

AN ABSTRACT OF THE THESIS OF

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Title: ION UPTAKE BY WHEAT (TRITICUM AESTIVUM VILL.,
HOST) AS A FUNCTION OF SOIL WATER SUCTION AND
SOIL TEMPERATURE

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The effects of soil temperature and soil water suction on the uptake of calcium, magnesium, and potassium by wheat (Triticum aestivum VILL., Host) were studied. Companion studies on uptake of nitrogen and phosphorus provided background for discussion of the results. Plants were grown in perlite slabs separated from an osmotic solution by a semi-permeable membrane. Five week old seedlings were used for the measurements made at root temperatures of 10.0, 18.3, 23.9, and 32.2°C, and soil water suctions of 0.35 and 2.5 bars. Air temperature remained constant at 23.9°C during these experiments. The dry weight of shoots and roots was determined at two-day intervals. Plant material extract was analyzed by atomic absorption spectrophotometry for concentrations of calcium, magnesium, and potassium.

Rates of dry weight accumulation for both shoots and roots were highest when temperature of the root environment was about 24°C. The rate of growth was higher at a soil water suction of 0.35 bar than at 2.5 bars for all root temperatures tried. Concentrations of potassium, nitrogen, and phosphorus increased with increasing root temperature in both shoots and roots. By contrast, concentrations of magnesium were minimally affected by temperature differences; concentration increased slightly in the roots as temperature increased but remained the same in the shoots. Concentration of calcium in both shoots and roots decreased as temperature increased. This was attributed to a combination of ion interaction and temperature effects. The rate of uptake for all five elements, i. e. , calcium, magnesium, potassium, nitrogen, and phosphorus increased to a maximum rate and then decreased with increasing root temperature.

The translocation of ions to the shoots was lowest for calcium. The fraction of total uptake translocated to the shoots was for: magnesium, 69%; potassium, 83%; nitrogen, 74%; phosphorus, 72%; and calcium less than 50%. Calcium content in the shoots was less than in the roots. The limited translocation of calcium to the shoots was attributed to its high degree of immobility. It was retained by the roots in relatively high concentration.

The mineral concentration of plants grown at soil water suctions of 0.35 and 2.5 bars were not significantly different statistically

while there was a significant reduction in the rate of plant growth at a soil water suction of 2.5 bars. As a result of the reduced growth rate at the higher suction the rate of ion uptake was also reduced even though the concentrations in the plant tissue at the two suctions were the same. Under the conditions of these experiments water availability affected plant growth apparently more by its effects on plant physiological functions other than mineral uptake.

Ion Uptake by Wheat (Triticum aestivum VILL.,
Host) as a Function of Soil Water Suction and
Soil Temperature

by

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ION UPTAKE BY WHEAT (TRITICUM AESTIVUM VILL., HOST)
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INTRODUCTION

The effect of soil temperature on growth and nutrition of plants has received increasing attention in recent years. Effect of temperature on ion uptake varies with different nutrient elements and different plant species. Generally, high root temperature accelerates the ion accumulation process, while low root temperature retards the ion uptake rate.

Temperature effects associated with physiological factors, such as the solubility of nutrients, root respiratory activity, and transpiration could be important factors in the nutrient absorption by plant. Suggestions are that low rates of nutrient uptake at low temperature result largely from decreased root elongation and slow plant growth. However, low soil temperatures can affect growth in many ways and it is difficult to isolate the specific causes for depressed nutrient absorption. Low soil temperatures for example markedly reduce the conversion rate of inorganic to organic nitrogen in the roots but many other physiological activities are altered also.

Soil water suction may limit plant growth by restricting ion absorption. Large decreases in the degree of root and shoot hydration accompanying increases in soil water suction may result in reduced

ion uptake. Effects on nutrient uptake are complex as a result of various effects on processes in the roots, but are attributed to two principle mechanisms: (1) decreased rate of water movement to the roots thereby decreasing the supply of nutrients at the root surface, and (2) the immediate effect on the hydrational status of the root tissue which in turn influences metabolic activities in the cells.

The purpose of this study was to measure rates of nutrient uptake of wheat seedlings at different root temperatures and soil water suctions. It was anticipated that an inspection of the results might lead to a better understanding of the effects of soil temperature and soil water suction on plant growth. The experiments were designed to eliminate rate of nutrient supply at the root surface as a variable, a confounding feature in other studies.

Also hopefully, the investigation of temperature effect on nutrient uptake may give an idea for further research work on the use of waste heat from power stations to control soil temperature for maximum agricultural production. Study of the moisture suction variable can lead to a better understanding of drought resistance of plants and aid in the selection of crops in drier areas. This study investigated both the temperature and moisture suction effect on ion uptake which differs from most previous work where only one factor was considered.

REVIEW OF LITERATURE

Ion Uptake

The absorption of ions by intact plants involves their movement from soil to root surfaces, accumulation in root cells, radial movement from root surfaces into xylem, and translocation to shoots. The ability of cells to accumulate ions to a concentration higher than that in their environment is an outstanding characteristic of living organisms. One theory of accumulation proposes (a) that anion accumulation is by active transport linked directly to metabolism and (b) that cations move passively along potential gradients established by the movement of anions. A more widely accepted theory assumes that ions form temporary combinations with special organic molecules called carriers, and that the resulting complex can move through cell membranes which are impermeable to ions alone. This theory says that ions then separate from the carriers at the membrane surface and move into the vacuoles, while the carrier molecules again become available to move more ions. Metabolic energy is required both for synthesizing the carrier molecules and maintaining the integrity of membrane structures. Organic acid metabolism is also involved in the maintenance of the ionic balance.

Experiments by Broyer (1950) and others indicate that shoots

tend to absorb ions directly from the root xylem rather than from the vacuoles of the root cells. Thus, the vacuoles probably function as diversionary sinks for salts rather than as a major pathway for movement, at least in low-salt plants (Broyer, 1950; Epstein, 1960).

Apparently ions also "move in" through the free space of the cell walls by diffusion and by mass flow in the transpiration stream, at least until they reach an ion barrier. This idea was proposed long ago by Scott and Priestley (1928). In this case, the controlling absorbing surfaces would be the outer surface of the ion barrier rather than the root epidermis. In contrast to this view, Lundegardh (1955) seemed to regard the epidermis as an important ion barrier in roots. Leggett and Gilbert (1967) reported that 90 percent of the calcium in soybean roots occurs in the epidermis, while potassium was uniformly distributed throughout the roots.

Hylmo (1953) suggested that the salt in the xylem sap is first accumulated by protoplasts which die and release the accumulated salt during the formation of xylem elements, a view advanced earlier by Priestley (1922).

Two processes involving ions occur simultaneously in roots, (1) the accumulation of ions in root cells and (2) the radial movement of ions inward across the living cells to the xylem. By comparison to the first, not much is known about the second process. In 1951 Biddulph wrote that the radial movement of minerals through roots

into xylem is one of the least understood processes in the realm of mineral absorption and translocation. A decade later Russell and Barber (1960) expressed the same opinion, and a second decade later one could justifiably repeat it.

It is generally assumed that once ions or other solutes have reached the xylem, they are carried upward in the sap stream. A number of investigators have supplied radioactive tracers to roots and found translocation to the shoots at rates up to 60 m/hr, the higher rates occurring in rapidly transpiring trees (Kramer and Kozlowski, 1960). Tracers supplied to the roots of herbaceous plants also often reach the shoot in less than an hour. All these observations support the view that ions move upward chiefly by mass flow in the xylem. Some have questioned mass-flow transport for ions such as calcium, however. Bell and Biddulph (1963) concluded from their data that calcium moved by exchange rather than mass flow. On the other hand, O'Leary (1965) observed the translocation of radioactive calcium paired with phosphorus or rubidium and concluded that they moved by mass flow.

Evaluating the upward movement of ions is complicated by the fact that not all the transport of salt occurs as inorganic ions. In many species, most or all of the nitrogen is probably transported in organic compounds such as amides, amino acids, and ureides. Limited evidence also suggests transport of at least small amounts of

sulfur (Pate, 1965) and phosphorus as organic compounds in the xylem. Additional complications include recycling of ions--back down through the phloem and again up the xylem--plus the tendency of certain ions to be precipitated in the xylem. Hewitt and Gardiner (1956) reported that considerable amounts of zinc are absorbed on the walls of the xylem vessels in grape.

Attempts to mathematically describe the movement of ions to the plant root by diffusion and by mass flow continue to be made. Some examples are cited below. Frere's (1969) analysis of a plant root system taking up ions at a constant rate showed that the apparent diffusion coefficient of each ion can change with time, distance from root, composition of the solution, and the rates of uptake of all the ions. The flux of an ion in solution, ($\text{eq}/\text{cm}^2\text{-sec}$), under the influence of concentration and potential gradients can be described by

$$\frac{\partial Q}{\partial t} = \frac{\mu}{|Z|} \left(\frac{RT}{T} \frac{\partial C}{\partial x} + Z_c \frac{\partial E}{\partial x} \right)$$

where Q = ion flux ($\text{eq}/\text{cm}^2\text{ sec}$), R = universal gas constant (8.31 joules/deg mole), F = Faraday (96,500 coul/eq), T = Kelvin temperature ($^{\circ}\text{C}$), Z = valence, C = concentration (eq/cm^3), μ = ion mobility (cm/sec), at infinite dilution under an electrical gradient of 1 v/cm, t = time (sec), E = electrical potential (volts), and x = linear distance (cm).

Barber (1962) proposed a linear model that satisfactorily described movement of ions to plant roots as follows:

$$J = D_1 \frac{dC_1}{dx} + D_2 \frac{dC_2}{dx} + C_3 v + a$$

where J = total quantity of ions reaching the root per unit time per unit area of root surface (moles/cm²sec), D_1 = the diffusion coefficient of the ions in the soil solution (cm²/sec), D_2 = the diffusion coefficient for the movement of ions on the particle surface (cm²/sec), C_1 = the concentration of the ions in soil solution that are not associated with the particle surface (moles/cm³), C_2 = the concentration of the ions moving on the solid surfaces (moles/cm³), C_3 = the concentration of the ions in the solution that is flowing through the soil with a velocity v toward the root surface, x = linear distance (cm), v = velocity of ions flowing through the soil toward the root surface (cm/sec), and a = replenishment factor.

Movement of ions through the soil to the root surface involves mass flow, and diffusion. The process having greatest effect on availability of a particular nutrient depends on: the concentration of the nutrients in the water reaching the root; the amount of water uptake, which affects the flow rate of water to the roots; and the rate of absorption of the nutrients by the plant root. When more nutrient is moved by mass-flow to the root than the root absorbs, the nutrient

accumulates at the root interface and mass-flow clearly is the dominant factor. Diffusion is the dominant factor controlling availability when mass-flow brings only a small fraction of the nutrients required by the plant root. Porter et al. (1960) considered that the environment of metabolically active plant roots was a function of "Diffusion processes, mass flow processes and immobilization processes."

Eaton and Bernardin (1964) measured the effect of "mass flow of soil solutions to root surfaces" on salt accumulations in plants. They compared differences in salt uptake by barley, cotton, and tomatoes grown in parallel in soil and aerated water cultures. Results showed that, with transpiration, the mass flow of the soil solution to root surfaces accentuated the accumulation of some ions in plants.

Danielson and Russell (1957) examined the relationship between soil-moisture content and uptake of rubidium by corn roots. They believed an increased uptake of rubidium at higher moisture levels was due to the existence of thicker moisture films through which the ions could diffuse. Wiersum (1958) also indicated that greater soil water content increased ion uptake at low ion concentrations because it increased the rate of diffusion. Apparently, many investigators assume that the ions at the root surface are replenished from the soil as rapidly as the ions are absorbed by the plant. The nutrient environment of the root is thus assumed to be the same as the average nutrient content of the soil.

In contrast to the preceding, 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 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. Barber (1962) stated that the mass flow of water to the root surface may cause an increase in concentration relative to the soil and diffusion will occur away from the root. Oliver and Barber (1966), and Olsen and Kemper (1968) illustrated this phenomenon. Ion uptake by the plant would create a concentration gradient so that ions might then diffuse along the soil particle toward the root.

Interaction Between Calcium, Magnesium, and Potassium Uptake

Ion uptake by plants involves interactions between the major nutrient cations, K^+ , Ca^{2+} , and Mg^{2+} as well as Na^+ and H^+ . Leggett and Gilbert (1969) studying the uptake of magnesium by soybean roots from $MgCl_2$ solutions over a concentration range of 0.1 to 10 mM, found that an increase in Mg^{2+} concentration depressed Ca^{2+} and K^+ content in roots. Conversely, magnesium uptake was only slightly reduced in the presence of either calcium or potassium alone. Simultaneous addition of K^+ and Ca^{2+} to the Mg^{2+} solution drastically reduced magnesium uptake. Inhibiting effect of $K^+ + Ca^{2+}$ on magnesium uptake depressed Mg^{2+} concentrations in the root tissue more

than in shoot tissue. Further observations were that changes in the external calcium concentration over the range of 10^{-4} to 10^{-2} M caused only slight change in calcium content of roots but greatly enhanced that of shoots as the calcium concentration was increased or the K concentration was decreased. These effects on calcium content were explained as arising from transport to the shoot without involvement of the vacuoles of root cells.

Often, calcium and magnesium are considered as similar ions with respect to their absorption by higher plants. Moore et al. (1961) found that a large fraction of the magnesium absorption by excised barley roots was blocked very effectively by small amounts of calcium. The blocking action was quite pronounced, even at calcium concentrations where there was a net loss of calcium from the root to the nutrient solution. They further concluded that calcium markedly decreased the permeability of cells but implied that uniform depression of all ions moving into the cells was not true. Although it markedly decreased the uptake of magnesium, and almost completely blocked the uptake of lithium and hydrogen, calcium either stimulated or had little effect on absorption of potassium, rubidium and cesium from acid solutions.

Elzam and Hodges (1967) found that calcium (or magnesium) sulfate or chloride inhibits energy dependent potassium transport in excised corn roots. This Ca^{2+} (or Mg^{2+}) inhibition of K^+ transport

was most pronounced during the initial phases of transport. They indicated that kinetic analysis showed both corn and barley to have efficient K^+ transporting systems but barley roots were approximately five times more active than corn roots.

The role of calcium in regulating the absorption of ions is well recognized. Its effect on the uptake of the monovalent, alkali ions ranges from highly stimulatory to strongly inhibitory, depending on the ion and H^+ concentration. Maas et al. (1969) studied the interaction effects between manganese, calcium and magnesium during steady-state absorption experiments with excised roots of 5-day-old barley seedlings. They found that calcium enhanced the rate of manganese absorption, whereas magnesium was highly depressive. Of additional interest was that potassium absorption was greatly enhanced in the presence of calcium, magnesium, and manganese. Their data also showed that in the presence of calcium and potassium, the absorption rate of magnesium was reduced. These observations are consistent with those of Leggett and Gilbert (1969). This observation is especially important as it emphasized the fact that both stimulatory and inhibitory effects may be exerted by the same cations at the same time, while no mutually competitive effects are involved.

Rains and Floyd (1970) investigated the influence of calcium on the aging processes of bean stem slices and on the absorption of potassium and sodium by fresh and aged slices. The effect of calcium on

potassium absorption differed in aged and fresh tissue. Increasing concentrations of calcium accelerated potassium absorption by aged tissue but depressed it in fresh tissue. The effect of calcium on sodium uptake in aged stem tissue was qualitatively similar to that found in fresh tissue. The reduction of sodium absorption was attributed to the presence of calcium in addition to an already substantially reduced capacity for sodium uptake as the result of aging. In the presence of calcium, sodium absorption by aged tissue was almost zero. The positive response of potassium absorption to calcium, as well as the requirement of calcium for maximal development of potassium absorption, indicated that potassium uptake by aged tissue is mediated by a mechanism different from the one responsible for sodium uptake, and it was proposed that a new mechanism for potassium transport develops with aging.

Influence of calcium on ion absorption by excised barley roots appears distinctive in that its effect depends upon the species of the monovalent cation undergoing absorption. Jacobson et al. (1961) found that calcium was a very effective inhibitor of lithium absorption and a moderately effective inhibitor of sodium absorption. Calcium drastically altered the ratio of absorption of sodium and potassium from a mixture of the two. With Li and Na + K solutions, the absorption system was extremely sensitive to small concentrations--as little as 10^{-6} M calcium caused a detectable change in absorption rates.

The effect of calcium was enhanced in mixtures compared to single salt solutions of sodium and potassium.

Increasing the concentration of potassium generally depresses the calcium content of plants. Johansen et al. (1968) used barley plants growing in nutrient solutions of low calcium concentrations (250 and 2500 μM). They found that increasing concentrations of potassium (20, 200, 2000 μM) in the nutrient solution depressed calcium content and concentration. They reasoned that the strong depression of calcium absorption at low concentration of potassium must involve a process different from that of high concentrations of potassium. They suggested that at the low concentrations of potassium and calcium, as are likely to be found at the root surface in many soil solutions, the effect of potassium inhibiting calcium absorption may become important in the calcium nutrition of the plants.

Maas (1969) using 5-day-old excised maize roots to investigate calcium uptake, with the tissue inhibited by dinitrophenol and at low temperature, showed that the uptake of Ca^{2+} is influenced by the counter ion, the pH, and concentration of the ambient solution. He pointed out that K^+ and H^+ greatly interfered with Ca^{2+} absorption. Ca^{2+} uptake was essentially blocked at pH 3. The Ca^{2+} to H^+ ratio regulated the uptake as well as the loss of other cations by plant tissue. The increase in potassium concentration greatly reduced the uptake of calcium at pH 6. He suggested that the reduction in calcium

absorption closely associated with the increasing uptake of potassium was due to a competitive effect.

Epstein (1961), using excised barley roots, showed that potassium and rubidium are mutually competitive in the presence of calcium. He indicated that in the absence of calcium, sodium interfered with potassium absorption, and potassium with sodium absorption, at all concentration ratios examined. In the presence of calcium, and at low sodium concentration, sodium interfered only slightly with potassium absorption; at higher concentrations of sodium, there was little or no further inhibition of potassium absorption.

Water Stress and Ion Uptake

The limiting effect of soil moisture deficiencies on plant development is usually attributed to transpirational, photosynthetic, respiratory, and assimilatory changes associated with excessive water stress within the plant. However, as Brown (1953) stated, there is a possibility that low soil water content, or high soil water stress may also limit growth by restricting ion absorption. Increased soil water stress reduced the rate of water supply to the plant root and may thereby decrease the rate of nutrient supply to root surface. Richards and Wadleigh (1952) reported that most experimental evidence showed decreasing moisture supply to be associated with an increased nitrogen content, decreased potassium content, and a variable effect upon the

calcium, magnesium and phosphorus content of the plant tissue.

Mederski and Wilson (1960) used a split-root technique in which the top portion of the roots of corn plants developed in sand culture and the remaining portion of the root system developed in soil adjusted to seven different moisture contents all in the range of wilting point to field capacity. The soil moisture levels were 12.1, 13.2, 14.9, 16.1, 17.8, 19.7 and 20.8%. They found for plant tops and roots that dry weight increased linearly with increasing soil moisture, i. e., decreasing moisture stress. Both percent and total content of potassium, phosphorus, and magnesium in the plants increased with increasing levels of soil moisture. The relative humidity appeared to interact with the effect of soil moisture on ion absorption. Their postulated reasons as to why ion absorption varied with soil moisture were: (a) the continuity of the moisture films was broken at low soil moisture content thus impeding ion transfer from soil to root; (b) the solvent properties of soil water decreased as the thickness of the moisture films decreased; and (c) the amplitude of the cationic swarm surrounding soil particles decreased as moisture content decreased. They also believed that a considerable portion of ions accumulated by the plant were absorbed from the solution phase although contact exchange between root and soil surface may exist. If so, the quantity of soil moisture present would have influenced ion accumulation through a change in the quantity, quality, and mobility of the soil

solution.

Brouwer (1954), Petterson (1966), Greenway and Klepper (1968) indicated that water flow can accelerate ion movement to shoots even when ion transfer depends on active transport. Reasons suggested for this observation are that the mass flow of solution might increase ion delivery to sites of active uptake or alternatively 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 across the root (Brouwer, 1954; Jackson and Weatherley, 1962a).

Rahman et al. (1971) studied metabolic products and accumulated ions at the different developmental stages of a number of plant species grown under different conditions of moisture stress. For levels of water supply corresponding to 125, 200, 275 and 350 mm, they found that decreased water supply favored an increase in total available carbohydrate and total nitrogen. With deficiency in soil moisture, the concentration of the majority of accumulated ions in me/100 g dry wt (K, Na, Ca, Mg, and Cl) increased; for some (P and Fe) it decreased. The sum of total ions accumulated in the plant tissues became greater as the soil water content decreased.

Danielson and Russell (1957) evaluated the uptake of rubidium-86 by corn seedlings from soil and from osmotic solutions. They found that the uptake rate decreased rapidly with initial increases in

soil water suction but leveled out at high suctions to give a nearly logarithmic curve. They concluded that the rate of ion diffusion from the soil to the root decreased as the film thickness decreased. Reduced water intake by roots at high soil water suction would also presumably reduce the movement of water and nutrients to the absorbing surfaces and thus reduce the amount of ions in the proximity of the root.

Hylmo (1953) found a positive correlation to exist between water transport to the root and the uptake of both calcium and chloride ions. He perceived that the magnitude of the ion uptake was dependent on the amount of water transpired but independent of the method used to vary the transpiration and hence the water transport. He presumed that water was drawn passively through cell walls and cytoplasm, but ions could not passively penetrate the vacuoles. The ions were detained at the root surface, or were stopped at the epidermal vacuoles; they were mostly returned to the medium when not absorbed by the plant.

Shapiro et al. (1960) pointed out that a moisture gradient develops in the soil near the root surface as water is absorbed by roots. Consequently, there is a movement of soil moisture from the bulk soil to the layer near the root surface. The mass fluid transfer of soil water under a moisture tension gradient masks any diffusion concentration gradients that may exist. Thus, transpiration may

affect ion uptake in the plant by inducing moisture gradients in the soil. If the soil near the root surface becomes so dry that the transfer of soil moisture through this soil layer to the root takes place in the vapor phase, the soil water diffusivity coefficient is still ten fold greater than the diffusion coefficient of phosphate ion in free solution. Philip (1958) pictures this layer of dry soil acting as a vapor gap which Bonner (1959) describes as a semipermeable membrane, permeable to the passage of water but impermeable to the passage of ions.

Dean and Gledhill (1956) used excised root mats of young rye seedlings that were pressed upon sand containing a known amount of P_{32} labelled phosphate. They found that active roots preconditioned at low moisture stress and subsequently placed in contact with dry soil, absorbed phosphorus rapidly from this soil, while water was simultaneously being drawn from the roots to the dry soil. On the other hand, roots conditioned at high moisture stress absorbed phosphorus at a reduced rate.

Wiersum (1958) determined the rate of rubidium-86 uptake by excised young root pieces of the broad bean (Vicia faba) buried in 100 g of washed sand to which $\pm 2 \mu\text{c}$ rubidium-86 and a varying amount of water were added. He found that if only a minute amount of rubidium was present in the sand, the uptake greatly increased as the amount of water used increased from 2 to 20 ml. If, however, a large amount of unlabelled rubidium was added, the reverse trend occurred

and uptake decreased slightly with increasing moisture content. He concluded that the relation between moisture content of the medium and rate of uptake depended on the amount of soluble substance.

Fawcett and Quirk (1960) investigated the effect of soil-water-stress on the uptake of phosphorus by wheat plants (Triticum aestivum). They suggested that as the soil water-stress increases, the large 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 found that increasing water-stress did not affect the rate of phosphorus uptake by young wheat plants--provided that the plants were not damaged by wilting. They also concluded that the available soil phosphorus was mainly held in fine pores that remained full of water even when the plants were wilting.

Water Stress and Calcium, Magnesium, and Potassium Uptake

Ion uptake by plants can be influenced by a number of environmental factors, including soil moisture supply. As growth is limited materially by soil moisture, total ion uptake will also be limited. Miller and Daley (1925) found appreciably higher percentages of nitrogen, potassium, and calcium in greenhouse corn plants grown at a minimum level compared with an optimum level of soil moisture.

Jenne et al. (1958) from an irrigation study on corn plants stated that the two irrigation treatments involved one with which plots were irrigated to reach a soil moisture tension of 400 cm of water, and the other with no irrigation water applied during the period from June 9 to September 27. They found that the magnesium percentage of whole corn plants was greater for those plants grown under moisture stress than for those plants adequately supplied with water, the difference first becoming apparent at the July 21 sampling. Most of the difference was accounted for by increased accumulation of magnesium in the stalks. Potassium percentages in the leaves, stalks, and the whole corn plant were increased materially by moisture stress. Although potassium accumulation in the plant essentially ceased by the time all the available soil moisture was depleted from the upper 30 inches of the soil, by this time the plants already contained a large proportion of the total amount accumulated under favorable moisture conditions. Calcium percentages in the leaves, stalks, husks, and the whole plant were also increased materially by moisture stress. This effect was apparent at the August 4 sampling. After that time there was essentially no change in calcium percentage of the whole plant where soil moisture was limited, whereas there was a marked decline where moisture was adequate.

Jackson and Weatherley (1962b) using plants growing in nutrient solution imposed a pressure gradient between the medium and xylem

elements of ricinus and tomatoes. Applying a pressure difference of 2 atm, resulted in a doubling of the sodium flux from medium to xylem. The Na flux under a pressure gradient appeared therefore to be metabolism-facilitated. The "metabolism facilitated process" appeared to predominate in the flux of calcium to the xylem of ricinus, but not in the flux through tomato roots.

Wiersum (1966) stated that there are two modes of water supply to fruits. The calcium content of fruits and storage tissue was related to the mode of water supply. He explained the phenomenon by accepting the existence of a mass flow transport in the phloem that restricted transpiration of the tomato fruits, which eliminated accessory entrance of water via the xylem, resulting in a lower calcium content. Reducing the water supply through the phloem by restricting growth rate, resulted in a higher calcium content. This was explained by accepting the xylem as an accessory water supply mode.

Temperature Effect on Water Uptake

Hylmo (1953) found that for many plant species, the water uptake is strongly reduced by lowering the temperature of the roots. At 0-2°C the water transport averaged only 53%, and at 7-11° only 77% of that for plants with a root temperature of 20°C. The drop in water transport was more or less proportional to the drop in root temperature. Kramer (1940) observed that water flow through root systems

increased as the temperature was increased to 35°C, the highest temperature studied.

There are several reasons why a decrease in soil temperature reduces water absorption. Kramer (1969) concluded the most important ones are: (1) decreased root growth, (2) increased viscosity of water--the viscosity of water is about twice as great near 0°C as at 25°C, (3) increased resistance to movement of water into roots, caused by decreased permeability of cell membranes and, (4) decreased metabolic activity of the root cells.

Kuiper (1964a) re-examined the effects of low temperature on water absorption by plants. For a short time at low temperatures, water intake was controlled by the viscosity of water as in nonliving membranes, but after an exposure of 30 minutes an added effect appeared which he attributed to change in permeability of protoplasm. The effect of low soil temperature on transpiration as observed by Tew et al. (1963), was also explained on the basis of decreased permeability of the roots. Kuiper (1964b) further concluded that the temperature effect on water uptake consisted of a low-temperature range with high Q_{10} values, and a high temperature range with low Q_{10} values. The change was rather abrupt at a "critical temperature" which differs according to the temperature at which the plant was grown. He postulated that above this "critical temperature" only the effects of change in viscosity of water limited water uptake. He

believed this indicated the existence of "permanent" water-filled pores in the root cell membranes. Below this critical temperature, the root cell membranes were assumed to be more homogenous and characterized by a high potential energy barrier for water.

Jensen and Taylor (1961) pointed out that the rate of water movement through the plant with respect to time was linear over the temperature range, 10-40°C, studied. This relationship is described by a zero order rate equation, suggesting that the flow of water through the plant was independent of the amount of water that had passed through the tissue. They also suggested that the interaction of the water with the colloids in the root tissues resulted in a molecular mechanism for water flow having an energy barrier greater than that for simple viscous flow or diffusion, but not as great as needed for breaking hydrogen bonds or for vaporization.

Bohning and Lusanandana (1952) studied the change in rate of water absorption as influenced by gradual and abrupt changes in root temperature within the range of 25° to 5°C. They measured the daily decrease in volume of the culture solution in which sunflower, tomato, and red kidney bean plants were growing. A gradual decrease in temperature resulted in a gradual reduction in the absorption rate. Abrupt changes in temperature resulted in correspondingly abrupt decreases in absorption rate to a value slightly below that of plants which had been gradually cooled to that same temperature. They indicated that

the water absorption rate of sunflower and tomato plants showed greater reduction at temperatures below 10°C than at higher temperatures. They also found that none of the plants showed wilting symptoms over the range of 25° to 5°C, when the root temperature was decreased gradually. However, tomato and sunflower plants wilted severely on the day when the temperature was dropped abruptly from 25° to 5°C and gradually recovered on subsequent days with little or no permanent injury; but bean plants wilted severely and were greatly damaged from desiccation of the foliage, and showed very slow recovery of the uninjured portion of the foliage. Ullery (1970) noted similar wilting and recovery of beans in recent related studies.

Temperature Effect on Ion Uptake

Increased plant growth accompanying increasing root temperature has been ascribed to increased ion absorption resulting from increased diffusion rates, reaction velocities, solubility, synthesis, and translocation (Mederski and Jones, 1963). Mederski and Jones (1963) found that plant samples taken from heated (vs. unheated) corn rows 30 days after planting contained about 25% more nitrogen and potassium, 100% more phosphorus, and about 25 to 30% less calcium and magnesium. Attributing the observed dry weight and yield increase entirely to the greater uptake of nitrogen, phosphorus and potassium is probably an oversimplification of the causal effect of temperatures.

Hylmo (1953) concluded that a lowering of the root temperature, lowered the uptake of ions by itself. Parks and Fisher (1958) reported that nitrogen absorption was greatest at temperatures between 20° and 30°C. The uptake of phosphorus was significantly reduced at 10°C. Woolley (1963) grew Thatcher wheat to the 4- to 6-leaf stage in nutrient solution to find that root temperature had a significant effect on growth. Over the range of temperatures used (45°, 55°, 67° and 80°F), shoot phosphorus increased 38% and shoot nitrogen increased 17%.

In two pot experiments designed to investigate the effects of temperature and temperature changes on the mineral composition of perennial ryegrass, Dijkshoorn and 't Hart (1957) found that a transition from cold to warm usually led to an increase in the cation content of the plants. A transition from warm to cold led to a decrease in cation content.

Sullivan and Sprague (1949) found new top growth of ryegrass to be most rapid at 60° to 70°F, and least rapid at 80° to 90°F. They concluded that high temperature adversely affects ryegrass by rapidly dissipating reserve carbohydrates, by slowing down the production of new leaf growth, and by generally inhibiting recovery after clipping. At the highest temperatures, the soluble nitrogen, expressed as a percentage of total nitrogen, was found to increase in the tops and stubble of the ryegrass. Associated with the nitrogen increase was a

decrease in carbohydrate. The calcium content of the roots and stubble was slightly higher at the highest temperature studied.

The reverse situation of low rather than high soil temperature also depresses growth of plants. Such growth depressions from low root-zone temperatures reportedly resulted from restricted uptake, translocation or assimilation of plant nutrients. Knoll et al. (1964) found that low root-zone temperature severely restricted growth of young corn plants. High phosphorus levels in the nutrient solution never fully counteracted this harmful effect. They concluded that reduced phosphorus uptake at low root temperatures was caused primarily by a depression in root growth.

Nielsen et al. (1960) grew oats supplied with different nutrient levels in temperature-controlled soil in the greenhouse. Yields of grain and straw were higher when soil temperature was increased from 41° to 67° F. Increasing the soil temperature from 41° to 67° F increased the uptake of nitrogen, phosphorus, and potassium. The effect of soil temperature on uptake was more consistent for phosphorus than for other elements.

Temperature Effect on Calcium, Magnesium and Potassium Uptake

Soil temperature affected the concentration of chloride, calcium and magnesium and the uptake of calcium and magnesium in the plants;

it had little influence on the uptake of nitrogen, phosphorus, sulfur, sodium, and potassium except when it affected yield (Nielsen and Cunningham, 1964). Change et al. (1968) found that an increase in environmental temperature resulted in an increase in calcium accumulation in the stems of tobacco grown at 20°, 23°, 26°, 29° and 30°C in controlled-environment growth chambers. Calcium reportedly was immobilized in the stems at high temperatures, hence, failed to reach the meristem and terminal leaves, the critical portion of the plant with respect to calcium deficiency. The tobacco varieties used developed very severe calcium deficiency symptoms when grown at either 29 or 30°C.

Roberts and Kenworthy (1956) found a significant increase in potassium level of strawberry leaves when the root temperature was increased. Root temperature appeared to have little effect on plant contents of other nutrient elements during the vegetative period of development.

When grown without added phosphorus, Nielsen et al. (1961) found that the phosphorus content of bromegrass and tomato tops increased with rising soil temperatures (from 41 to 80°F). Plant uptake of nitrogen, phosphorus, calcium, magnesium, and potassium usually increased with increasing temperature to at least 67°F. Handley and Overstreet (1961) have shown that vacuolated segments of excised maize roots readily absorbed Ca^{2+} at rates approaching those

of other actively absorbed cations; the uptake was highly temperature dependent indicating metabolism was involved.

Johnson and Jackson (1964) found that the rate of calcium accumulation in wheat root was reduced from 0.64×10^{-7} to 0.26×10^{-7} moles Ca per g roots per hour when temperature was decreased from 25 to 3°C.

Proebsting (1957) using Shasta and Lassen strawberries grown with their roots at six different temperatures (45, 55, 65, 75, 85, and 90°F) found a higher K^+ percentage in leaves and petioles of both varieties at 85°F than at other temperatures, although dry weight was lower at that temperature. Roots showed a sharp decrease in potassium content with increase in temperatures. Peak total potassium contents occurred near 75°F.

Dijkshoorn and 't Hart (1957) working with ryegrass found that increasing root temperatures increased potassium uptake markedly but increased calcium and magnesium uptake only slightly. Nielsen and Cunningham (1964) indicated that the reasons for these increases in cation uptake may be linked with the interaction between soil temperature and nitrogen uptake, and between soil temperature and rates of chemical reactions in the soil.

Nitrogen Uptake and Ion Uptake

Application of nitrogen fertilizer has an influence upon cation

contents of plants. Russell et al. (1954) concluded that the greater effect of nitrogen fertilizer was from rate of application rather than from form of material or time of application. There was some increase in total cation content of bromegrass forage due to nitrogen fertilizer. Increasing rates of nitrogen fertilizer influenced magnesium and phosphorus percentages similarly, with some increases at the first sampling and either no effect or slight decreases at the last sampling. Potassium percentage was increased to nearly the same degree as the nitrogen percentage, while calcium percentage was decreased slightly during the last stages of growth.

Arnon (1939) found that ammonium fertilized plants had a higher phosphorus and a lower calcium, magnesium, and potassium content than nitrate fertilized plants. He explained that the rapid absorption of ammonium ions would tend to depress the absorption of other cations and to increase the absorption of anions. Conversely, the rapid absorption of nitrate ions by nitrate fertilized plants would tend to depress the absorption of other anions such as phosphate, and to increase the absorption of cations, calcium, magnesium, and potassium.

In contrast to Russell et al. (1954), Cunningham (1962) recently showed that cation-anion relationships in plants grown in soil depend on form of nitrogen and concentration of nitrogen. Nielsen and Cunningham (1964) found that yields of tops of Italian Ryegrass grown at 19.5°C with $\text{NO}_3\text{-N}$ were maximal at 100 ppm and with $\text{NH}_4\text{-N}$ at

200 ppm. He also found that form of nitrogen greatly influenced the composition of the grass. Increasing NO_3 -N decreased the concentrations of phosphorus, chloride, and sulfur, and increasing NH_4 -N decreased the concentrations of calcium. Percent N was larger with NO_3 -N than with NH_4 -N.

Grunes and Krantz (1958) found that addition of nitrogen to oats in the spring, 2 to 3 weeks before the "boot" stage, resulted in increasing nitrogen, phosphorus, and potassium concentrations in oat tops. They suggested that this effect was due in part to increased root growth, especially of fine roots which were probably high in absorbing capacity per unit weight. Also the absorption of nutrients by this new root was occurring more rapidly than was the plant growth response to the increased nutrient absorption.

Contrary to the above, Cole et al. (1963) concluded that the presence of nitrate or ammonium ions in the test solution during the uptake period had negligible effects on phosphorus uptake rates, although phosphorus uptake rate was highly correlated with total nitrogen levels in the roots. They also concluded that increased phosphorus absorption rates at the higher plant nitrogen levels suggested a connection between nitrogen metabolism and phosphorus uptake processes.

Conclusion

Temperature on Ion Uptake

Generally speaking, soil temperature effects on the nutrient uptake and composition of plants are associated with its influence on plant growth. Most evidence showed that at low root temperatures, the uptake of nutrients is reduced, and this correlated with a depression in root growth. Normally, as the root temperature increases, the yield of dry plant material and the nutrient content are increased. This trend continues until a maximum uptake of ions occurs at a temperature which is best for plant growth; rate of ion uptake then decreases as the temperature continues to increase. Hence, too low or too high a root temperature may restrict plant growth accompanied by reduced ion uptake. The optimum temperature for ion uptake and plant growth differs for different plant species.

Water Stress on Ion Uptake

Ion uptake rate may be influenced by the amount of water transport. Most evidence showed increasing moisture stress, or decreasing water supply, is associated with an increase in nitrogen content, decrease in potassium content, and a variable effect on the calcium, magnesium, and phosphorus content in the plant tissue. Some of the conflicting observations arise because ion accumulation may vary as a

consequence of changes either in ion entry or in rate of plant growth, or both, thereby confounding interpretation of the data. Physiological stage and length and severity of imposed stress also need consideration.

Ion Uptake and Its Supply Through Roots

Ion uptake by plants mostly occurs in the roots. Only a small amount is taken up through leaves and stems. The absorption of ions by intact plants involves (1) the movement of ions to the root surface and subsequently, into the root cells, and (2) translocation of ions from roots to shoots. How ions move radially from the root surface into the stele and xylem tissues remains arguable; hence more research is needed on the radial movement of ions in roots.

Ion Interaction Between Ca, Mg, and K

Ion interactions between the major nutrient cations, K^+ , Ca^{2+} and Mg^{2+} may exist during the absorption process. The role of calcium in regulating the absorption of ions is well recognized. Its effects on the uptake of the monovalent, alkali cations range from highly stimulatory to strongly inhibitory, depending on the ion and the H^+ concentration. Generally, calcium stimulates the absorption of potassium at low pH, while it markedly depresses the absorption of magnesium. In general, increased potassium concentration may

depress the calcium content, in some other cases, calcium has an inhibiting effect on potassium absorption. Because of the different species of plants, the inhibition between ions may not be the same in all cases.

MATERIALS AND METHODS

Control of Soil Water Suction and Soil Temperature

The technique used for the control of soil water suction and soil temperature in the experiment was the same as recently used by several other colleagues (Babalola et al., 1968; Sedgley and Boersma, 1969; Kuo, 1970; Amujo, 1970; Fazilat, 1971; Sepaskhah, 1971). It was first suggested by Zur (1961), and developed by Cox (1966) who incorporated several modifications to overcome some limiting problems. Control of soil water suction was obtained by inserting thin slabs of soil, encased in semi-permeable membranes, into solutions of different osmotic pressure. Osmotic solutions were prepared by mixing Carbowax-6000 (polyethylene glycol) with distilled water. Two concentrations corresponding to osmotic pressures of 0.35 (48.0 g/liter) and 2.5 (150.0 g/liter) were used in these experiments. Required concentrations were derived from Zur's (1961) work.

The chambers containing the carbowax solutions were surrounded by a water-jacket which was connected to a constant temperature water bath. Water pumped from the bath through the jacket and recirculated to the water bath gave a positive temperature control for the osmotic solution and perlite slabs immersed therein. Measurements of dry weight were made for root temperatures of 10.0, 18.3,

23.9, and 32.2°C.

In order to prevent concentration gradients from developing in the chambers, the osmotic solution was stirred by hand periodically.

One serious drawback of this technique was that microorganisms attacked the cellulose acetate membrane especially at higher temperatures, higher N rates, and lower water suction. With 100 ppm nitrogen as free ammonium nitrate in the solution it sometimes took less than a week for the organisms to destroy the membrane. To at least partially inhibit microbial attack on the membrane, 10 ppm pimara-cin was added to the nutrient solutions. This did not eliminate the problem completely, but controlled the fungi to some extent.

Other Environmental Parameters

All experiments were carried out in a controlled environment. Air temperature was maintained at 23.9°C; relative humidity at 40 to 50%; light intensity, from fluorescent tubes and incandescent bulbs, at 1800 ft-c. at the tops of plants; and air movement over the plants, by means of an electric fan, at about 5 m/sec. Nutrients were made available by mixing them with the carbowax solution. The composition of the nutrient solution used is shown in Table 1.

Table 1. Composition 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
Fe EDTA	0.001
$CoCl_2 \cdot 4H_2O$	0.00005
<u>Micronutrients (mixture)</u>	
$ZnSO_4 \cdot 7H_2O$	0.067
$MnSO_4 \cdot 4H_2O$	0.876
$CuSO_4 \cdot 5H_2O$	0.078
H_3BO_3	0.00025
$Na_2MoO_4 \cdot 2H_2O$	0.00001

Experimental Procedure

Pregerminated wheat seedlings (Triticum aestivum VILL., Host), Gaines variety, were grown in perlite filled cells for five weeks in growth chambers, at a day temperature of 23.9°C and a night temperature of 21.1°C. The plants were supplied with water and 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 perlite cells (0.8 x 30 x 10 cm) in which the plants were grown consisted of a frame of lucite with removable sides. The arrangement was described in detail by Kuo (1970). The commercially obtained perlite was a nitrogen-free, lightweight material, made by exploding sand grains at high temperatures. After five weeks, 54 cells with uniformly growing plants were selected. By random selection, six of the 54 cells were taken for zero day determination of plant dry weight and mineral composition. The side covers of the remaining 48 cells were replaced by the semi-permeable cellulose acetate membranes. The membranes were sealed at the lower end by folding them over several times and clamping the fold with a plastic clip, and were held in place at the upper end by braces. Water and nutrients passed freely through the membrane to the plant roots in the perlite bed when the cells were inserted into the osmotic solutions contained in the chambers.

Each osmotic chamber held three cells. Sixteen chambers were used for each experimental run. Eight chambers each had osmotic solutions of 0.35 and 2.5 bars respectively. At 2 day intervals during the 8 day growing period, cells (total of 6) from two chambers at each suction were removed for plant harvest. The experiments were repeated a second time at each temperature.

Measurement

Dry Matter Production

Plants from two chambers containing six perlite cells were harvested on day 0, 2, 4, 6, and 8 of each experiment. The roots were carefully washed; and the 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. Roots and shoots were ground in a blending mill to a uniform meal-like fineness, redried in an oven at 52°C for 24 hours, and stored in a dessicator until weighed.

Plant Material Extraction

Approximately one gram of the ground sample was weighed and prepared for chemical analysis by wet washing with perchloric acid (Jackson, 1958). One scoop of glass beads and two ml of concentrated nitric acid was added to each flask. The flasks were heated slowly until brown fumes (NO_2) came off, and foaming ceased, then removed from the hot plate and left to cool. When cool, 6 ml of 70% perchloric acid was added after which the flasks were heated in a perchloric acid-proof hood until the reaction mixture became colorless. Flasks were removed from the hot plate and cooled for about 30 seconds. Approximately 10 ml of water was added and the solution was swirled to dissolve any existing solids. Solutions were immediately filtered

through an 11 cm Watman No. 5 filter paper in 100 ml volumetric flasks.

Determination of Nutrient Ions

Calcium, magnesium, and potassium were determined by atomic absorption of the perchloric acid digest using a Perkin Elmer Model 303 spectrophotometer.

One ml of the extract from shoot or root material was pipetted into 50 ml volumetric flasks, five ml of 1000 ppt SrCl_2 then added and the whole diluted to 50 ml.

Nitrogen was determined by micro-Kjeldahl modified to include nitrates (Johnson and Ulrich, 1959).

Phosphorus was determined by the Molybdate-Vanadate colorimetric method; the color intensity being measured on a Bausch and Lomb Spectronic 20 spectrophotometer (Jackson, 1958).

RESULTS

Rate of Dry Matter Accumulation

Rates of dry matter accumulation at various soil temperatures and soil moisture suctions, as summarized in Table 2, are shown graphically in Figure 1. Some of the values shown in Table 2 were obtained from Figure 1. These data were reported in a companion thesis (Fazilat, 1971). From the dry weight of plants harvested every second day, the daily increase in dry matter weight was calculated. It appeared that the plants approached a constant rate of growth during the first several days of the experiment. Final equilibrium rate of dry matter gain was obtained by drawing the best fitting line of dry weight increase as a function of time at various temperatures. The data shown in Table 2 were derived from Figure 1.

Table 2. Rate of dry matter accumulation in 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	10.2
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

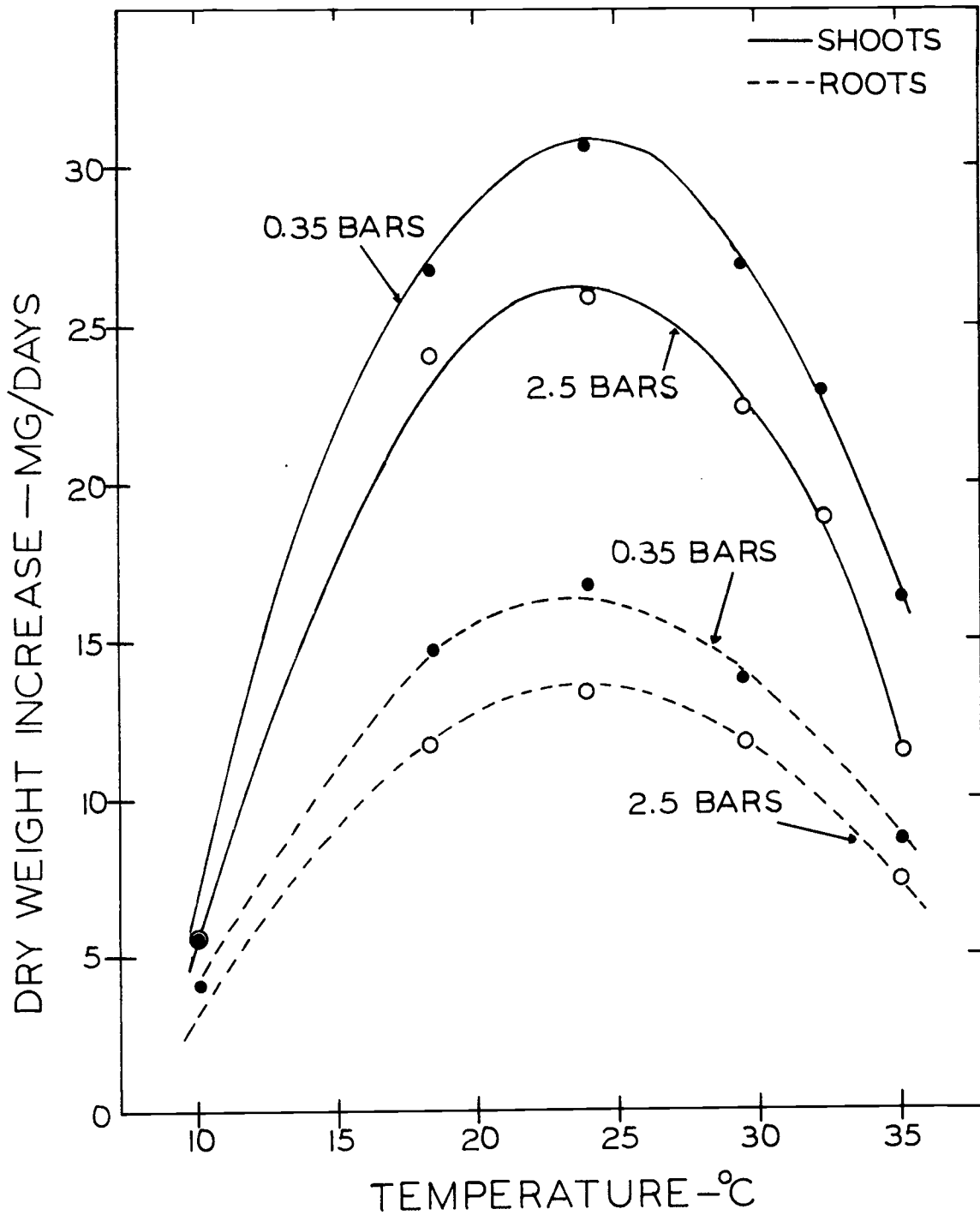


Figure 1. Rate of increase in dry matter weight (mg per day) of shoots and roots of 5-week old wheat seedlings as a function of root temperature at soil water suctions of 0.35 and 2.5 bars.

Calcium, Magnesium, and Potassium Content
of Plant Material

Percentages of calcium, magnesium and potassium in the dry plant material are shown in Table 3. The concentration of calcium was highest in the roots, whereas concentrations of both magnesium and potassium were highest in the shoots.

The concentrations shown in Table 3 were plotted as a function of time (Figures A-1 through A-12). The graphs indicate that the concentration of Ca, Mg and K in the shoot and root material at various treatment combinations approached an equilibrium value as time progressed, which was approached from a higher or lower value depending on the initial concentration. Final equilibrium concentrations of Ca, Mg, and K obtained from empirical "best fit" curves (Table 4) were plotted as a function of root temperature (Figures 2, 3, and 4). Results at the two soil water suctions were not significantly different statistically, hence average values of the two suctions were used.

Observation of the graphs shown in Figure 2 make it clear that the concentrations of calcium in both shoot and root tended to decrease as the temperature increased. At the same temperature, the calcium concentration in the roots was roughly twice as high as in the shoots. Concentrations of magnesium (Figure 3) were higher in shoots than in roots. As with Ca, Mg concentrations in shoots decreased with

Table 3. The content of calcium, magnesium, and potassium, as percent dry weight of shoots and roots of 5-week old wheat seedlings subjected for eight days to water suction of 0.35 and 2.50 bars and soil temperatures of 10, 18.3, 23.9 and 32.2°C.

Plant Part	Day No.	Concentration - %					
		0.35			2.50		
		Ca	Mg	K	Ca	Mg	K
-----10°C-----							
Shoots	0	0.691	0.150	3.93	0.690	0.150	3.93
	2	0.594	0.140	3.48	0.650	0.149	3.39
	4	0.603	0.149	3.17	0.648	0.163	3.44
	6	0.622	0.154	3.21	0.624	0.155	3.20
	8	0.609	0.150	2.99	0.648	0.172	3.28
Roots	0	---	0.134	1.45	---	0.134	1.45
	2	1.388	0.132	1.32	1.088	0.124	1.27
	4	1.220	0.126	1.26	1.358	0.122	1.26
	6	1.147	0.124	1.36	1.234	0.117	1.23
	8	0.942	0.114	1.22	1.201	0.112	1.20
-----18.3°C-----							
Shoots	0	0.511	0.142	3.63	0.511	0.142	3.63
	2	0.476	0.149	3.70	0.478	0.147	3.82
	4	0.464	0.151	3.60	0.486	0.156	3.70
	6	0.465	0.159	3.50	0.471	0.158	3.25
	8	0.488	0.159	3.40	0.478	0.150	3.46
Roots	0	---	0.137	1.48	---	0.137	1.48
	2	1.561	0.142	1.43	1.491	0.143	1.28
	4	1.388	0.142	1.39	1.582	0.159	1.31
	6	1.170	0.139	1.46	1.392	0.136	1.43
	8	1.047	0.138	1.49	1.229	0.124	1.42
-----23.9°C-----							
Shoots	0	0.516	0.119	3.88	0.516	0.119	3.88
	2	0.586	0.129	4.16	0.546	0.171	4.13
	4	0.590	0.138	4.15	0.566	0.139	3.99
	6	0.567	0.144	4.06	0.565	0.139	4.03
	8	---	---	--	0.550	0.150	4.18

(continued)

Table 3. Continued.

Plant Part	Day No.	Concentration - T					
		0.35			2.50		
		Ca	Mg	K	Ca	Mg	K
Roots	0	---	0.129	1.57	1.258	0.129	1.57
	2	1.200	0.127	1.43	1.258	0.131	1.33
	4	1.012	0.124	1.37	1.247	0.139	1.25
	6	1.037	0.126	1.25	1.095	0.117	1.26
	8	---	---	--	0.956	0.117	1.25
----- 32.2° C -----							
Shoots	0	0.430	0.133	3.65	0.430	0.134	3.65
	2	0.435	0.157	4.08	0.444	0.161	4.03
	4	0.421	0.150	3.96	0.439	0.140	3.92
	6	0.430	0.162	4.12	0.458	0.140	3.75
	8	---	---	4.05	---	0.155	--
Roots	0	---	0.136	1.73	---	0.136	1.73
	2	---	0.147	1.53	---	0.142	1.48
	4	---	0.152	1.50	---	0.143	1.43
	6	---	0.136	1.45	---	0.144	1.44
	8	---	0.182	--	---	---	--

Table 4. Equilibrium concentration of calcium, magnesium, and potassium in dry matter of shoots and roots of 5-week old wheat seedlings as a function of soil temperature at soil water suctions of 0.35 and 2.50 bars.

Soil Temperature	Shoots			Roots		
	0.35	2.50	Ave.	0.35	2.50	Ave.
<u>°C</u>	<u>%</u>	<u>%</u>	<u>%</u>	<u>%</u>	<u>%</u>	<u>%</u>
----- Calcium -----						
10.0	0.61	0.64	0.62	0.98	1.21	1.10
18.3	0.48	0.48	0.48	1.08	1.18	1.13
23.9	0.57	0.56	0.56	0.99	0.98	0.99
32.2	0.43	0.44	0.44	1.00	0.96	0.98
----- Magnesium -----						
10.0	0.152	0.161	0.157	0.120	0.114	0.117
18.3	0.159	0.158	0.158	0.137	0.126	0.130
23.9	0.149	0.149	0.149	0.124	0.120	0.122
32.2	0.157	0.147	0.152	0.146	0.149	0.145
----- Potassium -----						
10.0	3.05	3.23	3.14	1.25	1.22	1.23
18.3	3.45	3.50	3.50	1.45	1.35	1.40
23.9	4.05	4.05	4.05	1.28	1.25	1.26
32.2	4.08	4.00	4.04	1.45	1.45	1.45

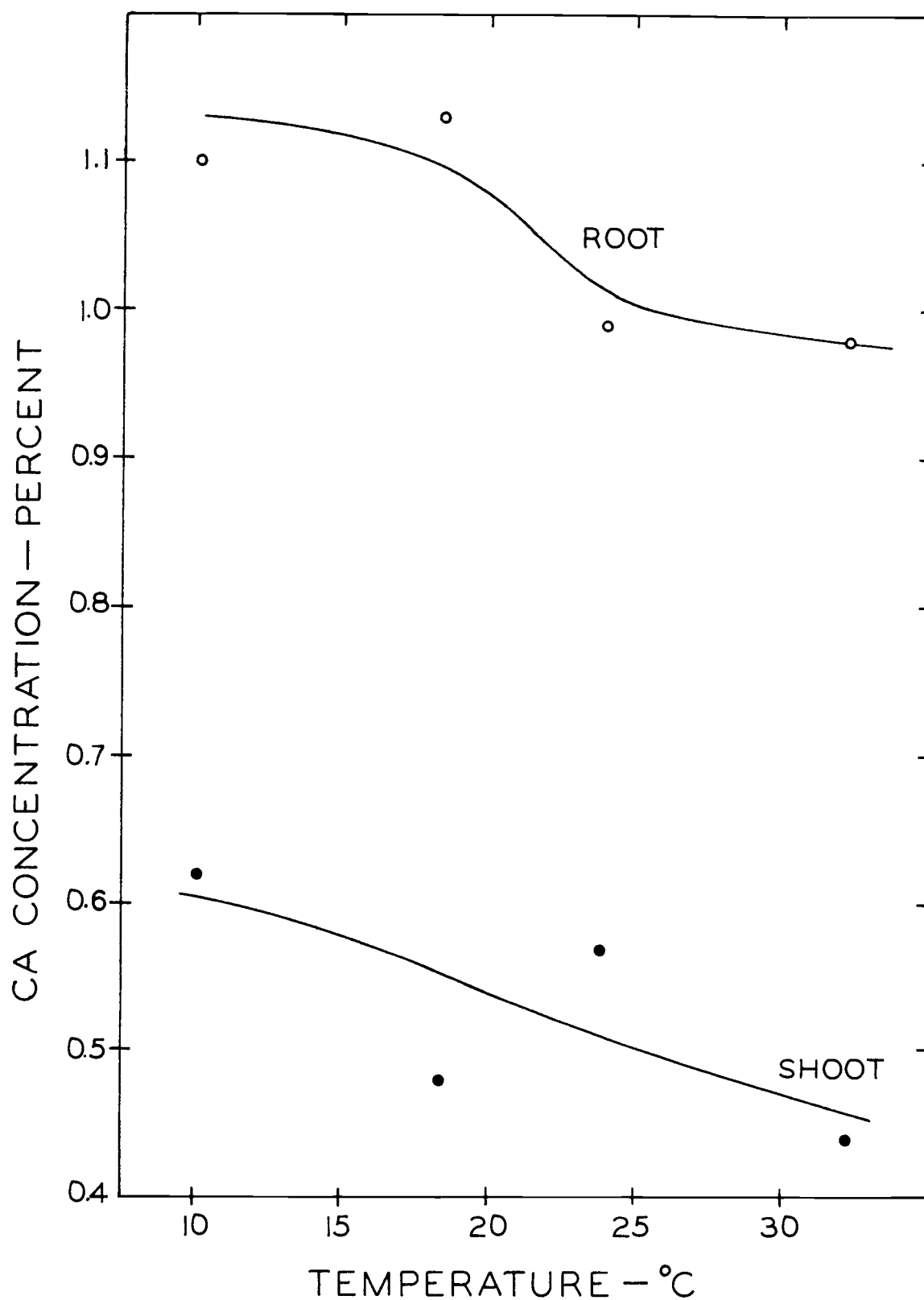


Figure 2. Concentration of calcium in percent dry weight of shoots and roots of 5-week old wheat seedlings as a function of root temperature.

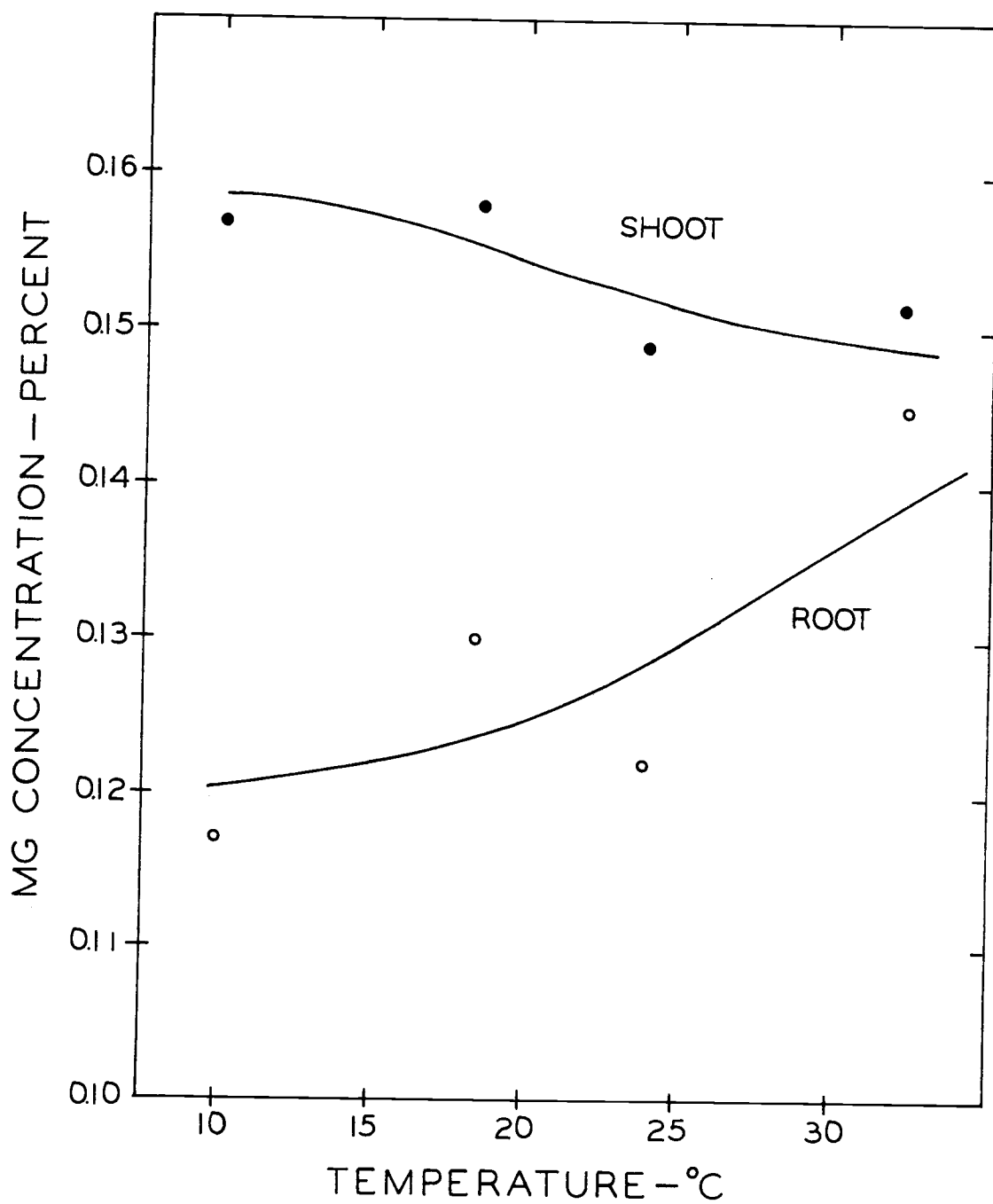


Figure 3. Concentration of magnesium in percent dry weight of shoots and roots of 5-week old wheat seedlings as a function of root temperature.

increasing temperature; but in the roots, Mg increased as the temperature increased. The concentration of potassium (Figure 4) in both shoots and roots increased as the temperature increased. The concentration in the shoots was about twice that in the roots, just the reverse of calcium.

Rate of Calcium, Magnesium, and Potassium Uptake

Plant material concentration of calcium, magnesium, and potassium at temperatures of 10.0, 15.5, 21.2, 26.6, and 32.2°C were derived from Figures 2, 3, and 4 in order to make comparisons with N and P uptake data from companion theses. Using the data shown in Tables 1 and 4 uptake rates of these ions were calculated. Results of these calculations are shown in Table 5. Uptake rates of nitrogen and phosphorus by the same plants are shown in Table 5 also. Data for P and N were reported by Fazilat (1971) and Sepaskhah (1971), respectively.

Observation of data in Table 5 reveals that the uptake rate of calcium, magnesium, and potassium increased with increasing root temperature for both shoots and roots. The calcium uptake was highest at a root temperature of 21.1°C and decreased as the temperature increased. For magnesium, maximum uptake rate was attained at root temperatures around 21.1° to 26.6°C. Potassium had a maximum uptake rate at root temperature of 26.6°C in the shoots and

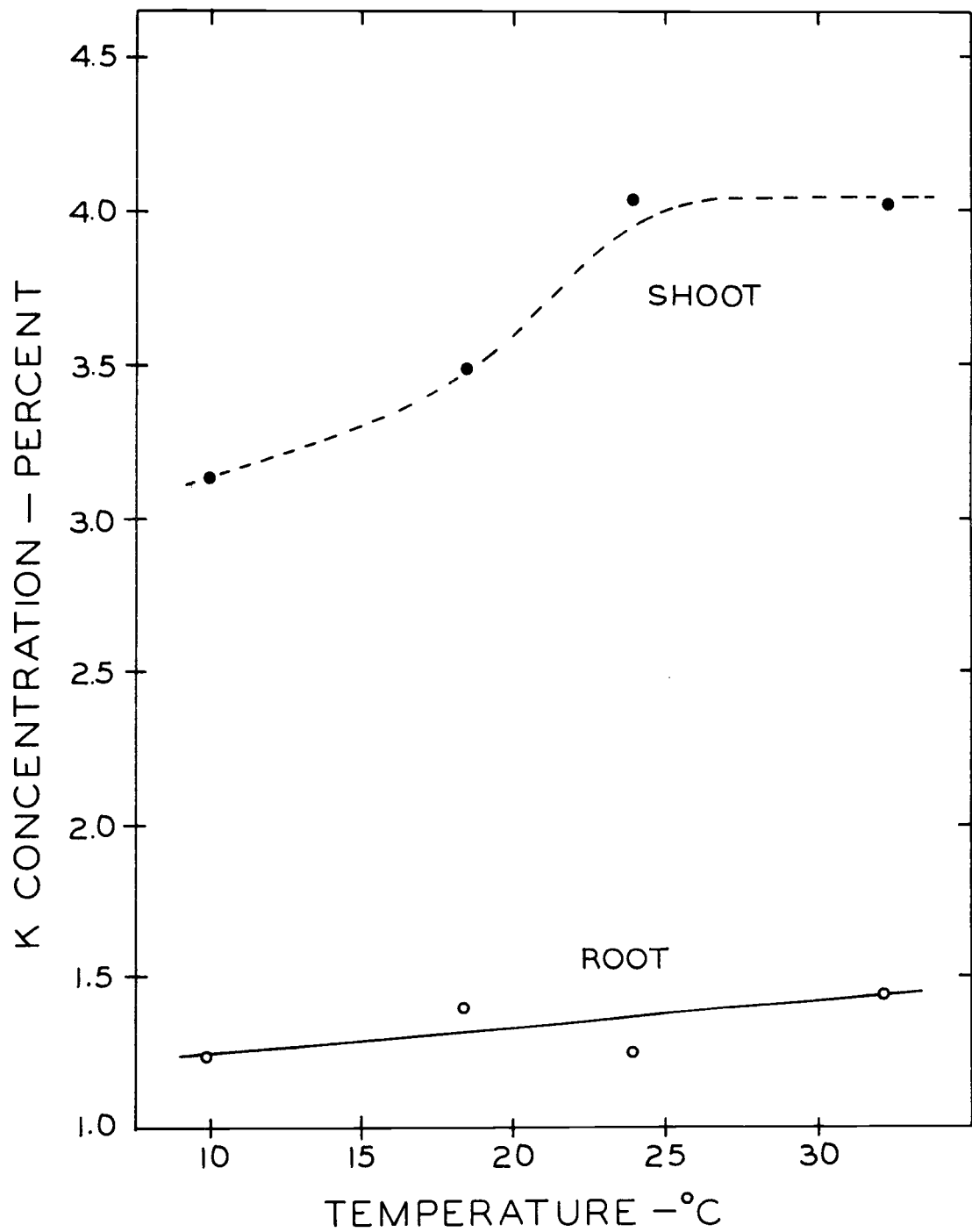


Figure 4. Concentration of potassium in percent dry weight of shoots and roots of 5-week old wheat seedlings as a function of root temperature.

Table 5. Calcium, magnesium, potassium, nitrogen, and phosphorus content, rate of uptake and fraction of total uptake translocated to shoots of 5-week old wheat seedlings, all as a function of soil water suction and soil temperature.

Soil Water Suction	Soil Temp.	Shoots		Roots		Fraction to Shoot
		Nutrient Content	Uptake Rate	Nutrient Content	Uptake Rate	
<u>bars</u>	<u>°C</u>	<u>%</u>	<u>µg/day</u>	<u>%</u>	<u>µg/day</u>	<u>%</u>
----- Calcium -----						
0.35	10.0	0.605	42	1.130	51	45
	15.5	0.575	132	1.118	136	49
	21.1	0.530	159	1.060	173	48
	26.6	0.490	148	0.997	156	49
	32.2	0.468	107	0.980	114	48
2.5	10.0	0.605	35	1.130	38	48
	15.5	0.575	108	1.118	118	48
	21.1	0.530	136	1.060	141	49
	26.6	0.490	124	0.997	131	49
	32.2	0.468	88	0.980	98	47
----- Magnesium -----						
0.35	10.0	0.159	11	0.120	5	69
	15.5	0.157	36	0.122	15	71
	21.1	0.154	46	0.126	21	69
	26.6	0.151	46	0.132	21	69
	32.2	0.149	34	0.139	16	68
2.5	10.0	0.159	9	0.120	4	69
	15.5	0.157	29	0.122	12	71
	21.1	0.154	39	0.126	17	70
	26.6	0.151	38	0.132	17	69
	32.2	0.149	28	0.139	14	67
----- Potassium -----						
0.35	10.0	3.14	220	1.25	56	80
	15.5	3.33	766	1.30	159	83
	21.1	3.72	1116	1.35	220	84
	26.6	4.05	1223	1.40	218	85
	32.2	4.05	923	1.45	168	85

(continued)

Table 5. Continued.

Soil Water Suction	Soil Temp.	Shoots		Roots		Fraction to Shoot
		Nutrient Content	Uptake Rate	Nutrient Content	Uptake Rate	
<u>bars</u>	<u>°C</u>	<u>%</u>	<u>µg/day</u>	<u>%</u>	<u>µg/day</u>	<u>%</u>
2.5	10.0	3.14	182	1.25	43	81
	15.5	3.33	623	1.30	130	83
	21.1	3.92	952	1.35	180	84
	26.6	4.05	1025	1.40	183	85
	32.2	4.05	757	1.45	145	84
----- Nitrogen -----						
0.35	10.0	3.10	217	2.11	95	70
	15.5	3.50	805	2.31	282	74
	21.1	3.87	1161	2.42	394	75
	26.6	4.04	1220	2.44	381	76
	32.2	4.08	930	2.44	283	77
2.5	10.0	3.10	180	2.14	72	71
	15.5	3.50	655	2.31	231	74
	21.1	3.87	991	2.42	322	75
	26.6	4.04	1022	2.44	320	76
	32.2	4.08	763	2.44	244	76
----- Phosphorus -----						
0.35	10.0	0.374	26	0.300	14	65
	15.5	0.428	98	0.286	35	74
	21.1	0.493	148	0.293	48	76
	26.6	0.555	168	0.343	54	76
	32.2	0.633	144	0.482	56	72
2.5	10.0	0.368	21	0.330	11	64
	15.5	0.429	80	0.305	31	72
	21.1	0.479	123	0.300	40	75
	26.6	0.531	134	0.329	43	76
	32.2	0.544	102	0.514	51	67

21.1°C in the roots. Nitrogen showed the same tendency as calcium, magnesium, and potassium uptake. Maximum uptake rate of nitrogen occurred at the same root temperatures as observed for potassium which were 26.6°C in shoots and 21.1°C in roots. Phosphorus uptake in shoots also increased as temperature increased until it reached a maximum rate and then decreased as temperature increased further. Phosphorus uptake rate by roots behaved differently. The maximum uptake for phosphorus in shoots occurred at root temperature of 26.6°C while in roots the uptake rate increased as a function of temperature up to 32.2°C. From this study, it is suggested that a soil temperature of about 24°C was optimal for nutrient uptake and production of dry weight in wheat.

Results of all experiments are summarized in Table 6.

Table 6. Summary of the rate of nutrient uptake in μg per day of 5-week old wheat seedlings as a function of soil temperature at soil water suctions of 0.35 and 2.50 bars.

Plant Part	Soil Water Suction	Soil Temp.	Element				
			N	K	Ca	Mg	P
	<u>bars</u>	<u>°C</u>	----- $\mu\text{g/day}$ -----				
Shoots	0.35	10.0	217	220	42	11	26
		15.5	805	766	132	36	98
		21.1	1,161	1,116	159	46	148
		26.6	1,220	1,223	148	46	168
		32.2	930	923	107	34	144
Roots	0.35	10.0	95	56	51	5	14
		15.5	282	159	136	15	35
		21.1	394	220	173	21	48
		26.6	381	218	156	21	54
		32.2	283	168	114	16	56
Shoots	2.50	10.0	180	182	35	9	21
		15.5	655	623	108	29	80
		21.1	991	952	136	39	123
		26.6	1,022	1,025	124	38	134
		32.2	763	757	88	28	102
Roots	2.50	10.0	72	43	38	4	11
		15.5	231	130	118	10	31
		21.1	322	180	141	17	40
		26.6	320	183	131	17	43
		32.2	244	145	98	14	51

DISCUSSION

Dry Weight IncreaseRoot Temperature

The rate of dry weight increase of shoots and roots as a function of root temperature was shown in Table 2 and Figure 1. A maximum rate of dry weight accumulation was attained at a root temperature of about 24°C. Above this temperature the accumulation rate decreased. The rate of growth of shoots and roots at all temperatures was higher at 0.35 bars than at 2.50 bars soil water suction. Table 7 shows the dry matter accumulation rates in percent of the rate at 23.9°C and 0.35 bar.

Table 7. Rate of dry matter accumulation in shoots and roots of 5-week old wheat seedlings as a function of soil temperature at soil water suctions of 0.35 and 2.50 bars. Rates are shown in percent of the rate at 23.9°C and 0.35 bar.

Root Temperature		Shoots		Roots	
		0.35	2.50	0.35	2.50
<u>°F</u>	<u>°C</u>				
50	10.0	23	19	27	20
60	15.6	74	60	73	61
65	18.3	87	76	88	72
70	21.1	97	82	97	80
75	23.9	100	84	100	78
80	26.7	97	82	94	78
85	29.4	87	71	85	72
90	32.2	74	60	69	60
95	35.0	53	38	54	44

These results agree in general with literature reports. Idealized growth curves for several plant species are shown in Figure 5. Data obtained in this experiment are also shown in this diagram. The growth curve for wheat obtained in this experiment at a soil water suction of 0.35 bars has the same general shape as those for the crops shown in the original diagram. Its position between tomato and cucumber, somewhat unexpected, may result from a difference in experimental conditions. The curves for lettuce, tomato, and cucumber represent growth when the entire plant was exposed to the indicated temperature; results for wheat were obtained with only the roots exposed to the indicated temperature, while the shoots were maintained at 75°F.

Other workers investigating the effects of temperature on plant growth showed different results. Woolley (1963) grew Thatcher spring wheat to the 4- to 6-leaf stage in nutrient solutions at four different temperature levels. His results showed (Table 8) dry weight of both shoots and roots increased with increasing root temperature up to 80°F. Because growth was not tested above 80°F, dry weight production at higher temperatures could not be predicted. In the present experiment, the maximum rate of growth occurred at a temperature around 75°F. Also, growth depression at lower temperatures was not nearly as large in Woolley's experiment as in ours. Comparative rates at 10°C were 84 and 23 percent of the maximum rate. This discrepancy could arise from differences in experimental conditions, varieties, or both.

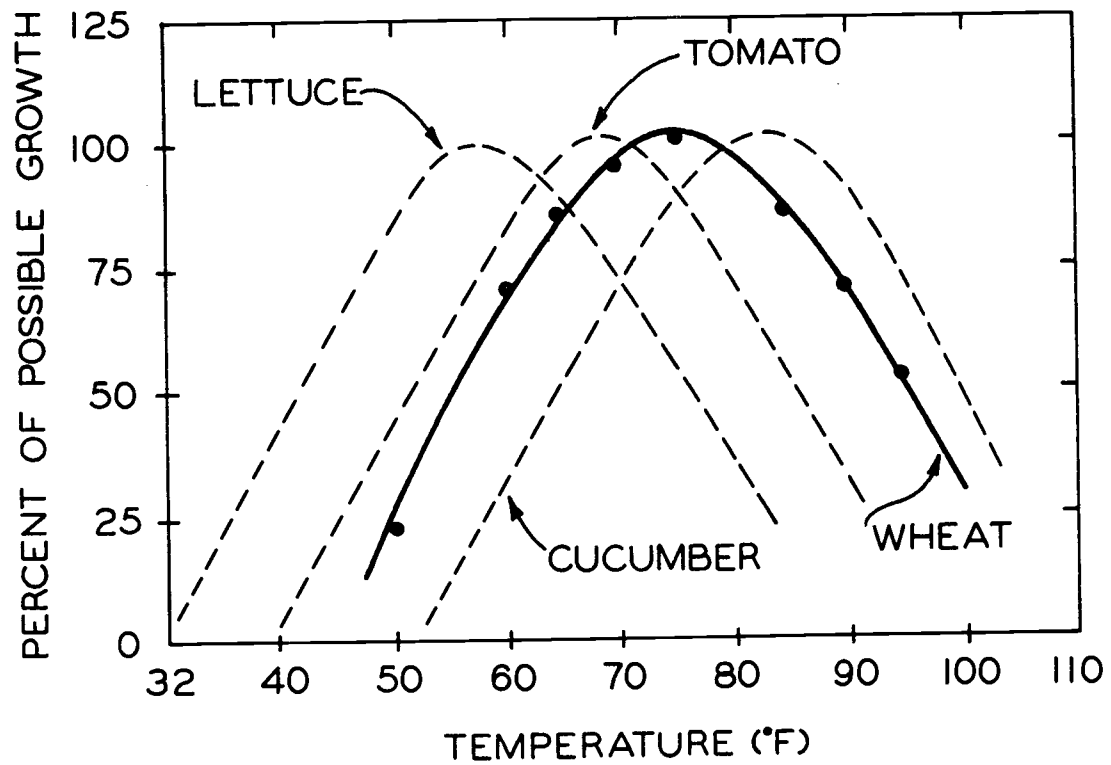


Figure 5. Idealized growth curves for lettuce, tomato, wheat, and cucumber at different temperature levels. The dotted lines were redrawn after Beall and Samuels (1971). The solid line is based on data reported in this study.

Table 8. Yield of shoots and roots of spring wheat at the 4- to 6-leaf stage as a function of root temperature (after Woolley, 1963).

Root Temperature	Dry Weight (per 100 plants)	
	Shoots	Roots
<u>°F</u>	<u>%</u>	<u>%</u>
45	82	62
54	87	74
67	92	76
80	100	100

Nielsen et al. (1961) using NPK fertilized soil in temperature-controlled pots in the greenhouse, found that yields of corn and bromegrass tops increased with increments in temperature from 41° to 80°F (Table 9). Yields of potato tops showed a less consistent relationship with temperature. Yields of corn roots also increased with temperature. Potato tubers and bromegrass roots appeared to have an optimum temperature at 67°F. Results in percent of the dry weight at 80°F are shown in Table 9. The response of corn to changes in root temperature was very similar to that of wheat, while bromegrass and potatoes behaved differently. The difference in response for the last two plant types is an indication of the thermal adaptation of different plants. Grasses in general have lower optimum temperatures than wheat or corn.

Table 9. Yield of corn, bromegrass, and potatoes grown at four soil temperatures (after Nielsen *et al.*, 1961).

Soil Temperature	Corn		Bromegrass		Potato		
	<u>Yield per Pot</u> Tops	<u>Yield per Pot</u> Roots	<u>Yield per Pot</u> Tops	<u>Yield per Pot</u> Roots	<u>Yield per Pot</u> Tops	Tubers	Roots
<u>°F</u>	<u>%</u>	<u>%</u>	<u>%</u>	<u>%</u>	<u>%</u>	<u>%</u>	<u>%</u>
41	20	13	38	68	86	60	127
54	59	46	52	146	95	95	127
67	83	96	86	177	83	139	73
80	100	100	100	100	100	100	100

Soil Water Suction

The reductions in growth rate which occurred as a result of increased soil water suction (Tables 2 and 7) were greatest at the optimum temperatures. At 23.9°C, the decreases were 16 and 22 percent for shoots and roots, respectively, while at 10°C, the reductions were 4 and 7 percent and at 35.0°C, 15 and 10 percent. This observation agrees with literature reports that the effect of low root temperatures on growth is often similar to that of increased plant water suction.

The magnitude of growth reductions observed in these experiments were similar to those reported in the literature. Mederski and Wilson (1960) measured yields of tops and roots of corn plants that developed in the soil at seven given moisture levels. They found a generally linear increase in dry weight with increasing soil moisture content at both high and low levels of humidity (Table 10).

Table 10. Dry weight of shoots and roots of corn plants as a function of soil moisture content at high and low atmospheric humidity.

Soil Moisture	Dry Weight			
	High Humidity		Low Humidity	
	Shoots	Roots	Shoots	Roots
<u>%</u>	<u>g</u>	<u>g</u>	<u>g</u>	<u>g</u>
12.1	2.0	1.3	2.2	1.3
13.2	2.3	1.6	2.4	1.7
14.9	2.4	1.5	2.3	1.8
16.1	2.6	1.5	2.5	1.8
17.8	2.8	1.7	2.8	2.2
19.7	2.8	1.7	3.0	2.4
20.8	3.1	1.9	2.6	2.1
r	0.98	0.89	0.85	0.86

r = regression coefficient

Thomas and Wiegand (1970) found that cotton lint yield decreased significantly as the total soil suction increased. Mean yields were 689, 465, 397, and 300 kg/ha at 3.6, 4.5, 5.0, and 7.2 bars, respectively. The yield decreased from 689 kg/ha to 300 kg/ha or about 56% as the total soil suction increased from 3.6 bars to 7.2 bars.

Temperature Effect on Ion Content

Statistical significance of the temperature and moisture suction effect on calcium, magnesium, potassium, nitrogen, and phosphorus content (Table 5) was inspected with a variance analysis. Results are shown in Table 11. Significance of temperature effect on nutrient content at both 0.01 and 0.05 levels is summarized in Table 12.

Table 11. Variance analysis of the data on content of Ca, Mg, and K in shoots and roots of 5-week old wheat seedlings grown at temperatures of 10.0, 15.6, 21.1, 26.6, and 32.2°C and soil water suctions of 0.35 and 2.50 bars.

Plant Part	Source of Variation	Degree of Freedom	Sum of Square	Mean Square	F
----- Ca -----					
Shoots	Temperature	3	0.04345	0.01448	98.53
	Moisture	1	0.00010	0.00010	0.67
	Residuals	3	0.00045	0.00015	
Roots	Temperature	3	0.0350	0.0117	1.56
	Moisture	1	0.0098	0.0098	1.31
	Residuals	3	0.0225	0.0075	
----- Mg -----					
Shoots	Temperature	3	0.000112	0.000037	1.43
	Moisture	1	0.000002	0.000002	0.08
	Residuals	3	0.000078	0.000026	
Roots	Temperature	3	0.000926	0.00309	41.4
	Moisture	1	0.000021	0.00021	3.0
	Residuals	3	0.000022	0.000007	
----- K -----					
Shoots	Temperature	3	1.2001	0.4000	67.3
	Moisture	1	0.0028	0.0028	0.47
	Residuals	3	0.0178	0.006	
Roots	Temperature	3	0.0647	0.0216	23.9
	Moisture	1	0.0032	0.0032	3.56
	Residuals	3	0.0027	0.0009	
----- N -----					
Shoots	Temperature	3	1.27725	0.42575	1216.
	Moisture	1	0.00405	0.00405	11.57
	Residuals	3	0.00105	0.00035	
Roots	Temperature	3	0.17255	0.05752	15.65
	Moisture	1	0.001025	0.00103	0.28
	Residuals	3	0.011025	0.00368	

(continued)

Table 11. Continued.

Plant Plant	Source of Variation	Degree of Freedom	Sum of Square	Mean Square	F
----- P -----					
Shoots	Temperature	3	0.05926	0.01975	15.37
	Moisture	1	0.00045	0.00045	0.35
	Residuals	3	0.00386	0.00129	
Roots	Temperature	3	0.05400	0.01800	111.72
	Moisture	1	0.00086	0.00086	5.34
	Residuals	3	0.00048	0.00016	

Table 12. Summary of significance of temperature effect on nutrient content at 0.01 level (**), and at 0.05 level (*).

Element	Plant Part	
	Shoots	Roots
K	Yes (**)	Yes (*)
N	Yes (**)	Yes (*)
P	Yes (*)	Yes (**)
Mg	No	Yes (*)
Ca	Yes (**)	No

These results show that temperature had a significant effect on the calcium content in shoots but not in roots, the magnesium content in roots but not in shoots, and potassium content in both shoots and roots. There was no significant difference in the calcium, magnesium, and potassium content of plants grown at soil water suctions of 0.35

vs. 2.5 bars for either shoots or roots.

The content of calcium expressed as a percentage of the oven dried plant material decreased as the temperature increased in both shoots and roots, but the change in the roots was not statistically significant. Temperature had only a small effect on magnesium content; the concentration in the roots increased slightly as temperature increased. The content of N, P, and K increased as temperature increased in both shoots and roots.

Ion concentrations in the dry matter of shoots and roots as a percentage of the content at 10.0°C are shown in Table 13.

Table 13. Concentration of Ca, Mg, K, N, and P in the dry matter of shoots and roots of 5-week old wheat seedlings as a function of root temperature. Concentrations are shown in percent of the content at 10°C.

Plant Part	Ion	Temperature - °C			
		10.0	18.3	23.9	32.2
Shoot	Ca	100	77	90	71
	Mg	100	101	95	97
	K	100	111	129	129
	N	100	119	129	132
	P	100	117	146	164
Root	Ca	100	103	90	89
	Mg	100	111	104	124
	K	100	114	102	118
	N	100	114	119	114
	P	100	95	99	158

The effect of temperature on plant content of nitrogen, phosphorus, and potassium agreed with most of the previous work, but the results for calcium did not. Mederski and Jones (1963) indicated that soil heating significantly increased nitrogen, phosphorus, potassium concentrations in corn plants sampled 30 days after planting. Nielsen et al. (1960) found that increasing the soil temperature from 40° to 67° F increased the uptake of nitrogen, phosphorus, potassium and magnesium in oats, but they showed that the calcium content tended to decrease with increasing temperature to 67° F and then to increase at 80° F. Results in this experiment showed that the calcium content in shoots decreased as temperature increased and was significant at 0.01 level while the Ca content in roots also decreased as temperature increased but not significantly. Kenworthy (1956) pointed out that there was a significant increase in potassium in the leaves of strawberry plants as root temperatures were increased, but indicated that root temperature had very little effect on the composition of the plant for other nutrients during the vegetative period of development. Contradictory results regarding calcium uptake may have been due to ion interaction or competitive effects or differences among plant species. The temperature effect on the uptake of calcium and its role in different plants is not clear and further research seems indicated.

Low soil temperature has a depressing effect on the mineral accumulation process. Dean and Gledhill (1956) and Davis and Lingle

(1961) showed that cool root temperatures decreased mineral accumulation and reduced rates of mineral translocation. Parks and Fisher (1958) found that at 20°C and 30°C there was a greater percentage of potassium and magnesium in the forage than at 10°C. The difference was significant at 0.05 level but no significant difference between the means of these nutrients at 20°C and 30°C was found. Observations make it clear that nutrient uptake is temperature dependent.

Ion Uptake and Transpiration

A relationship between ion uptake and rate of transpiration is often discussed. Sepaskhah (1971) tested the hypothesis that nitrogen uptake depends on the rate of water uptake. He calculated the rate of nitrogen uptake per unit volume of water entering the plant and came to the conclusion that the rate of nitrogen uptake was not proportional to the rate of water uptake. A similar calculation was made for the rate of uptake of the sum of all ions considered in this study (Table 14).

Sepaskhah (1971) came to the conclusion that the reduced rates of nitrogen uptake at low root temperatures could not be explained on the basis of such physical phenomena as translocation rates or transpiration rates.

It has been suggested that there are a limited number of exchange sites on plant roots available for nutrient uptake and that these are occupied as soon as they are formed. Kramer (1969) was one who

reasoned that in nature the exchange sites on growing roots are occupied as rapidly as they are produced and that metabolic uptake alone is responsible for the steady, long-term movement of ions into root cells. The rate of formation of these exchange sites would then determine to a great extent the rate of nutrient uptake. If this is so, then an increase in the rate of nutrient uptake must be proportional to the increase in rate of root growth. To test this hypothesis, Table 15 was constructed from the data shown in Table 2 (rates of dry matter production) and Table 5 (rates of ion uptake). It shows the rate of ion uptake (N, K, Ca, P, and Mg) as a function of the rate of root growth in grams of nutrients taken up per gram of new root growth.

The rate of nutrient uptake per unit of new root growth was not a constant but increased as a function of temperature. The temperature effect (Figure 6) showed a rapid increase at the lower temperatures and little change at the higher temperatures. The rates were nearly the same at both soil water suctions (0.35 and 2.50 bars) and a statistical analysis failed to indicate significant difference between the two treatments. The transpiration rates were appreciably different at the two suctions. If the correlation between root growth and ion uptake is indeed meaningful, this would again indicate an absence of a direct link between transpiration and ion uptake.

The nature of the temperature effect on the rate of uptake shown in Table 15 was further explored by plotting the log rate of uptake per

Table 14. Rate of ion uptake (N + K + Mg + Ca + P) per unit volume of water transpired (ppm).

Soil Water Suction	Soil Temperature	Ion Uptake Rate	Transpiration Rate	Concentration
<u>bars</u>	<u>°C</u>	<u>μg/day</u>	<u>cm³/day</u>	<u>ppm</u>
0.35	10.0	737	12.2	60.4
	15.5	2464	14.9	165.4
	21.1	3486	18.8	185.4
	26.6	3635	25.6	142.0
	32.2	2775	31.6	87.8
2.50	10.0	595	8.5	70.0
	15.5	2015	9.6	209.9
	21.1	2941	11.5	255.7
	26.6	3037	14.4	210.9
	32.2	2290	17.0	134.7

Table 15. Rate of ion uptake as a function of the rate of root growth (10^{-2} g/g).

Soil Water Suction	Soil Temperature	Element Taken Up					
		N	K	Ca	P	Mg	Sum
<u>bars</u>	<u>°C</u>	<u>----- 10⁻² g/g -----</u>					
0.35	10.0	6.93	6.13	2.06	0.889	0.356	16.37
	15.5	8.91	7.58	2.20	1.090	0.418	20.20
	21.1	9.54	8.20	2.04	1.202	0.411	21.39
	26.6	10.26	9.24	1.95	1.423	0.429	23.30
	32.2	10.46	9.41	1.91	1.724	0.431	23.92
2.50	10.0	7.41	6.62	2.15	0.941	0.382	17.50
	15.5	8.69	7.38	2.22	1.088	0.382	19.75
	21.1	9.87	8.51	2.08	1.226	0.421	22.11
	26.6	10.24	9.22	1.95	1.351	0.420	23.18
	32.2	10.07	9.02	1.86	1.530	0.420	22.90

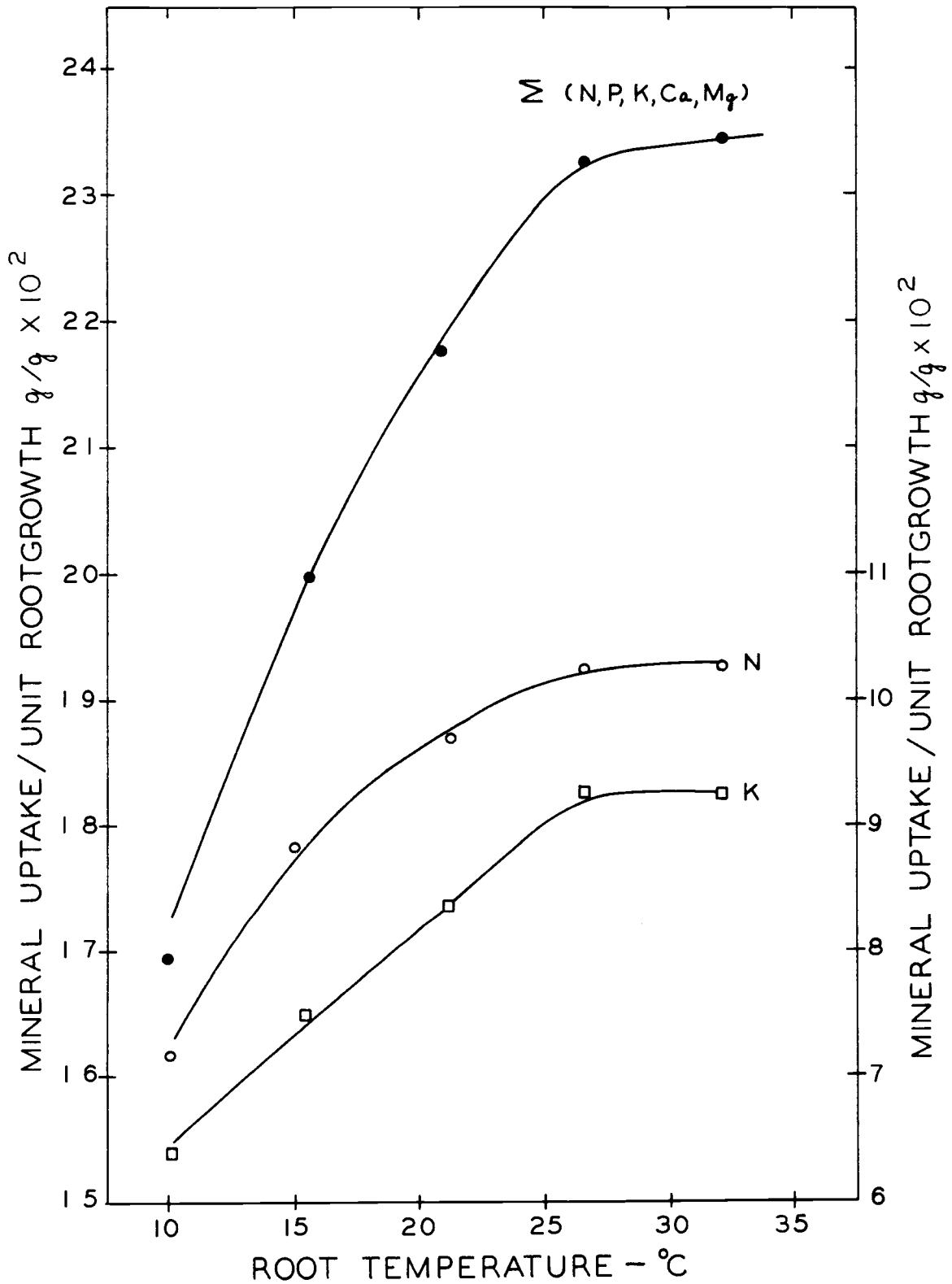


Figure 6. Nutrient uptake per unit of new root growth of 5-week old wheat seedlings as a function of root temperature.

gram of new root growth as a function of the reciprocal of the absolute temperature (Figure 7). The rates used were the average of those observed at 0.35 and 2.50 bars.

If the slopes of the lines in Figure 6 are viewed as reflecting the activation energy of the processes involved, two processes appear to exist--one with a higher activation energy at temperatures lower than 25°C and one with a lower activation energy at temperatures above 25°C. The process with the higher activation energy could be viscosity controlled whereas the process with the lower activation energy could be controlled by diffusion. Q_{10} values for the change in viscosity of water and change in diffusion coefficients as a function of temperature are shown in Table 16. At the low temperature range (10-20°C), Q_{10} values for the ion uptake per gram of new root growth and viscosity of water are of the same order of magnitude, suggesting that the ion uptake might be viscosity controlled. Viscosity influence could be exerted in several places, e.g., in the carrier molecule transfer across root cell membranes or in the transfer of metabolites in the vascular system.

Over the high temperature range (25-35°C), the Q_{10} values for the temperature effect on ion uptake and diffusion rates in aqueous solutions are of the same order of magnitude. This sort of control could only occur if the membranes of the root cells lost their controlling functions at high temperatures. Ions would then freely pass

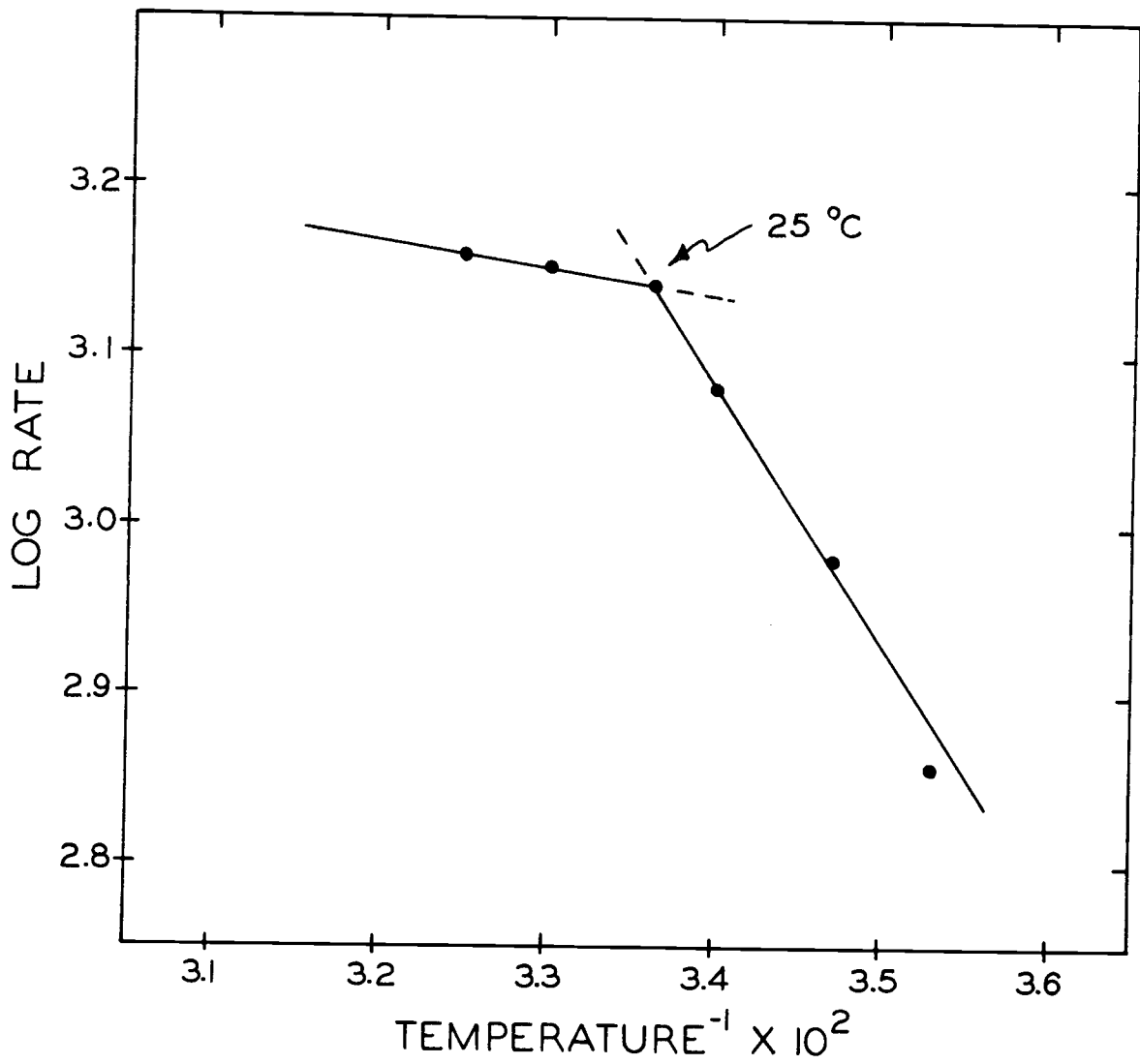


Figure 7. Log rate of nutrient uptake per unit of new root growth of 5-week old wheat seedlings as a function of the reciprocal of the absolute temperature.

and would do so at a rate controlled by the rate of diffusion into the cells. This reasoning implies that in addition to viscosity the membrane structure plays an important role in the control of mineral translocation. It agrees with the (1966) discussion of membrane controlled transport by Nielsen and Humphries.

Table 16. Q_{10} values for the change in rate of ion uptake shown in Table 15, the change in viscosity of water and the change in diffusion rates.

Temperature Range	Ion Uptake	Viscosity of water	Diffusion in Aqueous Solution
<u>°C</u>			
10-15	1.34	1.32	1.03
15-20	1.20	1.29	1.03
20-25	1.13	1.27	1.03
25-30	1.03	1.25	1.03
30-35	1.01	1.23	1.03

Ion Interactions

As previously stated, with an increase in root temperature came an increase in the content of nitrogen, potassium, phosphorus, and magnesium. At the same time, the calcium content of the shoots was found to decrease, though in roots it was little changed. It appeared the overall decrease in calcium content as temperature increased was due to ion inhibition from increased potassium and/or competition from increased magnesium. This agrees with Jones and Mederski (1963) who pointed out that the marked depressive effect of high

temperature on the uptake of calcium may be due to antagonism caused by increased uptake of potassium. They also observed that high temperature stimulated the uptake of magnesium.

Similar interaction between ions in different plants has been identified by many other workers, but there appear exceptions related to relative concentrations. Increasing concentrations of potassium generally depresses the calcium content of plants (Beeson et al., 1944; Freeman, 1967; Hylton et al., 1967; Lazaroff and Pitman, 1966; McEvoy, 1955; Osmond, 1966; York et al., 1953). Lazaroff and Pitman (1966) and Johansen et al. (1968) indicated that increasing concentrations of potassium in the nutrient solutions depressed the calcium content in barley plants growing in nutrient solutions of low calcium concentration (250 and 2500 μm). On the other hand calcium inhibits potassium transport during the initial phase of transport (Elzam and Hodges, 1967), but calcium can also stimulate absorption of potassium (Jacobson et al., 1961; Moore et al., 1961). Hooymans (1964) found that the influence of the calcium ion on the potassium uptake at pH 5.4 manifests itself as inhibitory, stimulatory, or neutral depending upon the potassium concentration and the duration of the experiment. Calcium can markedly depress the uptake of magnesium (Moore et al., 1961; Maas, 1969). Conversely, an increase in the magnesium concentration can also depress the calcium content in the roots (Leggett and Gilbert, 1969).

Distribution Between Shoots and Roots

It is generally assumed that soil temperature as well as soil water suction has an influence on the rate of translocation of ions within plants. The daily rates of calcium, magnesium, and potassium uptake derived from the rate of increase in dry weight (Table 2) and the calcium, magnesium, and potassium concentration of the dry weight (Table 3) and the fraction of total uptake translocated to shoots are shown in Table 5. Calcium stands out because its concentration in shoots was less than in roots at both soil water suctions at the various temperatures tried, and the amount translocated to the shoots was less than 50% of total uptake. In contrast, magnesium and potassium, nitrogen and phosphorus content was higher in shoots than in roots. The fraction of total uptake translocated to the shoots was about 69% for magnesium, 83% for potassium, 74% for nitrogen and 72% for phosphorus.

Biddulph et al. (1958) also found that calcium displayed a high degree of immobility. They indicated that the initial step in its delivery by the transpiration stream constituted the final step in its distribution and that calcium did not re-circulate. There are a number of reports in the literature of translocation which indicate that calcium is immobile in the phloem, or relatively so (Biddulph, 1953; Biddulph et al., 1958; Bledsoe et al., 1949; Bukovac and Wittwer, 1957;

Swanson and Whitney, 1953). However, the majority of these studies were not quantitative but merely indicated that translocation of calcium was considerably less than that of phosphorus, sulfur, potassium, and some other elements (Biddulph et al., 1959).

The translocated fraction of calcium, magnesium, potassium, nitrogen, and phosphorus to shoots was lowest at a temperature of 10°C, consistent with Strausberg's (1958) report that nutrient translocation to the aerial parts decreased as soil temperatures were lowered to 7°C.

A few comments can be made on the limitations of this experiment. (1) A membrane is needed which is more resistant to physical as well as microbial damage as breakage and bacterial deterioration presented problems. (2) A longer period may be necessary for the investigation of growth. (3) In order to investigate nutrient uptake as a function of water suction effect, a wider range of water suctions could be used.

SUMMARY AND CONCLUSION

The effect of soil temperature and soil water suction on the uptake of calcium, magnesium, and potassium by 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 were germinated and cultured for 5 weeks in a growth chamber set for 23.9°C day time and 21.1°C night time temperatures. During this period the plants were supplied daily with water and nutrients. At the age of 5 weeks, the cells were taken from the growth chambers, trimmed, and after removal of cell sides encased in a semi-permeable membrane. Replicate membrane covered cells were then immersed in constant temperature chambers containing osmotic solutions and plant nutrients and maintained at a given constant temperature. Plants were allowed to grow exposed to these conditions for 8 days with some of the plants being harvested at day 0, 2, 4, 6, and 8. Measurements included: dry weight and calcium, magnesium, and potassium contents of both shoots and roots. Experiments were repeated for soil temperatures of 10.0, 18.3, 23.9, and 32.2°C and soil water suctions of 0.35 and 2.5 bars.

The daily increase in dry weight at various temperatures and

soil water suctions was calculated from the plants harvested every second day, based on the assumption that the final equilibrium rate of dry weight gain was indicated by drawing the "best fit" line of dry weight increase as a function of time.

The rate of dry weight accumulation for both shoots and roots was slowest at the extreme temperatures with the maximum rate occurring at a root temperature of about 24°C. It was stated by Nielsen and Humphries (1966) that maximum growth is often greatest when root and shoot temperature are different, while in this experiment, the best development of wheat was when the roots and shoots were at the same temperature which is corresponding to Hall's (1950) report on buckwheat. The growth rate of shoots and roots at all temperatures was highest at a soil water suction of 0.35 bar. These results are in general agreement with literature reports. Indications were that the uptake of nutrients was restricted at low root temperatures, due to membrane structure, solution viscosity or other unknown factors. Restrictions in growth rate at the high temperatures was presumed due to the thermal destruction of enzymes and disruption of physiological processes.

Percent of calcium, magnesium, and potassium in the extract from shoots and roots of the harvested plants was determined with an atomic absorption spectrophotometer. As time progressed, the concentration of calcium, magnesium, and potassium in the shoot and

root material approached an equilibrium value for each ion at the various treatment levels.

Increasing root temperature resulted in an increase in the nitrogen, phosphorus, and potassium content in both shoot and root material. Magnesium content was decreased only slightly in shoots and hardly at all in the roots. The calcium content decreased in both shoots and roots. Statistically the effect of temperature was significant at the 0.01 level in the shoots for nitrogen and potassium content, and at the 0.05 level in the roots; for phosphorus at the 0.01 level in the roots, but only at the 0.05 level in the shoots; for calcium at the 0.01 level in the shoots. No significant effect of temperature was found for either calcium content of roots or magnesium content of shoots.

The decreased calcium content of the shoots paralleled an increased potassium content but little changed magnesium content in shoots as root temperature was increased. Further, the increased magnesium content of roots paralleled an increased potassium content but with little changed calcium content in roots. This suggested ion inhibition may have occurred due to the increase in potassium content. In both shoots and roots, the uptake rate of all ions analyzed--calcium, magnesium, potassium, nitrogen and phosphorus--increased to a maximum and then decreased with increasing temperature. The maximum uptake rate for calcium and magnesium occurred between 21.1°

to 26.6°C; for potassium and nitrogen at 26.6°C in the shoots and at 21.1°C in the roots; and for phosphorus at 26.6°C in the shoots, and greater than 32.2°C in roots. For the range of conditions imposed, a root temperature of about 24°C appeared best for nutrient uptake and optimal growth of wheat (Triticum aestivum).

The total content of calcium in the shoots was less than in roots at both water suctions and at all temperatures. The fraction of total uptake translocated to the shoots was for: calcium, less than 50%; magnesium, 69%; potassium, 83%; nitrogen, 74%; and phosphorus, about 72%. That the translocation to shoots was greater for all other ions than calcium agreed with previous literature. The fraction of calcium, magnesium, potassium, nitrogen, and phosphorus translocated to shoots was lowest at the lowest soil temperature used, i. e. , 10°C.

For both shoots and roots, no significant difference was found in concentration of calcium, magnesium, potassium, nitrogen or phosphorus of plants grown at soil water suctions of 0.35 and 2.5 bars. There was a significant reduction in growth rate of wheat for the 2.5 bar water stress.

The effect of water suction on ion uptake rate is woefully incomplete, partly because critical experiments are few and partly because of the range of water suctions used. Further research work in this field is also indicated.

BIBLIOGRAPHY

- Arnon, D. I. 1939. Effect of ammonium and nitrate nitrogen on the mineral composition and sap characteristics of barley. *Soil Science* 48:295-307.
- Barber, S. A. 1962. A diffusion and mass-flow concept of soil nutrient availability. *Soil Science* 93:39-49.
- Beall, S. E. and G. Samuels. 1971. The use of warm water for heating and cooling plant and animal enclosures. p. 7. Oak Ridge National Laboratory. ORNL-TM-3381.
- Beeson, K. C., C. B. Lyon and M. W. Barrentine. 1944. Ionic absorption by tomato plants correlated with variations in composition of the nutrient medium. *Plant Physiol.* 19:258-277.
- Bell, C. W. and O. Biddulph. 1963. Translocation of calcium exchange versus mass flow. *Plant Physiol.* 38:610-614.
- Biddulph, O. 1953. Translocation of radioactive mineral nutrients in plants. In: *The Use of Isotopes in Plant and Animal Research*, Report No. 4. Agr. Expt. Sta., Kansas State College, Manhattan, or U. S. A. E. C., Wash., D. C. T/D 5098.
- Biddulph, O., S. Biddulph, R. Cory and H. Koontz. 1958. Circulation patterns for phosphorus, sulfur, calcium in the bean plant. *Plant Physiol.* 33:293-300.
- Biddulph, O., R. Cory and Susann Biddulph. 1959. Translocation of calcium in the bean plant. *Plant Physiol.* 34:512-519.
- Bledsoe, R. W., C. L. Comar and H. C. Harris. 1949. Absorption of radioactive calcium by the peanut fruit. *Science* 109:329-330.
- Bohning, R. H. and B. Lusanandana. 1952. A comparative study of gradual and abrupt changes in root temperature on water absorption. *Plant Physiol.* 27:475-488.
- Bonner, James. 1959. Water transport. *Science* 129:447-450.
- Brown, D. A. 1953. Cation exchange in soils through the moisture range saturation to the wilting percentage. *Soil Sci. Soc. Amer. Proc.* 17:92-96.

- Brouwer, R. 1954. The regulating influence of transpiration and suction tension on the water and salt uptake by the roots of intact *Vicia Faba* plants. *Acta Bot. Neerl.* 3:264-312.
- Broyer, T.C. 1950. Further observations on the absorption and translocation of inorganic solutes using radioactive isotopes with plants. *Plant Physiol.* 27:367-377.
- Broyer, T.C. 1951. The nature of the process of inorganic solute accumulation in roots. *Mineral Nutrition of Plants*, E. Truog, Ed., Univ. of Wis. Press. Madison, Chap. 8:187-249.
- Bukovac, M.J. and S.H. Wittwer. 1957. Absorption and mobility of foliar applied nutrients. *Plant Physiol.* 32:428-435.
- Butler, G.W. 1953. Ion uptake by young wheat plants. I. Time course of the absorption of potassium and chloride ions. *Physiol. Plantarum* 6:594-616.
- Chang, S.Y., R.H. Lowe and A.J. Hiatt. 1968. Relationship of temperature to the development of calcium deficiency. *Agron. J.* 60:435-436.
- Cole, C.V., D.L. Crunes, L.K. Porter and S.R. Olsen. 1963. The effects of nitrogen on short-term phosphorus as absorption and translocation in corn (*Zea mays*). *Soil Sci. Soc. Amer. Proc.* 27:671-674.
- Cunningham, R.K. 1962. Cation-anion relationships in Italian ryegrass (*Lolium multiflorum*). *Nature* 196:1230-1231.
- Danielson, R.E. and M.B. Russell. 1957. Ion absorption by corn roots as influenced by moisture and aeration. *Soil Sci. Soc. Amer. Proc.* 21:3-6.
- Davis, R.M. and J.C. Lingle. 1961. Basis of shoot response to root temperature in tomato. *Plant Physiol.* 36:153-162.
- Dean, L.A. and V.H. Gledhill. 1956. Influence of soil moisture on phosphate absorption as measured by an excised root technique. *Soil Sci.* 82:71-79.
- Dijkshoorn, W. and M.L. 'T Hart. 1957. The effect of alteration of temperature upon the cationic composition in perennial ryegrass. *Netherland Journal of Agri. Sci.* 5:18-36.

- Eaton, F.M. and J.E. Bernardin. 1964. Mass-flow and salt accumulation in water versus soil cultures. *Soil Science* 97:411-416.
- Elzam, O.E. and T.K. Hodges. 1967. Calcium inhibition of potassium absorption in corn roots. *Plant Physiol.* 42:1483-1488.
- Epstein, E. 1960. Spaces, barriers, and ion carriers: ion absorption in plants. *Amer. J. Bot.* 47:393-399.
- Epstein, E. 1961. The essential role of calcium in selective cation transport of plant cells. *Plant Physiol.* 36:437-444.
- Fawcett, R.G. and J.P. Quirk. 1960. Effect of water-stress on the absorption of soil phosphorus by wheat plants. *Nature* 188:687-688.
- Fazilat, M. 1971. Growth rate and phosphorus uptake of wheat as a function of soil water suction and soil temperature. M.S. thesis, Corvallis, Oregon State University. 93 numb. leaves.
- Fraser, D.A. and C.A. Mawson. 1953. Movement of radioactive isotopes in yellow birch and white pine as detected with a portable scintillation counter. *Can. J. Bot.* 31:324-333.
- Freeman, G.G. 1967. Studies on potassium nutrition of plants. I. Effects of potassium concentration on growth and mineral composition of vegetable seedlings in sand culture. *J. Sci. Food Agr.* 18:171-176.
- Frere, M.H. 1969. Ionic interaction in diffusion. *Soil Sci. Soc. Amer. Proc.* 33:883-886.
- Furr, J.R. and C.A. Taylor. 1939. Growth of lemon fruits in relation to moisture content of the soil. U.S.D.A. Tech. Bull. No. 640.
- Greenway, H. and B. Klepper. 1968. Phosphorus transport to the xylem and its regulation by water flow. *Planta (Berlin)* 83:119-136.
- Grunes, D.L. and B.A. Krantz. 1958. Nitrogen fertilization increases N, P and K concentrations in oats. *Agron. J.* 50:729-732.
- Hall, W.C. 1950. Growth and development of buckwheat under different temperature gradients. *Bot. Gaz.* 111, 331-343.

- Handly, R. and R. Overstreet. 1961. Uptake of calcium and chlorine in roots of zea mays. *Plant Physiol.* 36:766-769.
- Hewitt, W.B. and M.E. Gardiner. 1956. Some studies of the absorption of zinc sulfate in Thompson seedless grape canes. *Plant Physiol.* 31:393-399.
- Hooymans, J.J.M. 1964. The role of calcium in the absorption of anions and cations by excised barley roots. *Acta Botanica Neerlandica* 13:507-540.
- Hylmo, B. 1953. Transpiration and ion absorption. *Physiol. Plantarum* 6:333-405.
- Hylton, L.O., A. Ulrich and D.R. Cornelius. 1967. Potassium and sodium interrelationships in growth and mineral content of Italian ryegrass. *Agron. J.* 59:311-314.
- Jackson, J.E. and P.E. Weatherley. 1962a. The effect of hydrostatic pressure gradients on the movement of potassium across the root cortex. *J. Exp. Bot.* 13:128-143.
- Jackson, J.E. and P.E. Weatherley. 1962b. The effect of hydrostatic pressure gradients on the movement of sodium and calcium across the root cortex. *J. Exp. Bot.* 13:404-413.
- Jacobson, L., R.J. Hannapel, D.P. Moore and M. Schaedle. 1961. Influence of calcium on selectivity of ion absorption process. *Plant Physiol.* 36:58-61.
- Jenne, E.A., H.F. Rhoades, C.H. Yien and O.W. Howe. 1958. Change in nutrient element accumulation by corn with depletion of soil moisture. *Agron. J.* 50:71-74.
- Jenny, H. and R. Overstreet. 1939. Surface migration of ions and contact exchange. *J. Phys. Chem.* 43:1185-1196.
- Jensen, R.D. and S.A. Taylor. 1961. Effect of temperature on water transport through plants. *Plant Physiol.* 36:639-642.
- Johansen, C., D.G. Edwards and J.F. Loneragan. 1968. Interactions between potassium and calcium in their absorption by intact barley plants. I. Effects of potassium on calcium absorption. *Plant Physiol.* 43:1717-1721.

- Johnson, R. E. and W. A. Jackson. 1964. Calcium uptake and transport by wheat seedlings as affected by aluminum. *Soil Sci. Soc. Amer. Proc.* 28:381-386.
- Jones, J. B., Jr. and H. J. Mederski. 1963. Effect of soil temperature on corn plant development and yield: II. Studies with six inbred lines. *Soil Sci. Soc. Amer. Proc.* 27:189-192.
- Kaufmann, M. R. 1968. Water relations of pine seedlings in relation to root and shoot growth. *Plant Physiol.* 43:281-288.
- Knoll, H. A., D. J. Lathwell and N. C. Brady. 1964. The influence of root zone temperature on the growth and contents of phosphorus and anthocyanin of corn. *Soil Sci. Soc. Amer. Proc.* 28:400-403.
- Kramer, P. J. 1940. Root resistance as a cause of decreased water absorption by plants at low temperatures. *Plant Physiol.* 15:63-79.
- Kramer, P. J. and T. T. Kozlowski. 1960. *Physiology of trees.* McGraw-Hill Book Company. New York. p. 198-201.
- Kramer, P. J. 1969. Factors affecting the absorption of water. *Plant and soil water relationships.* Chapter 6:174-213.
- Kuo, T. 1970. Soil physical conditions and nitrogen fixation of soybeans. M.S. thesis. Corvallis, Oregon State University. 69 numb. leaves.
- Kuiper, P. J. C. 1964a. Water transport across root cell membranes: effect of alkenylsuccinic acids. *Science* 143:690-691.
- Kuiper, P. J. C. 1964b. Water uptake of higher plants as affected by root temperature. *Meded Landbouwhogeschool Wageningen* 64-4:1-11.
- Lazaroff, N. and M. G. Pitman. 1966. Calcium and magnesium uptake by barley seedlings. *Austral. J. Biol. Sci.* 19:991-1005.
- Leggett, J. E. and W. A. Gilbert. 1967. Localization of the Ca-mediated apparent ion selectivity in the cross-sectional volume of soybean roots. *Plant Physiol.* 42:1658-1664.
- Leggett, J. E. and W. A. Gilbert. 1969. Magnesium uptake by soybeans. *Plant Physiol.* 44:1182-1186.

- Lundegardh, H. 1955. Mechanisms of absorption, transport, accumulation and secretion of ions. *Ann. Rev. Plant Physiol.* 6:1-24.
- Maas, E. V., D. P. Moore and B. J. Mason. 1969. Influence of calcium and magnesium on manganese absorption. *Plant Physiol.* 44:796-800.
- Maas, E. V. 1969. Calcium uptake by excised maize roots and interactions with alkali cations. *Plant Physiol.* 44:985-989.
- McEvoy, E. T. 1955. Interaction of sodium and potassium on growth and mineral content of flue-cured tobacco. *Can. J. Agr. Sci.* 35:294-299.
- Mederski, H. J. and H. J. Wilson. 1960. Relation of soil moisture to ion absorption by corn plants. *Soil Sci. Soc. Amer. Proc.* 24:149-152.
- Mederski, H. J. and J. B. Jones, Jr. 1963. Effect of soil temperature on corn plant development and yield. I. Studies with a corn hybrid. *Soil Sci. Soc. Amer. Proc.* 27:186-189.
- Meyer, R. E. and J. R. Gingrich. 1966. Osmotic stress effects on wheat using a split root solution culture system. *Agron. J.* 58:377-381.
- Miller, M. F. and F. L. Duley. 1925. The effect of a varying moisture supply upon the development and composition of the maize plant at different periods of growth. *Missouri Agr. Expt. Sta. Res. Bul.* 76.
- Moore, D. P., R. Overstreet and L. Jacobson. 1961. Uptake of magnesium and its interaction with calcium in excised barley roots. *Plant Physiol.* 36:290-295.
- Nielsen, K. F., R. L. Halstead, A. J. Maclean, R. M. Holmes and S. J. Bourget. 1960. The influence of soil temperature on the growth and mineral composition of oats. *Can. J. of Soil Science* 40:255-263.
- Nielsen, K. F., R. L. Halstead, A. J. Maclean, S. J. Bourget and R. M. Holmes. 1961. The influence of soil temperature on the growth and mineral composition of corn, bromegrass and potatoes. *Soil Sci. Soc. Amer. Proc.* 25:369-372.

- Nielsen, K. F. and R. K. Cunningham. 1964. The effects of soil temperature and form and level of nitrogen on growth and chemical composition of Italian ryegrass. *Soil Sci. Soc. Amer. Proc.* 28:213-218.
- Nielsen, K. F. and E. C. Humphries. 1966. Effects of root temperature on plant growth. *Soils and Fertilizers* 29:1-7.
- O'Leary, J. W. 1965. Root pressure exudation in woody plant. *Bot. Gaz.* 126:108-115.
- Oliver, S. and S. A. Barber. 1966. An evaluation of the mechanisms governing the supply of Ca, Mg, K, and Na to soybean roots (*Glycine max*). *Soil Sci. Soc. Amer. Proc.* 30:82-86.
- Olsen, S. R. and W. D. Kemper. 1968. Movement of nutrients to plant root. *Advan. Agron.* 20:91-151.
- Osmond, C. B. 1966. Divalent cation absorption and interaction in *Atriplex*. *Austral. J. Biol. Sci.* 19:37-48.
- Parks, W. L. and W. B. Fisher, Jr. 1958. Influence of soil temperature and nitrogen on ryegrass growth and chemical composition. *Soil Sci. Soc. Amer. Proc.* 22:257-259.
- Pate, J. S. 1965. Roots as organs of assimilation of sulfate. *Science* 169:547-548.
- Petterson, S. 1966. Active and passive components of sulfate uptake in sunflower plants. *Physiol. Plantarum (Copenh.)* 19:459-492.
- Philip, J. R. 1958. The osmotic cell, solute diffusibility, and the plant water economy. *Plant Physiol.* 33:264-271.
- Porter, L. K., W. D. Kemper, R. D. Jackson and B. A. Stewart. 1960. Chloride diffusion in soil as influenced by moisture content. *Soil Sci. Soc. Amer. Proc.* 24:460-463.
- Priestley, J. H. 1922. Further observation upon the mechanism of root pressure. *New Phytol.* 21:41-48.
- Proebsting, E. L., Sr. 1957. The effect of soil temperature on the mineral nutrition of the strawberry. *Proc. Am. Soc. Hort. Sci.* 69:278-291.

- Rahman, A. A. A., A. F. Shalaby and M. D. El Monayeri. 1971. Effect of moisture stress on metabolic products and ions accumulation. *Plant and Soil* 34:65-90.
- Rains, D. W. and R. A. Floyd. 1970. Influence of calcium on sodium and potassium absorption by fresh and aged bean stem slices. *Plant Physiol.* 46:93-98.
- Richards, L. A. and C. H. Wadleigh. 1950. Soil physical conditions and plant growth. *Agronomy Monograph* 2:73-251. Academic Press, Inc., New York.
- Roberts, A. N. and A. L. Kenworthy. 1956. Growth and composition of the strawberry plant in relation to root temperature and intensity of nutrition. *Proc. Am. Soc. Hort. Sci.* 68:157-168.
- Russell, J. S., C. W. Bourc and H. F. Rhoades. 1954. Effect of nitrogen fertilizer on the nitrogen, phosphorus and cation contents of bromegrass. *Soil Sci. Soc. Amer. Proc.* 18:292-296.
- Russell, R. S. and D. A. Barber. 1960. The relationship between salt uptake and the absorption of water by intact plants. *Ann. Rev. Plant Physiol.* 11:127-140.
- Scott, L. I. and J. H. Priestley. 1928. The root as absorbing organ. I. A reconsideration of the entry of water and salts into the absorbing region. *New Phytol.* 27:125-141.
- Sepaskhah, A. R. 1971. Nitrogen uptake by wheat as a function of root temperature and plant water stress. M.S. thesis. Corvallis, Oregon State University. 81 numb. leaves.
- Shapiro, R. E., W. H. Armigen and M. Fried. 1960. The effect of soil water movement vs. phosphate diffusion on growth and phosphorus content of corn and soybeans. *Soil Sci. Soc. Amer. Proc.* 24:161-164.
- Strausberg, D. V. 1958. The utilization of nutrients by plants in the polar region under various temperature conditions. *Fizio. Rast.* 5:228-234.
- Stevenson, D. S. and L. Boersma. 1964. Effect of soil water content on the growth of adventitious roots of sunflower. *Agron. J.* 56:509-512.

- Sullivan, J. T. and U. G. Sprague. 1949. The effect of temperature on the growth and composition of the stubble and roots of perennial ryegrass. *Plant Physiol.* 24:706-719.
- Swanson, C. A. and J. B. Whitney. 1953. The translocation of foliar applied phosphorus-32 and other radioisotopes in bean plants. *Amer. Jour. Bot.* 40:816-823.
- Taylor, H. M. and L. F. Ratliff. 1969. Root elongation rates on cotton and peanuts as a function of soil strength and soil water content. *Soil Sci.* 108:113-119.
- Tew, R. K., S. A. Taylor and G. L. Ashcroft. 1963. Influence of temperature on transpiration under various environmental conditions. *Agron. J.* 55:558-560.
- Thomas, J. R. and G. L. Wiegand. 1970. Osmotic and matric suction effects on relative turgidity, temperature and growth of cotton leaves. *Soil Sci.* 109:85-92.
- Wiersum, L. K. 1958. Influence of water-content of sand on rate of uptake of rubidium-86. *Nature* 181:106-107.
- Wiersum, L. K. 1966. Calcium content of fruits and storage tissue in relation to the mode of water supply. *Acta Botanica Neerlandica* 15:406-418.
- Willis, W. O., W. E. Larson and D. Kirkham. 1957. Corn growth as affected by soil temperature and mulch. *Agron. J.* 49:323-328.
- Woolley, D. G. 1963. Effects of nutrition, osmotic pressure, and temperature of the nutrient solution on plant growth and chemical composition. *Can. J. Plant Sci.* 43:44-50.
- York, E. T., R. Bradfield and M. Peech. 1953. Calcium-potassium interactions in soils and plants: II. Reciprocal relationship between calcium and potassium in plants. *Soil Sci.* 76:481-491.

APPENDIX

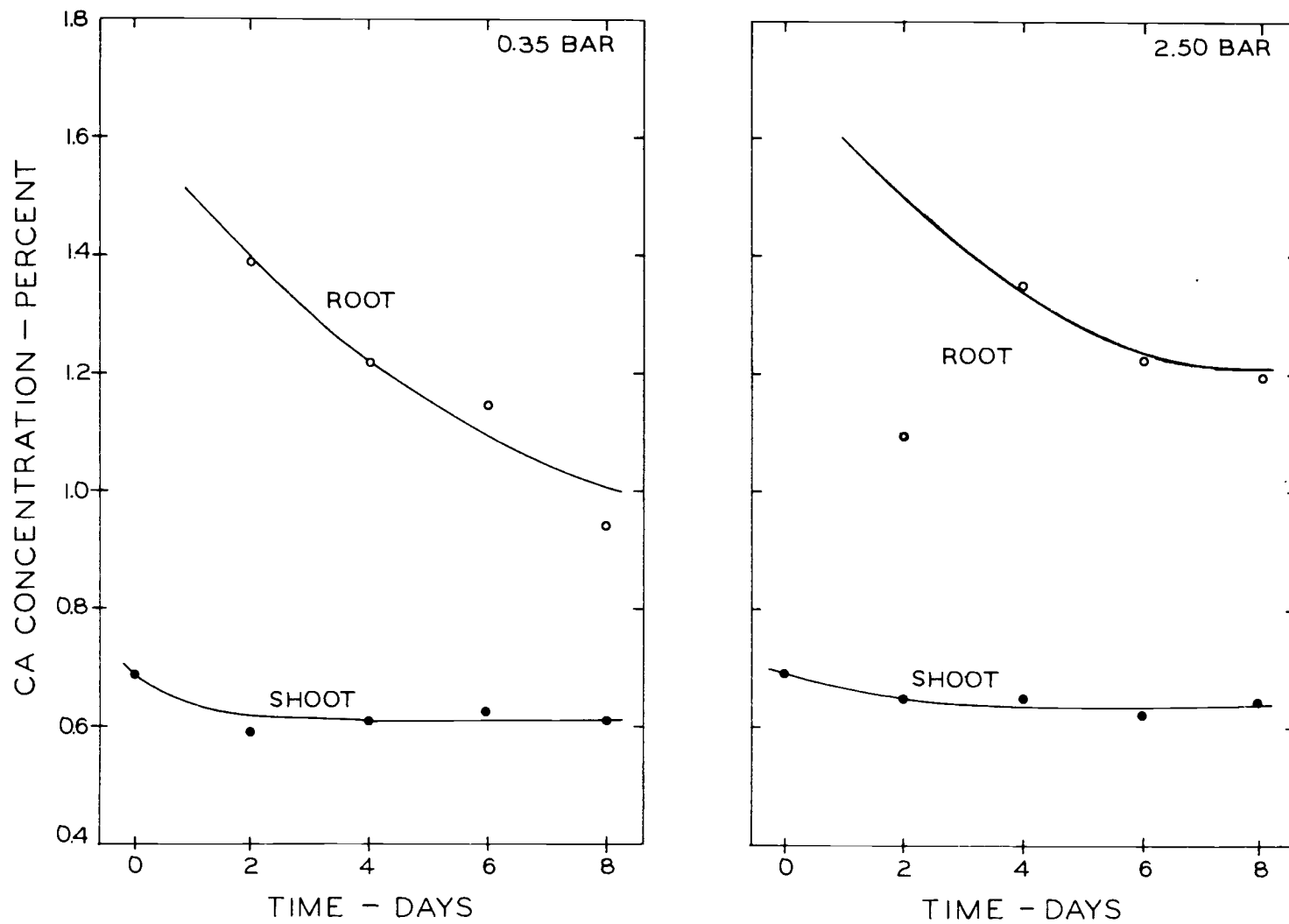


Figure A-1. Percent calcium in shoots and roots of 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars at a root temperature of 10.0°C.

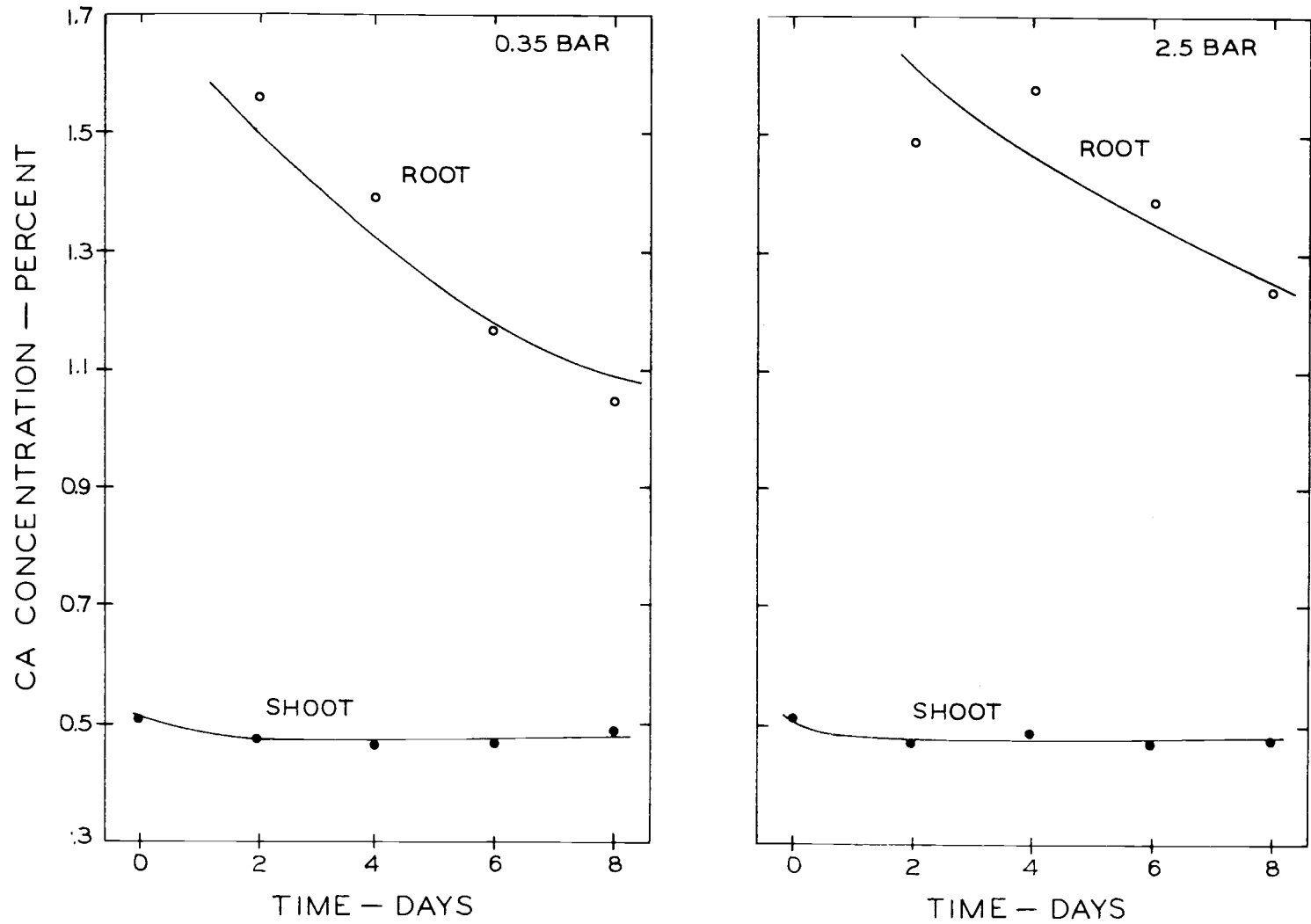


Figure A-2. Percent calcium in shoots and roots of 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars at a root temperature of 18.3°C.

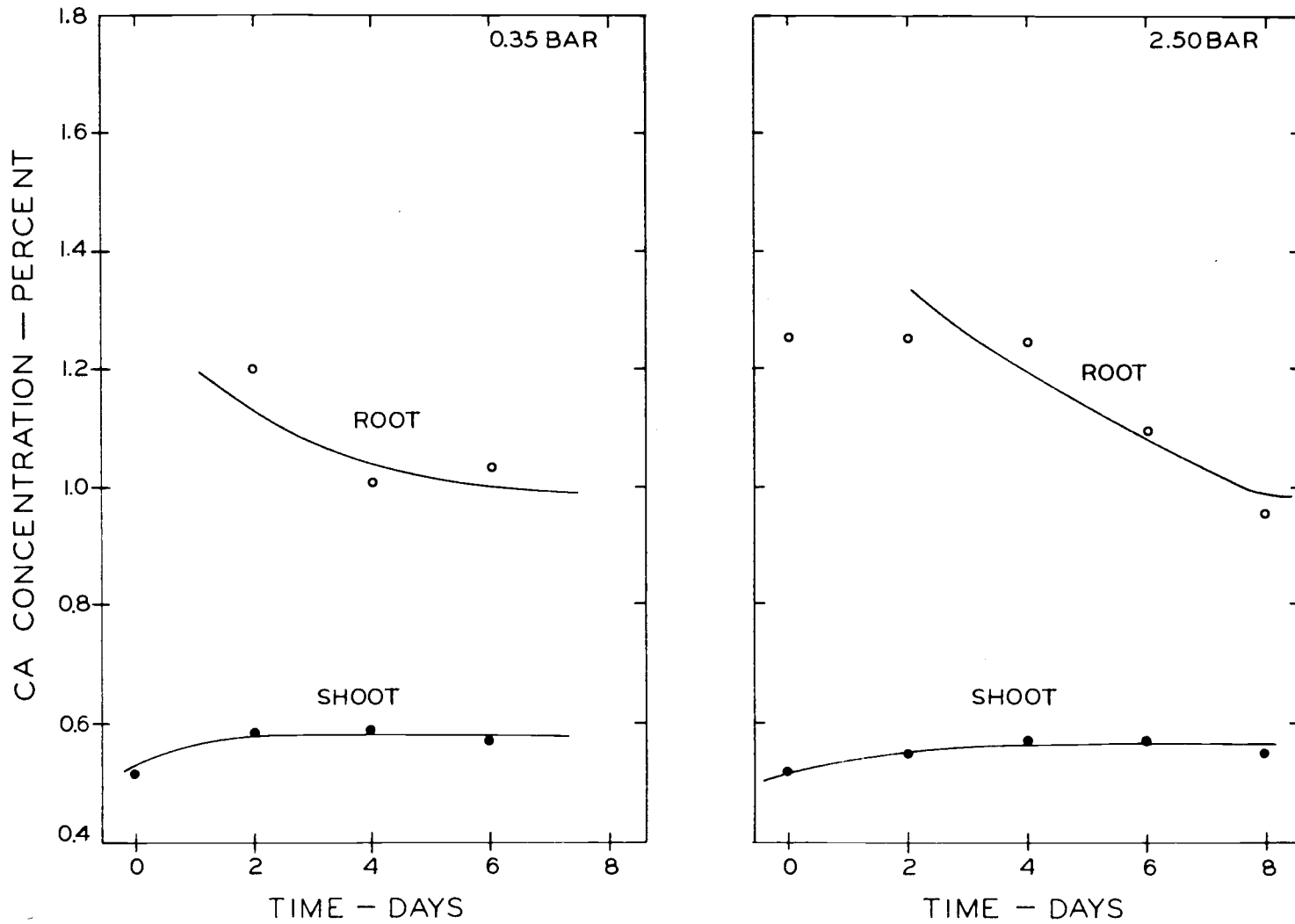


Figure A-3. Percent calcium in shoots and roots of 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars at a root temperature of 23.9°C.

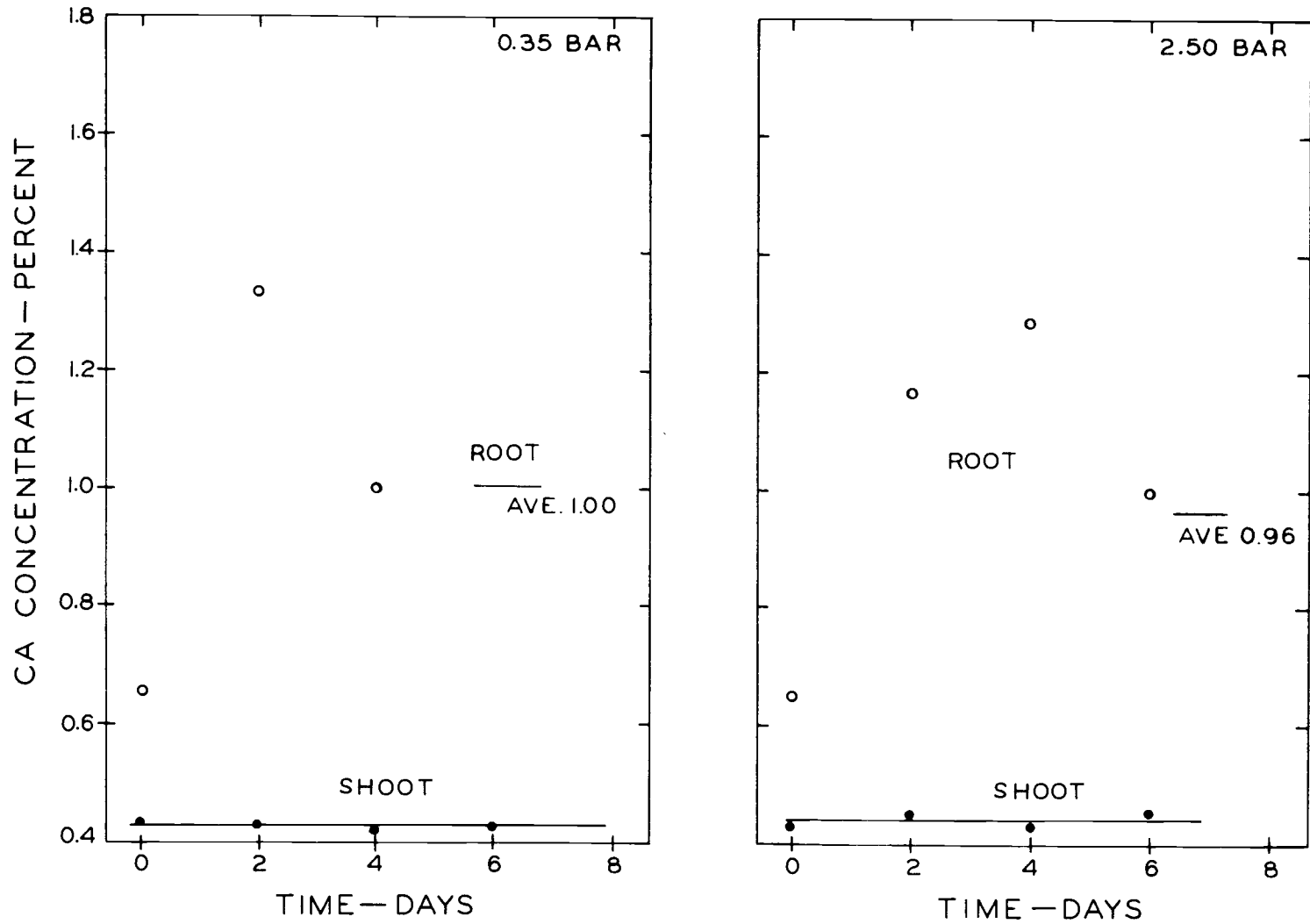


Figure A-4. Percent calcium in shoots and roots of 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars at a root temperature of 32.2°C.

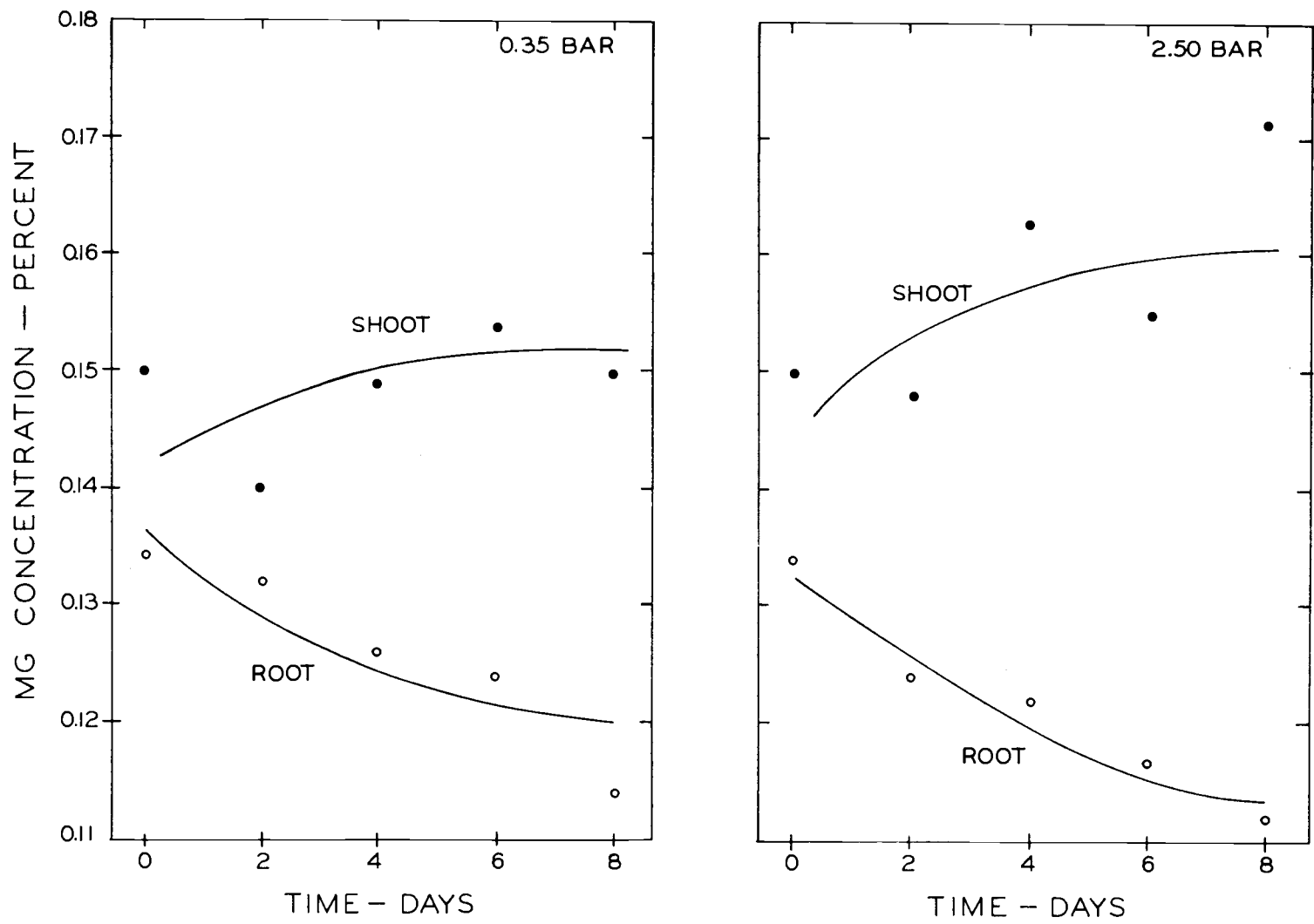


Figure A-5. Percent magnesium in shoots and roots of 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars at a root temperature of 10.0°C.

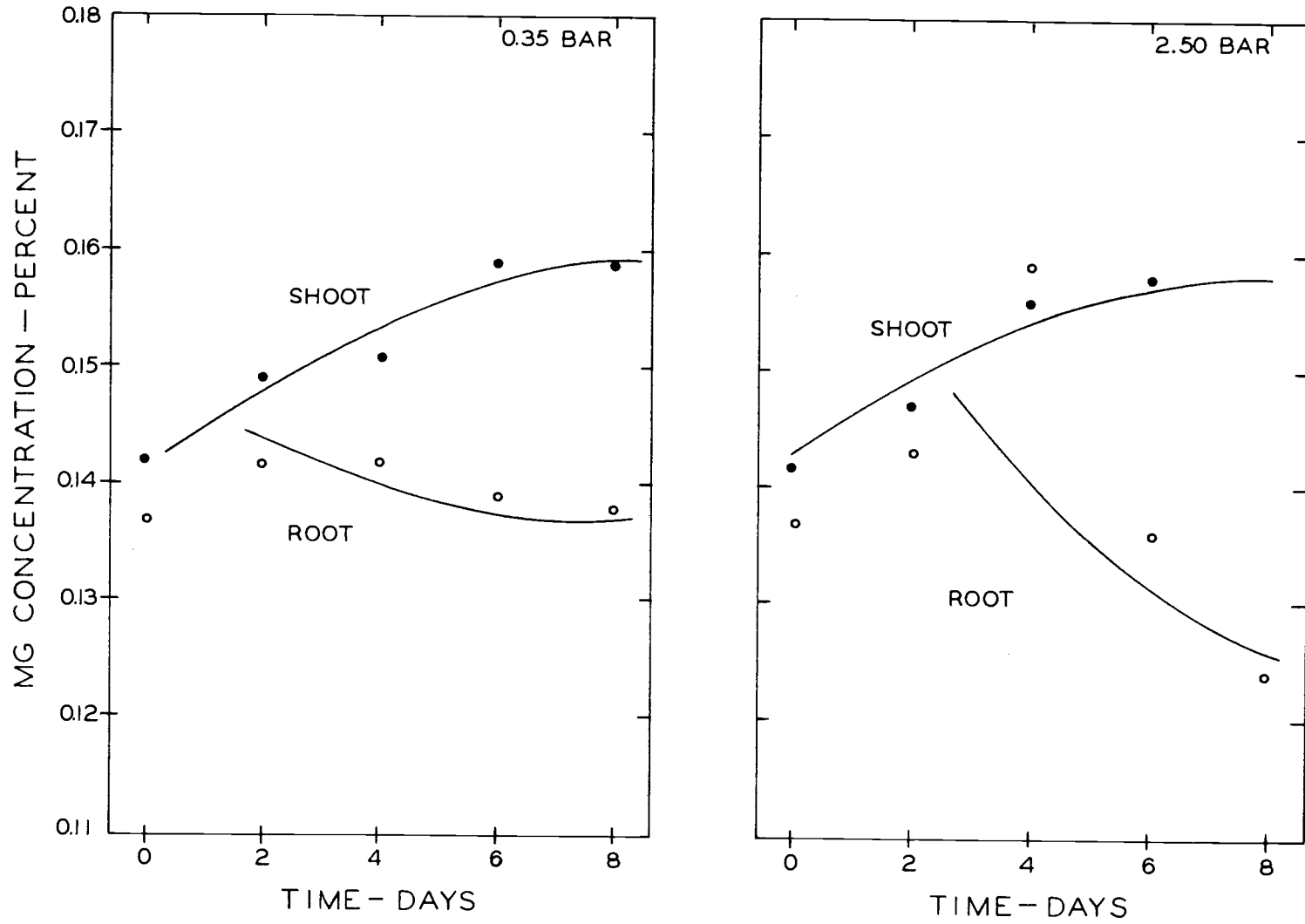


Figure A-6. Percent magnesium in shoots and roots of 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars at a root temperature of 18.3°C.

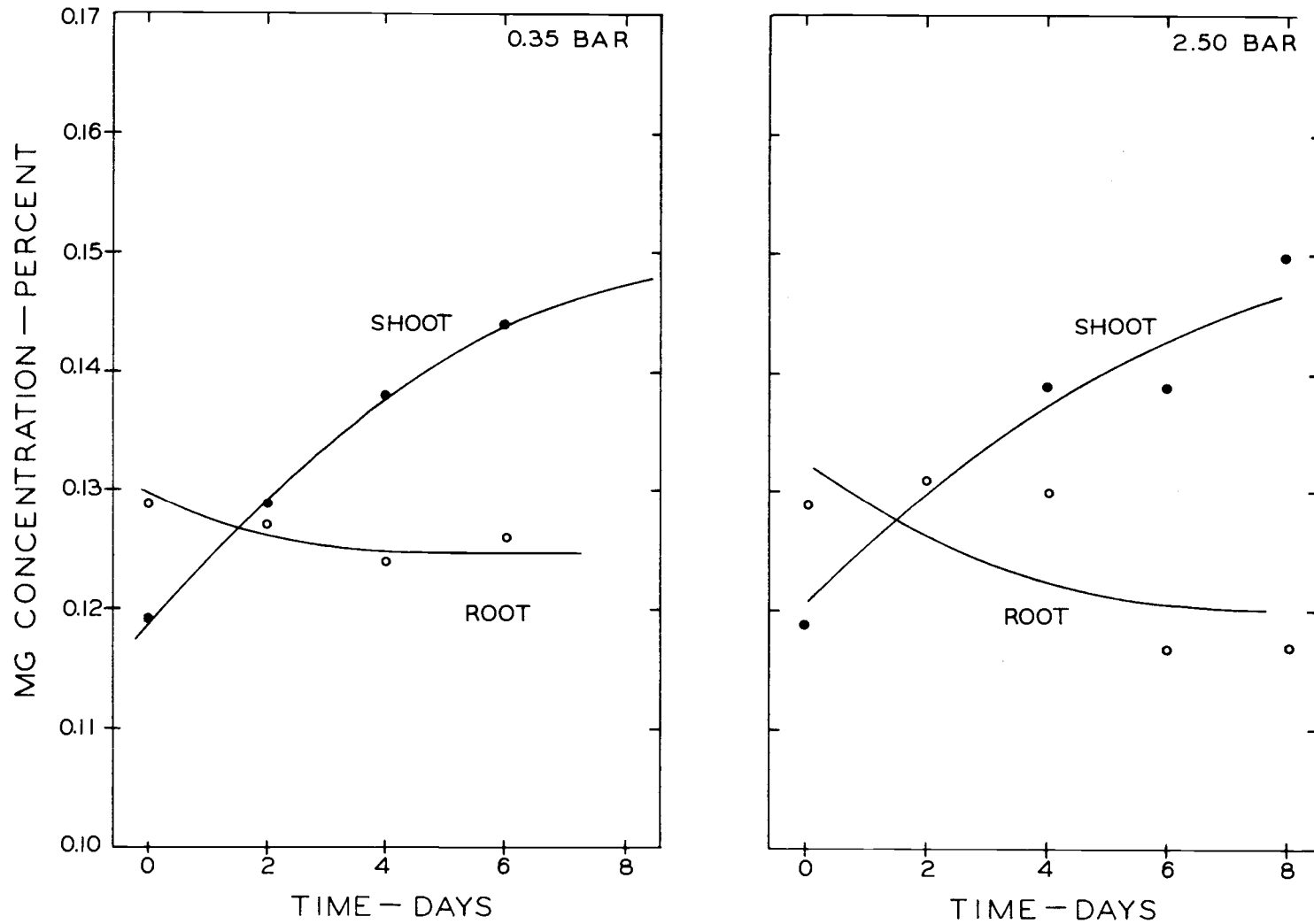


Figure A-7. Percent magnesium in shoots and roots of 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars at a root temperature of 23.9°C.

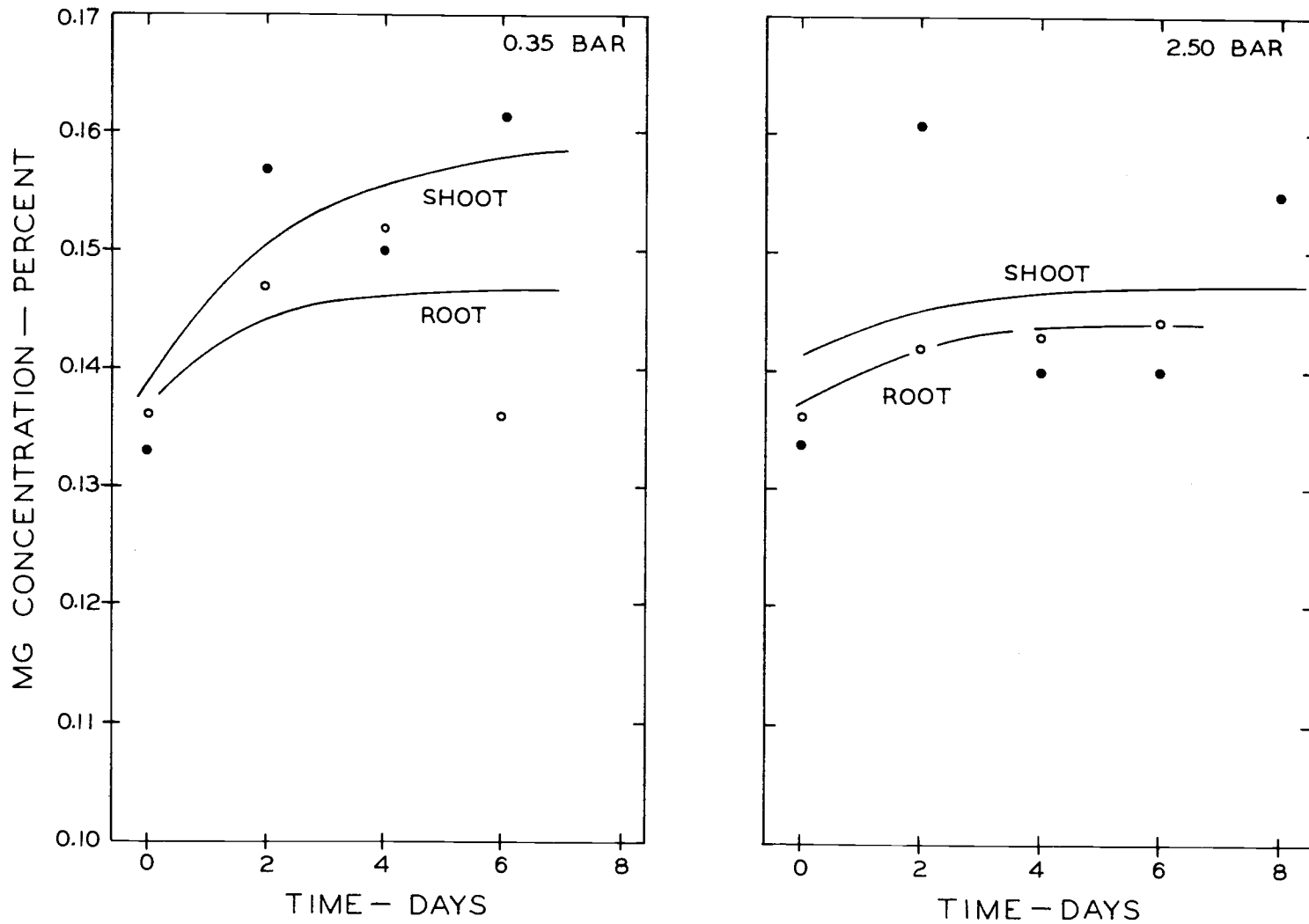


Figure A-8. Percent magnesium in shoots and roots of 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars at a root temperature of 32.2°C.

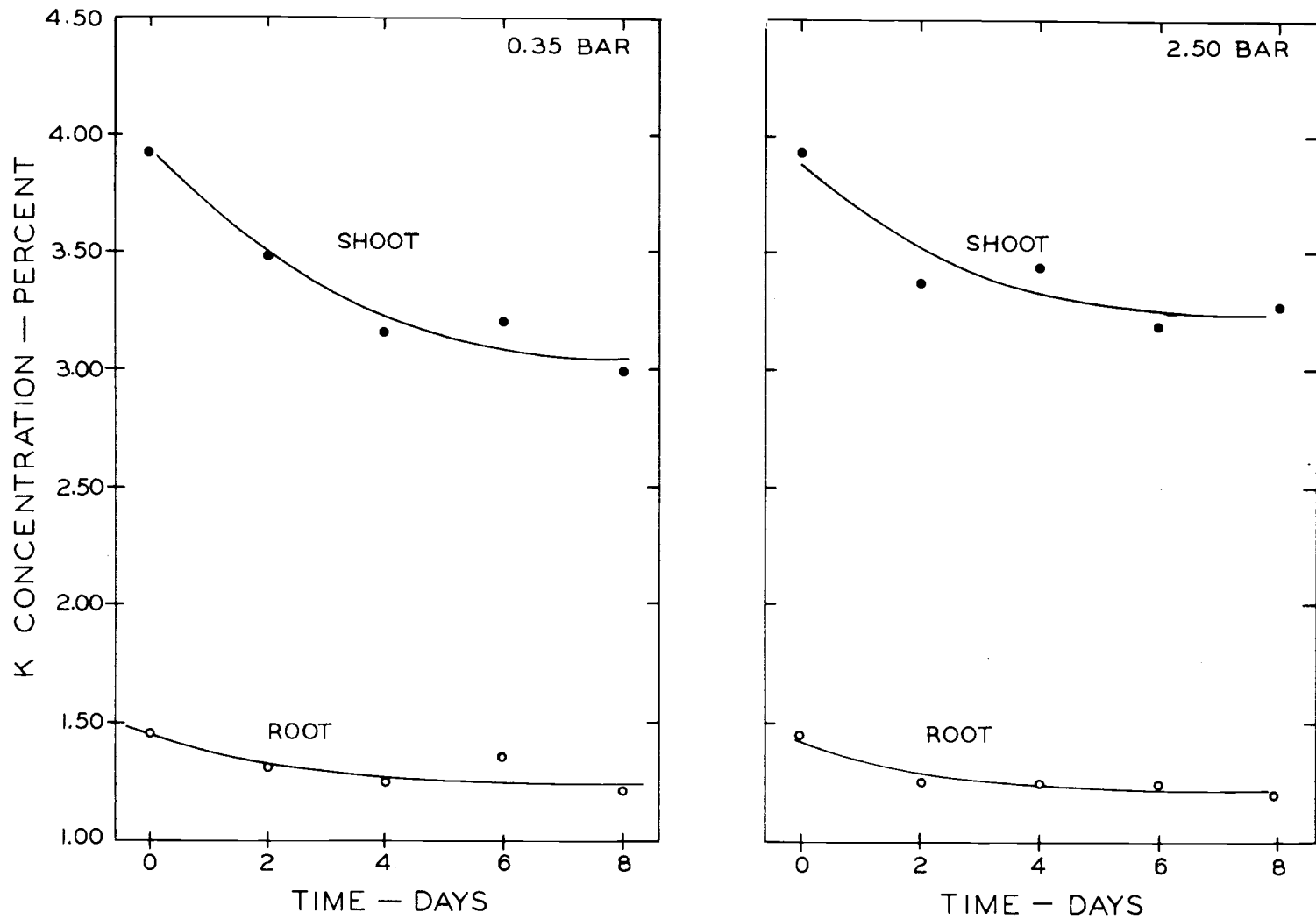


Figure A-9. Percent potassium in shoots and roots of 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars at a root temperature of 10.0°C.

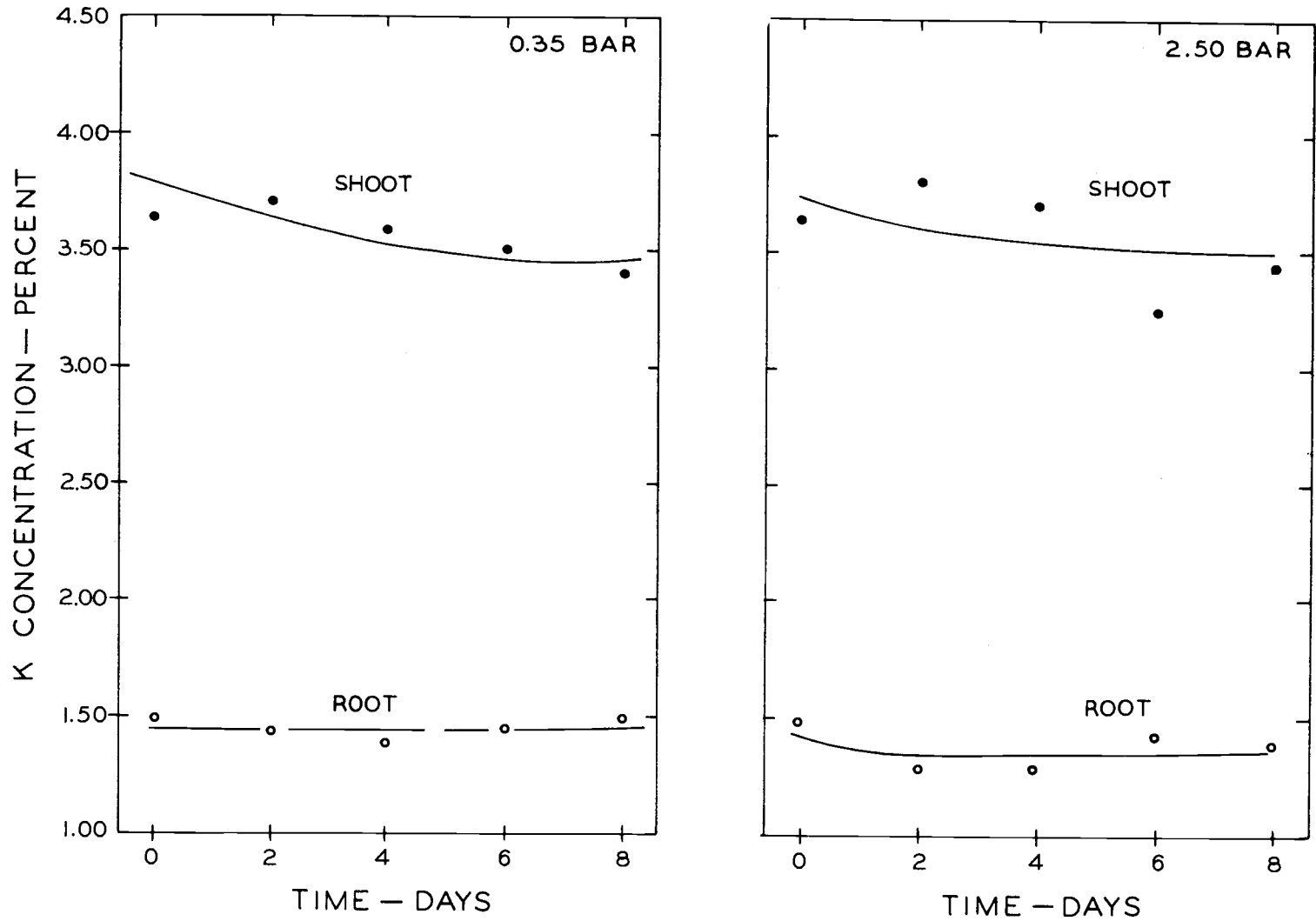


Figure A-10. Percent potassium in shoots and roots of 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars at a root temperature of 18.3°C.

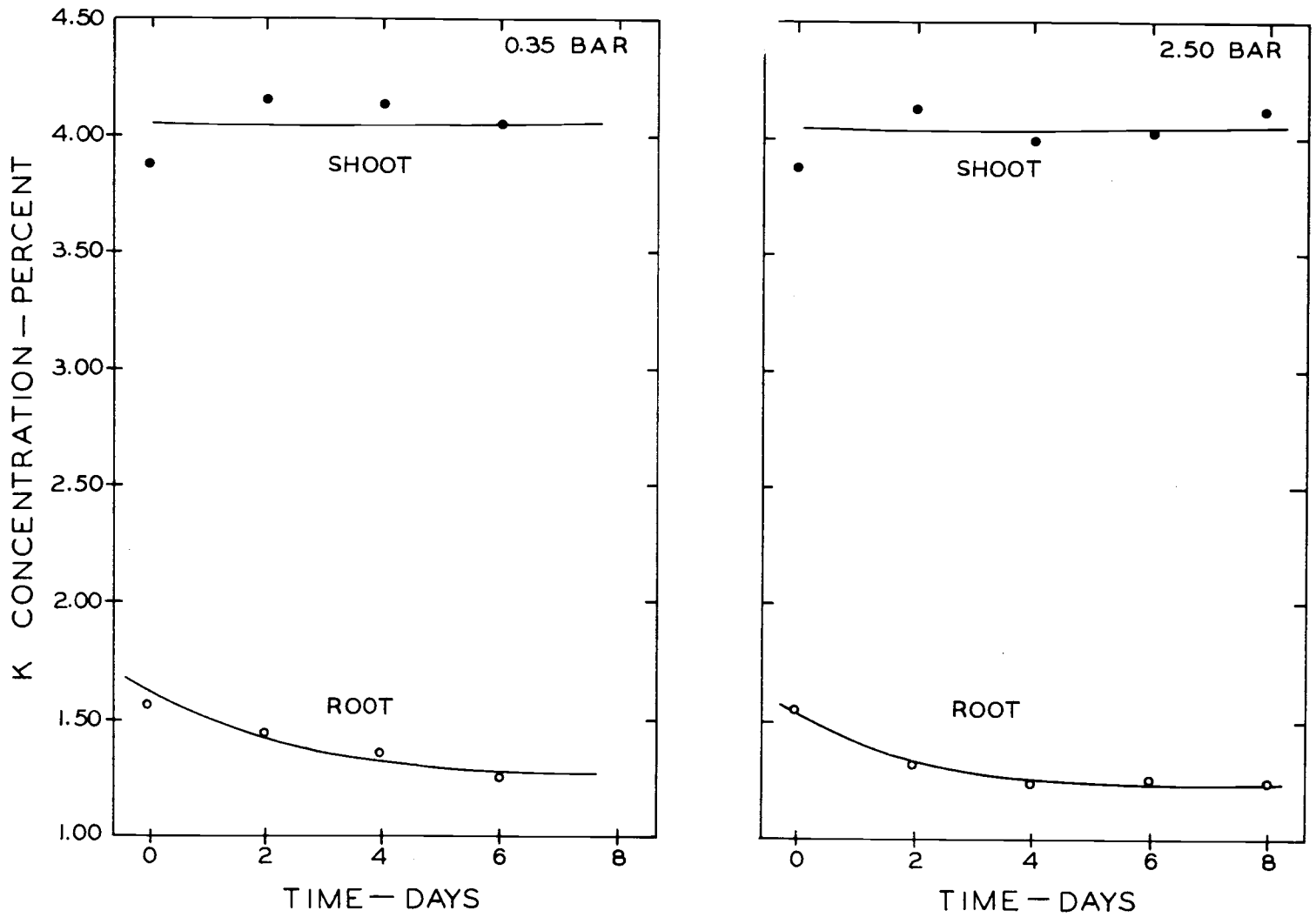


Figure A-11. Percent potassium in shoots and roots of 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars at a root temperature of 23.9°C.

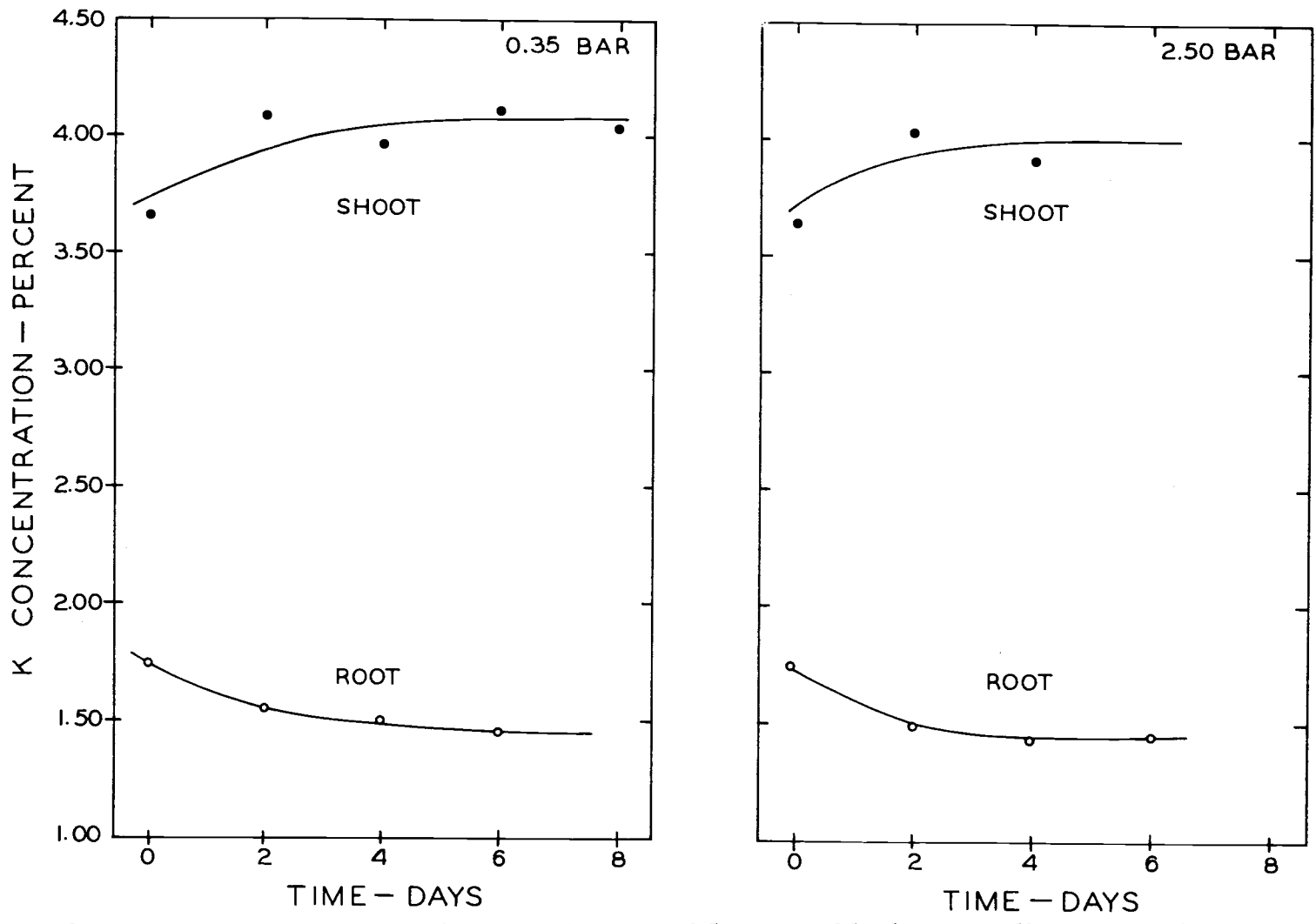


Figure A-12. Percent potassium in shoots and roots of 5-week old wheat seedlings as a function of time at soil water suctions of 0.35 and 2.5 bars at a root temperature of 32.2°C.