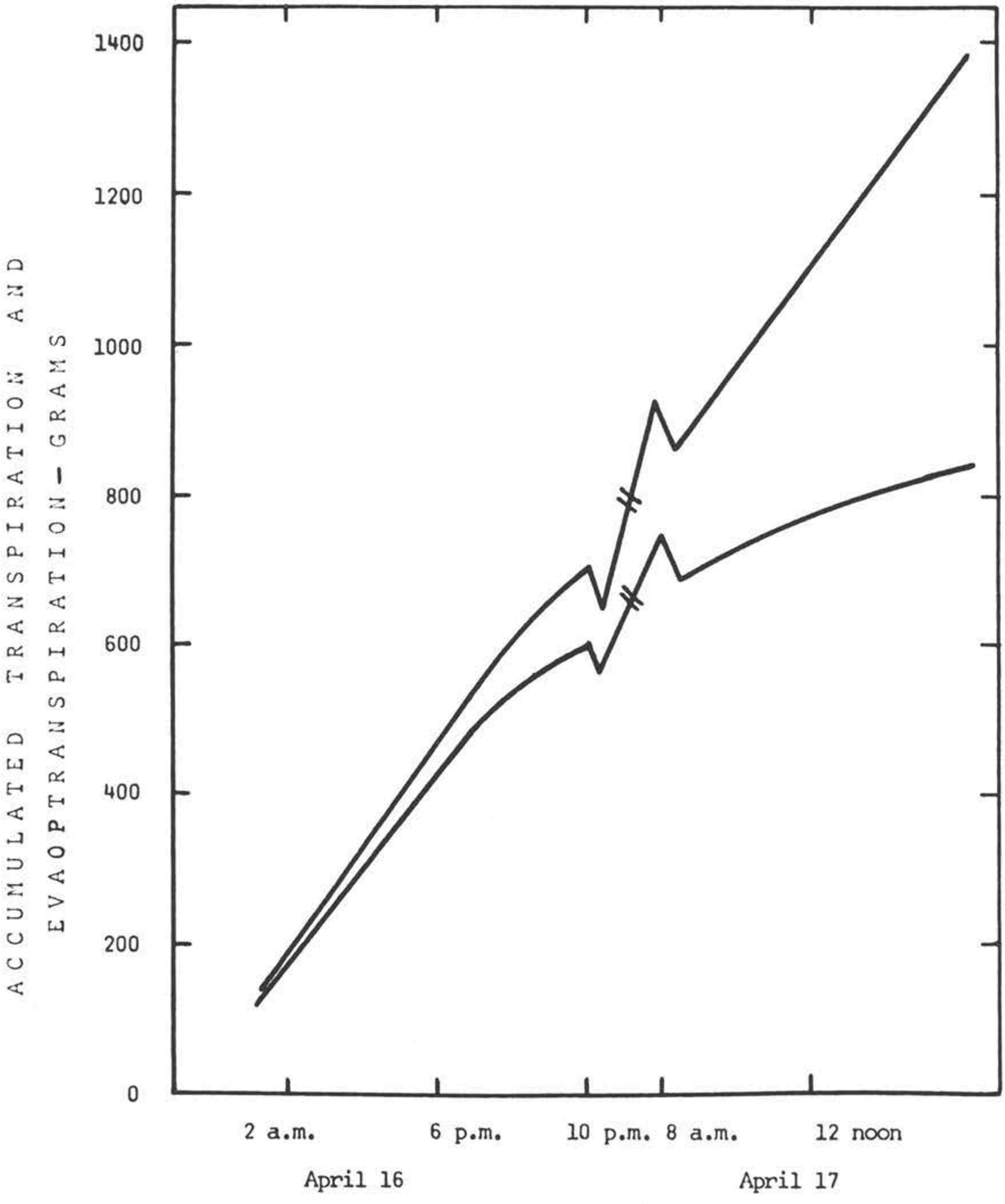

Figure 12. Accumulated water losses via transpiration from vermiculite-covered soil and via evapotranspiration from frequently rewatered soil. Sunflowers grown in clay loam soil.

samples and the highest reading for the rubidium samples is taken, it would represent the maximum number of transmittance units attributable to rubidium. For the stem tissue this maximum is 4 transmittance units; for the leaf and petiole tissue it is 6.5 and 6.5 transmittance units, respectively. By comparison, the maximum range of transmittance units attributable to rubidium after potassium corrections from the interference curve is 4.4, 5.3, and 6.4 units for stem, leaf, and petiole, respectively. The two sets of figures compare very favorably and leave reasonable assurance that almost all of the interference was from potassium. The potassium interference corrections then, were taken as reasonably accurate. There is no possible way to apply a correction from the control samples which would be any more accurate than the correction for the potassium interference.

Because potassium interference was not adequately accounted for in the samples from the plants grown in the sandy loam soil, the data for rubidium uptake are not presented here but are tabulated in the appendix. Covariance analysis, in which the uptake means are adjusted for root growth, showed no significant effects from the moisture treatments. There was also no correlation between root growth and rubidium uptake.

Table 13 gives the rubidium uptake which occurred with the three moisture treatments on clay loam soil in test number two by plant parts and by replicates to show the nature of the variability encountered in the tests. However, for analysis the figures are summed over the three parts of each plant. For the remaining tests only the means for these sums are given with the complete data tabulated in the appendix.

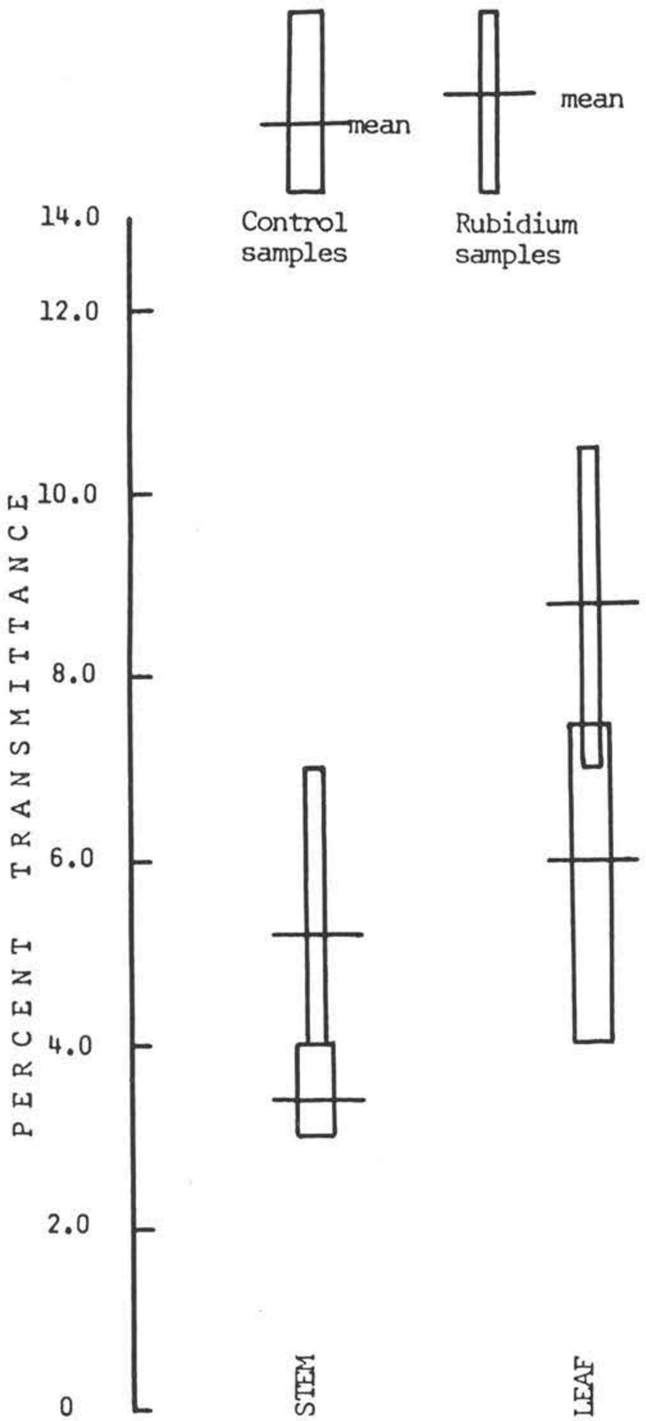

Figure 13. Comparison of percent transmittance readings between control samples and samples containing rubidium.

Table 13. Rubidium uptake through adventitious roots of sunflower plants as related to soil moisture treatments in test 2.

Plant part	Replicate		Total rubidium uptake, miligrams per plant part Soil moisture treatment 1	2	3
Stem	1		0.644	0.919	0.991
	2		0.834	0.952	0.874
	3		1.104	0.826	0.972
	4		0.928	1.062	0.679
	5		0.625	0.826	0.715
	6		0.887	1.034	0.876
		Mean	0.837	0.937	0.851
Leaf	1		0.749	0.563	0.758
	2		0.864	0.663	0.997
	3		0.779	0.721	0.702
	4		0.691	0.653	0.651
	5		0.482	0.624	0.439
	6		0.614	0.514	0.563
		Mean	0.696	0.623	0.685
Petiole	1		0.163	0.219	0.236
	2		0.300	0.304	0.338
	3		0.189	0.154	0.159
	4		0.090	0.147	0.176
	5		0.114	0.213	0.120
	6		0.150	0.131	0.145
		Mean	0.168	0.195	0.196

Table 14 gives the root growth means and the corresponding rubidium uptake means for each moisture treatment in tests two, four, and five. The moisture treatments have been fully described previously but to permit easy comparisons, the approximate initial soil moisture tensions are given. The corresponding initial water contents for tests two and four are 17.5 percent, 21 percent, and 25 percent for treatments 1, 2, and 3, respectively. The corresponding initial water contents for test number five are 20 percent, 25 percent, and 30 percent for treatments

1, 2, and 3, respectively.

In test two the rubidium concentration was 5.0 milliequivalents per 100 grams of soil and in test four and five the rubidium concentration was 15 milliequivalents per 100 grams of soil.

Table 14. Total rubidium uptake through adventitious roots of sunflower plants by treatments in tests 2, 4, and 5.

Test No.	Treatment No.	Soil moisture treatment initial tension (atms.)	Root growth means (grams)	Rubidium uptake per plant means (milligrams
2	1	1.50	0.1852	1.701
	2	0.60	0.4198	1.754 [1]
	3	0.30	0.7342	1.732
4	1	1.50	0.1228	2.260
	2	0.60	0.3001	1.989 [2]
	3	0.30	0.5048	2.764
5	1	0.80	0.2830	1.721
	2	0.30	0.4769	2.381 [3]
	3	0.16	0.4039	2.086

[1]Statistic F for adjusted means for uptake = 0.399 for 2 and 9 d.f.

Required F = 4.256 at 5 per cent

[2]Statistic F for unadjusted means for uptake = 11.204 for 2 and 2 d.f.

Required F = 19.00 at 5 per cent

[3]Statistic F for unadjusted means for uptake = 12.77 for 2 and 6 d.f.

Required F = 10.92 at 1 per cent

Analysis of covariance was made on each of these tests. The covariance analysis was made to test the possibility of regression between root growth and rubidium uptake. Wherever there was a significant regression, the F test was made on the uptake means adjusted for regression. In test two the regression was significant and therefore the F value is for the adjusted means. In tests four and five the regression was not significant and therefore the F value is for the unadjusted means for uptake as in ordinary analysis of variance. The correlation coefficient for each test was very small indicating little correlation between root growth and rubidium uptake.

In test two the statistic F for both adjusted and unadjusted means was far from showing significance despite the fact there appeared to be a slight regression between root growth and uptake. In test four there was no significance for either regression or for the difference between treatment means for uptake. In test five there was no significance for regression between root growth and uptake, but the statistic F shows significance for the differences between both the adjusted means and the unadjusted means for rubidium uptake.

Despite the significance which appeared in test number five there appears to be little dependence of the rubidium uptake upon the water content or tension to which the adventitious roots were exposed. The amount of rubidium taken up into the plants was very small and small differences undoubtedly would tend to be obscured because of the variability. If some of the variability could be removed, perhaps differences could be detectable even at the low levels of uptake encountered in these experiments. Certainly within the ranges of soil moisture tensions imposed upon the adventitious root system it can be said that the higher water contents or lower tensions did not induce any great uptake of rubidium over and above that at the lower water contents or higher tensions.

The fact that rubidium uptake was almost the same at all levels of moisture in tests two, four,and five, respectively, may point to a concentration effect in the soil solution. If the concentration increased with decreasing water content there may have been some compensating effect for the decreasing amount of solution. This possibility agrees with the statement of Eaton (4, p. 332), who stated that upon drying the soil from 0.1 atmosphere at 16 atmospheres the salt concentration tends to double. As was stated earlier most of this doubling probably occurs over a relatively narrow range of tensions more proportionately with water contents than with tension. In this regard, by comparing the rubidium uptake in test two with that in test four and five it appears that there was a slight increase in the total rubidium uptake in the latter two tests where the rubidium concentration was three times that in test two. However, the increase is certainly not proportional to the increased concentration in the soil.

It is interesting to note that even though root growth increased almost linearly with increasing water in the clay loam soil the rubidium uptake did not follow this trend. This is verified by the lack of correlation between root growth and rubidium uptake. If it could be shown that uptake is not correlated with root growth over the entire range of moisture tension from close to zero to the wilting percentage, the amount of root growth which takes place need not be accounted for when interpreting ion uptake results as related to moisture levels. In addition, much of the data, now in the literature, can be interpreted with some assurance that whatever particular effects are reported are not the result of increased root growth but may indeed be moisture effects on uptake itself.

In this study it has been shown that rubidium uptake through adventitious roots is not related to root growth over a range of moisture tensions from as low as 0.14 atmospheres to as high as about 1.50 atmospheres initial tensions. The highest final tension when the roots were harvested was about 2.40 atmospheres. Test number six gave some evidence of what may happen at tensions lower than 0.14 atmospheres. The means for rubidium uptake and the corresponding mean root growth are given in Table 15. The more complete data are given in the appendix.

Table 15. Rubidium uptake by adventitious roots of sunflower at 40 per cent soil moisture in test 6.

Treatment number*	Root growth means (grams)	Rubidium uptake means (milligrams per plant)
1	2.1268	3.922
2	1.1719	3.846

Statistic F for unadjusted means for uptake = 0.8793 for 1 and 2 d.f.

Required F = 18.51 at 5 percent

*Treatment 1 - plants subjected to soil moisture stress
2 - plants rewatered frequently

In this test the correlation coefficient for the relationship between root growth and rubidium uptake is very small indicating an absence of correlation. While the evidence from this particular test is somewhat limited it is encouraging to note that at a moisture tension of less than 0.10 atmosphere, indeed a tension very close to zero, there was still no correlation between the amount of roots and the amount of rubidium uptake into the plant. If this result holds for ion uptake generally, interpretations of moisture effects on ion uptake are greatly simplified. There is no intention here, however, to claim that this lack of correlation may hold true in general because certainly there is little evidence to support such a claim. There is also no evidence to show what happens at tensions higher than about 2.50 atmospheres.

The rubidium uptake which was measured was only that which moved into the plants. The amount which was taken up and held in the roots is not known. The amount of adventitious root tissue which developed was too small for adequate analysis. However, it is important that the distinction be made that uptake in this study refers to rubidium in the plant top, exclusive of the rubidium which may have remained in the roots.

In all of these tests with the clay loam soil, even though water uptake into the roots appeared to be correlated to some degree with root growth, the rubidium uptake again did not appear to follow this trend. As root growth increased water intake increased but rubidium content in the plants remained relatively constant for each test. Yet the uptake shown in Table 15 is somewhat higher than that shown in Table 14. This means that more rubidium appeared in the plants in 28 hours at a soil water content of 40 per cent than appeared in the plants in six days at any level from 17.5 per cent to 30 percent moisture. Admittedly there was a great deal more root growth than in the previous tests, but in none of the tests was there any correlation between the amount of roots and the rubidium uptake. Neither was there any apparent correlation between water intake and rubidium uptake. What then might the reason be for the greater uptake in a shorter time in test six than in all the previous tests?

To speculate a little, perhaps the fact that the adventitious roots in test six were at a lower tension than were the main roots had some effect. In all previous tests the reverse was true. There appeared to have been much greater translocation of water from the adventitious roots to the main transpiration stream of the plants in test six that that which occurred in all of the other tests. This factor alone could well be the link between the moisture conditions at the root surface and the uptake of both water and nutrients. Perhaps the uptake of ions will not correlate with soil moisture tension unless rapid translocation into the plant itself takes place. Transport of water and nutrients from parts of the root system into the plant may be rather slow as long as those particular roots are at a higher tension than are the other parts of the system. Certainly in test six, the degree of tension to which the main roots were subjected appeared to make little difference. The statistic F in Table 15 indicated that plants which were allowed to dry out contained no more rubidium than those which were rewatered. The interesting feature is that the main roots of both sets of plants were subjected to higher tension than were the adventitious root systems. If more was known of the ultimate fate of the water lost from the soil in the small containers, perhaps the question could be answered. These speculations agree in a general way with some of the statements made by Hylmo (9, p. 384, 385) and Shapiro et al. (24, p. 164) whose discussions have been referred to in the review of literature.

Limitations and Criticisms

An important limitation to the procedure used in this study is the problem of increasing the range of soil-moisture tension over which to measure the root growth and rubidium uptake. Some preliminary tests had indicated that it was very difficult to obtain satisfactory adventitious root growth at tensions above 1.5 to 2.0 atmospheres. In this regard the soil moisture tensions referred to throughout this thesis are subject to the criticism that the figures obtained are from moisture-tension curves as determined by laboratory equipment and because of this the actual tensions in the soil around the sunflower stems may be somewhat different from the tension figures used in the text. At the lower tensions, particularly, the moisture tension depends in part upon the structure or packing of the soil, and any differences in structure between the soil for the laboratory determination of the moisture-tension curves and the soil packed into the small containers around the plant stems would be reflected in some differences between the tension determined in the laboratory and that actually imposed upon the soil. However, these laboratory estimates for moisture-tension are the best estimates obtainable under these experimental conditions. In addition, while the estimated tensions may be slightly different from those actually occurring, the magnitudes of the tension ranges would probably not be very much different but simply shift upwards or downward depending upon which direction the estimate was in error.

Another criticism of the study is in connection with the use of rubidium as an indicator ion. This ion is not known to be essential for plant growth or metabolism and in fact is normally found in only trace amounts or not at all. However, since rubidium is very similar to potassium chemically and has been used for uptake studies by many workers, it was thought that it would serve well as the indicator ion. Cations normally present in the plant in even small quantities could not be used unless labelled radioactively or deleted entirely from the growth medium for the main root system. Labelled cations may prove useful for future work with the procedure but if the uptake through the adventitious roots is as small as was encountered in this study there may be difficulty in separating the radioactivity from background radiation.

The small amounts of rubidium which were taken up placed some limits on the interpretation of the data. Small differences in uptake may have been lost in the normal variability of the plant materials. It would be unwise to conclude that small differences are not important just because they are small. Small differences can be of very great importance in the study of certain phenomena at the root-soil interface. Here again, despite the fact that the amounts of rubidium taken were small and possible differences from moisture treatments perhaps obscured, it is felt that leads obtained may prove valuable even if somewhat inclusive at this time.

SUMMARY AND CONCLUSIONS

A technique involving the growth of adventitious roots into soil pre-established at various water contents or moisture-tensions was developed in order to examine the effects of the moisture conditions upon root growth and the uptake of rubidium into plants. Sunflower plants were grown for about six weeks before each individual test. Soil containing rubidium and at various water contents, was placed around the sunflower stems and the adventitious roots allowed to grow for six days. The plants were then harvested. In these tests the main roots were always at a lower tension than were the adventitious roots. In one test only, the roots were allowed to grow for six days before the rubidium was added to the soil. In this test some of the plants were permitted to deplete the soil moisture while others were kept watered. In both groups of plants the main roots were at a higher moisture tension than were the adventitious roots. This test lasted only 28 hours.

Uptake data were obtained by analyzing the plant tissue for rubidium content. Adventitious root growth was measured by obtaining the fresh weights of the roots which had been washed free of soil and blotted dry on filter paper. Water losses from the soil into which the adventitious roots grew were determined by calculation from the moisture percentages of the soil before and after each test. Treatment comparisons were made with respect to root growth, water losses, and rubidium uptake.

One of the main premises of the thesis is that any absorption phenomena which is directly related to the amount of root growth would be subject to misinterpretation if root growth was in turn directly related to water content or soil moisture tension. Water absorption, at least in the clay loam soil, appeared to be related to the amount of root growth present but rubidium uptake did not. Root growth was almost linearly related to water content in the soil. Water transport out of the adventitious roots into the plant may be a major factor tending to overwhelm or mask any tension effects on absorption of both water and nutrients at the root surface. The relationships found for the clay loam soil did not appear in the sandy loam soil.

The technique which was developed permitted the study of moisture tension ranges not possible if the main root system is used. The main root system must be subjected to very near zero tension many times and the effects of this may mask the effects of tensions higher than zero. Under these conditions it is not possible to attribute a particular response or lack of it to any particular tension because all moisture treatments have a considerable portion of the tension range in common.

The following conclusions are drawn from this study:

1. Adventitious root growth increases almost linearly in the clay loam soil as the water content increases, within the moisture tension range from 0.3 atmospheres to about 2.5 atmospheres. It is reasonable to assume that the main root system would react the same way.
2. Water absorption increased with the amount of root growth within the tension ranges in these experiments.
3. Rubidium uptake was not correlated with the amount of

adventitious root growth.

4. Rubidium uptake was not related to the soil water content or moisture tension.

5. The rate of water transport out of the adventitious roots into the plants was enhanced when these roots were at lower moisture tensions than were the main root systems.

6. The degree of water transport out of the roots may be a determining factor masking tension effects on water and ion absorption at the root surface.

The author believes that, although some of the relationships which appeared in this study are not so clear cut as might be desired, there are some valuable leads which merit much more investigation than was possible in this study. The technique appears promising for future studies of this kind.

BIBLIOGRAPHY

1. Bennett, O. L. and B. D. Doss. Effect of soil moisture level on root distribution of cool-season forage species. Agronomy Journal 52:204-207. 1960.

2. Danielson, R. E. and M. B. Russell. Ion absorption by corn roots as influenced by moisture and aeration. Soil Science Society of America Proceedings 21:3-6. 1957.

3. Dean, L. A. and V. H. Gledhill. Influence of soil moisture on phosphate absorption as measured by an excised root technique. Soil Science 82:71-79. 1956.

4. Eaton, F. M. Water uptake and salt accumulation. California Citrograph 44:322, 332-336. 1959.

5. Freeland, R. O. Effect of transpiration upon absorption and distribution of mineral salts in plants. American Journal of Botany 23:355-362. 1936.

6. ________________. Effect of transpiration on the absoprtion of mineral salts. American Journal of Botany 24:373-374. 1937.

7. Gates, C. T. The response of the young tomato to a brief period of water shortage. III. Drifts of nitrogen and phosphorus. Australian Journal of Biological Science 10:127-146. 1957.

8. Gonzalez, j de D. L. and H. Jenny. Modes of entry of strontium into plant roots. Science 128:90-91. 1958.

9. Hylmo, B. Transpiration and ion absorption. Physiologia Plantarum 6:333-405. 1953.

10. Jean, F. C. and J. E. Weaver. Root behaviour and crop yield under irrigation. Washington, Carnegie Institute, 1924. 66p. (Carnegie Institute Publication 357)

11. Jenne, E. A. et al. Change in nutrient element accumulation by corn with depletion of soil moisture. Agronomy Journal 50:71-74. 1958.

12. Jenny, H. Contact phenomena between absorbents and their significance in plant nutrition. In: E. Truog's Mineral Nutrition of Plants. Madison, University of Wisconsin Press, 1951. p. 107-132.

13. Jenny, H. and R. Overstreet. Cation interchange between plant roots and soil colloids. Soil Science 47:257-272. 1939.

14. Kilmer, V. J. et al. Yield and mineral composition of eight forage species grown at four levels of soil moisture. Agronomy Journal 52:282-285. 1960.

15. Kmoch, H. G. et al. Root development of winter wheat as influenced by soil moisture and nitrogen fertilization. Agronomy Journal 49:20-25. 1957.

16. Loustalot, A. J. Influence of soil moisture conditions on apparent photosynthesis and transpiration of pecan leaves. Journal of Agricultural Research 71:519-532. 1945.

17. Mederski, H. J. and J. H. Wilson. Relation of soil moisture to ion absorption by corn plants. Soil Science Society of America, Proceedings 24:149-152. 1960.

18. Mendiola, N. B. Effect of differnt rates of transpiration on dry weight and ash weight of tobacco plants. Phillippine Journal of Science 20:639-655. 1922.

19. Muenscher, W. C. The effect of transpiration on the absorption of salts by plants. American Journal of Botany 9:311-329. 1922.

20. Olsen, R. A. and M. Peech. The significance of the suspension effect in the uptake of cations by plants from soil-water systems. Soil Science Society of America Proceedings 24:257-261. 1960.

21. Richards, L. A. Pressure membrane apparatus--construction and use. Agricultural Engineering 28:451-454. 1947.

22. ________________. Porous plate apparatus for measuring moisture retention and transpiration by soil. Soil Science 66:105-110. 1948.

23. Schneider, G. W. and N. F. Childers. Influence of soil moisture on photosynthesis, respiration and transpiration of apple leaves. Plant Physiology 16:565-583. 1941.

24. Shapiro, R. E. et al. The effect of soil water movement vs phosphate diffusion on growth and phosphorus content of corn and soybean. Soil Science Society of America Proceedings 24:161-164. 1960.

25. Slayter, R. O. The influence of progressive increases in total soil moisture stress on transpiration, growth and internal water relationships of plants. Australian Journal of Biological Science 10:320-336. 1957.

26. Steward, F. C. and J. F. Sutcliffe. Plants in relation to inorganic salts. In F. C. Steward's Plant Physiology: A treatise. Vol. 2. New York, Academic Press, 253-478. 1959.

27. Walker, T. W. Uptake of ions by plants growing in soil. Soil Science 89:328-331. 1960.

28. Weaver, J. E. Root development of field crops. New York, McGraw-Hill, 1926. 291p.

29. West, E. S. and O. Perkman. Effect of soil moisture on transpiration. Australian Journal of Agricultural Research 4:326-333. 1953.

30. Wright, K. E. Transpiration and the absorption of mineral salts. Plant Physiology 14:171-174. 1939.

31. Wright, K. E. and N. L. Barton. Transpiration and distribution of radioactive phosphorus in plants. Plant Physiology 30:386-388. 1955.

APPENDIX

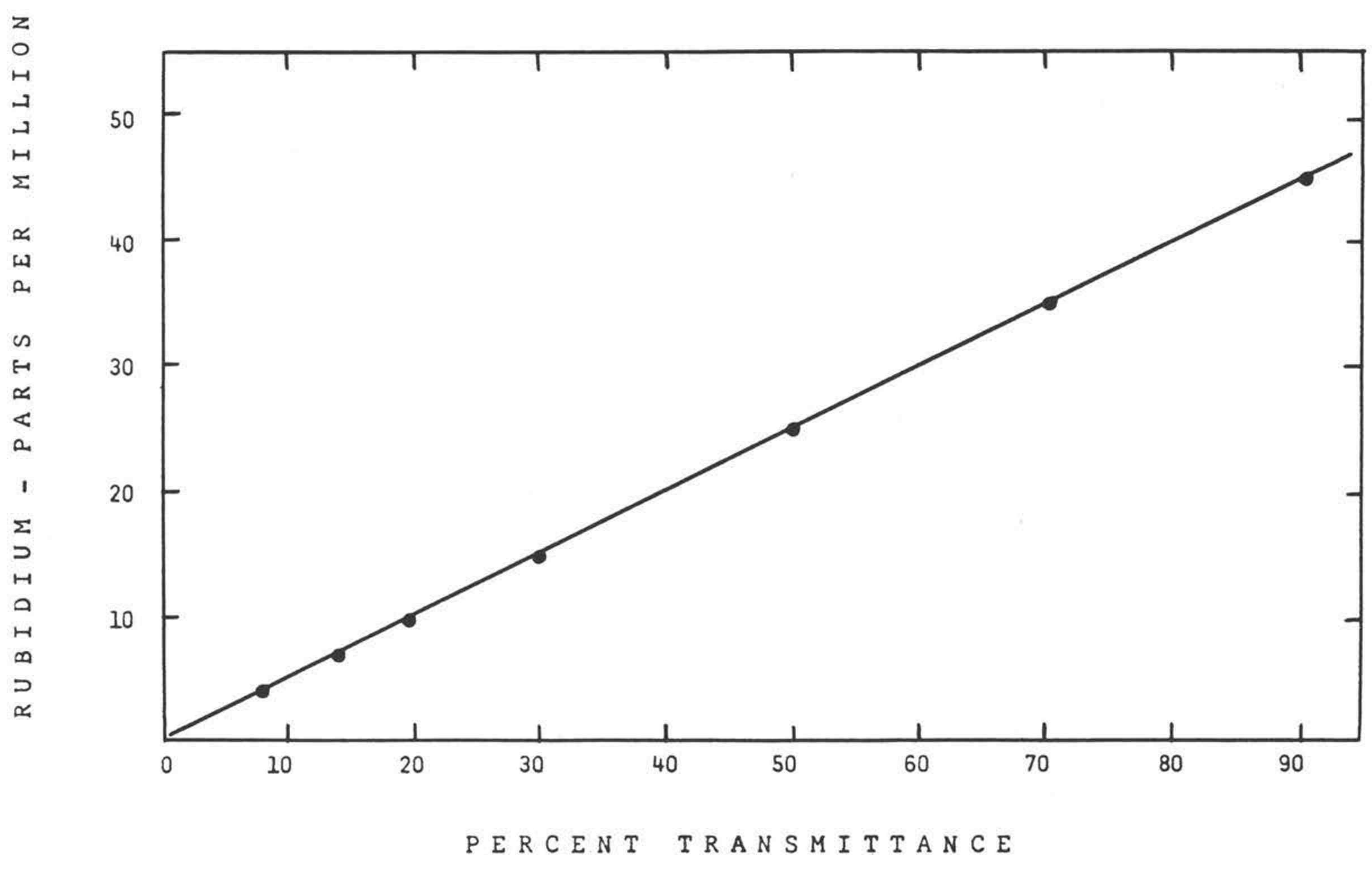

Figure 14. Standard curve for rubidium determination on the flame photometer.

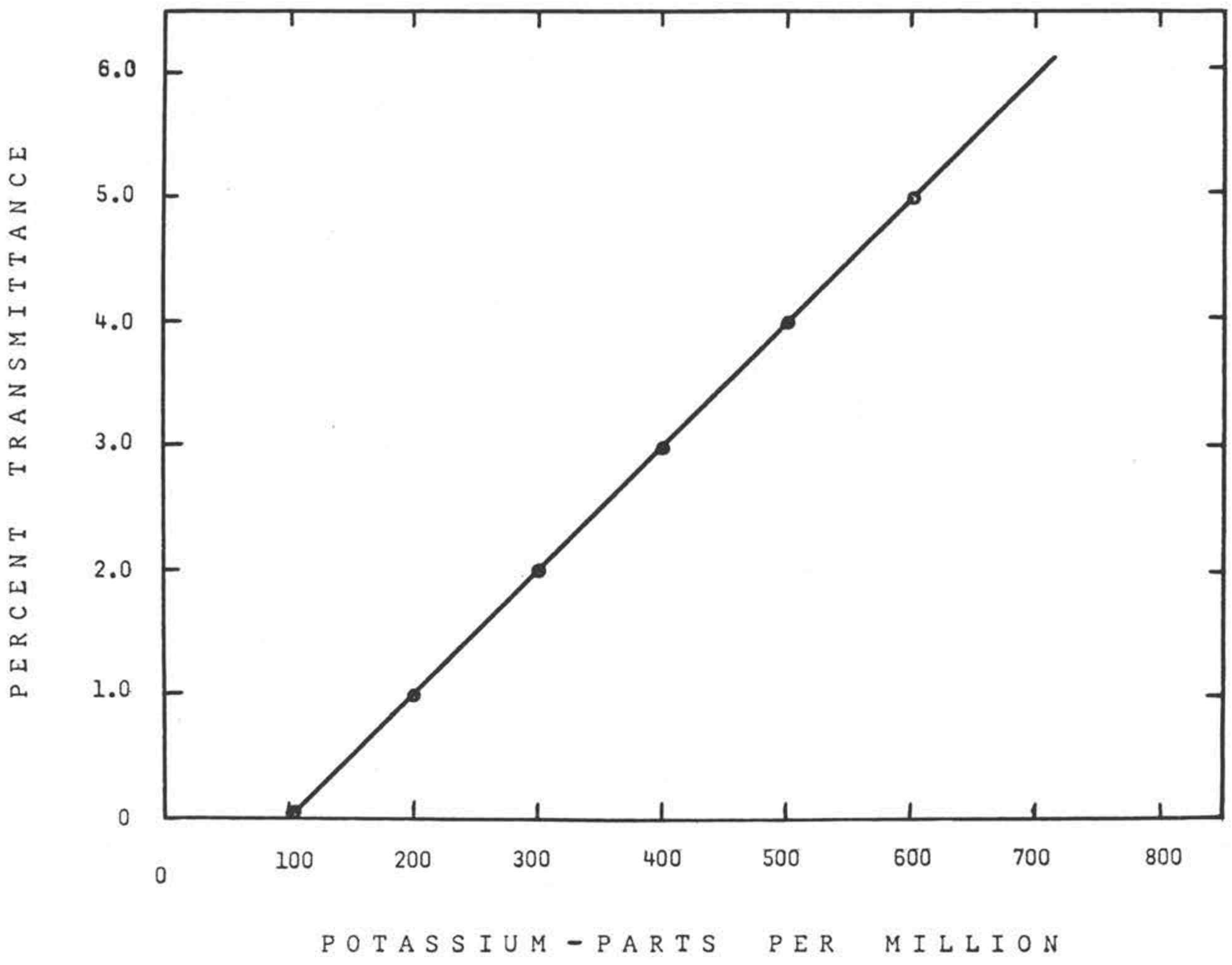

Figure 15. Interference from potassium at the flame photometer settings for rubidium readings.

Table 16. Rubidium uptake by sunflowers on sandy loam soil in test 1.

Moisture treatment*	Replicate	Rubidium uptake (milligrams per plant+) Stem	Leaves	Petioles	Total	Treatment mean
	1	1.1749	4.6721	0.6787	6.5257	
	2	1.1497	2.2989	0.8087	4.2573	
1	3	2.0160	1.0035	0.5436	3.5531	
	4	2.1049	2.3150	0.5353	4.9552	
	5	0.8949	1.6732	0.4154	2.9835	
	6	2.6795	1.6576	0.3108	4.6479	4.4873
	1	1.5226	2.7567	0.8547	5.1340	
	2	1.4939	3.2740	1.0296	5.7975	
2	3	2.6182	2.7420	0.6249	5.9891	
	4	1.9714	2.5717	0.3894	4.9325	
	5	1.5067	1.8919	0.7578	4.1564	
	6	1.1932	2.0933	0.4096	3.6961	4.9509
	1	1.7190	2.7247	0.8216	5.2653	
	2	1.2565	3.9674	0.7271	5.5910	
3	3	1.6288	1.9671	0.5037	4.0996	
	4	1.7444	2.2678	0.6202	4.6324	
	5	1.8180	1.4250	0.4354	3.6784	
	6	1.7466	1.3311	0.4355	3.5132	4.5233

* See table 3, page 45.

+ Data uncorrected for potassium interference.

Table 17. Rubidium uptake by sunflowers on clay loam soil in test 2.

Moisture treatment*	Replicate	Rubidium uptake (milligrams per plant) Stem	Leaves	Petioles	Total	Treatment mean
	1	0.644	0.749	0.163	1.556	
	2	0.834	0.864	0.300	1.998	
1	3	1.104	0.779	0.189	2.072	
	4	0.928	0.691	0.090	1.709	
	5	0.625	0.482	0.114	1.221	
	6	0.887	0.614	0.150	1.651	1.701
	1	0.919	0.563	0.219	1.701	
	2	0.952	0.663	0.304	1.919	
2	3	0.826	0.721	0.514	1.701	
	4	1.062	0.653	0.147	1.862	
	5	0.826	0.624	0.213	1.663	
	6	1.034	0.514	0.131	1.679	1.754
	1	0.991	0.758	0.236	1.985	
	2	0.874	0.997	0.338	2.209	
3	3	0.972	0.702	0.159	1.833	
	4	0.679	0.651	0.176	1.506	
	5	0.715	0.439	0.120	1.274	
	6	0.876	0.563	0.145	1.584	1.732

* See Table 3, page 45.

Table 18. Rubidium uptake by sunflowers on clay loam soil in test 4.

Moisture treatment*	Replicate	Rubidium uptake (milligrams per plant) Stem	Leaves	Petioles	Total	Treatment mean
1	1	1.202	0.805	0.283	2.289	
	2	1.143	0.846	0.242	2.231	2.260
2	1	1.030	0.894	0.313	2.237	
	2	0.895	0.609	0.239	1.742	1.988
3	1	1.328	1.157	0.492	2.977	
	2	1.304	1.020	0.226	2.550	2.764

* See table 3, page 45.

Table 19. Rubidium uptake by sunflowers on clay loam soil in test 5.

Moisture treatment*	Repli-	Rubidium uptake (milligrams per plant) Stem	Leaves	Petioles	Total	Treatment mean
1	1	0.741	0.738	0.310	1.789	
	2	1.311	0.695	0.249	2.255	
	3	0.763	0.573	0.163	1.499	
	4	0.649	0.534	0.157	1.340	1.721
2	1	0.994	0.982	0.440	2.416	
	2	1.193	0.927	0.362	2.482	
	3	1.304	0.718	0.296	2.318	
	4	1.340	0.701	0.266	2.307	2.381
3	1	0.980	0.710	0.224	1.914	
	2	1.194	0.865	0.341	2.400	
	3	1.022	0.761	0.251	2.034	
	4	0.886	0.775	0.335	1.996	2.086

* See table 3, page 45.