

11. HAGEN, C. E. AND H. T. HOPKINS. 1955. Ionic species in orthophosphate absorption by barley roots. *Plant Physiol.* 30: 193-99.
12. HAGEN, C. E., J. E. LEGGETT, AND P. C. JACKSON. 1957. The sites of orthophosphate uptake by barley roots. *Proc. Natl. Acad. Sci.* 43: 496-506.
13. HODGES, T. K. AND Y. VAADIA. 1964. Uptake and transport of radiochloride and tritiated water by various zones of onion roots of different salt status. *Plant Physiol.* 39: 104-8.
14. HODGES, T. K. AND Y. VAADIA. 1964. Chloride uptake and transport in roots of different salt status. *Plant Physiol.* 39: 109-14.
15. HOFSTEE, B. H. J. 1952. On the evaluation of the constants V_m and K_m in enzyme reactions. *Science* 116: 329-31.
16. JACKSON, P. C. AND H. R. ADAMS. 1963. Cation-anion balance during potassium and sodium absorption by barley roots. *J. Gen. Physiol.* 46: 369-86.
17. LEGGETT, J. E. 1961. Entry of phosphate into yeast cells. *Plant Physiol.* 36: 277-84.
18. LEGGETT, J. E. AND E. EPSTEIN. 1956. Kinetics of sulfate absorption by barley roots. *Plant Physiol.* 31: 222-26.
19. NOGGLE, J. C. AND M. F. FRIED. 1960. A kinetic analysis of phosphate absorption by excised roots by millet, barley, and alfalfa. *Soil Sci. Soc. Am. Proc.* 24: 33-35.

Effect of Water Movement on Ion Movement into the Xylem of Tomato Roots^{1, 2, 3}

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It is generally accepted that an increase in transpiration can, in some circumstances, cause an increase in the rate of salt uptake by plants (17). However, there is considerable disagreement as to how transpiration causes increased salt uptake. Many workers regard salt absorption as involving an active transport process in which salt transport into the root xylem is dependent upon energy released in respiration (7, 17, 18). According to this view, water movement through roots affects salt uptake indirectly by reducing the salt concentration in the root xylem, thereby accelerating the inward movement of salt by active transport. Other investigators have concluded that ions can move through roots with mass flow of water. According to their view, salt movement into the root xylem of rapidly transpiring plants involves mass flow as well as active transport (12, 13).

Estimates of the amount of salt moved by the 2 processes vary considerably. Hylmo (8), working with pea plants, reported that more than 75 % of the total uptake of Ca and Cl ions could occur directly by mass flow with water, whereas Brouwer (6), investigating Rb and Cl uptake by *Vicia faba* plants, con-

cluded that only approximately 15 % was moved passively with water.

In the present paper, experiments are described in which water was moved through detopped root systems by increasing the hydrostatic pressure of the solution surrounding the roots. Using this method with tomato root systems, Jackson and Weatherley (10) found that application of a pressure of 2 atm caused approximately a fourfold increase in the rate of K movement into the root xylem. They concluded that the increase was caused in part by an increase in permeability of the root cells to K ions. Jensen (11) found that when vacuum was applied to the stumps of detopped tomato roots, NO_3 uptake increased with increase in water uptake but not in proportion to water uptake.

In the present experiments, the effect of water movement on the rate of movement of P^{32} , Ca^{45} , and total salts was studied. Particularly, an effort was made to determine accurately what fraction of the total salt moved into the root xylem was associated with water movement.

Materials and Methods

Tomato plants (*Lycopersicon esculentum* Mill. var. Marglobe), grown in full strength Hoagland's solution in the greenhouse, were used in the experiments. Solutions were aerated continuously and changed every 5 days. After 3 to 4 weeks in nutrient solution, the plants were 40 to 50 cm in height,

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weighed 40 to 110 g, and had large, extensively branched root systems. Plants were 7 to 9 weeks old when used.

Plants were conditioned overnight before each experiment by immersing the roots for 16 hours in a radioactive or nonradioactive pre-experimental solution identical to the particular experimental solution to be used. The next morning the plants were detopped and the stumps sealed into the lid of a pressure chamber in such a way that the roots could be immersed in the experimental solution and subjected to hydrostatic pressure while the stumps projected through the lid of the chamber. Stem tissues external to the stele were removed from the stumps above the seal so that measurements were confined to solutions exuding mainly from the xylem. During the experiments, the experimental solution was aerated continuously and pressures were closely regulated.

Iron as Geigy Sequestrene 330 Fe was present in the culture solutions but was omitted from the pre-experimental and experimental solutions which, in all experiments, were half-strength Hoagland's solutions. The radioactive tracers used were P^{32} and Ca^{45} at a concentration of 0.5 mc/liter. P^{32} was obtained as H_3PO_4 and Ca^{45} as $CaCl_2$, each in weak HCl solution, from Oak Ridge National Laboratory. Isotope activity was determined by placing a measured amount of solution on disks of filter paper and counting the dried disks with a thin end-window GM tube. Rates of salt movement into the root xylem were determined by measuring the volume and salt concentration of exudate collected from the stumps. Plants were conditioned and experiments carried out in a constant temperature room at $25 \pm 1^\circ$. Most experiments were carried out with 6 plants, and the results shown are average values. The results shown in figures 2, 3, and 7 are average values for 3 plants.

Experiments and Results

Effect of Pressure on Water Movement. After conditioning overnight, root systems were enclosed in the chamber and subjected to successive increments of pressure from 5 to 40 lb/in². Exudation was measured for 15 minutes at each pressure. Root pressure exudation was measured for 15 minutes before and after each pressure application. Half of the root systems were placed in the chamber in Hoagland's solution containing 10^{-3} M NaN_3 , and subjected to pressure under the same conditions as the control roots. The rate of water movement through the control roots increased with increasing pressure from 0 to 40 lb/in², but not as a linear function of pressure except at pressures above 15 lb/in² (fig 1A). The shape of the curve suggests that the permeability of the roots to water increased with increasing pressure up to 15 lb and then remained constant with further increase in pressure. The change in slope from curvilinear to straight line at 15 lb suggests that, at pressures above 15 lb, water was moving through all of the pathway available for water flow through the roots.

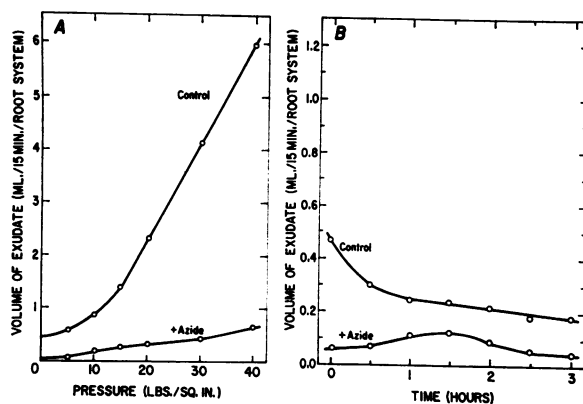


FIG. 1. A, Effect of pressure on rate of water movement through control and 10^{-3} M sodium azide-treated tomato roots. Azide-treated roots were preconditioned with azide for 1 hour before the experiment. B, Rate of root pressure exudation, from control and azide-treated tomato roots, occurring during the experiment shown in part A.

The rate of water movement through azide-treated roots increased more slowly over the same pressure range and, at 40 lb/in², was only 11% of the rate through the control roots. Thus azide drastically reduced the permeability of the roots to water.

The rate of root pressure exudation from control roots decreased during the experiment (fig 1B). This was found later to be a time effect which also occurred in roots not subjected to pressure. The rate of root pressure exudation from azide-treated roots was much less than that from control roots. The rate of exudation increased gradually, reaching a maximum 1.5 hours after the start of the experiment, and then decreased during the remainder of the experiment.

Effect of Time on P^{32} Content of Exudate. In the first experiment conducted with P^{32} , roots were subjected to successive increments of pressure from 5 to 40 lb. The rate of P^{32} movement into the xylem decreased with increasing pressure up to 20 lb and then increased with increasing pressure above 20 lb. The amount of P^{32} in root pressure exudate also decreased rapidly during the first half of the experiment, suggesting a time effect which probably was responsible for the initial decline in the rate of P^{32} movement under pressure. To study this effect more closely, changes in total P^{32} content of exudate with time, after detopping, were followed (fig 2).

During the first 4 hours after detopping, the total amount of P^{32} in the root pressure exudate increased slightly and then decreased greatly. The P^{32} content of the root pressure exudate continued to decrease during the remainder of the experiment but at a slower rate. Since salts are known to accumulate to high levels in the xylem sap of slowly transpiring plants (18), the rapid decline in total P^{32} content of exudate after detopping probably occurred because excess accumulated P^{32} was washed out of the xylem

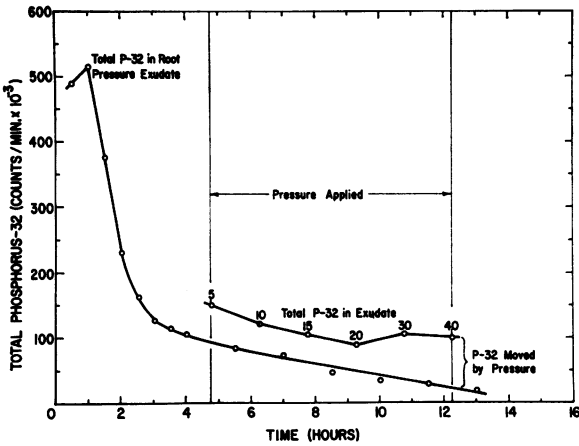


FIG. 2. Effect of time and pressure on total P³² in root pressure exudate and in exudate collected during periods of applied pressure. Values 5 to 40 indicate lb of pressure applied. P³² moved by pressure represents the fraction of the total P³² which was associated with water movement under applied pressure. Root pressure exudate was collected every 30 minutes before pressure applications were begun. After the beginning of pressure application, roots were conditioned for 30 minutes at each applied pressure and each 0 lb pressure before collection of exudate. Exudate was collected for 15 minutes at each pressure and for 15 minutes before and after each pressure application.

elements by water moving upward through the xylem. Successive periods of increasing pressure apparently had no effect on the P³² content of root pressure exudate measured before and after each pressure application. The total amount of P³² moved during pressure applications decreased with increasing pressure from 5 to 20 lb, perhaps because the P³² content of root pressure exudate was still decreasing at a considerable rate. Total P³² increased slightly at 30 lb pressure and remained unchanged at 40 lb. The additional amount of P³² moved into the root xylem as a result of applied pressure remained essentially constant from 5 to 20 lb and then increased slightly at higher pressures.

Changes in P³² concentration of the exudate with time were also followed (fig 3). During pressure applications, the P³² concentration of exudate initially decreased and then became relatively constant. P³² concentration decreased more at 40 lb than at 10 lb and also became constant more quickly at the higher pressure, probably because the greater amount of water moved through the roots at the higher pressure removed P³² from the root xylem more quickly. After pressure was released, the P³² concentration of root pressure exudate increased rapidly, becoming relatively constant after approximately 20 minutes. The P³² concentration of root pressure exudate decreased during the experiment, probably reflecting the time effect discussed earlier. The results emphasize the importance of allowing sufficient time for the

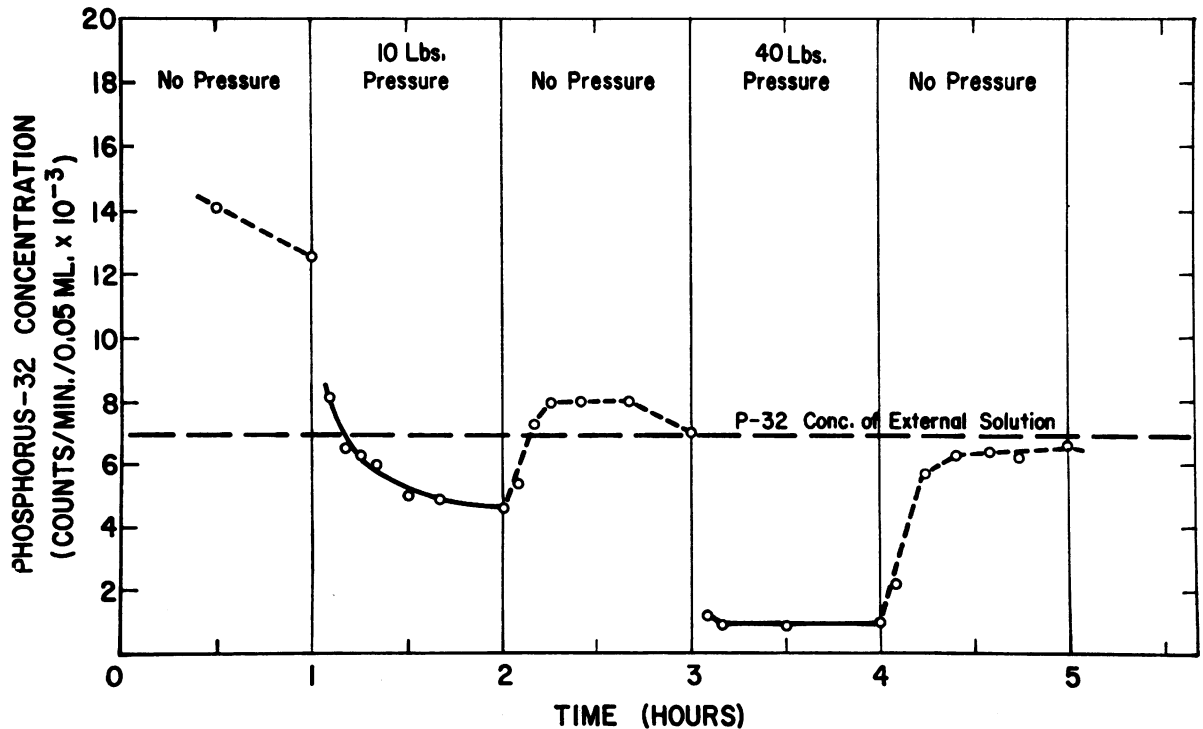


FIG. 3. Effect of time and pressure on P³² concentration of root pressure exudate (small dashed lines), and exudate collected during periods of applied pressure (solid lines). Applied pressure was maintained constant at 10 and 40 lb/in². Exudate was collected for 5 minutes at intervals during the periods of applied pressure and no pressure.

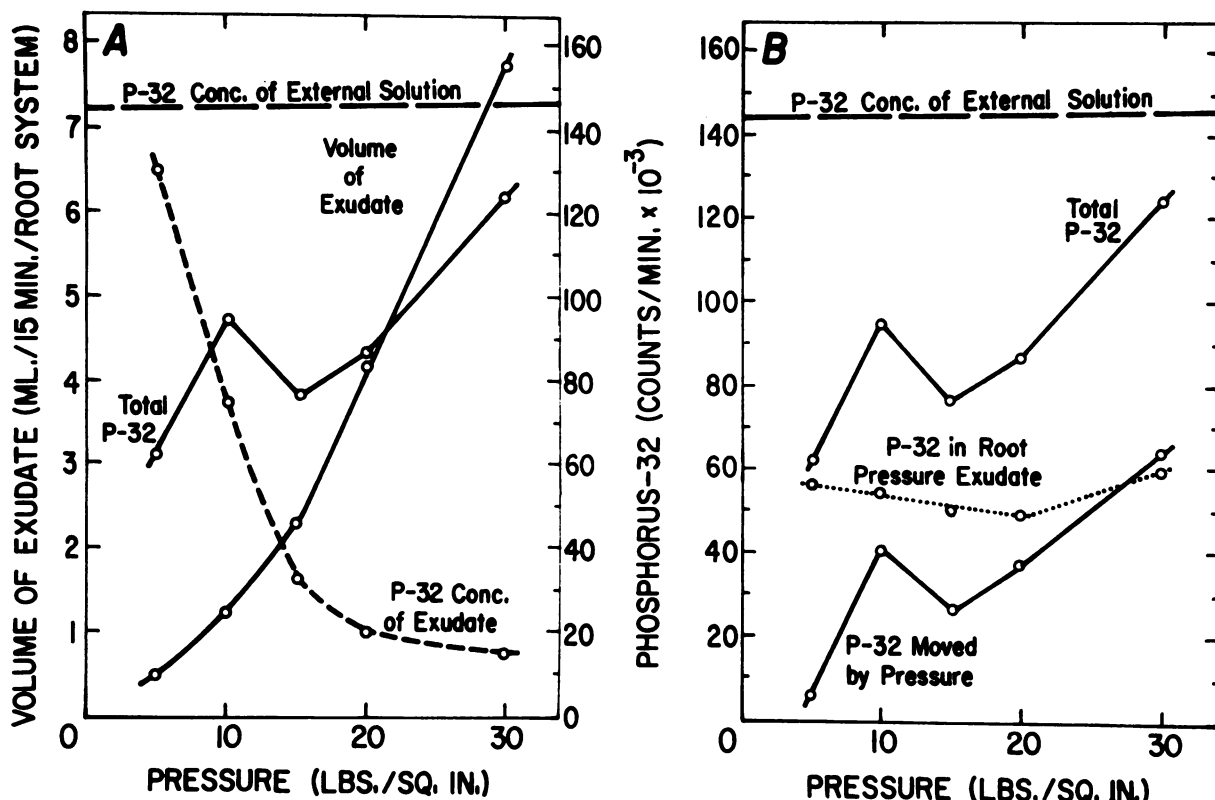


FIG. 4. A, Effect of pressure on rates of water and P³² movement into the xylem of tomato roots. P³² concentrations (dashed lines) are in count/min./ml. B, Effect of pressure on rate of P³² movement. P³² in root pressure exudate represents the amount of P³² moved into the root xylem in the absence of applied pressure. The value for P³² in root pressure exudate shown for each pressure is really an average of measurements taken before and after that pressure application. P³² moved by pressure represents the fraction of the total P³² which was associated with water movement under applied pressure.

ion concentration of the xylem exudate to attain equilibrium before collecting samples.

Effect of Pressure on P³², Ca⁴⁵, and Total Salt Contents of Exudates. An attempt was made to minimize the time effects which influenced the results of earlier experiments. Roots were conditioned before each experiment to remove excess accumulated salts from the xylem, and sufficient time was allowed for the concentration of the xylem sap to reach a steady state before samples of exudate were collected.

In the experiment with P³², roots were subjected to a pressure of 5 lb for 1.5 hours before the experiment. During the experiment, roots were conditioned for 1.5 hours at 5 lb and 0.5 hour at all other applied and 0 lb pressures. The results shown in figure 3 indicated that these times should permit the concentration of the xylem sap to reach a steady state. Exudate was collected for 15 minutes at each pressure and root pressure exudate was collected for 30 minutes before and after each pressure application.

The results are shown in figure 4A where total P³² is the product of the volume and P³² concentration of the exudate. As the rate of water movement through the roots increased, the P³² concentration of the exudate decreased. The total amount of P³² moved into

the root xylem increased with increasing pressure and rate of water movement, except from 10 to 15 lb where it decreased.

The amount of P³² in root pressure exudate during the experiment and the effect of pressure on rate of P³² movement are shown in figure 4 B. Pressure increased the rate of P³² movement into the root xylem as shown by the fact that the total amount of P³² in exudate obtained under applied pressure was always greater than the amount in root pressure exudate. The additional amount of P³² moved into the xylem as a result of applied pressure increased with increasing pressure, except from 10 to 15 lb where it decreased. At 30 lb pressure, the total amount of P³² in the exudate was 2.0 times the amount in root pressure exudate.

A similar experiment was carried out with Ca⁴⁵ (fig 5). Roots were conditioned and subjected to pressure as described above for P³² (fig 4), except that roots were conditioned for 1.5 hours at each applied pressure. It was assumed that these times would be sufficient to permit the concentration of the xylem sap to reach a steady state. Exudate was collected for 15 minutes at each applied pressure. Root pressure exudate was collected for 30 minutes.

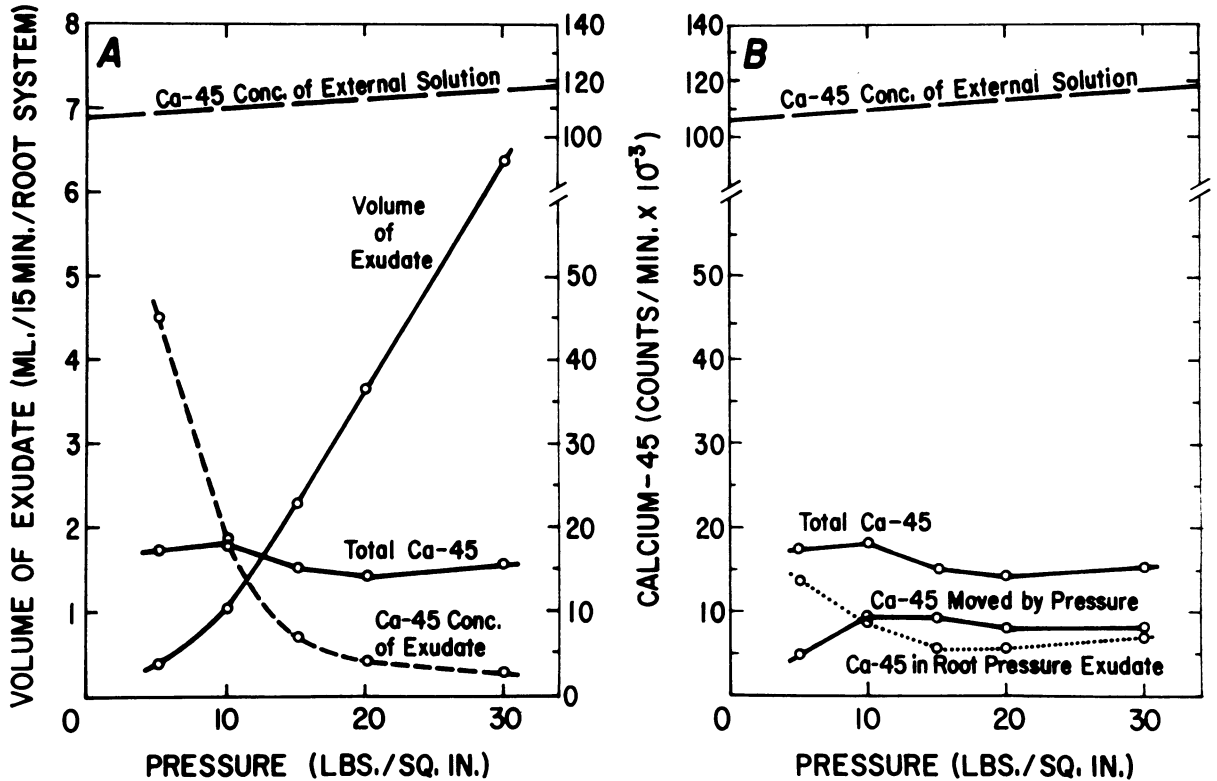


FIG. 5. Effect of pressure on rates of water and Ca^{45} movement into the xylem of tomato roots. For detailed explanation of the relationship of the curves, see figure 4.

As water movement through the roots increased with increasing pressure, the Ca^{45} concentration of the exudate decreased. At the same time, the total amount of Ca^{45} moved into the root xylem remained essentially constant.

The amount of Ca^{45} in root pressure exudate during the experiment and the effect of pressure are shown in figure 5B. Application of pressure definitely increased the amount of Ca^{45} moved into the root xylem; however, the additional amount of Ca^{45} moved under pressure remained relatively constant over most of the pressure range. At 30 lb pressure, the total amount of Ca^{45} in the exudate was 2.2 times the amount of Ca^{45} in the root pressure exudate.

In view of the differences obtained with P^{32} and Ca^{45} , it is interesting to note the effect of pressure on the movement of total salts into the xylem. Before the experiment, roots were conditioned for 2 hours at 0 lb pressure. During the experiment, roots were conditioned for 1.5 hours at 5 lb and 0.5 hours at all other applied and 0 lb pressures as in the experiment with P^{32} . It was assumed that these times would be sufficient to permit attainment of concentration equilibrium in the xylem sap. Exudate was collected for 30 minutes at each pressure. Root pressure exudate was collected for 60 minutes. Salt concentration of the exudate was determined by measuring its electrical conductivity with a conductivity bridge calibrated with KCl solutions.

The results, shown in figure 6, agree in general with those obtained for P^{32} . As water movement through the roots increased, the salt concentration of the exudate decreased. Total salt increased with increasing pressure, except in the pressure range of 10 to 20 lb where it remained relatively constant. Total salt in root pressure exudate and the effect of pressure are shown in figure 6 B. Application of pressure increased the rate of salt movement into the root xylem, with more total salt occurring in the exudate during pressure applications than in the absence of pressure. As in the case of P^{32} , the additional amount of salt moved by pressure increased with increasing pressure, except from 10 to 20 lb where relatively little increase occurred. At 30 lb, the total amount of salt in the exudate was 2.4 times the amount of salt in root pressure exudate.

Effect of Sodium Azide. A sufficient amount of NaN_3 was added to P^{32} -labeled Hoagland's solution in the chamber to produce a concentration of 10^{-3} M NaN_3 while a constant pressure was maintained. The amount of water moved through the roots under pressure initially decreased after the addition of azide (fig 7). One hour after the addition of azide, the rate of water movement was only 9% of the rate before treatment. Water movement remained at this low rate for 4 hours after treatment was started and then began to increase.

The total amount of P^{32} moved into the root xylem

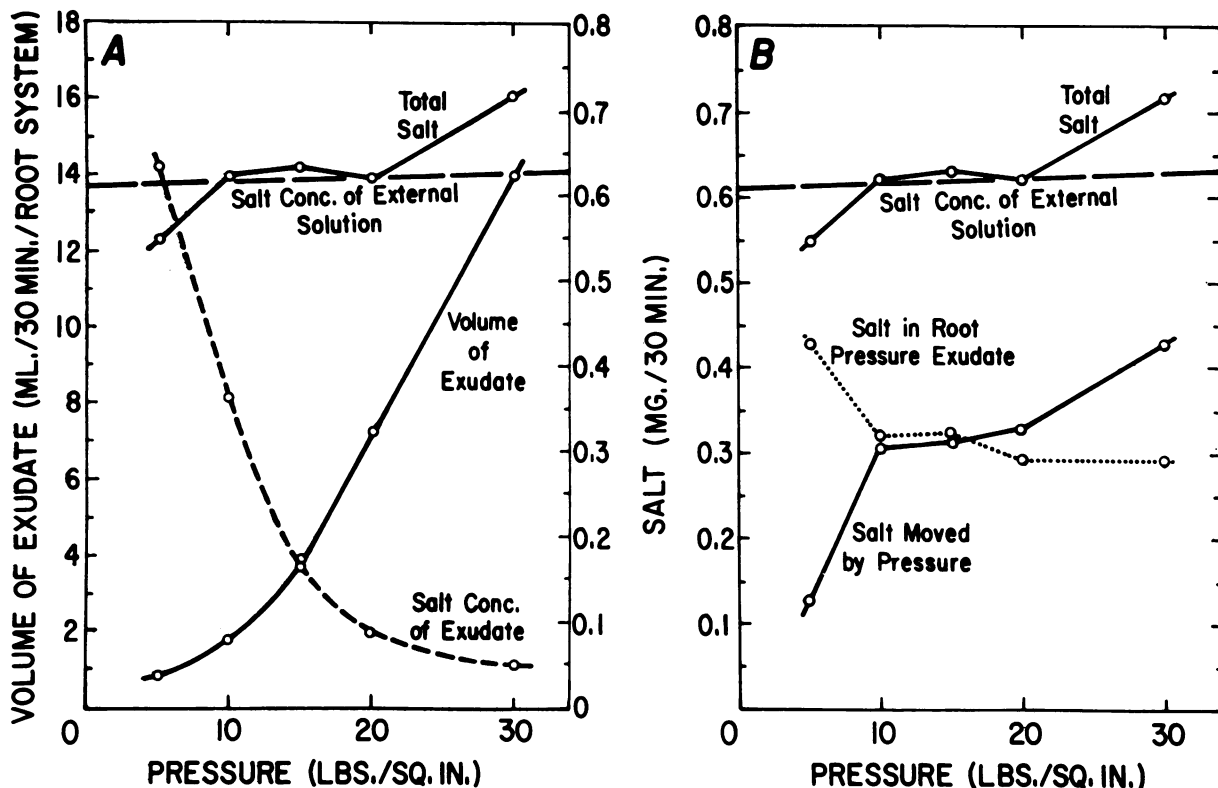


FIG. 6. Effect of pressure on rates of water and total salt movement into the xylem of tomato roots. Salt concentrations are in mg/ml. For detailed explanation of the relationship of the curves, see figure 4.

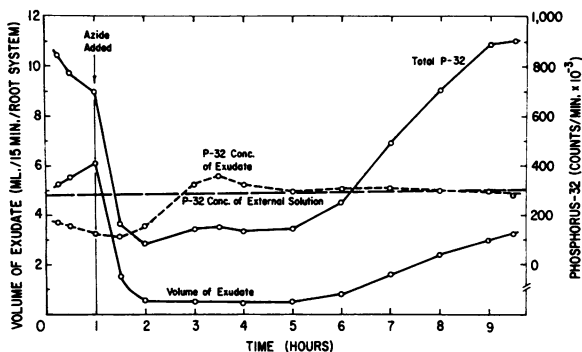


FIG. 7. Effect of 10^{-3} M sodium azide on rates of water and P^{32} movement into the xylem of tomato roots. Pressure was maintained constant at 30 lb/in². P^{32} concentrations (dashed lines) are in count/min/ml. pH was adjusted with HCl to 4.9 at the time azide was added.

initially decreased after the addition of azide and, one hour after treatment was begun, was only 12% of the amount moved before treatment. The rate of P^{32} movement remained at this low level for 4 hours and then began to increase. Two hours after treatment with azide, the P^{32} concentration of the exudate increased to a level exceeding the P^{32} concentration of the external solution. Four hours after the addition of azide, the P^{32} concentration of the exudate was the

same as that of the external solution, suggesting that the roots had lost their differential permeability to phosphate ions. Quite similar results were obtained in an experiment with Ca^{45} in which nitrogen was bubbled through the experimental solution while roots were maintained under constant pressure.

Discussion

The results of the above experiments show that when water is moved through roots by increasing the hydrostatic pressure of the external solution, the rate of ion movement into the root xylem increases but not in proportion to the increase in rate of water movement. At 30 lb/in², 50% or more of the salt transported into the root xylem was moved as a result of applied pressure. The remaining fraction was moved into the xylem by active transport.

The way in which pressure causes increased ion movement is not clear. One explanation, suggested by Broyer and Hoagland (7), is that water movement through roots reduces the salt concentration of the xylem sap, thereby stimulating active transport of ions into the xylem. Also, Bernstein and Niemen (2) have pointed out that a more rapid movement of water than salts through roots should result in an increase in salt concentration in the root cortex. These 2 factors operating together, an increase in concentration in the cortex plus a decrease in the xylem, would

steepen the concentration gradient from cortex to xylem and perhaps accelerate ion transport into the xylem.

An examination of figures 4A and 6A shows that while a decrease in exudate concentration might explain the initial increase in rate of salt movement at low pressures, it cannot explain the subsequent increase which occurred at higher pressures where only a slight reduction in concentration occurred. This increase in rate of salt movement at higher pressures was found in all experiments, except in the case of Ca^{45} , and suggests that the permeability of the roots to ions increased when pressures of more than 15 to 20 lb were applied. An increase in permeability of root cells to ions, brought about by increased suction tension in the xylem, has been reported by Brouwer (4). More recently, Jackson and Weatherley (10) found that externally applied pressure increased the rate of K movement into the xylem of detopped tomato roots even when the concentration of K in the xylem sap increased at the same time. They concluded that the increased rate of K movement under pressure must result, at least partly, from an increase in permeability of the roots to ions.

As mentioned earlier, the shape of the curve for rate of water movement under pressure (fig 1A) suggests that pressure also increased the permeability of the roots to water. Mees and Weatherley (14) also found that externally applied pressure increased the permeability of detopped tomato roots to water, and Brouwer (5) found an increase in water permeability in roots of intact broad bean plants with an increasing diffusion pressure gradient across them. Brouwer attributed the increased permeability to a decrease in turgidity of the root cells. According to Hylmo (9), increase in hydrostatic pressure causes flow of water through smaller and smaller pores in the water pathway until all available pore space is being utilized. Thereafter, the rate of water movement is proportional to pressure in accordance with Poiseuille's law.

In the present experiments, no increase in rate at higher pressures was noted with Ca^{45} . Ca, however, is known to be less mobile in plant roots than P (3, 19), and at the higher pressures, Ca movement may have been less responsive to permeability changes than was P movement.

Whether the increased rate of ion movement under pressure is the result of mass flow, increased diffusion, or increased active transport is not known. However, a more general explanation for the over-all increase in rate of salt movement can be suggested. That is, perhaps pressure increases the rate of salt movement indirectly in 2 ways: A) at all pressures by increasing the rate of water movement through the roots, thereby creating a steeper salt concentration gradient from the cortex to the xylem which possibly accelerates the rate of salt movement into the xylem, and B) at higher pressures by increasing the permeability of the root cells to ions. Thus at low rates of water movement, salt movement into the root xylem occurs primarily by active transport. In view of the increase in ion permeability which seems to occur at

higher pressures, the possibility exists that at high rates of water movement, some ion movement may occur by diffusion and mass flow in addition to that occurring by active transport.

The question also arises whether the increased rate of salt movement under pressure represents increased salt movement from the medium or increased "tissue exudation" (1) from sites in the root tissues. According to Jackson and Weatherley (10), all of the increased K movement under pressure in their experiments could be accounted for as increased tissue exudation from the root cells. In the present experiments, however, when roots conditioned overnight with P^{32} were transferred to nonradioactive Hoagland's solution and subjected to pressure, less P^{32} appeared in the exudate than when roots were transferred to a solution containing P^{32} . At 5 lb pressure, 60% of the total P^{32} moved into the xylem could be accounted for as tissue exudation. At 40 lb, tissue exudation amounted to only 30% of the total, the remaining fraction presumably entering from the external solution. Thus, at least at higher pressures and rates of water movement, much of the salt transported into the xylem entered directly from the external medium.

In all of the experiments, as the rate of water movement through roots increased with increasing pressure, the salt concentration of the exudate decreased to a small percentage (11% or less) of the external solution. This indicates the existence of a barrier in the roots, possibly the endodermis, which prevents free movement of ions into the xylem.

The initial effect of treatment with NaN_3 was to reduce the rate of both water and P^{32} movement into the xylem. The effect on water movement is consistent with results obtained by numerous investigators with various respiration inhibitors (14, 15, 16). In one experiment, the rate of water movement through roots under pressure was reduced almost instantaneously (2 min) after addition of azide, suggesting that azide had directly affected the permeability of the root cells to water.

The decrease in rate of P^{32} movement may be explained in several ways. First, azide is a respiration inhibitor and probably reduced the rate of active transport of P^{32} into the xylem. Second, azide may have caused a decrease in the permeability of the root cells to P^{32} as was found to occur for water. Third, by decreasing the rate of water movement, azide may have reduced the amount of P^{32} moved into the xylem in response to changes in the concentration gradient. Finally, if any movement of P^{32} occurred directly with mass flow of water, reduction in water movement would also result in reduced P^{32} movement. It seems most likely that a combination of these factors was involved.

Prolonged exposure to azide resulted in an increase in the rate of water and P^{32} movement, indicating that azide had begun to damage the root cells, thereby increasing their permeability to water and P^{32} . It is interesting to note that although the exudate concentration exceeded the external solution con-

centration 2 hours after addition of azide, indicating leakage of accumulated P^{32} from the root cells, the rate of water movement did not increase until 5 hours after treatment. This suggests that azide increased the permeability of the roots to P^{32} before increasing their permeability to water. The drastic effect of azide on the permeability of the roots to water and P^{32} indicates that the major resistance to both water and salt movement is located in the protoplasm of the root cells.

Summary

The relationship between water movement and salt movement through tomato roots was studied. Water movement through detopped root systems was increased by increasing the hydrostatic pressure of the solution surrounding the roots. The rate of salt movement into the root xylem was determined by measuring the volume and salt concentration of exudate collected from the stumps. Comparisons were made of amounts of salt moved into the root xylem when water was moved under pressure with amounts moved by active transport in the absence of external pressure.

Application of pressure increased the amount of P^{32} , Ca^{45} , and total salts moved into the root xylem, but not in proportion to the increased rates of water movement. At 30 lb/in², the amount of ions moved into the root xylem was 2.0 to 2.4 times the amount moved by active transport in the absence of pressure. The salt concentration of exudates obtained under pressure usually was less than the concentration of the external solution.

Treatment of roots with 10^{-3} M sodium azide initially reduced the rates of both water and P^{32} movement to about 10 % of the control rates. Longer exposure to sodium azide resulted in an increase in the rates of both water and P^{32} movement.

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Literature Cited

- ANDEL, O. M. VAN. 1953. The influence of salts on the exudation of tomato plants. *Acta Botan. Neerl.* 2: 445-521.
- BERNSTEIN, L. AND R. H. NIEMAN. 1960. Apparent free space of plant roots. *Plant Physiol.* 35: 589-98.
- BIDDULPH, O., S. BIDDULPH, R. CORY, AND H. KOONTZ. 1958. Circulation patterns for phosphorus, sulfur, and calcium in the bean plant. *Plant Physiol.* 33: 293-300.
- BROUWER, R. 1953. Transpiration and anion uptake. *Proc. Koninkl. Ned. Akad. Wetenschap.* C 56: 639-49.
- 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 Botan. Neerl.* 3: 264-312.
- BROUWER, R. 1956. Investigations into the occurrence of active and passive components in the ion uptake by *Vicia faba*. *Acta Botan. Neerl.* 5: 287-314.
- BROYER, T. C. AND D. R. HOAGLAND. 1943. Metabolic activities of roots and their bearing on the relation of upward movement of salts and water in plants. *Am. J. Botany* 30: 261-73.
- HYLMO, B. 1953. Transpiration and ion absorption. *Physiol. Plantarum* 6: 333-405.
- HYLMO, B. 1955. Passive components in the ion absorption of the plant. I. The zonal ion and water absorption in Brouwer's experiments. *Physiol. Plantarum* 8: 433-49.
- JACKSON, J. E. AND P. E. WEATHERLEY. 1962. The effect of hydrostatic pressure gradients on the movement of potassium across the root cortex. *J. Exptl. Botany* 13: 128-43.
- JENSEN, G. 1962. Active and passive components in ion uptake processes. Experiments with intact and excised tomato root systems. *Physiol. Plantarum* 15: 363-68.
- KRAMER, P. J. 1956. Relative amounts of mineral absorption through various regions of roots. *Atomic Energy Comm. TID-7512: 287-95.* Washington, D.C.
- KYLIN, A. AND B. HYLMO. 1957. Uptake and transport of sulphate in wheat. Active and passive components. *Physiol. Plantarum* 10: 467-84.
- MEES, G. C. AND P. E. WEATHERLEY. 1957. The mechanism of water absorption by roots. II. The role of hydrostatic pressure gradients across the cortex. *Proc. Roy. Soc. (London), B*, 147: 381-91.
- ORDIN, L. AND P. J. KRAMER. 1956. Permeability of *Vicia faba* root segments to water as measured by diffusion of deuterium hydroxide. *Plant Physiol.* 31: 468-71.
- ROSENE, H. F. 1947. Reversible azide inhibition of O_2 consumption and water transport in root tissues. *J. Cellular Comp. Phys.* 30: 15-30.
- 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: 127-40.
- RUSSELL, R. S. AND V. M. SHORROCKS. 1959. The relationship between transpiration and the absorption of inorganic ions by intact plants. *J. Exptl. Botany* 10: 301-16.
- WIEBE, H. H. AND P. J. KRAMER. 1954. Translocation of radioactive isotopes from various regions of roots of barley seedlings. *Plant Physiol.* 29: 342-48.