

AN ABSTRACT OF THE THESIS OF

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(TRITICUM AESTIVUM VILL., HOST) AS A FUNCTION OF
SOIL WATER SUCTION AND SOIL TEMPERATURE

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The effect of soil temperature and soil water suction on the rate of phosphorus uptake and growth rate of wheat (Triticum aestivum VILL., Host) was studied. Plants were grown in perlite slabs separated from an osmotic solution by a semi-permeable membrane. Measurements were made at temperatures of 10.0, 18.3, 23.9, 32.2, and 35.0°C, and soil water suctions of 0.35 and 2.5 bars. Five week old wheat seedlings were exposed to these conditions. The dry weight of shoots and roots was determined at two day intervals. Plant material extracted was analyzed for phosphorus concentration. The color intensity was measured on a Bausch and Lomb spectronic 20 spectrophotometer of 420 millimicrons.

In general, a constant growth rate, which was approached exponentially during the experimental period was found in all

treatment combinations. Growth rate for both shoots and roots was slow at low root temperatures and had a maximum rate at a root temperature of 24.0°C. High soil water suction was a limiting factor in growth rate.

Phosphorus concentration of shoots and roots was found to approach a constant value during the experimental period according to the equation

$$y = a + be^{-0.07t^{3/2}}$$

where y is the phosphorus concentration, t is the time in days, and a and b are constants. Over the entire range of soil temperatures considered the phosphorus concentration of the shoots increased linearly with the root temperature, but the phosphorus concentration of the roots slightly decreased by increasing soil temperature and did not increase until the root temperature was about 32.0°C. There was no evidence of much variation in percent of total phosphorus uptake transported to the shoot in the experiments. Translocation of phosphorus from roots to shoots did not appear to be a limiting factor for phosphorus uptake at the low root temperature. It was suggested that the low rates of phosphorus uptake at the low root temperatures resulted from the low level of metabolic activity.

Growth Rate and Phosphorus Uptake of Wheat (Triticum
aestivum VILL., Host) as a Function of Soil
Water Suction and Soil Temperature

by

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GROWTH RATE AND PHOSPHORUS UPTAKE OF WHEAT
(TRITICUM AESTIVUM VILL. , HOST) AS A FUNCTION
OF SOIL WATER SUCTION AND SOIL TEMPERATURE

INTRODUCTION

Soil temperature is an important factor in plant growth and ion uptake. High root temperatures accelerate the ion accumulation process, while low root temperatures usually retard the rate at which ions are taken up. Physiological factors, such as the solubility of nutrients, root respiratory activity, favorable effect of warmer temperatures on growth and water uptake could be important factors in increasing the absorption of solutes at elevated temperatures.

It has been suggested that low rates of phosphorus uptake at low soil temperature is caused largely by decreased root growth. Low soil temperatures can effect growth in many ways and it is difficult to isolate a specific effect on salt absorption. Low soil temperatures for example reduce the conversion rate of inorganic to organic nitrogen as well as other physiological activities in the roots significantly.

The effect of water stress on nutrient uptake is equally complex as a result of its various effects on processes in the roots. Two principle mechanisms by which water stress affects plant nutrition are the decreased rate of water movement to the roots thereby decreasing the supply at the root surface and the immediate effect on the

hydrational status of the root tissue which in turn influences the physiological activity in the cells. Large increases in the degree of hydration resulting from increases in soil water suction have been shown to result in decreased ion uptake.

This study was initiated to evaluate the effect of root temperature and soil water suction on the rate of uptake of phosphorus and the growth rate of shoots and roots of young wheat seedlings.

REVIEW OF LITERATURE

Ion Uptake

The ability of living plant cells to absorb ions from the surrounding medium and to accumulate these ions in their vacuoles at concentrations greatly exceeding those of the medium has been the subject of considerable research activity. The majority of studies of ion absorption have been made with algae, tissue-segments or excised roots, often completely immersed in the medium. It has generally been possible to differentiate the ion uptake by totally immersed cells or cell-groups, into separate phases, namely an initial phase, which is completed a short time after the initial contact with the medium, and a second phase which operates thereafter.

The first phase is regarded as a diffusion of ions from the medium to the root, governed by existing concentration gradients (Hylmo, 1953). When carrot slices were transferred from water or very dilute salt solutions to solutions of higher concentration, Stiles and Skelding (1940) found that an intensive ion uptake occurred during the first few hours. Using storage tissues Robertson (1944) and Robertson and Turner (1945) made similar observations. Brooks (1940) considered the initial phase to be an absorption of ions in or on the plasma-surface in exchange with ions already present in the

plasma. Robertson and Turner (1945) were able to identify a primary uptake phase of non-metabolic character which was completed within a few minutes after the medium-change. The initial absorption was independent of temperature, having the same value at 7°, 13°, 19°, and 25°C. Hylmo (1953) pointed out that the ions which have diffused into the roots may exist there in the free state, or may be held adsorbed on colloids either through simple adsorption or through ion exchange.

The ion accumulation during the second phase is a process dependent on aerobic respiration (Hylmo, 1953). He concluded that it is this second phase which is usually considered in ion accumulation studies using totally immersed cells or cell groups.

In this process ions are accumulated in the vacuoles to concentrations which greatly exceed that of the external medium. All the uptake which cannot be referred to the momentary initial absorption is customarily regarded as accumulation. Hylmo demonstrated an extensive storage of calcium and chloride, which was regarded as an accumulation in the plants. Kramer (1969) indicates that it is generally assumed that two kinds of processes are involved in salt accumulation: nonmetabolic adsorption exchange or "passive" uptake and metabolic or "active" uptake. He summarized the characteristics of the two processes as follows:

Adsorption exchangeActive transport

Equilibrium attained rapidly	Equilibrium attained slowly
Not dependent on metabolism	Dependent on metabolism
Little affected by temperature, aeration, and respiration inhibitors	Much affected by temperature, aeration, and respiration inhibitors
Reversible	Relatively irreversible
Non selective, but mostly concerned with cations	Highly selective; involves both anions and cations

Alberda (1948) states that ions or groups of ion-species with mutual antagonistic effects are taken up individually, independently of other ions or ion groups. In short-time experiments with intact plants sufficient amounts of sugar should be generally present in the roots to allow the steady state to be attained for ions which are not accumulated in especially large quantities. Robertson and Turner (1945) found that the accumulation phase accelerated with an increase in temperature.

Ion Supply to the Plant Roots

Ion absorption leads to further ion transport to the roots through diffusion. The rate of movement from a relatively concentrated soil solution to the root surface was expressed by Bull (1951) by an equation similar to Equation (1) and used by Shapiro et al. (1960) in this form

$$\frac{Q}{t} = DA \frac{c}{h} \quad (1)$$

where Q (moles) is the amount of material that diffuses in the time, t (sec), elapsed, D is the diffusion coefficient (cm^2/sec), A is the cross sectional area (cm^2), c is the concentration of the soil solution (moles/liter) and h is the thickness of the boundary layer across which the dissolved ion diffuses (cm). This equation is based on the assumption that the concentration at the root surface remains zero.

Barber (1962) further studied the effects of diffusion, mass flow, and water content of the soil on nutrient availability. He visualized three main steps in the nutrient absorption process. First, the movement of the nutrient from the soil to the root surface; second, the movement of the ions from the exterior of the root to the interior of the root; third, the translocation of the nutrients from the root to the shoot. He expressed this in the form of a linear model illustrating the processes involved in the movement of ions to the root.

$$J = D_1 \frac{dc_1}{dx} + D_2 \frac{dc_2}{dx} + c_3 v + a. \quad (2)$$

where J is the total quantity of ions reaching the root per unit time per unit area of root surface ($\text{moles}/\text{cm}^2 \text{sec}$), D_1 , the diffusion coefficient of the ions in the soil solution (cm^2/sec), D_2 , the

diffusion coefficient for the movement of ions on the particle surfaces (cm^2/sec), c_1 , the concentration for the ions in the soil solution that are not associated with the particle surfaces (moles/cm^3), c_2 , the concentration of the ions moving on the solid surfaces (moles/cm^3), c_3 , the concentration of the ions (moles/cm^3) in the solution that is flowing through the soil with a velocity v (cm/sec) toward the root surface, and a , replenishment factor. The importance of the first two processes in Equation (2) depends upon both the diffusion coefficients and the concentration gradients; the importance of the third process depends on the velocity of flow and the concentration of the solution. If the concentration of ions is so low that mass-flow does not bring as much to the root surface as the root absorbs, then additional quantities of the ion reach the root by diffusion and ion diffusion becomes the determining factor in supplying the plant root.

Later Barber et al. (1963) elaborated on the mechanisms for the movement of plant nutrients from the soil to the plant root. They suggested that the plant nutrients in the soil reach the root by root extension, mass flow, and diffusion. Root extension involves the growth of the root to the nutrients, mass flow, describes the flow of nutrients to the root, and diffusion describes movement of nutrients from the soil to the root by diffusion and occurs when the first two processes do not supply enough to meet the plant requirement. The maximum amount of nutrients that can come in direct contact with the plant

roots as they grow through the soil is the amount in a volume of soil equal to the volume of the roots. This usually amounts to less than 3% of the available nutrients in the soil, and depends upon the total amount of available nutrients in the soil. Much of the plant's need for calcium and magnesium but very little of the plant's need for nitrogen, phosphorus and potassium are satisfied in this manner in saline and arid soils. Mass-flow must supply the roots with much of its need for calcium, magnesium and nitrogen if root extension is not developed. The amount of nutrients that are moved to the plant root by this mechanism depends upon the amount of water used by the plant and the concentration of nutrients in the soil solution. This process does not supply much of the requirement for potassium or phosphorus in many soils because of low ion concentrations. These two nutrients are usually tied up with soil colloids or are present in insoluble forms and must reach the roots by diffusion. Absorption by the roots lowers the phosphorus and potassium content in the soil at the root-soil interface, and a concentration gradient is established along which diffusion occurs. Mass flow occurs when plant roots absorb water developing a suction gradient along which the water flows to the plant. It contains plant nutrients that are transported to the root surface where they become positionally available for nutrient uptake. The amounts of nutrients that are moved to the plant root by this mechanism depend upon the amount of water used by the plant and the concentration of

nutrients in the water. This mechanism would explain in part the relationship between transpiration and nutrient uptake which has been reported (Mederski and Wilson, 1960; Meyer and Gingrich, 1966).

The observed relationship between transpiration and nutrient uptake may in part also be associated with the removal of nutrients from root to shoot. A high rate of translocation would reduce the nutrient concentration inside the root and thus provide conditions for an increased rate of uptake, particularly if translocation were the rate-limiting step.

Jenny and Overstreet (1939) proposed that ions may move directly from the exchange site on a soil particle to the exchange site on the plant root without associating with an anion in the soil solution, as an intermediary step. They also proposed that ions would diffuse within the electric double layer on the soil particle surface. Ion uptake by the plant would create a concentration gradient so that the ions might then diffuse along the soil particle towards the root. This was also discussed by Barber (1962).

Phosphorus Uptake

Phosphorus uptake by plants grown in soil is affected by both plant and soil characteristics. The source of phosphorus is the soil, the medium of uptake is the soil solution and the agent of uptake is the plant. Thus plant uptake of phosphorus from a soil system is a

consequence of a series of consecutive reactions. In the soil plant system involving phosphorus uptake, the slowest process is associated with a reaction in either the soil or the plant system (Fried et al., 1957). They indicate that the rate of phosphorus release by the soil is at least 250 times as great as the rate of plant uptake. In their experiments the soil was leached with distilled water until the amount of phosphorus in the leachate became constant. This was considered the rate of formation of soil solution phosphorus at that leaching rate. The rate measurements suggest that the uptake of phosphorus by plants from a soil system may reflect not only the phosphate status of the soil but also other factors mentioned by Parker (1927) which influence the rate of plant uptake of phosphorus. These other factors are: Viets effect and enzyme catalyts or poisons.

He found that the maximum growth of corn and soybeans was obtained in a solution containing 0.5 ppm PO_4 .

Shapiro et al. (1960) point out that the soil and plant factors effect phosphorus uptake by plants as follows: (1) transfer of phosphate ions from solid to solution phase, (2) movement of phosphate ions to the solution root interface, and (3) uptake of phosphate from the soil solution by the plant. This system is described in general terms by Equation (1), which was used by these investigators to determine the nature of the transport mechanism involved. They experimentally determined the rate of phosphorus uptake (Q/t) by

the plant. This value was substituted in Equation (1) for Q along with appropriate values for D , A , c , and h . The equation was then solved for " t ." If the calculated value for t was less than or equal to one, diffusion was considered to be the sole mechanism of phosphate transport to the root surface at a rate equal to or greater than the rate of phosphate uptake by the roots. On the other hand, if the calculated value for t was greater than one, diffusion alone would not have been able to replenish the phosphate ions as fast as the plant was taking them up.

Hagen and Hopkins (1955) showed that hydroxide is competitive with phosphate in the plant-uptake process. The competitive nature of the hydroxyl ion OH^- , indicates the formation and breakdown of the labile, intermediate complexes involving the cleavage of an R-O bond. The cleavage of such R-OPO₃ bonds is known to be involved in such reactions as the acid hydrolysis of glucose-1-phosphate and numerous examples of phosphorylase action on glucosyl-OPO₃. Other ions or compounds may also affect phosphorus uptake by such mechanisms as the Viets effect or enzyme catalysts or poisons. The Viets effect is defined as the stimulatory effect of polyvalent cations localized on or near cytoplasmic surfaces of root cells. Those substances which inhibit glycolysis and the Krebs cycle may be caused by enzymes or catalysts (Cyanide, heavy metals like Hg^{++} , Cu^{++}) (Fried et al. 1957).

Soil Water Stress Effects on Plant Growth

Water stress has a marked effect on all plant functions. It may be expected to be pronounced on active processes which have their expression in elongation or vegetative growth as well as predominantly passive processes such as transpiration. As soil water stress increases, turgescence decreases (Slatyer, 1957). The degree of turgidity which can be maintained by a plant is limited by the total soil moisture stress (TSMS) since the absorption gradient for water is eliminated at the point of DPD (diffusion pressure deficit) TSMS equilibrium. Progressive decrease in plant turgor which accompanies the increase in soil water stress, usually causes a progressive decrease in growth and elongation.

Thomas and Wiegand (1970) studied the osmotic and matric suction effect on relative turgidity, temperature and growth of cotton leaves. They found that the ability of a plant to obtain water from a drying soil decreases as the total soil water suction increases. They point out that environmental conditions (total soil water suction and meteorological conditions) largely determine the relative turgidity of plant leaves. Their study showed that plant growth and cotton lint yields decreased significantly as the total soil water suction and osmotic suction increased.

Furr and Taylor (1939) showed that with decreasing soil water

content the growth rate of lemon fruits was retarded before the average soil water content reached the wilting range.

There is evidence in the literature that decreasing soil water content is associated with increases in the osmotic pressure of the tissue fluids, in both roots and tops of plants, a decrease in rate of vegetative growth and modification in the stomatal opening. A depletion in starch reserves, a decrease in apparent photosynthesis, and an increase in respiration are other effects of decreasing soil water content.

MacDougal (1920) studied hydration and growth. He found two main requirements for plant growth. The first is the formation of protoplasm for new cells, and the second, the hydration of that protoplasm together with vacuolation to bring about cell enlargement. He showed that the condition of stress, which brought about marked growth reduction, actually caused an increase in the proportion of proteinaceous material in the tissues, especially in the leaves.

It has been suggested (Loomis, 1938; Nightingale, 1937) that under conditions of stress inhibitory to growth, certain phases of protein synthesis may become limiting. Consequently, limited swelling of the protoplasmic proteins and decreased vacuolation of the protoplasm were undoubtedly main factors inhibiting growth. Whether the water stress was brought about by high soil water stress or by high osmotic pressure of the soil solution made no difference (Wadleigh

et al., 1943).

Thut and Loomis (1944) observed the diurnal growth of plants in relation to diurnal temperature, light and humidity. They state that the growth was checked by water deficits within the plant, and that such deficits were usually proportional to light intensity, temperature and air movement and inversely proportional to relative humidity and the available soil moisture. They state that higher light intensity, increased air temperature, and air movement caused more evaporation and thus greater water deficits. When there was a high relative humidity, water deficits were low because of low evaporation.

Wadleigh and Ayers (1945) stated that the effect of salt in the soil solution is sometimes regarded as chemical (toxicity) rather than physical. They indicate that in certain experiments the effect of depletion of soil moisture on increasing the salt concentration of the soil solution suggests the possibility that salt toxicity rather than the increase in soil water stress was the active factor in depressing growth. Certainly, the increase in osmotic pressure associated with decrease in soil moisture cannot be disregarded, whatever the basis for interpretation.

Peters' (1957) experiments indicate that the uptake of water by corn roots is a function of the specific water content as well as the soil water suction. His data show that uptake of water and elongation of corn roots decreased as the soil water suction increased and that

the uptake of water and root elongation per unit suction decreased as the water content decreased. It was shown that the plant roots would have to extract water from larger distances as the water content per unit suction decreased.

Gingrich and Russell (1957) found that as plant roots absorb water, soil water suction increases in the immediate proximity of the roots. Since transmission of water in unsaturated soils is known to decrease greatly as suction increases, the rate of such flow could possibly also be a factor in root growth. In their experiments fresh weight was higher throughout the entire suction range for seedlings grown in osmotic media rather than in soil.

Mederski and Wilson (1960) found that the dry weight of plant tops and roots developed in soil, decreased linearly with increasing soil water suction. Stevenson and Boersma (1964) found that dry weights of adventitious sunflower roots that developed in soil cores were not affected by soil water suctions between 0.3 and 1.1 bars in a fine sandy loam soil, but weights decreased as soil suction increased from 0.3 to 1.6 bars in a clay loam soil. Taylor and Ratliff (1969) supported this idea in their studies on root elongation rates of cotton and peanuts as a function of soil strength and soil water content. They concluded that cotton and peanut seedling root elongation rates responded to changes in soil strength but did not respond to changes in soil water suction between 0.17 and 7 bars for cotton, and between

0.19 and 12.5 bars for peanuts. But for cotton as well as peanuts, top weights and lengths increased as soil matric suction decreased. Barley et al. (1965) point out that the root elongation rate is reduced by higher soil water suctions in compressed soil layers.

Meyer and Gingrich (1966) discussed the effect of the osmotic stress on wheat. The increase in percent dry matter of the shoots appeared to reflect the osmotic stress applied to the roots after a period of time, but the response was slow. Percent dry matter of the roots increased more quickly in response to an applied stress. The degree of increase reflected the magnitude of stress applied.

Water Stress and Ion Uptake

The effect of water stress in ion uptake can exert itself by two principle mechanisms. Increased soil water suction affects the rate of water supply to the plant roots and may thereby reduce the rate of nutrient supply to the root surface. At the same time functions of the plant itself are affected as a result of increased plant water stress.

Wiersum (1958) considered nutrient supply to the roots. He indicated that higher water content increases uptake at low ion concentrations in solution, because it increases the rate of diffusion. He indicated that as long as the soil has a low ion concentration, the rate of uptake will depend on the number of ions able to diffuse towards the roots from more distant layers. This diffusion is enhanced by increased

water content and uptake increases. This observation could be explained on the basis of increased cross sectional area available for diffusion. Danielson and Russell (1957) determined that large decreases in the degree of root and shoot hydration resulted from increases in soil water suction developed either in the soil or in an osmotic solution. They found that the ion uptake decreased rapidly with initial increases in soil water suction and leveled out at higher suctions to give a curve nearly logarithmic in nature.

Hylmo (1953) showed that in most species of plants tested, the roots strongly depend on water transport for their supply of ions, and in all species the ion uptake by stems and leaves was directly proportional to the water transport. He found a positive correlation between water transport through the root and the uptake of both calcium and chloride ions. The magnitude of the ion-uptake was dependent on the amount of water transported but independent of the method used to vary the transpiration and hence the water transport. He pointed out that possible uptake resulting from diffusion and ion exchange will proceed relatively unaffected under conditions of arrested metabolic activity. According to Hylmo's interpretation the transpiration stream draws water through cell walls, cytoplasm and vacuoles. Charged ions in solution pass by mass flow through the cell walls and cytoplasm but ions cannot be passively transported through the vacuole. Ions are detained at the medium-root surface, or more precisely at

the vacuoles of the epidermis and for the most part return to the nutrient solution when not absorbed by the plants.

According to Long (1943) the addition of sucrose to the culture solution greatly reduced water entrance into the roots of tomato plants but did not greatly disturb mineral entrance. Mederski and Wilson (1960) found that both percent and total quantity of P, K, and Mg in plants increased with increasing levels of soil water. The level of humidity interacts with the effect of soil water on ion absorption. At low levels of humidity the water loss was approximately 50-100% greater than that at the high levels of humidity.

Dean and Gledhill (1956) point out that the process involved in nutrient absorption and accumulation from soils by plant roots are not independent of soil water content.

Water Stress and Phosphorus Uptake

Dean and Gledhill (1956) found that active roots preconditioned at high soil water contents and subsequently placed in contact with dry soil, absorbed phosphorus rapidly from this soil, while water was simultaneously being drawn from the roots. On the other hand, roots conditioned at low soil water contents absorbed phosphorus at a reduced rate. They point out that soil water suction produced an effect which apparently reduced the absorbing capacity of roots. Two factors appear to determine the influence of soil water on phosphorus

absorption. Roots dehydrated as a result of contact with soils of high suction showed a decreased rate of phosphorus absorption and roots not seriously affected in this manner tended to absorb phosphorus more rapidly from the drier soils. They also demonstrated that the soil water was moving from root to soil and that the greatest movement of water occurred in the driest soil. In the meantime, measurements showed that phosphate ions were moving in the opposite direction of water movement. Since these observations raised a question regarding the nature of the process responsible for the phosphorus absorption and accumulation, the absorption was measured at 3.33 and 23.9°C. Approximately a five-fold increase in absorption rate was observed at the higher temperature. This was associated with the predominance of metabolic phenomena rather than exchange reactions.

Fawcett and Quirk (1960) studied the effect of water stress on the absorption of soil phosphorus by wheat. They suggest that as soil water suction increases the coarse soil pores drain and, therefore, the cross sectional area for diffusion of ions in the liquid phase is decreased. Hence the rate of absorption per unit area of root surface would decrease. They state that most nutrient ions are intimately associated with the surface of soil colloids. Since most nutrient ions are intimately associated with the surface of soil colloids, it is possible that the transfer of ions in the fine pores may be the dominant

path for nutrient transfer from soil surfaces to the plant root.

Meyer and Gingrich (1966) showed that the phosphorus and nitrogen percentages were decreased in an entire plant by osmotic stress. The sharp decrease apparent after 24 hours at a soil water suction of 1 bar indicates that uptake of these elements must have decreased immediately after application of the stress with dry matter production being essentially unchanged.

Soil Temperature Effects on Plant Growth

Soil temperature is recognized as one of the most important factors in the production of plants. Soil temperature varies with soil depth, amount and type of vegetative cover, color of the soil, amount of soil moisture, amount and distribution of soil pore space, angle of surface exposure to radiation, and amount of insolation (Baver, 1948). Table 1 shows soil temperatures at several depths measured in a Dayton soil near Corvallis, (Boersma and Simonson, 1970).

Temperature Effects on Elongation and Growth

Halsted and Waksman (1917) have shown that root temperature is an important factor in the growth of a plant. They point out that the higher soil temperatures give faster emergence, more viability, less variability in length, and more growth in terms of length and weight of corn seedlings. Culpepper and Moon (1939) indicate for

Table 1. Soil temperatures measured on a Dayton soil near Corvallis, Oregon. Measurements were made at 9:00 a. m. the first day of each month during 1964.

Months	Depth of Measurement - Inches									
	1.5	4.5	7.5	10.5	15	21	27	33	39	45
	<u>°F</u>	<u>°F</u>	<u>°F</u>	<u>°F</u>	<u>°F</u>	<u>°F</u>	<u>°F</u>	<u>°F</u>	<u>°F</u>	<u>°F</u>
Jan	46	46	46	44	45	46	47	47	48	47
Feb	43	43	44	43	43	44	46	46	47	47
Mar	37	38	40	40	42	43	45	45	46	45
Apr	51	48	49	48	48	48	48	47	47	47
May	47	48	49	48	49	50	51	50	50	48
June	64	63	63	62	61	60	58	61	56	54
July	63	62	63	62	62	61	61	60	59	58
Aug	64	64	64	64	64	63	63	63	62	60
Sept	60	60	61	61	62	62	62	62	62	61
Oct	55	55	57	57	59	59	60	60	60	60
Nov	49	51	52	52	52	53	53	54	55	55
Dec	50	48	48	47	47	48	48	50	50	51

temperatures between 11.4 and 30.9°C, the relationship between the growth rate and the temperature is represented by lines that are almost straight. The rate of total elongation approximately doubled with each increase of 10°C (18°F) over a limited range of temperatures. Later Willis et al. (1957) studied corn growth as affected by soil temperature and mulch. They found that an increase in soil temperature accelerated the rate of emergence, rate of growth, and promoted earliness in corn. Corn yields appeared to increase with increases in soil temperature up to a point and then decreased with further increases in soil temperature. Their results show that with an increase in soil temperature the rate of growth increased almost linearly, and the production of dry weight increased in the same proportion. The most favorable soil temperature at the 10 cm depth for corn growth in central Iowa appeared to be about 23.9°C.

Lingle and Davis (1959) conducted soil and sand culture experiments made on raised greenhouse benches which had been filled to a depth of six inches with Yolo fine sand loam. Soil temperatures were maintained at 10-12.8, 15.6-18.3, 21.1-23.9, and 26.7-29.4°C. Increases in soil temperature within the range included in these studies substantially increased growth. Plants in the range of 10-12.8°C and 15.6-18.3°C were stunted, had a dark green color, and extreme anthocyanin pigmentation in the leaves. The plants growing at soil temperatures of 21.1-23.9°C and 26.7-29.4°C had a lush green color

typical of rapidly growing plants. In both sand and soil cultures, tomato growth was greatest at the highest root temperature. Percent of dry weight decreased as root temperature increased but total dry matter production increased. Plants grown at low soil temperatures had a lower percentage of water than did plants grown at high soil temperatures. A subsequent report (Davis and Lingle, 1961) evaluated shoot response to root temperature for tomato plants. At the lower root temperatures growth of the shoot was independent of the nutrient status at least with respect to phosphorus and potassium. Their experiment indicates that the rate of nutrient supply is not the factor which limits shoot growth at a low root temperature. They point out that if shoot response to root temperature has a degree of independence from its nutritional and hydrational states, an endogenous mechanism must be proposed. Variation in root temperature may, for instance, induce differential production of root-produced substances having shoot regulatory activity. Esau et al. (1957) point out that the relatively low temperature may retard the rate at which materials are transported in the phloem. It was suggested (Davis and Lingle, 1961) that it would be reasonable to suspect that low root temperatures might diminish the root's effectiveness as a "sink" for phloem transported material.

Temperature Effect on Water Uptake

Comprehensive investigations of the temperature dependence of water transport have been carried out by Doring (1935). The reason for the phenomenon was thought to be a diminished permeability of the plant tissues for water and increased viscosity of water at low temperatures. The specific viscosity of water at 1°C is 1.7 times greater than that at 20°C (Kramer, 1969).

Studies of the effect of soil temperature on the absorption of water were summarized by Richards et al. (1952). This summary indicates that water absorption by plants is reduced at low soil temperatures. The reviewers indicate that it is the opinion of most authors that this is a primary cause of slower growth under these conditions.

Davis and Lingle (1961) point out that the slow growth might be due to the depressing effect of cool root temperature on the water absorption of plants. Low temperatures may retard the rate at which materials are transported through the phloem. It would be reasonable to suspect that low root temperatures diminish the root's effectiveness as a "sink" for phloem transported materials. Indeed, cool root temperatures decrease shoot growth and mineral accumulation in a manner which recalls the ringing of branches. In the case of tomatoes, it might be proposed that reduced rates of mineral transport are

responsible for slow growth at cool root temperatures.

Temperature Effects on Ion Uptake

Hoagland and Broyer (1936) found that the power of cells to accumulate ions is related to temperature. The uptake of K, NO_3 , and Br increased from 6° to 30°C. The same authors (Hoagland and Broyer, 1943) pointed out that the uptake of K, Ca, Mg, and NO_3 at 10°C was quite insignificant compared with that at 24°C. Broyer and Hoagland (1943) have taken these results as strong evidence for the theory that the uptake of ions by plants is an active process entirely dependent on energy derived from metabolic processes. According to Wanner (1948) the temperature coefficient is not the same for the accumulation of all ions. Temperature coefficients are higher for anion absorption than for cation absorption, and the coefficients for both cations and anions are lower at higher ionic concentrations.

Phosphorus availability to red clover seedlings was determined at 10, 15.6, 21.1 and 26.7°C by Robinson et al. (1959) in controlled temperature chambers. With increasing temperature, the rate of P uptake increased markedly and plant growth increased. It would appear that the more rapid uptake of phosphorus at higher temperatures is associated with the temperature coefficient of absorption rather than with an increase in phosphorus concentration in the soil solution. They state that as the temperature increases, plants

apparently are able to absorb phosphorus more rapidly from soil solutions containing very small amounts of phosphorus. Hylmo (1953) stated that the lowering of root temperature lowers the uptake of ions by the root itself, but does not affect transport of ions from the medium to the shoot, because accumulation is an active process but translocation is a passive process.

Lingle and Davis (1959) point out that as root temperatures are increased the mineral content of the shoot increases. This observation may be attributed to one or more of four possible physiological factors. First, an increased solubility of nutrients in the soil at higher temperatures might cause such an effect. But it is questionable that the solubility of the elements under consideration would change so much within such a narrow range of temperatures, as was studied. A second and more plausible relationship would be the effect of temperature on root respiratory activity. It has been amply demonstrated that respiratory energy is expended to absorb ions against a concentration gradient. It has also been demonstrated that the respiratory action of different plant tissues is materially slowed by lower temperature. It can then be reasonably assumed that the respiratory activity of root tissue would be materially slowed by a drop in temperature. A third factor to be considered is the favorable effect of warmer soil on the rate of root growth. This would provide a greater root area for the absorption of ions. A fourth factor which

might materially affect these reactions could be the influence of temperature on water absorption. Lingle and Davis (1959) reported that the absorption of all mineral constituents determined increased as soil temperatures increased from 10-12.8°C to 21.1-23.9°C. Phosphorus and potassium concentrations increased over the entire range of temperatures studied, while sodium and calcium concentrations were lower at 26.7-29.4°C than at 21.1-23.9°C. Magnesium concentrations had apparently stabilized at a point below the highest temperature.

Temperature Effects on Phosphorus Uptake

Apple and Butts (1953) found a greater response to phosphate application at low soil temperatures than at high soil temperatures but stated that other factors not under their control such as light intensity might have affected their results. Roberts and Kenworthy (1956) found that the soil temperature affected plant growth but not the phosphorus concentration of the plant material.

In a greenhouse experiment, corn seedlings were grown over a 2-week period in soil and in sand-resin media (Dormaar and Ketcheson, 1960). Soil temperatures of 15.6, 21.1, and 26.7°C were used. They found that the higher temperatures increased growth and nutrient uptake linearly in accordance with the observation of Willis et al. (1957).

Lingle and Davis (1959) found that the warm-rooted tomato plants responded more to an increased level of phosphorus than did cool-rooted plants. At all root temperatures, increased phosphorus in the root medium induced higher levels of phosphorus in the shoots. Thus, the phosphorus level in the shoots of cool-rooted plants did not appear to be the factor limiting their growth. In this experiment a cool-rooted system was maintained by circulating mechanically refrigerated water through copper tubing embedded in the soil. A warm-rooted system was obtained by means of thermostatically controlled heating cables embedded in the soil.

McEvoy (1960) found that there is a markedly higher rate of phosphorus uptake at 30°C and 35°C than at lower temperatures in tobacco plants. He showed that the uptake of phosphorus by the tobacco crop will be reduced significantly by low soil temperatures. The results of these studies are in agreement with Demidenko and Golle (1939) who found that the phosphorus uptake by sunflowers grown in soil was greater at 25° to 35°C than at 13° to 17.5°C.

Results by McEvoy (1960) indicate that the temperature effect on P uptake cannot be disassociated from the duration of exposure. The exact nature of the time factor involved in causing a reduction in P uptake at higher temperature is not known. One possible explanation is injury to the protoplasm and consequent inactivation of enzymes in the root tissue. Exposure of 2 and 4 days of different size

plants to higher temperature showed a positive relationship between P activity in the leaf tissue and the temperature of the culture medium. However, curves for a 6-day exposure had a maximum with the greatest P uptake at 35°C. Thus, the efficiency of P absorption by the root system decreased at 40°C when the absorption period was extended beyond 4 days.

Davis and Lingle (1961) found that the translocation of phosphorus and potassium from root to shoot was greater at higher root temperatures. Rapid shoot growth due to increased root temperature is accompanied by increased concentrations of potassium and phosphorus in the shoot.

A more recent study by McKell et al. (1962) indicated that top growth, root growth and phosphorus content usually increased with an increase in temperature or phosphorus fertility.

MATERIALS AND METHODS

Experimental Procedure

Five pregerminated wheat seedlings (Triticum aestivum VILL., Host) were planted in perlite filled cells and grown for five weeks in growth chambers, at day time temperature of 23.9°C and night time temperature of 21.1°C. The variety used was Gaines. The plants were given water and a nutrient solution on alternate days for the first ten days. During the rest of the growing period the cells were flooded with the nutrient solution for one hour each day. The make-up of the nutrient solution is shown in Table 2.

The perlite cells (0.8 cm thick, 30 cm high, and 10 cm wide) in which the plants were grown consisted of a frame of lucite with removeable covers (Figure 1). The perlite used for this study was a nitrogen-free, light weight material, made by exploding sand grains at high temperatures. After a period of five weeks, 54 cells of uniformly growing plants were chosen and trimmed for the experiment. Six of them were randomly selected for the initial analysis of dry weight and phosphorus content. The remaining 48 cells were moved into the growth room where with the sides removed they were encased in semi-permeable cellulose acetate membranes which allowed water and nutrients to pass freely into and out of the perlite. The cells

were then immersed in chambers containing osmotic solutions for the control of soil water suction.

Table 2. Make-up of the nutrient solution used for growing the wheat plants.

Compound	Concentration in Solution
	<u>gm/liter</u>
<u>Macronutrients</u>	
K_2SO_4	0.275
$MgSO_4 \cdot 7H_2O$	0.493
KH_2PO_4	0.122
$K_2HPO_4 \cdot 3H_2O$	0.031
$CaSO_4 \cdot 2H_2O$	1.033
$CaCl_2$	0.056
NH_4NO_3	0.500
<u>Micronutrients</u>	
$ZnSO_4 \cdot 7H_2O$	0.067
$MnSO_4 \cdot 4H_2O$	0.876
$CuSO_4 \cdot 5H_2O$	0.078
Fe EDDHA	1.000
$CoCl_2 \cdot 4H_2O$	0.00005

The technique used in these experiments for controlling soil water suction during plant growth was first suggested by Zur (1961) and developed by Cox (1966) who incorporated many modifications to overcome some problems found with the technique. It has been used

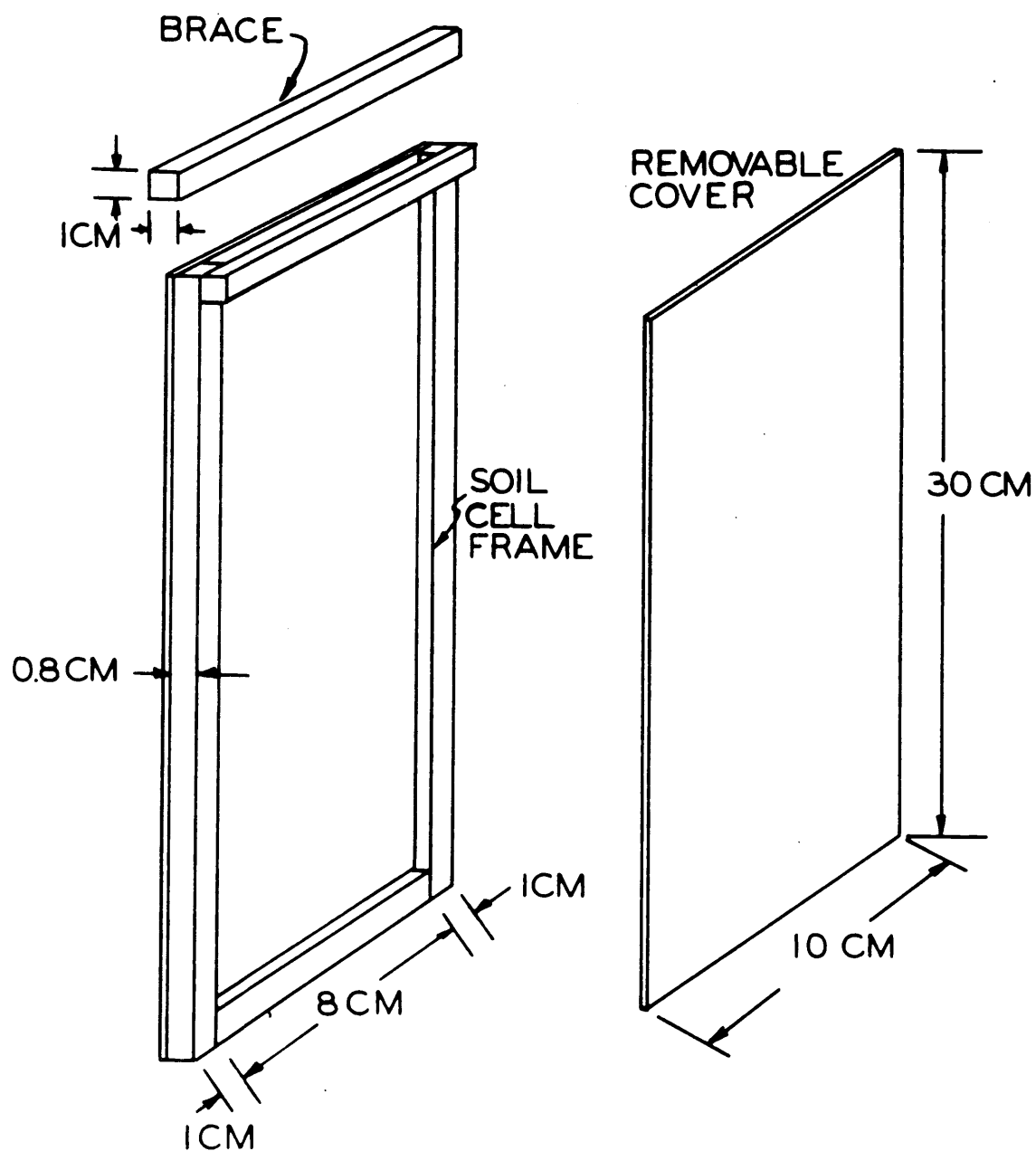


Figure 1. Schematic diagram of the perlite cell used, showing removable cover and braces.

by Babalola et al. (1968), Sedgley and Boersma (1969), Kuo (1970), and Amujo (1970). Predetermined quantities of carbowax 6000 were dissolved in distilled water to obtain the desired equivalent soil water suction. Required concentrations were derived from Zur's (1961) work. These are shown in Table 3. Nutrients were mixed with the carbowax solution at the proper concentration. The chambers were surrounded by a water-jacket which was connected to a constant temperature water bath to provide the root environment temperature control. In order to avoid the development of concentration gradients in the osmotic solutions adjacent to the membrane each osmotic solution was stirred by hand two times a day. Measurements of dry weight gain were made at temperatures of 10, 18.3, 23.9, 29.4, 32.2, and 37.8°C. Phosphorus uptake was measured at temperatures of 10, 18.3, 23.9, and 32.2°C. Concentrations of carbowax-6000 corresponding to soil water suctions of 0.35 and 2.5 bars were used in the experiment.

Table 3. Composition of osmotic solutions used to control the soil water suction.

Moisture Stress	Carbowax 6000
(bars)	g/liter
0.30	42.5
0.35	48.0
0.70	73.0
1.00	87.5
1.50	108.0
2.50	150.0
3.00	170.0

Each osmotic chamber contained three cells. A total of 16 chambers were used, eight each for a suction of 0.35 and 2.5 bars. Cells were removed for harvest from two chambers for each suction on day 2, 4, 6, and 8, so that duplicate measurements were obtained. The experiment was repeated twice at each temperature.

The most serious drawback for this technique is that the cellulose acetate membrane is very easily attacked by microorganisms. With about 100 ppm nitrogen as free ammonium nitrate in the solution it usually took less than a week for the organisms to destroy the membrane. The problem was most serious at high temperatures. Ten ppm pimaracin was applied to the nutrient solutions. This did not eliminate the problem completely, but controlled the fungus to some extent. The organisms did not grow on the membrane when the temperature was low (10° and 18.3°C) or when the osmotic pressure was 2.5 bars. At this suction, organism growth was limited even at high temperatures.

All experiments were carried out in a room in which the air temperature was 23.9°C and relative humidity ranged from 40 to 50%. The light intensity from fluorescent tubes and incandescent lamps was maintained at 1800 ft. c. at the tops of the plants. Air movement over the plants was maintained constant with one electric fan.

Measurements

Dry Matter Production

Plants from two chambers containing six perlite cells were taken randomly on day 2, 4, 6, and 8 of the experiment. The roots were carefully washed and roots and shoots were dried separately at 52°C for 48 hours. The weights of the roots and shoots were determined separately to the nearest milligram. Shoots and roots were ground in a blending mill to a uniform meal-like fineness. The ground plant materials were redried in an oven at 52°C for 24 hours. They were stored under sealed desiccant conditions until weighing.

Plant Material Extraction

The finely ground plant tissue was prepared for chemical analysis by wet washing with perchloric acid (Jackson, 1958). Approximately one gram of the finely ground plant tissue was weighed and put into 125 ml Erlenmeyer flasks. One scoop of glass beads was added to each flask. Ten ml of concentrated nitric acid was added. The flasks were heated slowly until the brown fumes (NO_2) came off, and foaming was over. Then the flasks were removed from the hotplate and left to cool. When the flasks were cool, 6 mls of 70% perchloric acid were added after which they were returned to the hotplate in a perchloric acid proof hood. After the nitric acid

boiled off the reaction mixture turned yellow, with black-brown pieces on it and boiled briskly, then dense white fumes came off and the reaction mixture became colorless. Flasks were removed from the hotplate and left to cool for about 30 seconds. Then approximately 20 mls of water were added and the solution swirled to dissolve any solids. Flasks were immediately filtered through Watman No. 5, 11 cm filter paper into 100 ml volumetric flasks.

Phosphorus Determination

Five ml of the extract from shoot material or seven ml of the extract from root material were pipetted in 50 ml volumetric flasks. Ten ml of color producing reagent (equal volume of ammonium vanadate and ammonium molybdate solution) were added to the flasks and diluted to 50 ml. The color intensity was measured on a Bausch and Lomb spectronic 20, spectrophotometer at 420 millimicrons. Blanks were set at 100% transmission. Each phosphorus determination had two replications.

Other Ions

The plant material extract was used for determination of the concentration of other ions. Results of these measurements are reported by Sepaskhah (1971) and Young (1971).

RESULTS

Dry Matter Accumulation

Results of the dry weight measurements, made every second day are shown in Tables 4 through 7. The measurements shown are averages of two separate experiments. At the high temperatures the number of observations is smaller than at the low temperatures. During the course of the experiments the cellulose membrane was attacked and decomposed by microorganisms, rendering the system inoperable after a period of time. The rate of organism growth was much higher at the high temperatures allowing fewer observations. The rate of organism growth was reduced by the increase in suction from 0.35 bars to 2.5 bars, allowing usually more observations at the higher stress level.

Table 4. Dry matter weight of shoots in mg per chamber of 5-week old wheat seedlings as a function of root temperature at 0.35 bars.

Day No.	Root Temperature - °C					
	10	18.3	23.9	29.4	32.2	37.8
	<u>mg</u>	<u>mg</u>	<u>mg</u>	<u>mg</u>	<u>mg</u>	<u>mg</u>
0	664	666	485	691	622	554
2	921	865	588	790	730	604
4	1000	897	674	799	774	644
6	959	1028	751	-	-	-
8	967	1039	-	-	-	-

Table 5. Dry matter weight of shoots in mg per chamber of 5-week old wheat seedlings as a function of root temperature at 2.5 bars.

Day No.	Root Temperature - °C					
	10	18.3	23.9	29.4	32.2	37.8
	<u>mg</u>	<u>mg</u>	<u>mg</u>	<u>mg</u>	<u>mg</u>	<u>mg</u>
0	664	667	587	691	622	554
2	846	798	701	839	716	608
4	862	838	707	791	763	623
6	851	936	782	849	-	-
8	895	970	871	-	-	-

Table 6. Dry matter weight of roots in mg per chamber of 5-week old wheat seedlings as a function of root temperature at 0.35 bars.

Day No.	Root Temperature - °C					
	10	18.3	23.9	29.4	32.2	37.8
	<u>mg</u>	<u>mg</u>	<u>mg</u>	<u>mg</u>	<u>mg</u>	<u>mg</u>
0	469	466	314	484	373	462
2	553	570	359	586	399	472
4	669	527	393	623	407	510
6	587	615	458	-	-	552
8	546	638	486	-	-	479

Table 7. Dry matter weight of roots in mg per chamber of 5-week old wheat seedlings as a function of root temperature at 2.5 bars.

Day No.	Root Temperature - °C					
	10	18.3	23.9	29.4	32.2	37.8
	<u>mg</u>	<u>mg</u>	<u>mg</u>	<u>mg</u>	<u>mg</u>	<u>mg</u>
0	469	466	386	484	373	461
2	479	497	487	639	415	584
4	570	531	477	560	396	547
6	510	564	507	599	-	571
8	599	571	500	-	-	-

Observation of Tables 4 through 7 makes it clear that the plants in the chambers did not grow at a constant rate. This is further indicated in Appendix Figures A-1 through A-11 which show the increase in shoot and root dry weight as a function of time at various temperatures. It has been indicated previously that the plants were grown in a growth chamber at a temperature of 25.0°C and were supplied with water daily. The change to an environment which changed temperature stress and soil water stress reduced growth gradually. This is well demonstrated by the difference in response at temperatures of 10.0°C and 23.9°C. At the lowest temperature (Figure A-1) the rate of growth decreased rapidly during the first several days. At 23.9°C (Figure A-3) the change in growth rate was much less as it should be since the change in environmental conditions was much less severe.

It was assumed that a constant growth rate eventually was

reached and that this constant rate was approached exponentially during the first several days of the experiment. Since difficulty was experienced in fitting the proper exponential equation to the data because of the lack of observations, the lines shown in the figures were drawn in without the benefit of a statistical approximation technique. From these graphs daily growth rates were obtained which are shown in Table 8. An example of a plant's daily growth rate as a function of time is shown in Figure 2. These results have been summarized in Table 9 and are shown graphically in Figure 3. This figure indicates that the rate of gain in dry weight at the equilibrium level was highest at 0.35 bars. Shoots had a higher growth rate than did roots. The maximum rate of gain for both roots and shoots at both levels of soil water suction was at 23.9° C.

Phosphorus Concentration

Results of the phosphorus concentration measurements made every second day are shown in Tables 10 and 11 and also have been graphically presented in Appendix Figures B-1 through B-8.

These figures suggest that, the phosphorus concentrations in the shoot and root material tended to attain a final constant value as time progressed. Depending on the initial concentration, this equilibrium was approached from a higher value or a lower value. Plants with an initially low phosphorus concentration absorbed phosphorus at

Table 8. Daily increase in dry matter weight in mg per day of shoots and roots of 5-week old wheat seedlings as a function of root temperature at soil water suctions of 0.35 and 2.50 bars. These data were obtained from Figures A-1 through A-11.

Plant Part	Soil Water Suction	Day No.	Root Temperature - °C						
			10.0	18.3	23.9	29.4	32.2	37.8	
			-----mg/day-----						
Shoot	0.35	1	100	122	57	44	61	28	
		2	40	59	49	33	41	24	
		3	17	47	44	30	31	22	
		4	11	40	40	27	27	20	
		5	9	35	37	27	23	18	
		6	6	31	34	27	23	17	
		7	6	29	32				
		8	6	28	32				
		2.50	1	84	79	46	33	53	24
	2		38	47	40	28	37	20	
	3		22	40	35	25	27	17	
	4		15	35	31	23	22	14	
	5		10	31	28	23	19	13	
	6		7	28	27	22	19	12	
	7		6	26	27				
	8		6	25	26				
Roots	0.35	1		33	31	60		18	
		2		28	28	30		13	
		3		24	26	21		11	
		4		21	23	18		10	
		5		18	21	16		10	
		6		16	20	15		10	
		7		16	18	14		10	
		8		15	18	14		10	
		2.50	1	42	28	23	26		29
	2		20	23	20	20		22	
	3		9	19	18	17		17	
	4		7	16	16	15		14	
	5		6	14	15	14		11	
	6		4	13	14	14		9	
	7		4	12	13	13		8	
	8		4	12	13	12		8	

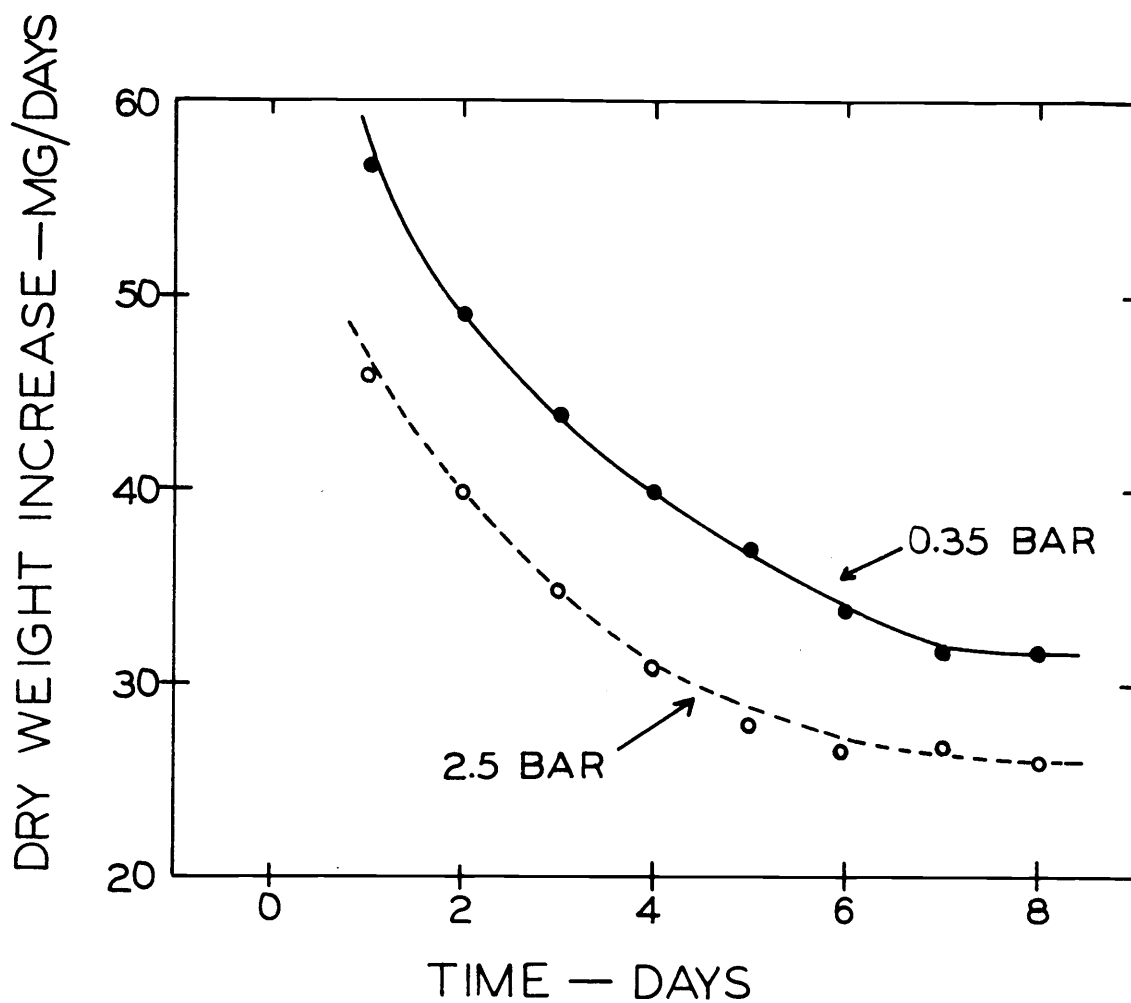


Figure 2. Rate of increase in dry matter weight in mg per day of shoots of 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars at a root temperature of 23.9°C.

a rapid rate to reach the equilibrium level. On the other hand, plants with an initially high phosphorus content absorbed phosphorus at a slow rate. In some instances the concentration remained constant during the experiment. The final equilibrium concentration was obtained by fitting the equation

$$y = a + be^{-0.07t^{3/2}} \quad (3)$$

to the data. In this equation y is the concentration and t is time in days. The parameter a represents the equilibrium concentration. Results of these calculations are shown in Tables 12 and 13 for all experiments. Correlation coefficients are also shown. The lines shown in Figures B-1 through B-8 were calculated by substituting the appropriate values of the parameters a and b in Equation 3.

Table 9. Rate of increase in dry matter weight in mg per day of shoots and roots of 5-week old wheat seedlings as a function of soil temperature at soil water suctions of 0.35 and 2.5 bars.

Root Temperature	Shoots		Roots	
	0.35	2.5	0.35	2.5
<u>°C</u>	<u>mg/day</u>	<u>mg/day</u>	<u>mg/day</u>	<u>mg/day</u>
10.0	7.0	5.8	4.5	3.4
15.6	23.0	18.7	12.2	10.0
18.3	27.0	23.6	14.7	12.0
21.1	30.0	25.6	16.3	13.3
23.9	31.0	26.0	16.7	13.0
26.7	30.2	25.3	15.6	13.1
29.4	27.0	22.0	14.2	12.0
32.2	22.8	18.7	11.6	10.0
35.0	16.5	11.7	9.0	7.4

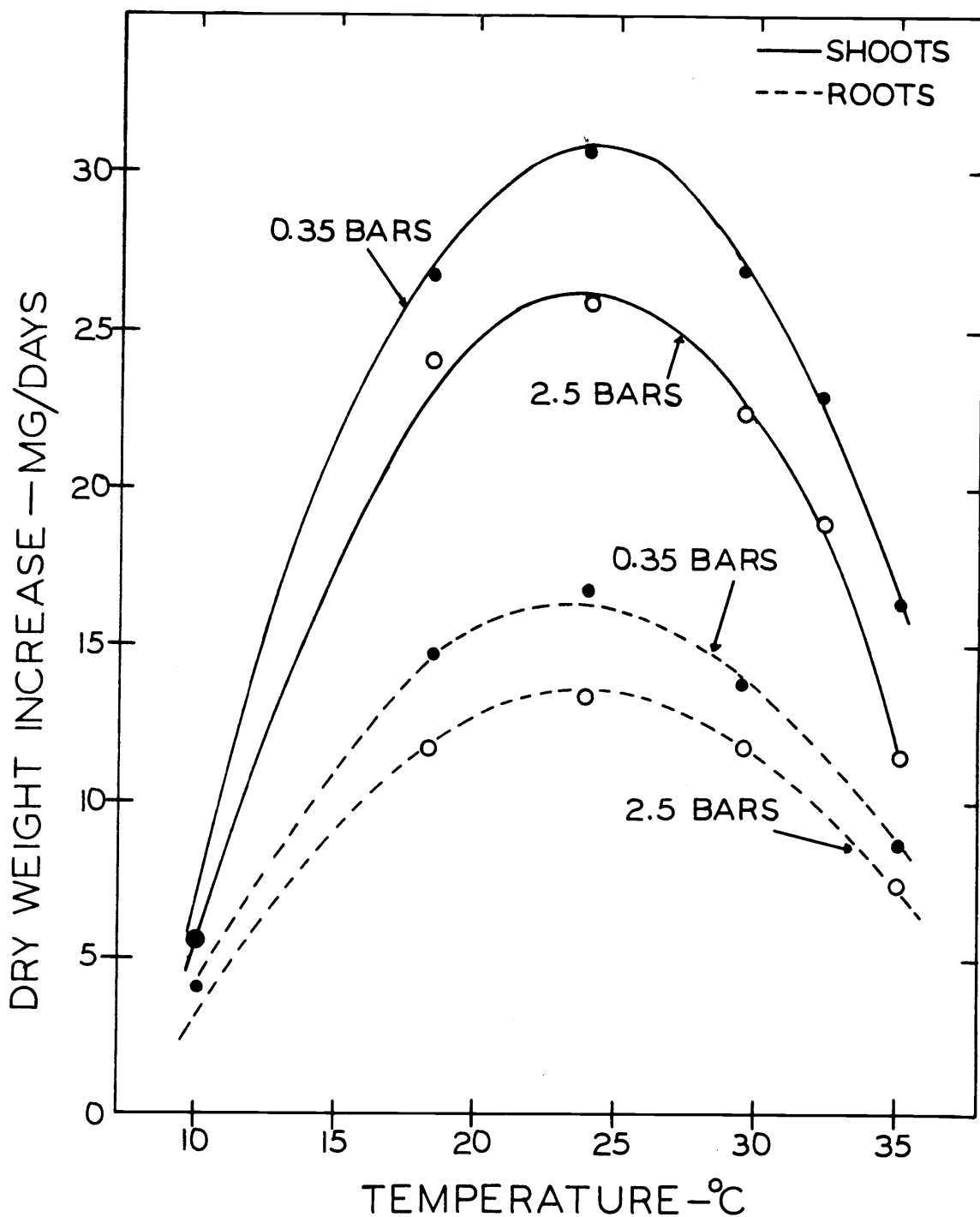


Figure 3. Rate of increase in dry matter weight in mg per day of shoots and roots of 5-week old wheat seedlings as a function of root temperature at soil water suctions of 0.35 and 2.5 bars.

Table 10. Phosphorus concentration of shoots of 5-week old wheat seedlings as a function of root temperature at soil water suctions of 0.35 and 2.50 bars. Results of duplicate experiments are shown.

Soil Water Suction	Root Temp.	Exp. No.	Day No.					
			0	2	4	6	8	
<u>bars</u>	<u>°C</u>		<u>%</u>	<u>%</u>	<u>%</u>	<u>%</u>	<u>%</u>	
0.35	10.0	I	0.50	0.46	0.41	0.38	0.38	
		II	0.37	0.36	0.39	0.37	0.39	
	18.3	I	0.46	0.48	0.43	0.44	0.45	
		II	0.45	0.42	0.44	0.43	0.42	
	23.9	I	0.40	0.45	0.49	0.52	--	
		II	0.67	0.61	0.56	0.53	0.54	
	32.2	I	0.57	0.57	0.57	--	--	
		II	0.65	0.66	0.67	--	--	
	2.50	10.0	I	0.50	0.44	0.42	0.39	0.41
			II	0.37	0.36	0.37	0.39	0.34
18.3		I	0.48	0.47	0.43	0.44	0.49	
		II	0.45	0.46	0.43	0.43	0.46	
23.9		I	0.40	0.50	0.47	0.50	0.51	
		II	0.66	0.55	0.50	0.55	0.58	
32.2		I	0.57	0.55	0.55	0.52	--	
		II	0.65	0.65	0.60	--	--	

Table 11. Phosphorus concentration of roots of 5-week old wheat seedlings as a function of root temperature at soil water suctions of 0.35 and 2.50 bars. Results of duplicate experiments are shown.

Soil Water Suction	Root Temp.	Exp. No.	Day No.					
			0	2	4	6	8	
<u>bars</u>	<u>°C</u>		<u>%</u>	<u>%</u>	<u>%</u>	<u>%</u>	<u>%</u>	
0.35	10.0	I	0.41	0.36	0.31	0.37	0.34	
		II	0.27	0.26	0.27	0.28	0.27	
	18.3	I	0.34	0.34	0.32	0.28	0.28	
		II	0.29	0.28	0.31	0.29	0.28	
	23.9	I	0.25	0.25	0.27	0.29		
		II	0.45	0.43	0.39	0.34	0.37	
	32.2	I	0.35	0.38	0.45	0.39		
		II	0.42	0.45	0.48			
	2.50	10.0	I	0.41	0.36	0.34	0.38	0.38
			II	0.27	0.28	0.28	0.30	0.31
18.3		I	0.34	0.31	0.34	0.33	0.31	
		II	0.29	0.30	0.28	0.29	0.32	
23.9		I	0.25	0.26	0.26	0.27	0.24	
		II	0.45	0.38	0.40	0.41	0.38	
32.2		I	0.35	0.42	0.41	0.51		
		II	0.42	0.43	0.47			

Table 12. Values of the parameters a and b obtained by fitting the equation $y = a + be^{-0.07t^{3/2}}$ to the P-concentration of the shoots.

Soil Temperature	Soil Water Suction	Exp. No.	Parameter		Correlation Coefficient (r)
			a	b	
<u>°C</u>	<u>bars</u>				
10.0	0.35	I	0.360	0.175	0.9711
		II	0.387	-0.025	-0.5380
	2.50	I	0.375	0.139	0.9530
		II	0.360	0.015	0.2228
18.3	0.35	I	0.432	0.057	0.8014
		II	0.415	0.040	0.7576
	2.50	I	0.453	0.018	0.2316
		II	0.439	0.019	0.3802
23.9	0.35	I	0.571	-0.231	-0.9903
		II	0.502	0.184	0.9851
	2.50	I	0.527	-0.127	-0.7953
		II	0.572	-0.169	-0.9032
32.2	0.35	I	0.679	-0.033	-0.9760
		II	0.586	-0.268	-0.9305
	2.50	I	0.518	0.059	0.8808
		II	0.570	0.108	0.8878

Table 13. Values of the parameters a and b obtained by fitting the equation $y = a + be^{-0.07t^{3/2}}$ to the P-concentration of the roots.

Soil Temperature <u>°C</u>	Soil Water Suction <u>bars</u>	Exp. No.	Parameter		Correlation Coefficient (r)
			a	b	
10.0	0.35	I	0.321	0.085	0.6954
		II	0.278	-0.017	-0.5553
	2.50	I	0.354	0.037	0.3924
		II	0.305	-0.044	-0.9465
18.3	0.35	I	0.281	0.098	0.9021
		II	0.288	0.004	0.0963
	2.50	I	0.320	0.015	0.2717
		II	0.303	-0.021	-0.4040
23.9	0.35	I	0.292	-0.053	-0.9269
		II	0.340	0.139	0.9376
	2.50	I	0.252	0.010	0.2471
		II	0.368	0.080	0.7106
32.2	0.35	I	0.435	-0.091	-0.6258
		II	0.529	-0.139	-0.9989
	2.50	I	0.526	-0.213	-0.8755
		II	0.502	-0.109	-0.9821

Results of duplicate experiments were averaged to obtain equilibrium concentrations of phosphorus in the plant material at different temperatures and soil water suctions. These averages are shown in Table 14. The same results are shown in Figures 4 and 5. The equilibrium concentration was highest in the shoots at soil water suctions of 0.35 and 2.50 bars. Indications are that this concentration is a linear function of soil temperature. The phosphorus concentration of the roots did not increase until the root temperature increased above 32°C.

Table 14. Rate of increase in phosphorus concentration of shoots and roots of 5-week old wheat seedlings as a function of root temperature at soil water suctions of 0.35 and 2.5 bars.

Root Temperature	Shoots		Roots	
	0.35	2.5	0.35	2.5
<u>°C</u>	<u>%</u>	<u>%</u>	<u>%</u>	<u>%</u>
10.0	0.374	0.368	0.300	0.330
18.3	0.424	0.446	0.285	0.312
23.9	0.537	0.550	0.316	0.310
32.2	0.633	0.544	0.482	0.514
r	0.9625	0.9893		

r - regression coefficient.

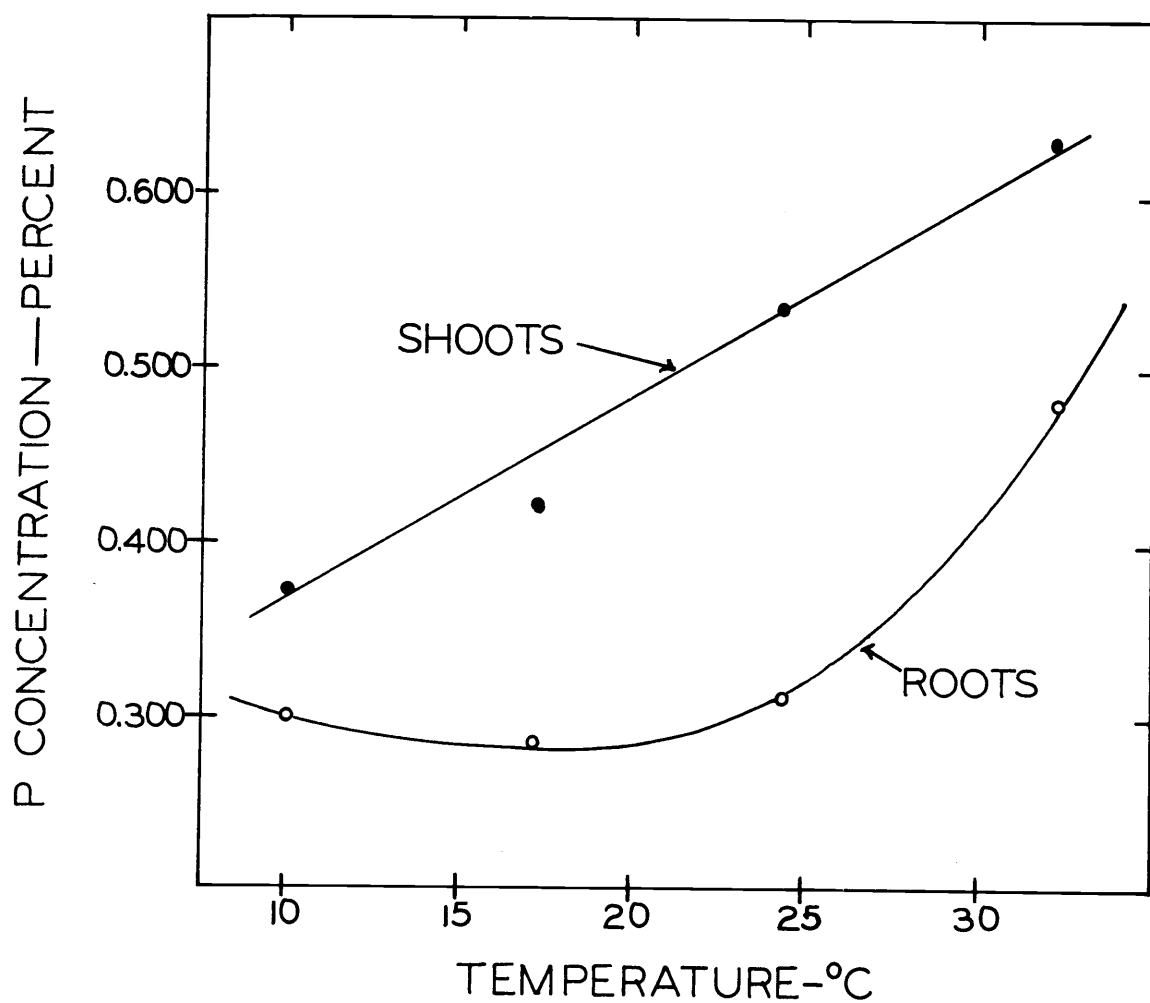


Figure 4. Phosphorus concentration of shoots and roots of 5-week old wheat seedlings as a function of root temperature at a soil water suction of 0.35 bars.

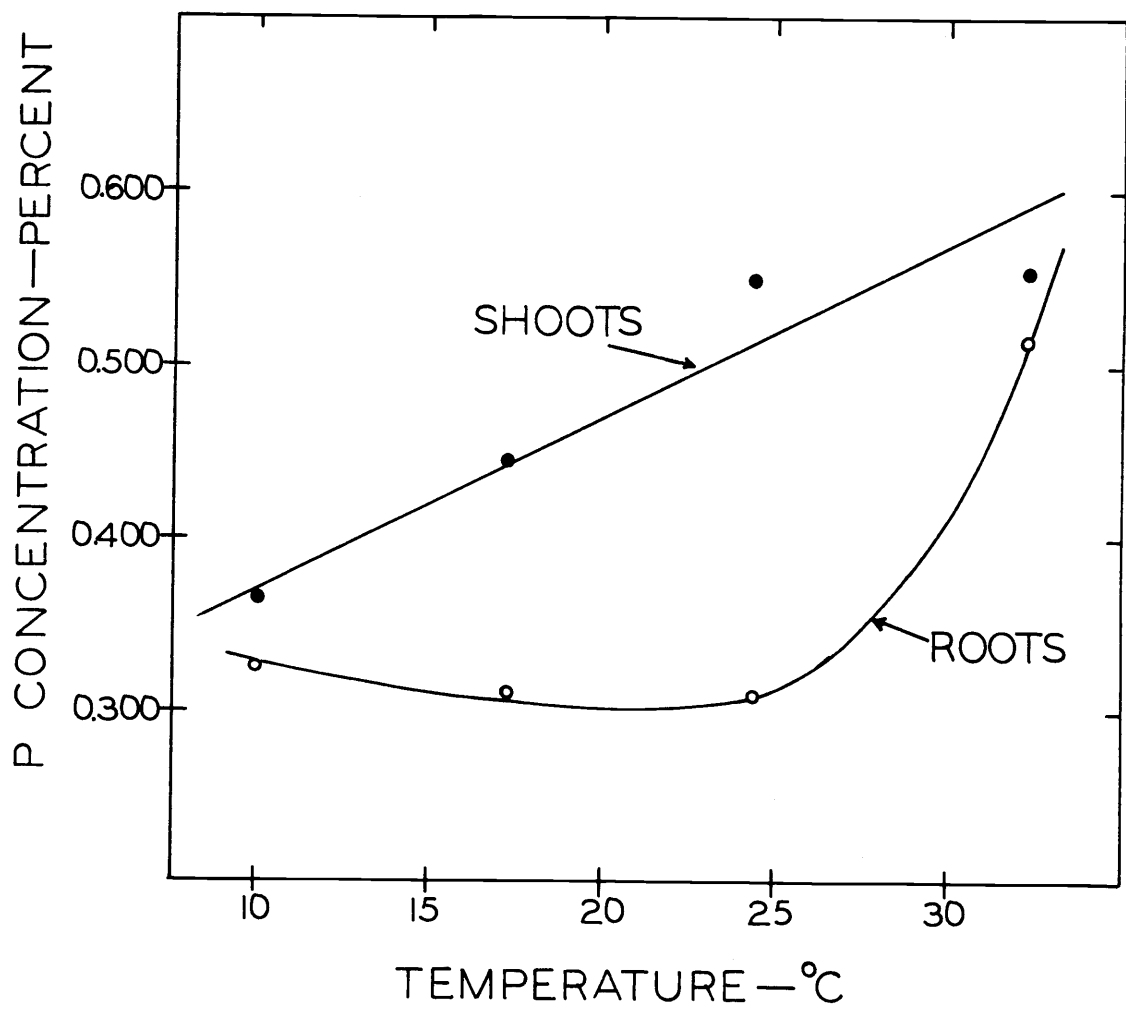


Figure 5. Phosphorus concentration of shoots and roots of 5-week old wheat seedlings, as a function of root temperature at a soil water suction of 2.5 bars.

DISCUSSION

Phosphorus Uptake

Hoagland and Broyer (1936), Robertson and Turner (1945), Dean and Gledhill (1956) and Davis and Lingle (1961) showed that cool root temperatures decrease mineral accumulation and reduce rates of mineral translocation. Conversely, temperature accelerates the mineral accumulation processes. Factors such as increased solubility of nutrients in the soil, effect of temperature on root respiratory activity, the favorable effect of warmer soil, and the influence of temperature on water absorption may have led to the higher phosphorus percentage at higher soil temperatures (Table 14). According to Demidenko and Golle (1939), Hylmo (1953), Willis et al. (1957), Robinson et al. (1959), Davis and Lingle (1961), Dormaar and Ketcheson (1960), McEvoy (1960), and McKell et al. (1962), phosphorus content usually increases with increased temperature. Roberts and Kenworthy (1956) found that the soil temperature affected plant growth but not phosphorus concentration. Also, Apple and Butts (1953) found a greater response to phosphate application at low soil temperatures than at high soil temperatures.

Meyer and Gingrich (1966) states that the phosphorus percentages in an entire plant were decreased by osmotic stress. This

report is not in agreement with water stress effects on phosphorus concentration observed here. In these experiments only a narrow range of soil water suction was considered. It is possible that a further increase in soil water suction would lead to more drastic changes in P-concentration.

Distribution Between Shoots and Roots

The daily rate of phosphorus uptake shown in Table 15 was derived from the rate of increase in dry weight (Table 9) and the phosphorus concentration of the dry weight (Table 14). This table also shows the portion of the total phosphorus uptake transported to the shoots. This fraction remained remarkably constant at the different temperatures and was nearly identical at the two soil water suctions considered. It is generally assumed that soil temperature as well as soil water suction have an influence on the rate of translocation of materials in the plant. One might logically have expected a much greater portion of the phosphorus to remain in the roots at the lower temperatures or at the higher suctions. Some increase in the fraction accumulated by the shoots was observed, but not nearly as much as could have been projected on the basis of changes in rate of translocation as a result of viscosity changes caused by changes in the root temperature. This observation suggests that the limited rate of uptake of phosphorus at the lower temperatures did not result from an

accumulation of the phosphorus in the roots due to restricted translocation to the shoots. Phosphorus concentrations in the root material actually decreased until a temperature of 21.1°C was attained, which supports this conclusion. Crossett and Loughman (1966) established that only a small portion of the P in the roots can be readily translocated to the shoots. This portion was called the "root pool." The existence of the "root pool" was further tested by Greenway and Klepper (1969). These results suggest that the quantity of phosphate ions in the "root pool" increases in proportion to the increase in number of ions taken up. These results also seem to indicate that the process limiting the rate of accumulation by the shoots was not restricted translocation to the shoots, except possibly at the lowest temperatures considered. If restricted translocation were the limiting factor a higher phosphorus content of the roots might have been expected. Since all ions available for translocation did go to the shoots the rate limiting process must have been the accumulation by the root cells or radial transport across the cells of the root to the xylem tissue.

Uptake in Relation to Water Flow

Water flow can accelerate ion movement to shoots even when ion transfer depends on active transport (Brouwer, 1954; Petterson, 1966; Jackson and Weatherly, 1962b; Greenway and Klepper, 1968).

Reasons suggested for this observation are that the mass flow of solution might increase ion delivery to sites of active uptake or alternately that ion transport might be increased by water flow after uptake either during ion movement through the cells or by rapid ion removal from the sites of release near the xylem, thus accelerating transport across the root (Brouwer, 1954; Russell and Shorrocks, 1959; Jackson and Weatherley, 1962a).

Table 15. Rate of phosphorus uptake in μg per day by shoots and root of 5-week old wheat seedlings as a function of soil temperature at soil water suctions of 0.35 and 2.5 bars.

Root Temperature	Shoots		Roots		Percent to Shoot	
	0.35	2.50	0.35	2.50	0.35	2.50
<u>$^{\circ}\text{C}$</u>	----- $\mu\text{g}/\text{day}$ -----				<u>%</u>	<u>%</u>
10.0	26	21	14	11	65.0	65.6
15.6	99	79	34	31	74.4	71.8
21.1	149	123	47	41	76.0	75.0
26.7	171	136	55	45	75.7	75.1
32.2	144	111	55	51	72.4	68.6

Hooymans (1969) stated that results of his experiments ruled out a significant contribution of any passive, transpiration-promoted ion flow to translocation of K to the shoot as visualized by Hylmo (1953) or implied by the reasons given above. He also ruled out enhancement of the rate of radial ion transport in the roots as postulated by Brouwer (1954) and Greenway and Klepper (1968). Rather he suggested that his results were consistent with the view that at low

transpiration rates the transfer of K ions from the root tissue to the xylem vessels is limited by the rate of removal of ions from the vessels to the upward plant parts. This does not appear to have been the case in these experiments. Had this occurred some increase in the phosphorus concentration of the shoots might have been expected.

If indeed the rate of mineral uptake is related to the transpiration rate it should be possible to show that the increased rates of P-uptake at the increased temperatures resulted from the higher transpiration rates. The rates of water uptake of similar plants were measured in a separate experiment (Sepaskhah, 1971). These rates are shown in Table 16, together with the rates of total phosphorus accumulation. The concentrations in the transpiration stream required to deliver the indicated quantity of phosphorus to the root was then calculated and is also shown in Table 16. The same calculation applied to the amount taken up by the shoots is not shown but follows a similar trend.

The concentration in the transpiration stream clearly was not constant. It was lowest at the 10.0°C root temperature and had a maximum value at a root temperature of around 20°C. Even at its highest value this concentration was well below the concentration of the nutrient solution which was 34 ppm.

Table 16. Total P-uptake, transpiration rate and concentration of phosphorus in the water taken up by 5-week old wheat seedlings as a function of soil temperature at soil water suctions of 0.35 and 2.5 bars.

Root Temp.	Total P-uptake		Transp. Rate		P-concentration	
	0.35	2.50	0.35	2.50	0.35	2.50
<u>°C</u>	---µg/day---		--cm ³ /day--		<u>ppm</u>	<u>ppm</u>
10.0	40	32	12.2	8.5	3.3	3.8
15.6	133	110	14.9	9.8	8.9	11.5
21.1	196	164	18.8	11.5	10.4	14.3
26.7	226	181	25.6	14.4	8.8	12.6
32.2	199	162	31.6	17.0	6.4	9.8

It could also be assumed that the rate of transpiration is an expression of the level of translocation occurring in the plant. This assumption presents an apparent contradiction. At the higher rates of translocation the concentrations per unit volume could then be expected to decrease rather than increase. It must be concluded that the higher concentrations occurred because the rate of phosphorus supply at the roots increased independently of the transpiration rates. Apparently all phosphorus available for translocation to the shoots is transferred through the xylem. This conclusion is further supported by the fact that the concentrations in the roots did not increase until a temperature of at least 20°C was reached. The mechanism which controls the rate of phosphorus uptake does not appear to be associated with the mechanism which controls the rate of transpiration. This conclusion is not surprising. It is surprising that so much effort

has been expanded trying to link the two processes since they are not similar in a cause and effect relationship sense. These results certainly seem to rule out a passive mechanism for phosphorus uptake as suggested by Hylmo (1953).

Greenway and Klepper (1968) stated that water flow might accelerate active transport in three ways: (1) if the rate of diffusion of ions limits active uptake by the roots, then the mass flow of solution to the sites of active uptake would increase the rate of ion uptake and consequently, the rate of ion transport to shoots; (2) radial movement through the roots might be accelerated presumably during transport in the symplast and cell walls; (3) if the concentration gradient between the symplast of the roots and the xylem sap limits ion release, then this release would be accelerated by a more rapid removal of ions from the stelar walls and the xylem. Not considered in this analysis is the fact that if the rate of uptake is controlled by a mechanism other than rate of diffusion any one of these three ways of changing the rate of transport could be of only minor consequence. The following factors may possibly play a role in the process of phosphorus uptake: (1) diffusion coefficients, (2) concentration gradients, rate of removal from the root, (3) viscosity of the various cell components, and (4) energy available for active uptake. Only the last factor can account for the rapid rate of increased uptake observed by increasing the root temperature. The three fold increase which

occurred by increasing the root temperature from 10.0°C to 15.6°C is too large to be accounted for by a change in diffusion coefficient. A change in concentration gradient cannot explain this increase in rate of uptake either, nor could a change in viscosity decrease since the Q_{10} of viscosity in this temperature range is smaller than 2.0. But a rapid increase in the rate at which energy is made available for active uptake is possible. This is demonstrated schematically in Figure 6. It shows an assumed rate of net photosynthesis and gain in dry matter with both quantities expressed in the same units. The difference between these two graphs is the rate of root respiration, which is also shown in the diagram (in percent of the rate at 10.0°C). When the difference is small between net photosynthesis and growth at low temperatures and the curves have the general shape as indicated, small changes in net photosynthesis and dry weight gain lead to a large increase in root respiration. The relative change in root respiration is also indicated in Figure 6. Actual data to construct these graphs were not obtained in these experiments.

Phosphorus Uptake and Nitrogen Uptake

In a separate experiment (Sepaskhah, 1971) the rate of nitrogen uptake was measured. The results of the phosphorus and nitrogen uptake studies are summarized in Table 17. Over the temperature range of 10.0°-30°C the ratio was more or less constant. A possible

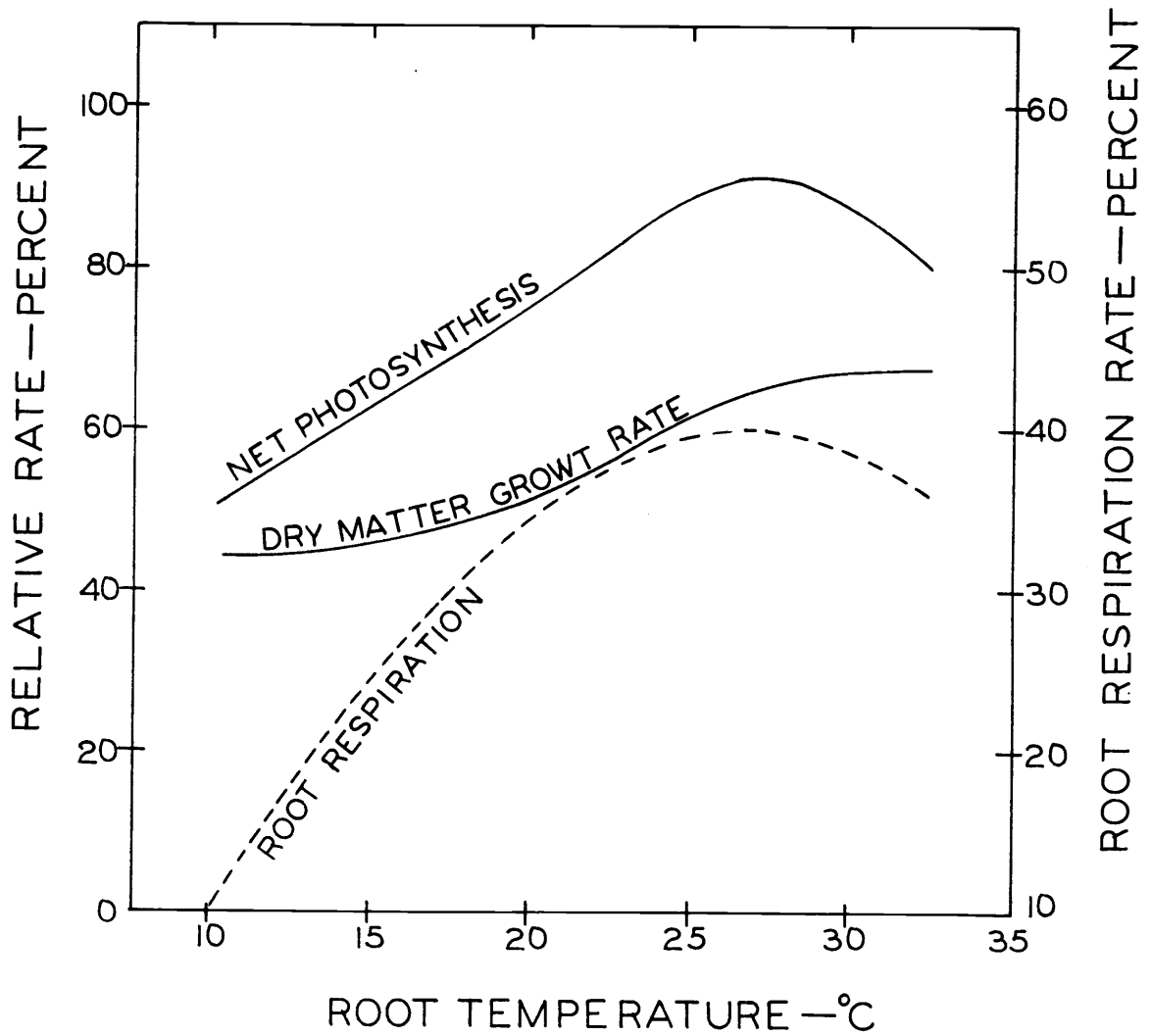


Figure 6. Rates of net photosynthesis and dry matter accumulation as a function of root temperature. The difference between the two curves is a measure of root respiration. This difference is also shown in percent of the rate at 10°C.

explanation might be that phosphorus was the growth limiting factor and that nitrogen was taken up as needed.

Table 17. Ratio of the rates of nitrogen and phosphorus uptake by 5-week old wheat seedlings as a function of soil temperature at soil water suctions of 0.35 and 2.50 bars.

Soil Temp.	N-uptake		P-uptake		Ratio	
	0.35	2.50	0.35	2.50	0.35	2.50
°C	---µg/day---		---µg/day---			
10.0	310	240	40	32	7.8	7.5
15.6	1090	870	133	110	8.2	7.9
21.1	1550	1260	196	164	7.9	7.7
26.7	1570	1260	226	181	6.9	7.0
32.2	1200	950	203	166	6.0	5.7

Dry Matter Accumulation

The results for the rate of dry weight accumulation are in agreement with literature reports. Culpepper and Moon (1939) and Willis et al. (1957) indicated this relationship between growth rate and temperature. Their results showed that with an increase in soil temperature the rate of growth increased almost linearly, and the production of dry weight increased in the same proportion. The most favorable soil temperature for corn growth appeared to be about 23.9°C (Willis et al., 1957). In Lingle and Davis' (1959) studies it was shown that an increase in soil temperature increased total dry matter production. Furr and Taylor (1939), Mederski and Wilson (1960), Stevenson and Boersma (1964), Taylor and Ratliff (1969), and

Thomas and Wiegand (1970) all are in agreement with results of this study indicating that growth rate decreases as the total soil water suction increases. These investigations concerned lemon fruits, corn, corn and sunflower, cotton and peanuts, and cotton respectively. According to MacDougal (1920) dehydration of plants under water stress may be the cause of a marked growth reduction. Under these conditions, certain phases of protein synthesis may become limiting (Loomis, 1938; Nightingale, 1937). Meyer and Gingrich (1966) found a slow response to changes in water stress with respect to growth of shoots, but the percentage dry matter of the roots increased more quickly in response to an applied stress.

Figure 7 shows the rate of dry matter accumulation as a function of the rate of phosphorus uptake for the temperature range of 10.0 to 21.1°C. Over this temperature range the curve has the general characteristics of a Mitscherlich growth curve. At higher temperatures the curve would show a maximum value and then decrease. Results obtained at 0.35 bars and 2.50 bars fall along the same curve. It appears that the rate of phosphorus uptake was limited by temperature effects as well as soil water suction effects and that growth occurred in proportion to the amount of phosphorus available. Earlier it was suggested that phosphorus supply might have been the growth limiting factor. This seems indeed to have been the case, with other processes becoming more important at higher temperatures.

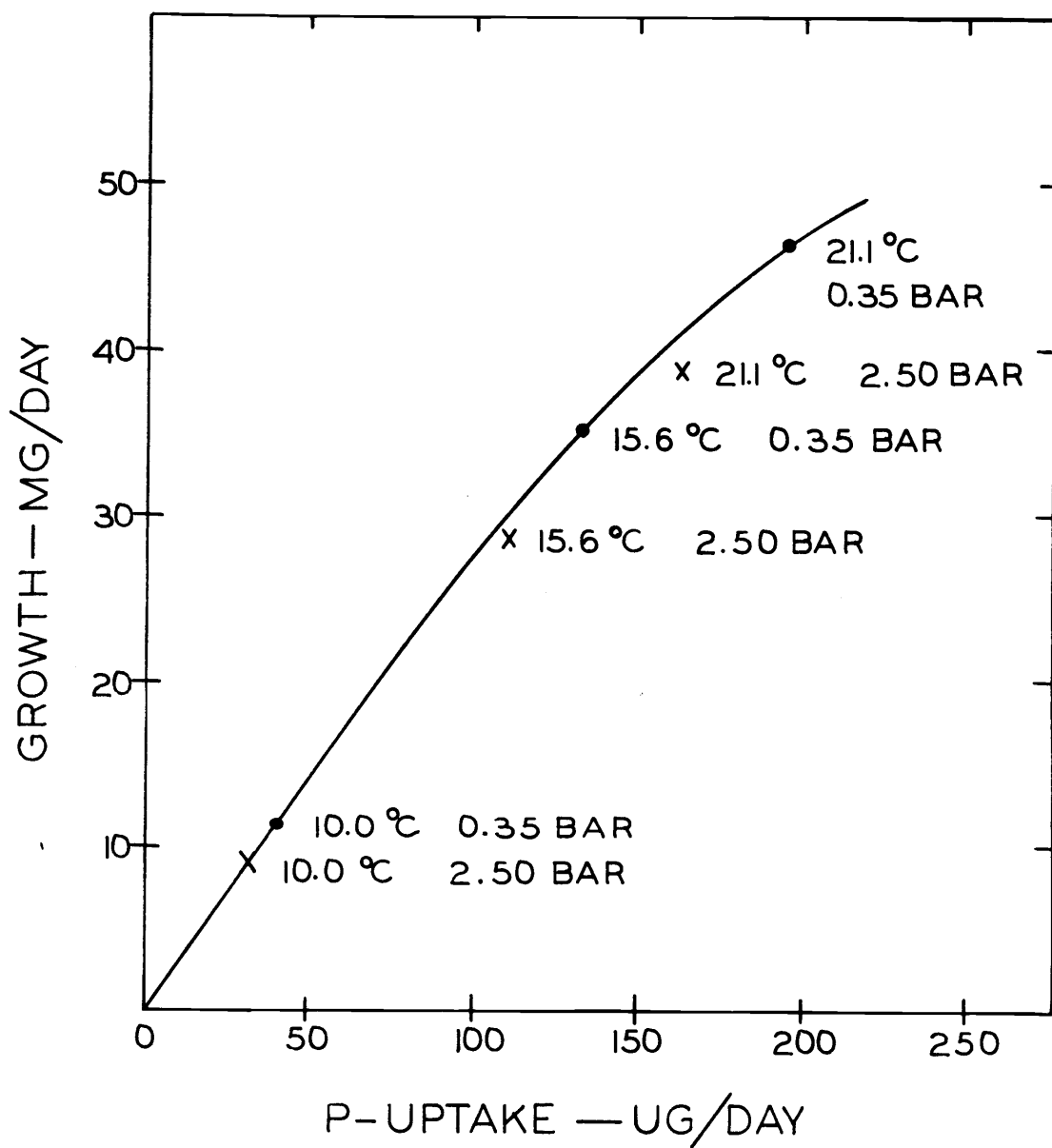


Figure 7. The rate of dry matter accumulation as a function of the rate of P-uptake at a range of root temperatures and soil water suctions of 0.35 and 2.50 bars.

SUMMARY AND CONCLUSION

The effect of soil temperature and soil water suction on the rate of growth and rate of phosphorus uptake of wheat (Triticum aestivum, VILL., Host) was studied. Wheat seeds were planted and grown in perlite, a nutrient free, non-adsorbing material made by exploding sand grains at high temperatures. The perlite was contained in thin slabs, 10 cm wide, 30 cm long and 0.8 cm thick. The seeds germinated and were cultured in a growth chamber at a day temperature of 23.9°C and a night temperature of 21.1°C, until they were 5 weeks old from the time of planting. During this time the plants were watered and supplied with nutrients daily. At the age of five weeks the cells were taken from the growth chambers and encased in a semi-permeable membrane after removal of the covers from the cells. The membrane covered cells were then immersed in an osmotic solution, maintained at a constant temperature. Nutrients were mixed with the osmotic solutions. Plants were allowed to grow exposed to these conditions for a period of 8 days with some of the plants being harvested at day No. 0, 2, 4, 6, and 8. The measurements made were: dry weight of roots, dry weight of shoots and phosphorus concentration of both shoots and roots. Experiments were done at temperatures of 10.0, 18.3, 23.9, 29.4, 32.2, and 37.8°C and soil water suctions of 0.35 and 2.50 bars.

Phosphorus concentrations were determined on plant material extracted by wet washing with perchloride acid. Color intensity was measured with a Bausch and Lomb spectronic 20 spectrophotometer at 420 millimicrons.

The growth rate of the plants in the chambers was obtained by plotting the change in dry weight of shoots and roots as a function of time. At all treatment combinations a constant rate of growth was approached exponentially during the experimental period. This constant rate of growth was assumed to be the growth rate at the temperature and soil water suction of the experiment. The phosphorus concentration of the plant material was obtained by plotting the concentration of shoots and roots as a function of time. These results were found to fit the equation

$$y = a + be^{-0.07t^{3/2}}$$

where y is the phosphorus concentration, t is the time in days and a and b are constant. The constant a represents the equilibrium phosphorus concentration at the temperature and soil water suction of the experiment. Values of a were obtained for all treatment combinations by averaging the results of duplicate experiments.

Growth rate of shoots and roots was slowest at the extreme temperature with the maximum rate occurring at a root temperature

of about 24.0°C. The growth rate was higher at a soil water suction of 0.35 bar than at a soil water suction of 2.5 bars. These results are in agreement with the literature. Indications were that phosphorus supply was the growth limiting factor at the low root temperatures. Restrictions in growth at the high root temperatures might be attributable to thermal death of enzymes and general disruption of physiological processes.

The phosphorus concentration of the shoots increased as a linear function of root temperatures over the entire range of temperatures considered. This was so for both soil water suctions considered. The phosphorus concentrations of the roots slightly decreased by increasing the root temperature from 10.0°C to 20.0°C and rapidly increased at the higher temperatures. The fraction of the phosphorus taken up by the plant that was transported to the shoots did not vary much over the entire temperature range. No relation was found between the rate of phosphorus uptake and the transpiration rate. No indications were found that the low rate of phosphorus uptake at the low root temperatures resulted from restricted translocation from root to shoot. Rather, the fact that the root concentrations remained low at low root temperatures was interpreted to mean that restricted translocation was not a limiting factor. Even though conclusive data were not available it was suggested that the low rate of phosphorus uptake resulted from limited energy availability.

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APPENDICES

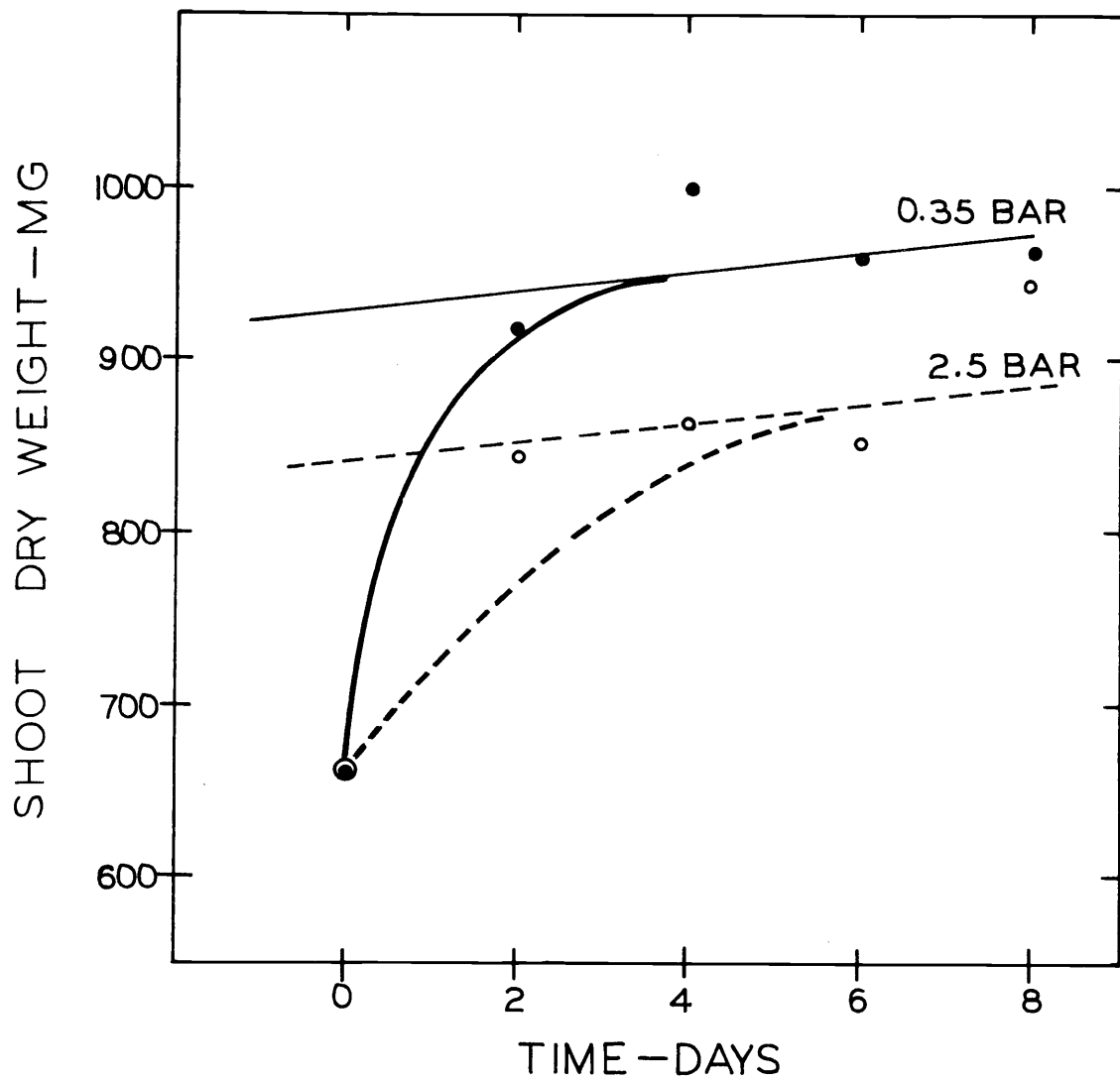


Figure A-1. Dry weight of shoots in mg per chamber for 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars and a soil temperature of 10.0°C.

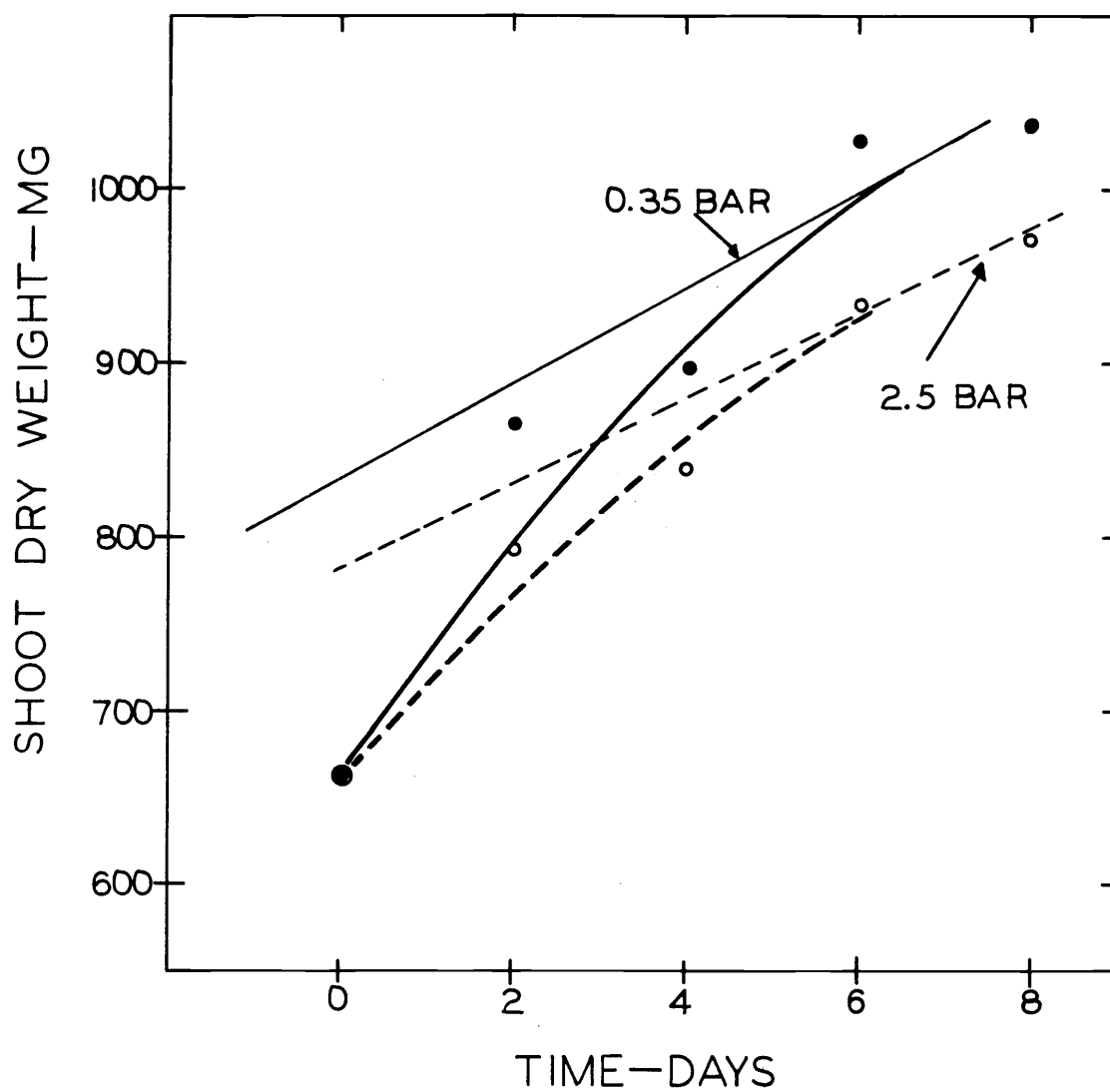


Figure A-2. Dry weight of shoots in mg per chamber for 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars and a soil temperature of 18.3°C.

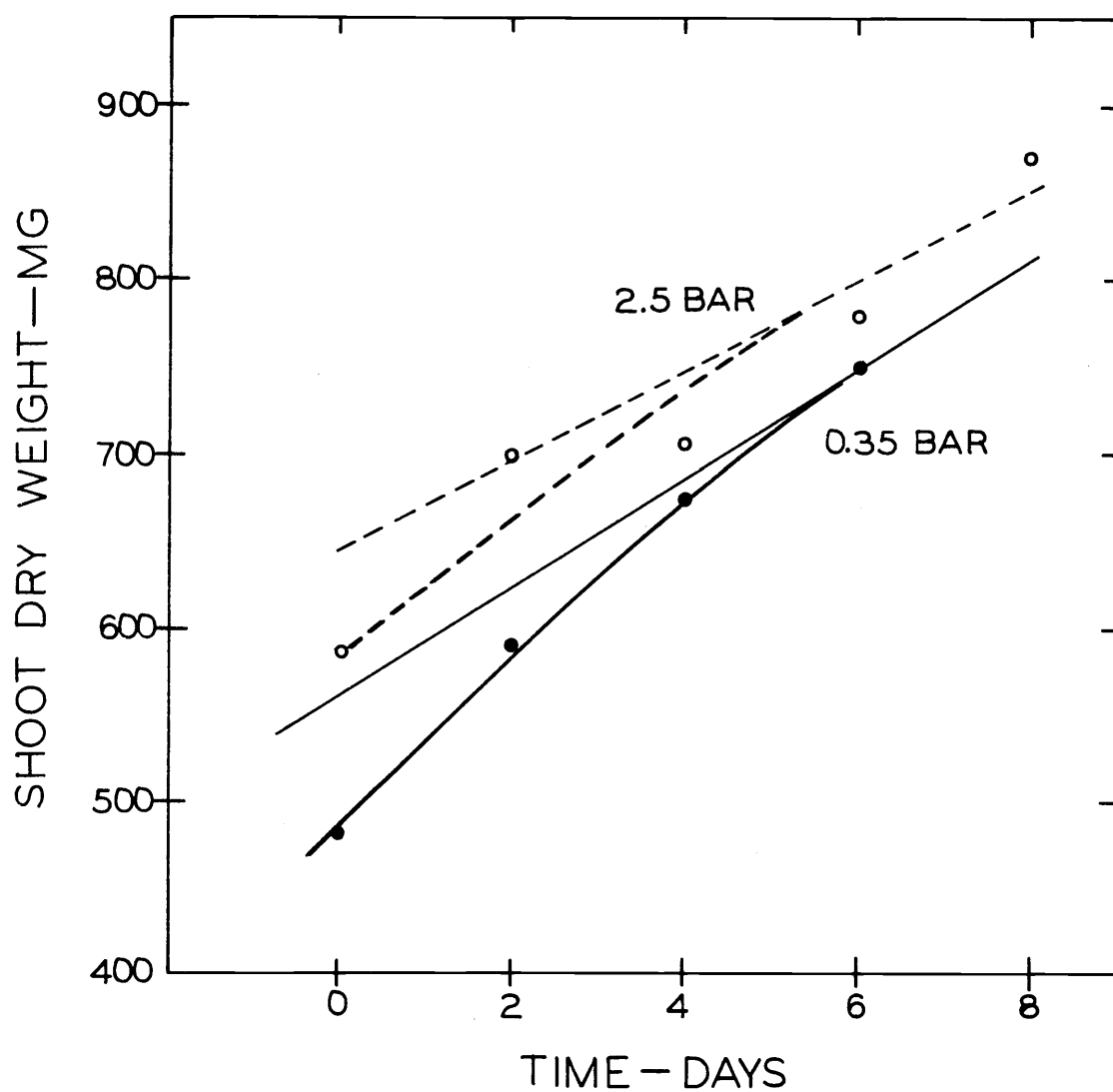


Figure A-3. Dry weight of shoots in mg per chamber for 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars and a soil temperature of 23.9°C.

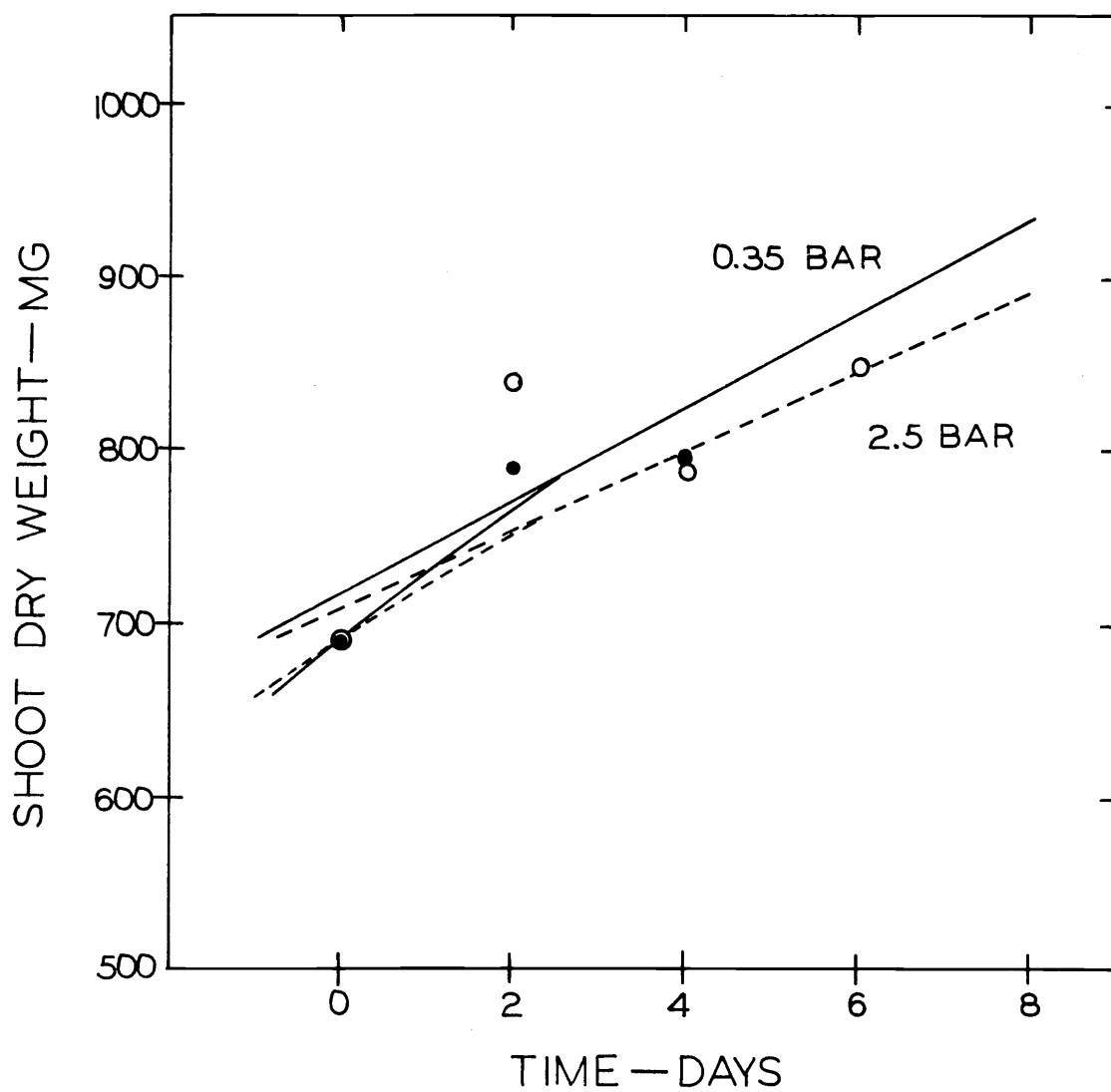


Figure A-4. Dry weight of shoots in mg per chamber for 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars and a soil temperature of 29.4°C.

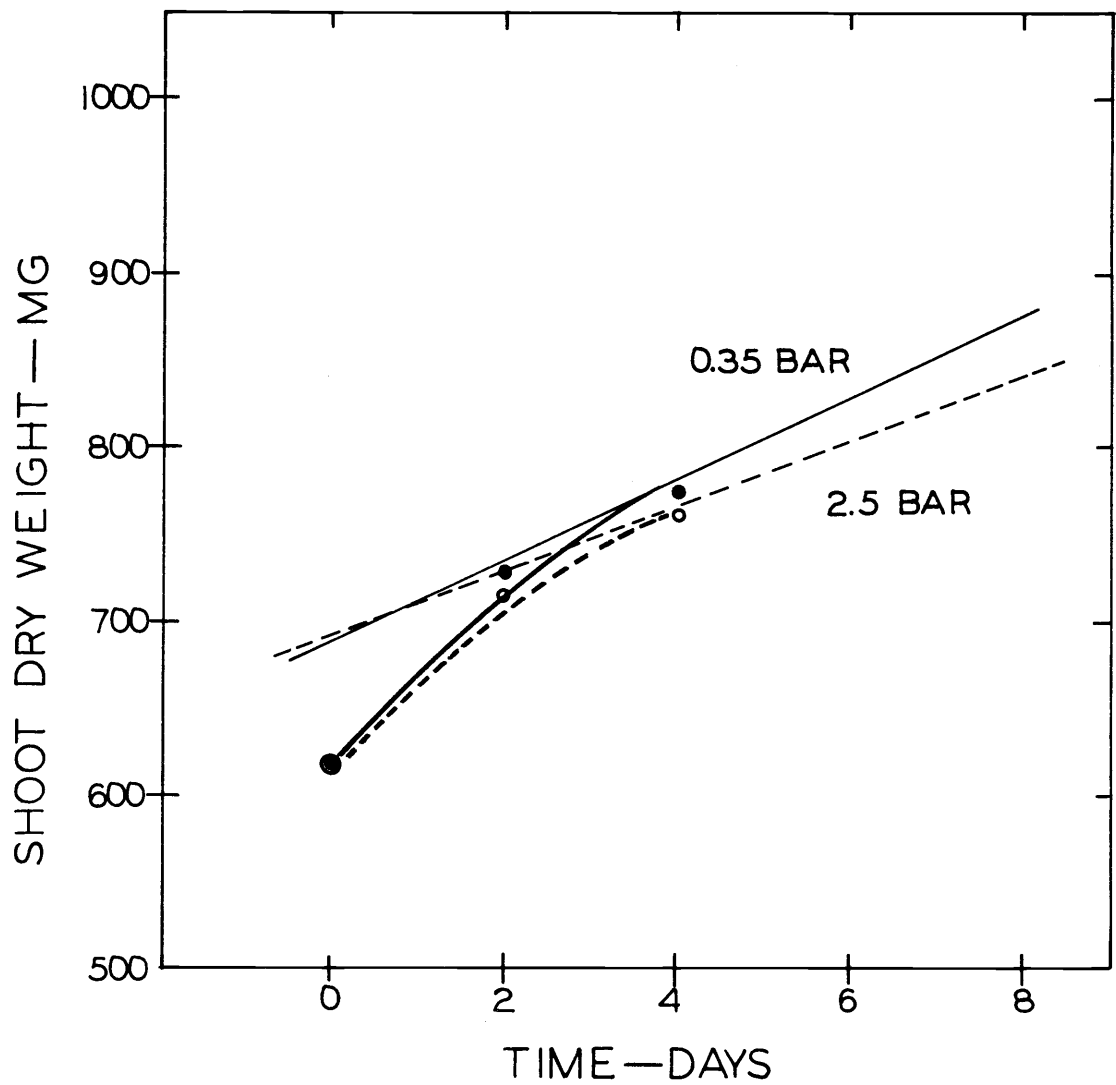


Figure A-5. Dry weight of shoots in mg per chamber for 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars and a soil temperature of 32.2°C.

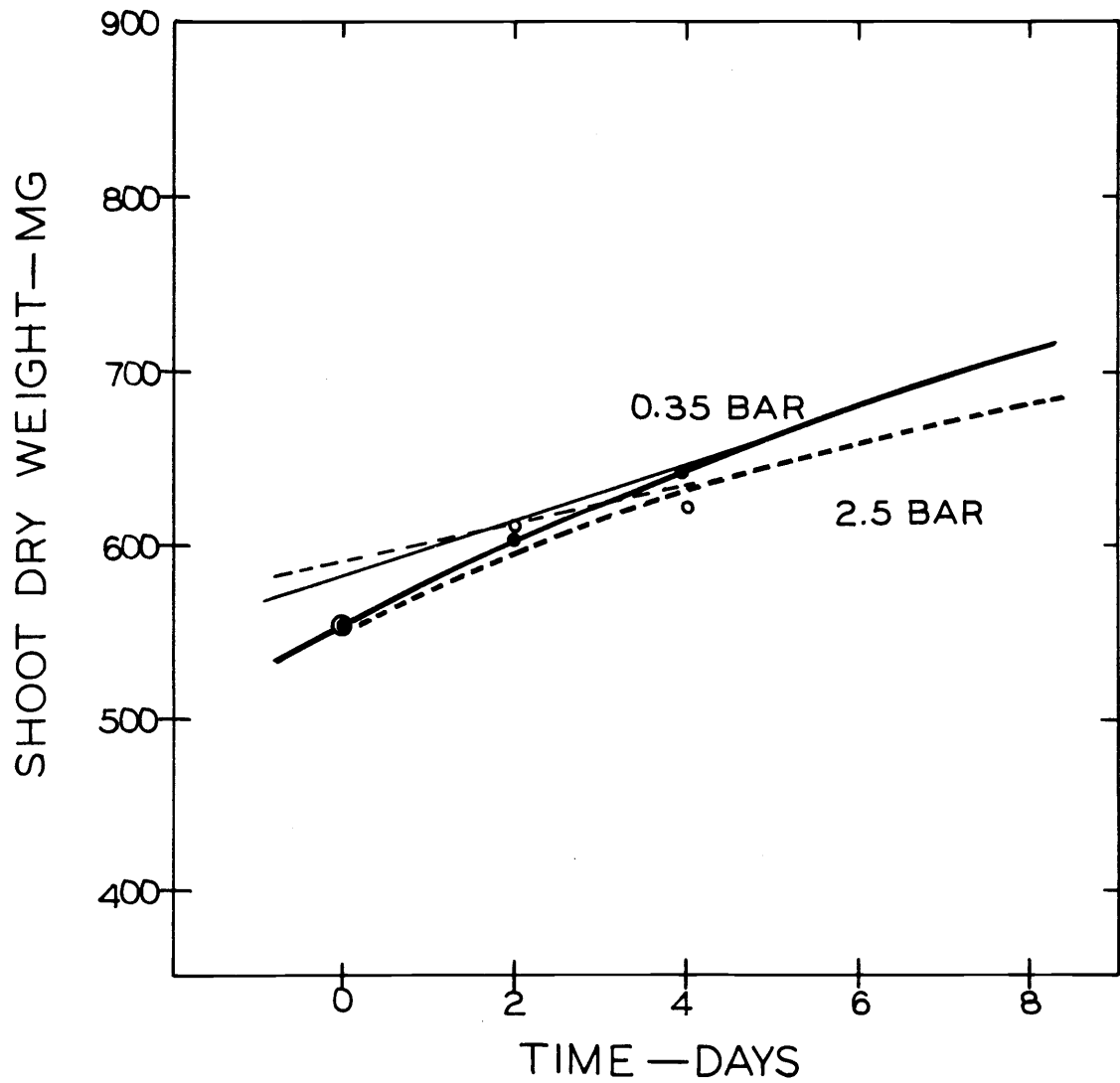


Figure A-6. Dry weight of shoots in mg per chamber for 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars and a soil temperature of 35.0°C.

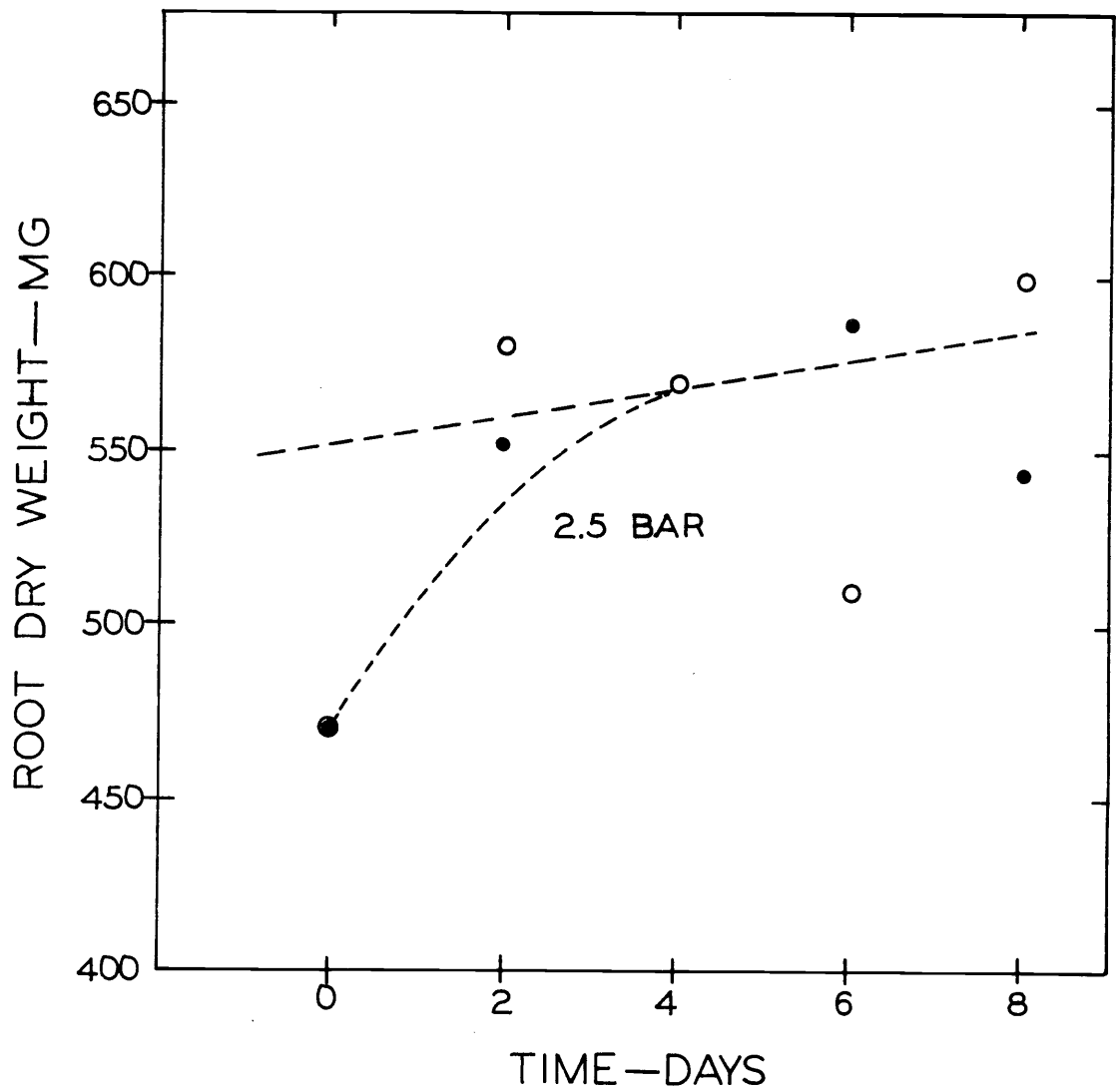


Figure A-7. Dry weight of roots in mg per chamber for 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars and a soil temperature of 10.0°C.

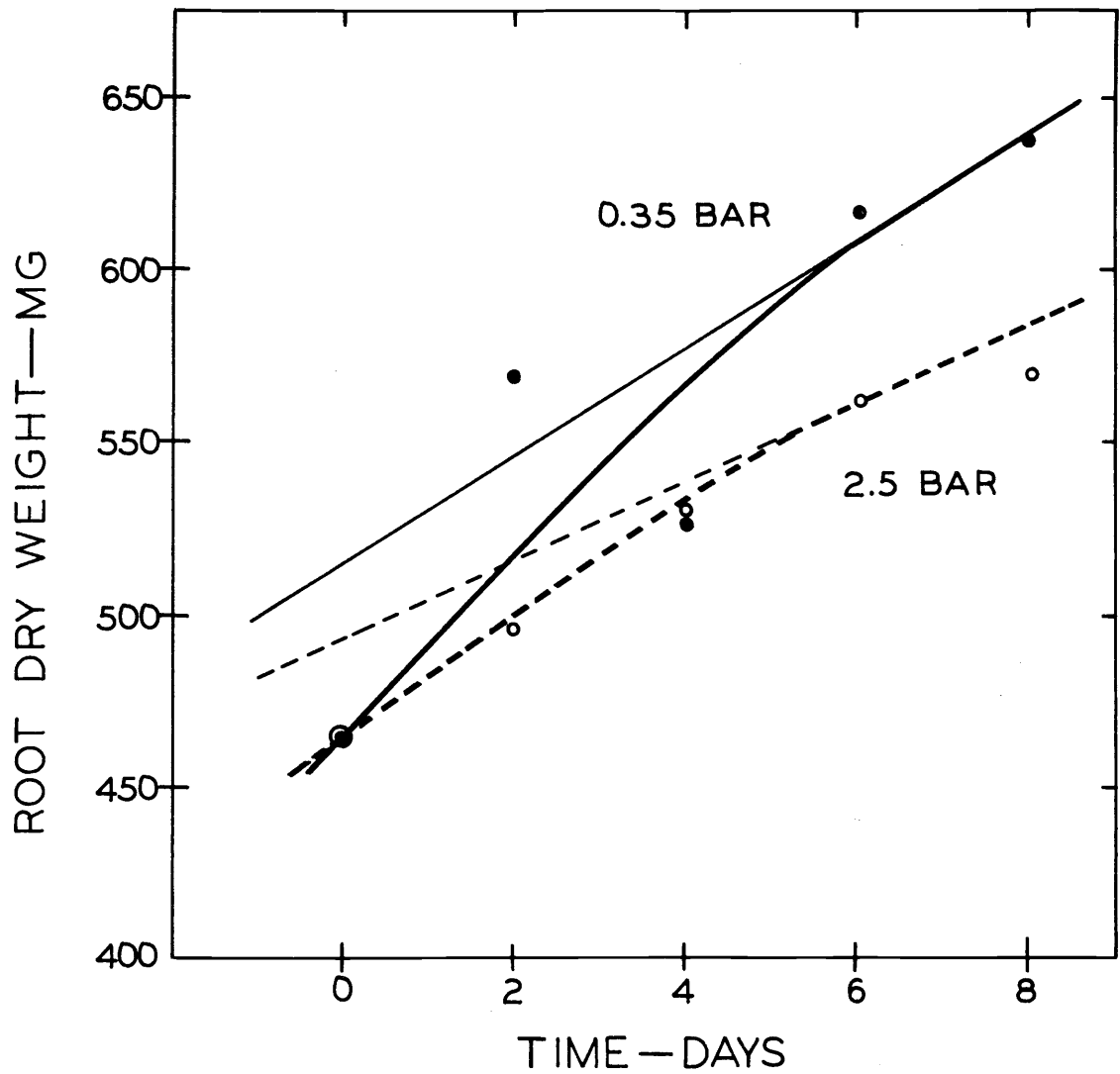


Figure A-8. Dry weight of roots in mg per chamber for 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars and a soil temperature of 18.3°C.

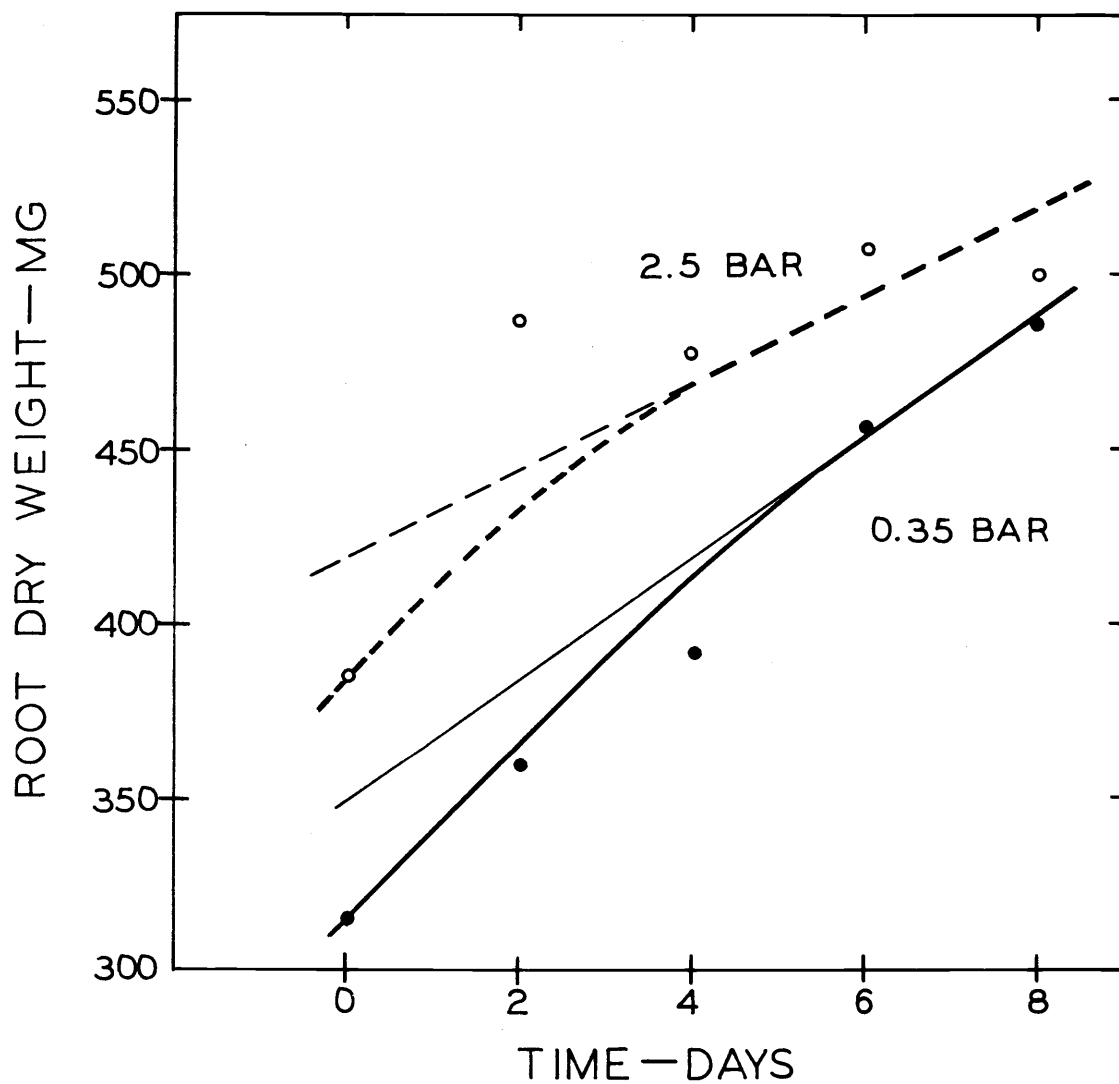


Figure A-9. Dry weight of roots in mg per chamber for 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars and a soil temperature of 23.9°C.

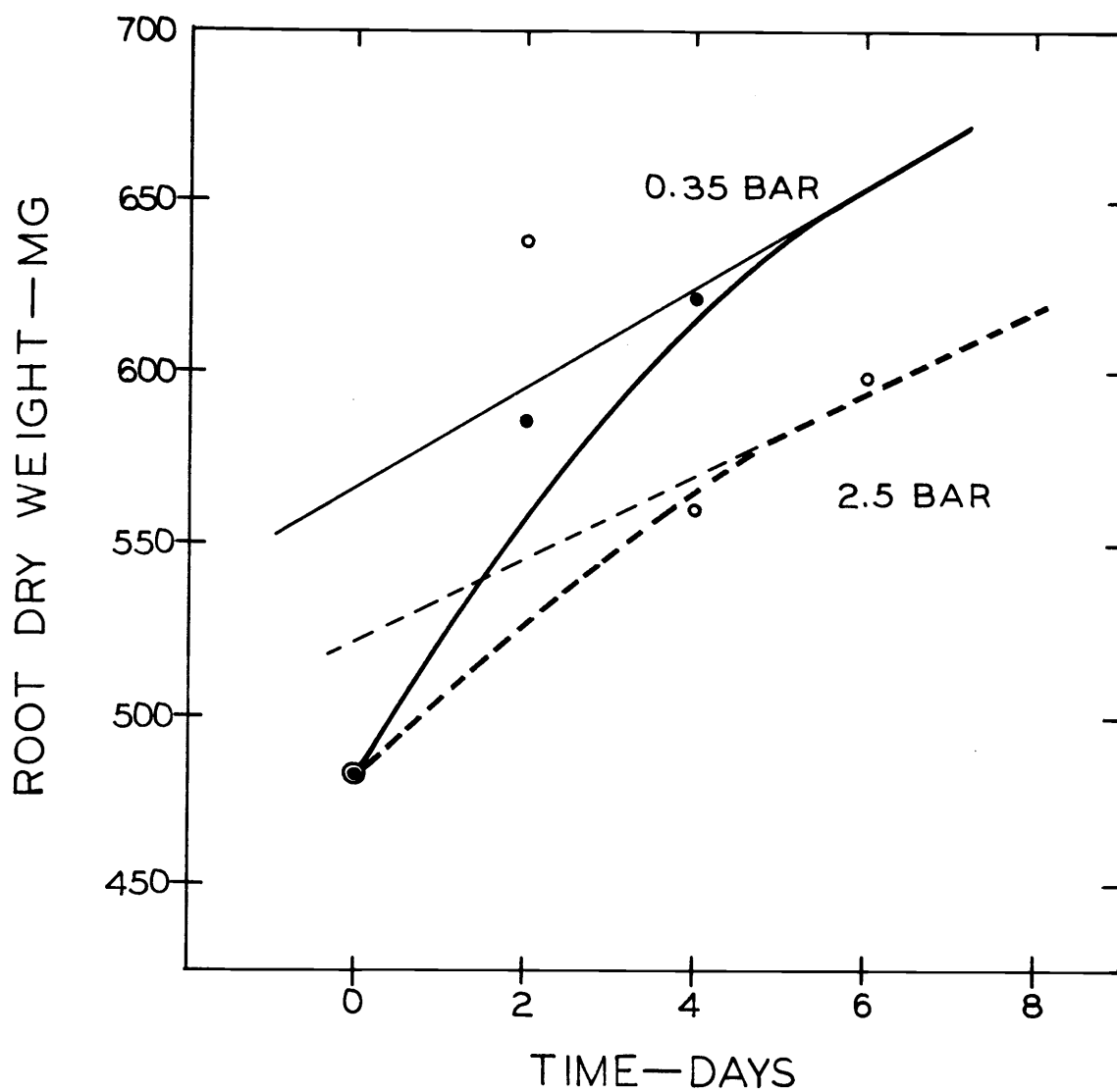


Figure A-10. Dry weight of roots in mg per chamber for 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars and a soil temperature of 29.4°C.

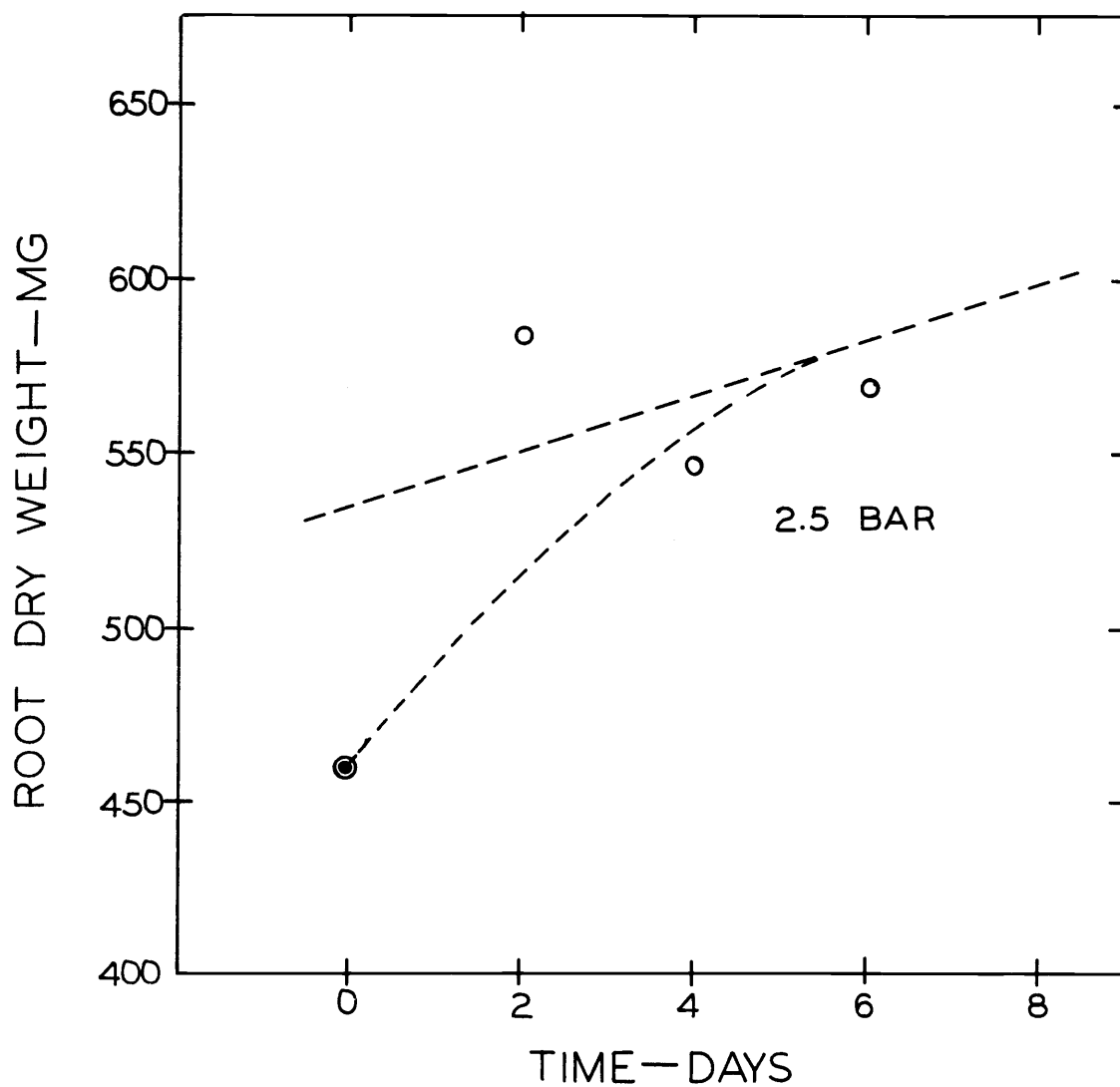


Figure A-11. Dry weight of roots in mg per chamber for 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars and a soil temperature of 35.0°C.

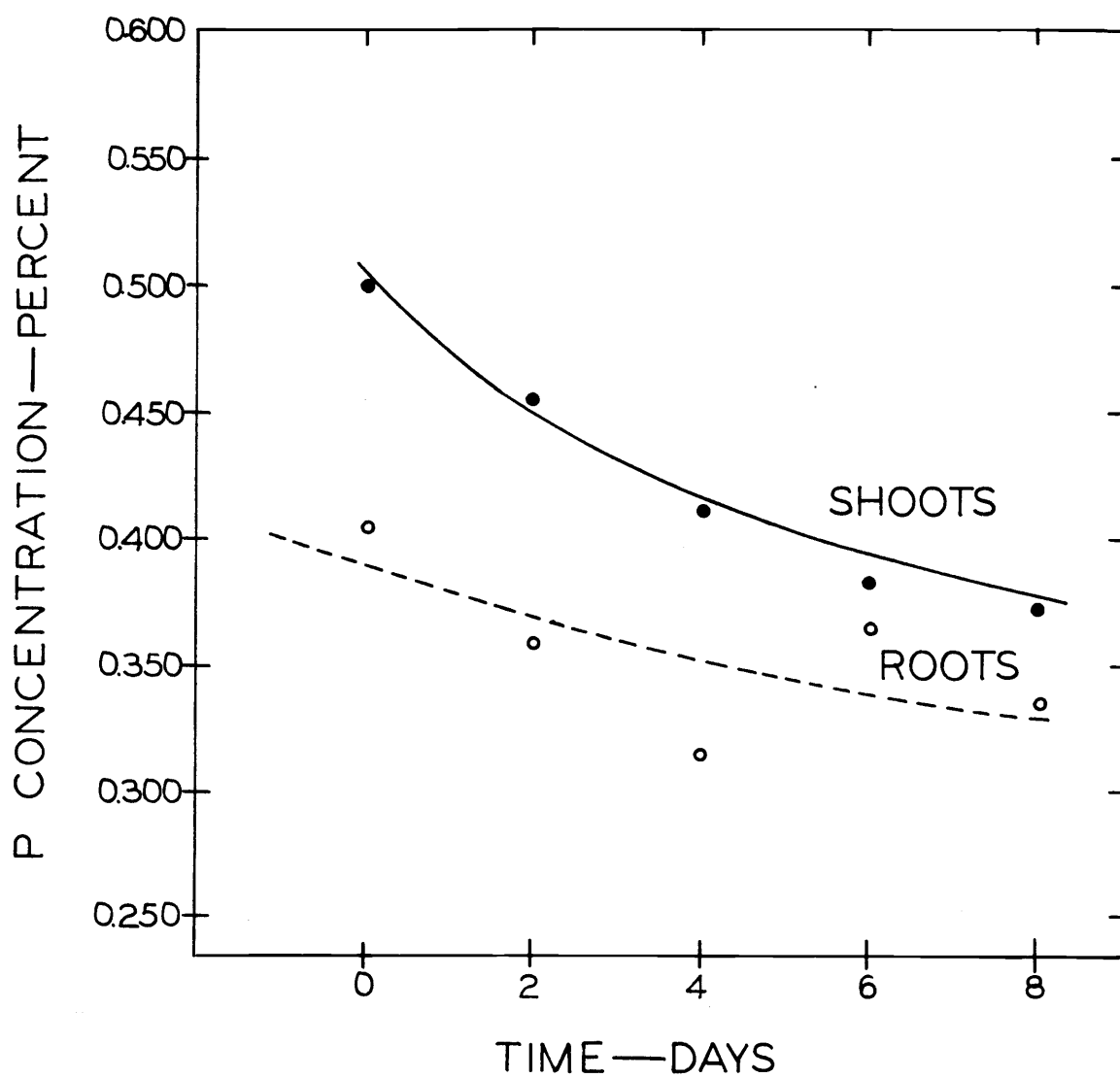


Figure B-1. Percent phosphorus in shoots and roots of 5-week old wheat seedlings as a function of time at a soil water suction of 0.35 bar and a soil temperature of 10.0° C.

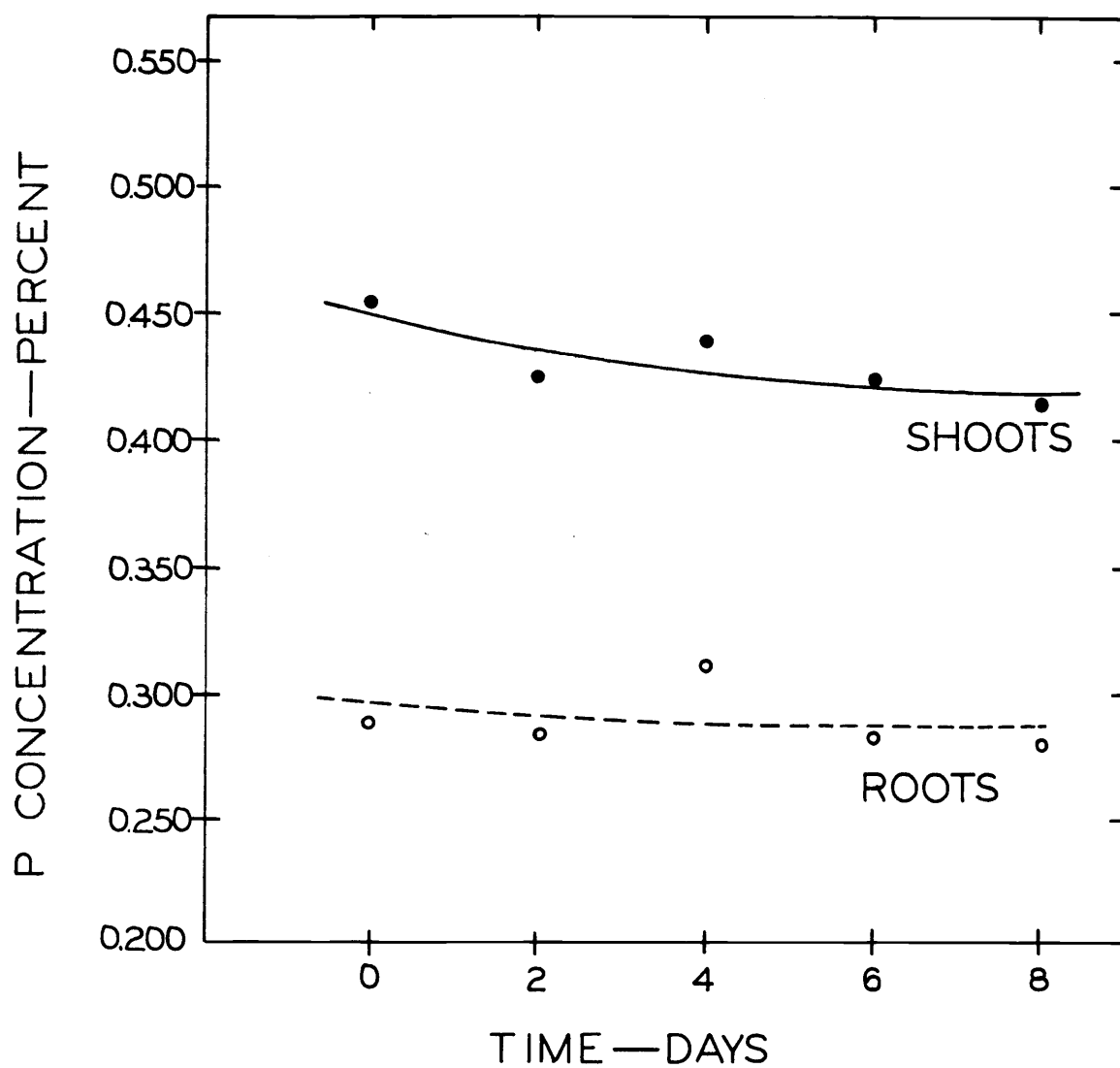


Figure B-2. Percent phosphorus in shoots and roots of 5-week old wheat seedlings as a function of time at a soil water suction of 0.35 bar and a soil temperature of 18.3° C.

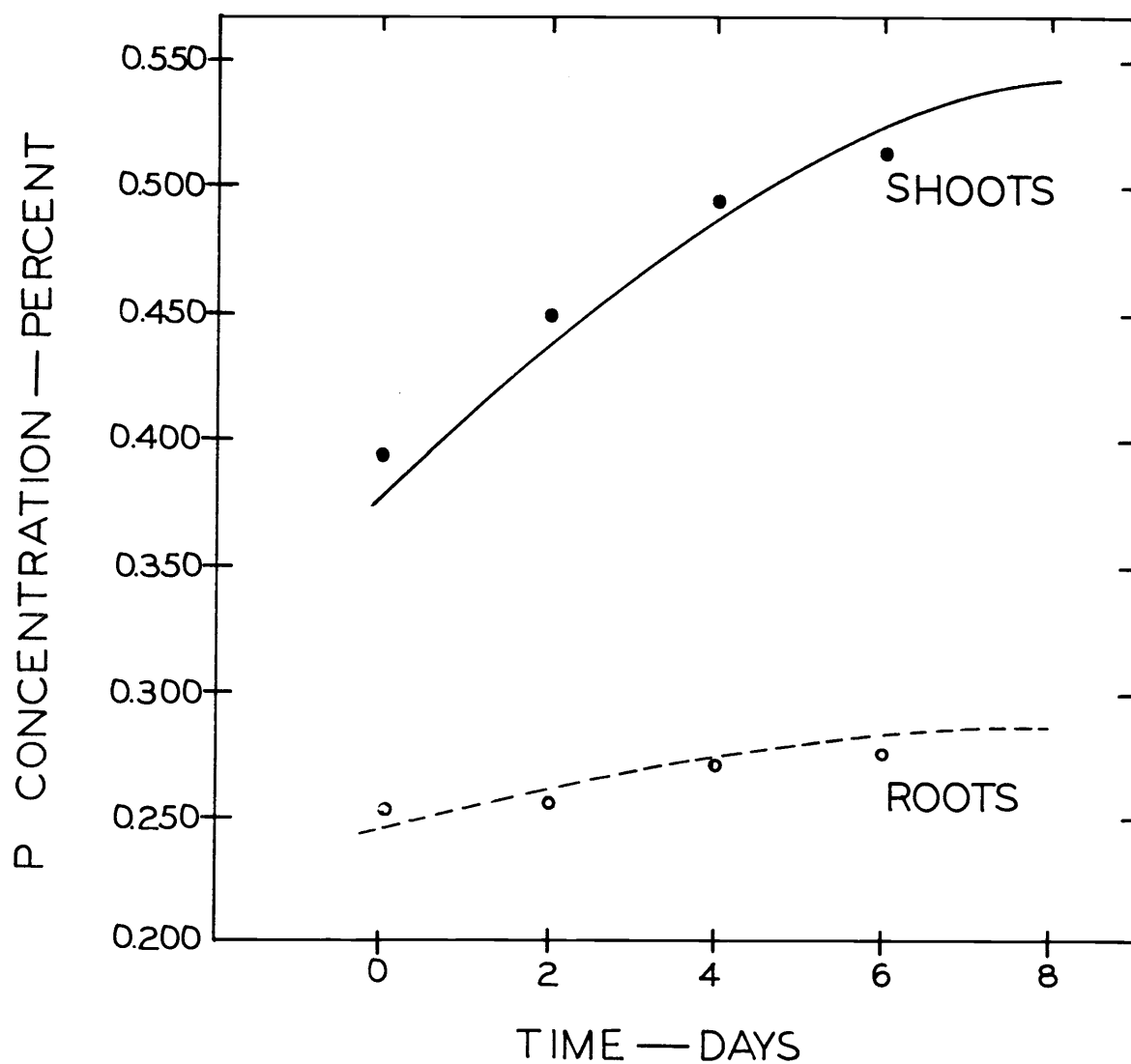


Figure B-3. Percent phosphorus in shoots and roots of 5-week old wheat seedlings as a function of time at a soil water suction of 0.35 bar and a soil temperature of 23.9°C.

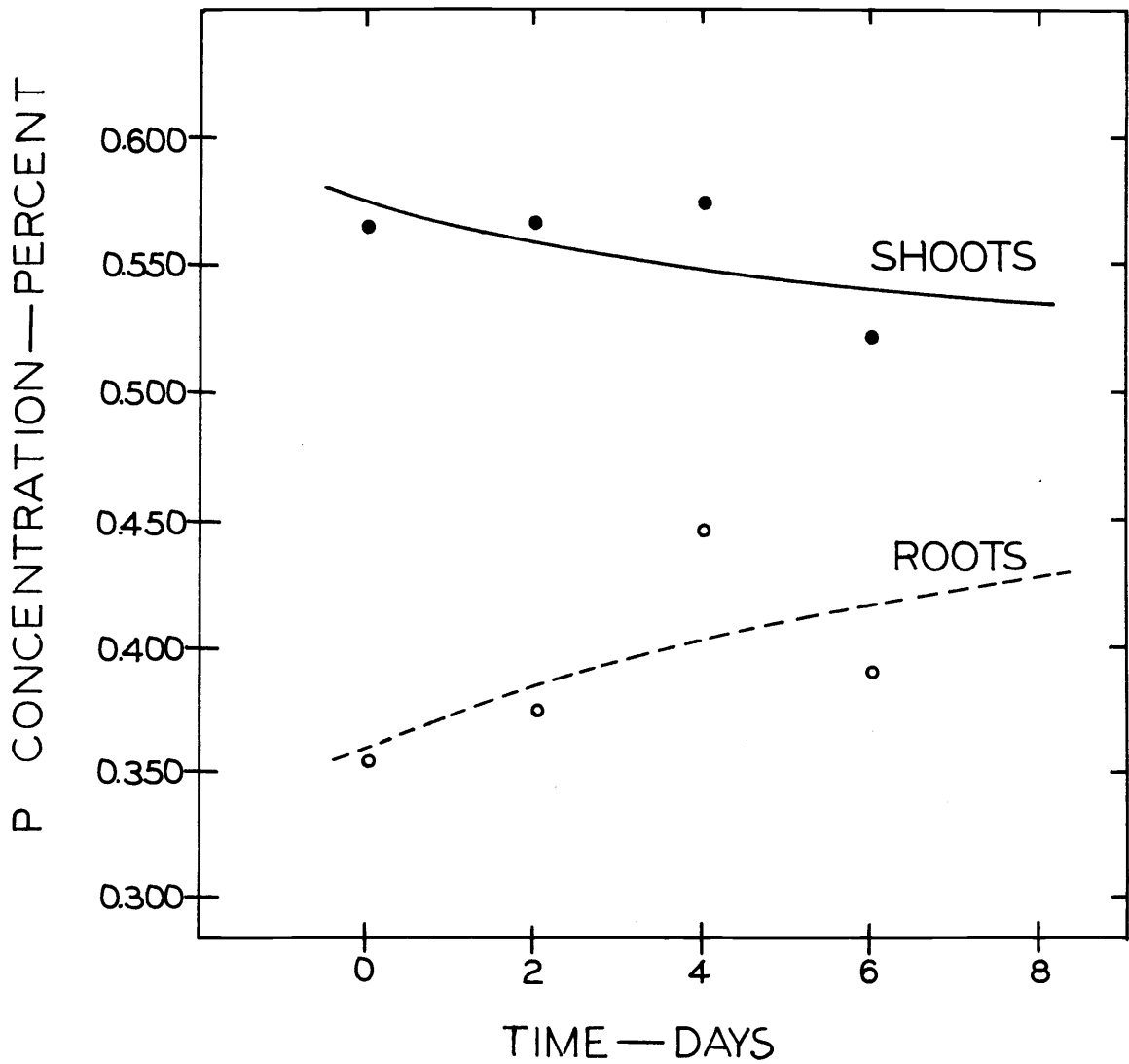


Figure B-4. Percent phosphorus in shoots and roots of 5-week old wheat seedlings as a function of time at a soil water suction of 0.35 bar and a soil temperature of 32.2°C.

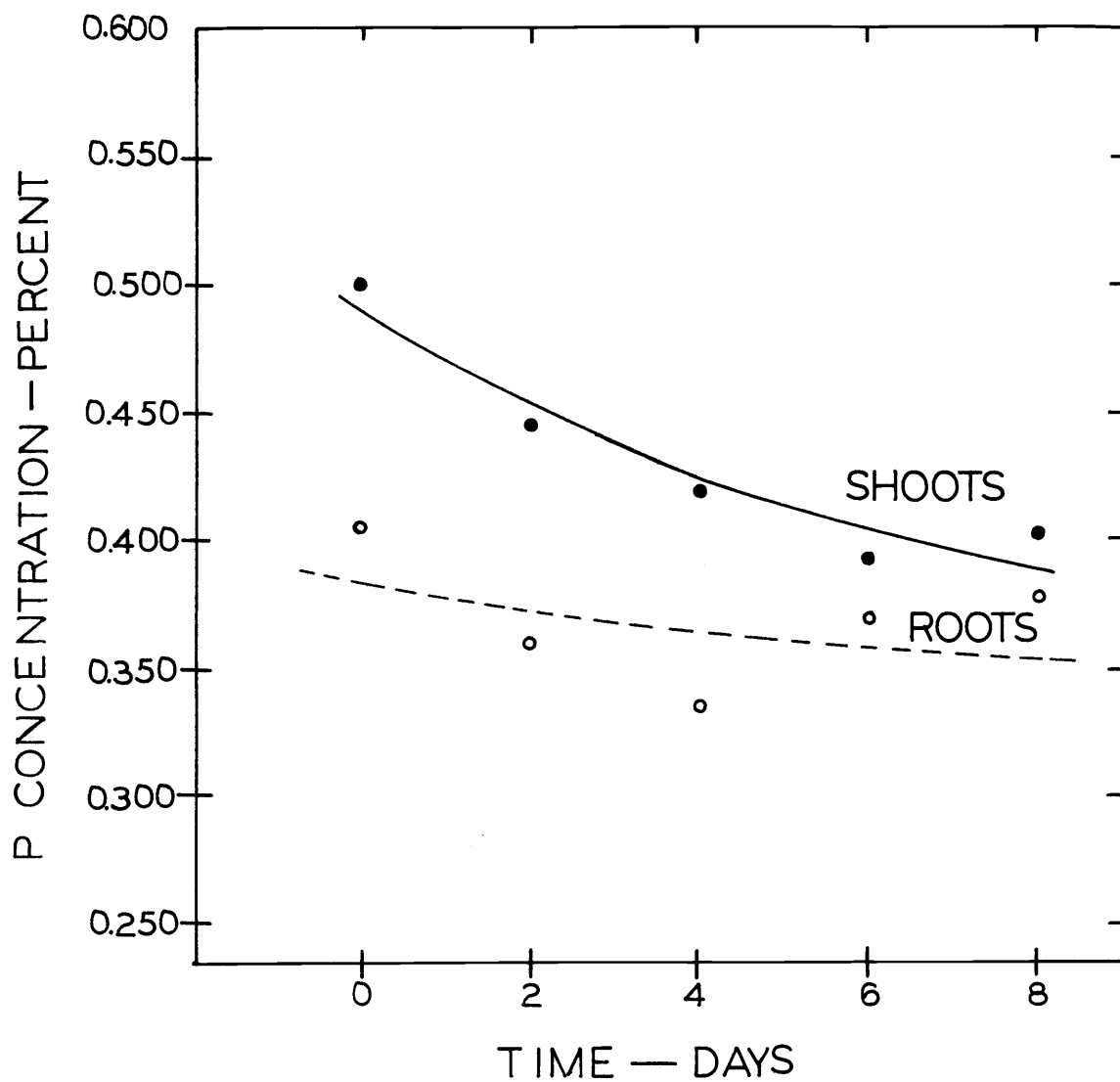


Figure B-5. Percent phosphorus in shoots and roots of 5-week old wheat seedlings as a function of time at a soil water suction of 2.5 bars and a soil temperature of 10.0°C.

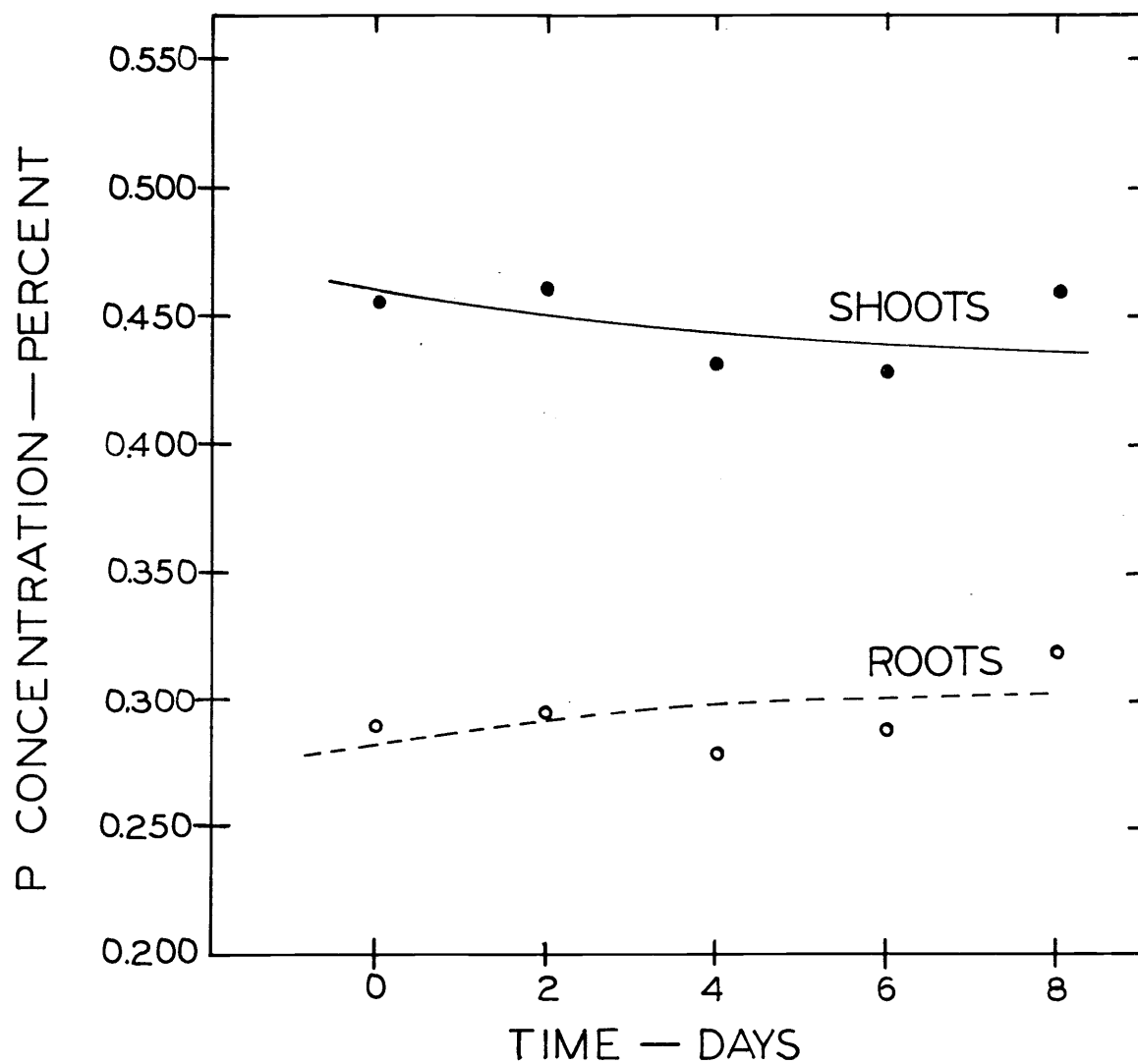


Figure B-6. Percent phosphorus in shoots and roots of 5-week old wheat seedlings as a function of time at a soil water suction of 2.5 bars and a soil temperature of 18.3°C.

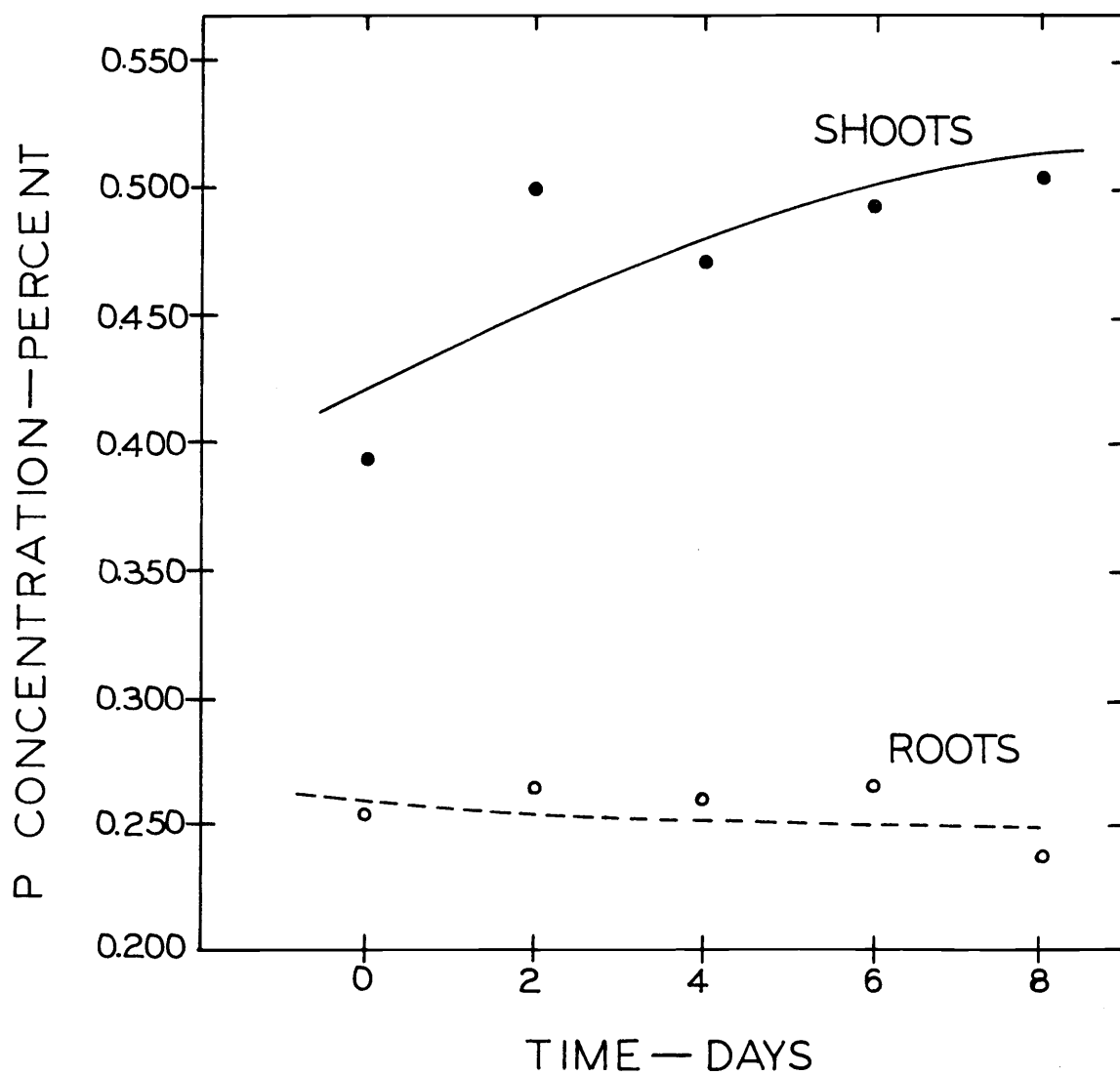


Figure B-7. Percent phosphorus in shoots and roots of 5-week old wheat seedlings as a function of time at a soil water suction of 2.5 bars and a soil temperature of 23.9°C.

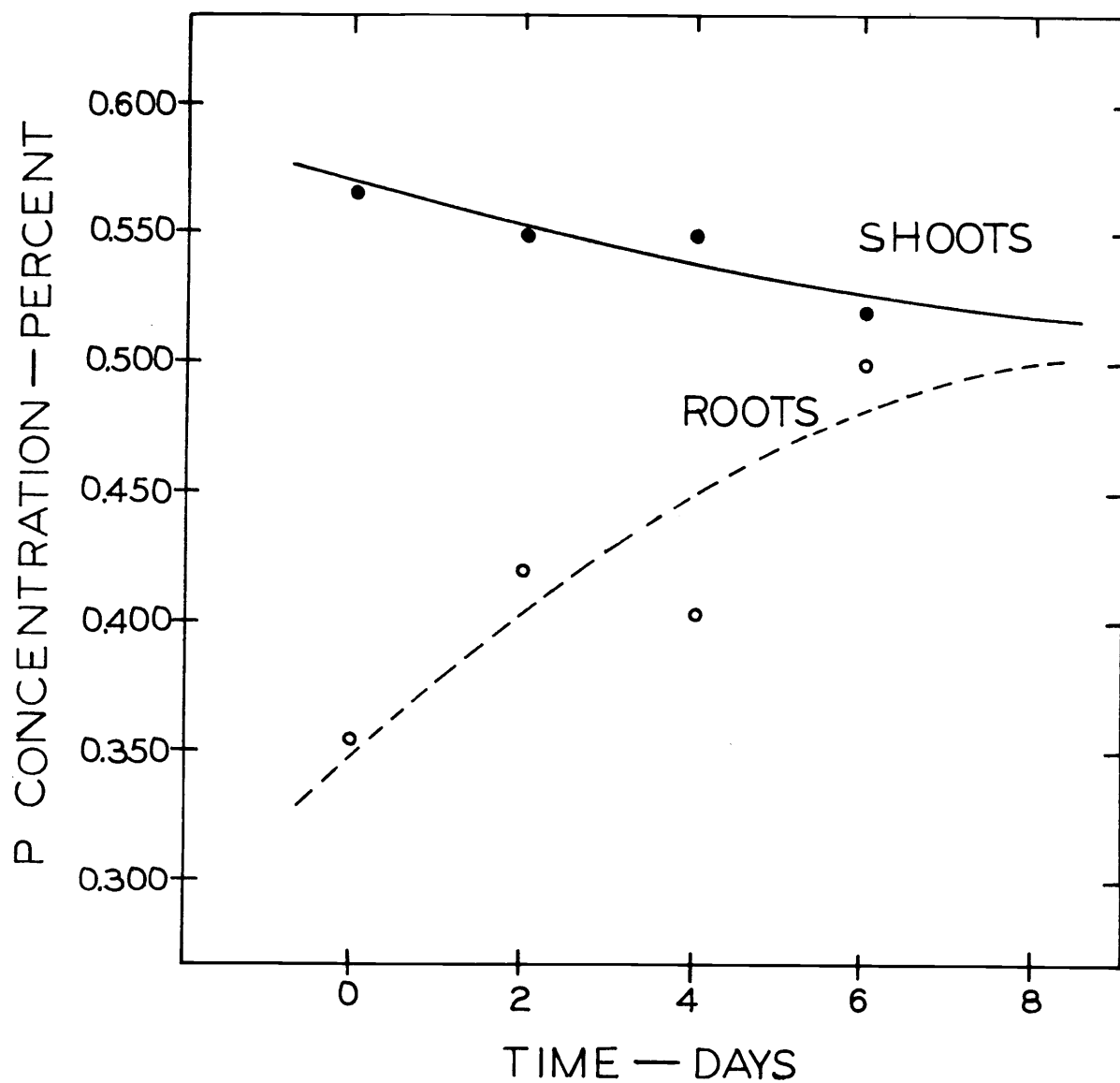


Figure B-8. Percent phosphorus in shoots and roots of 5-week old wheat seedlings as a function of time at a soil water suction of 2.5 bars and a soil temperature of 32.2°C.