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The Interaction Between Water Movement, Solute Uptake, and Respirational Energy in Plant Roots

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THE INTERACTION BETWEEN WATER MOVEMENT, SOLUTE UPTAKE, AND RESPIRATIONAL ENERGY IN PLANT ROOTS

by

Mohamed Sadek Tawakol

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

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M. S. Tawakol

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ABSTRACT

The Interaction Between Water Movement Solute Uptake, and Respirational Energy in Plant Roots

by

Mohamed Sadek Tawakol, Doctor of Philosophy

Utah State University, 1967

Major Professor: Dr. Sterling A. Taylor
Department: Soil Physics

Sunflower plants (Helianthus annus, var. Russian mammoth) were grown in Hogland nutrient solution. The roots (after being subjected to treatments with either respiratory inhibitors or respiratory stimulators) were used to measure the flux of water J_w, flux of solute J_s, and the rate of respiration J_o.

The thermodynamic theory of irreversible processes was used to examine the interaction between fluxes, and the changes in conductivity under different treatments. The rate equations for a root membrane of unit thickness were developed as:

$$J_w = L_{ww} \bar{V}_w \Delta p + L_{ws} RT \ln \frac{C^1_s}{C^2_s} + L_{wo} RT \ln \frac{C^1_o}{C^2_o}$$

$$J_s = L_{sw} \bar{V}_w \Delta p + L_{ss} RT \ln \frac{C^1_s}{C^2_s} + L_{so} RT \ln \frac{C^1_o}{C^2_o}$$

$$J_o = L_{ow} \bar{V}_w \Delta p + L_{os} RT \ln \frac{C^1_s}{C^2_s} + L_{oo} RT \ln \frac{C^1_o}{C^2_o}$$

Where: L_{ww}, L_{ss}, L_{oo} are the direct transfer coefficients for water, solute, and oxygen; and L_{ws}, L_{sw}, L_{wo}, L_{ow}, L_{so}, L_{os} are the interaction or linked transfer coefficients; $\overline{V}_w$ partial molal volume (or specific volume) of water, $\triangle p$ the difference in pressure between the external solution and xylem: C^1_s and C^2_s, C^1_o and C^2_o are the salt and oxygen concentration in external solution and xylem respectively.

The results showed that: 1. The nonlinearity of the flux of water through the root system of sunflower is due to causes associated with the membrane (mainly the permeability). 2. The increase in respiration did not increase the permeability of the membrane. 3. The uptake of water due to solute potential under transpiring conditions is small, but important. 4. The uptake of solute in normal root systems is by active process from solutions to the zylem and then moves passively to the leaves. 5. An increase in passive water uptake might cause an increase of respiration of the root.

(109 pages)

INTRODUCTION

During the processes of water movement from the soil to the atmosphere, in passive absorption, transpiration water must pass over two cellular barriers, between the soil and the xylem elements of the root, and between the xylem of the leaf vein and transpiring cell. Transpirational loss of water from surface cells induces a gradient of water potential within the leaf tissue which causes water movement from the vein. This results in the reduction of hydrostatic pressure in the xylem which induces the water to move from the soil across the root cortex. These transpirational forces are quite different in origin and nature from the forces responsible for "active water absorption" which occurs only in the presence of oxygen and depends on the energy produced by active living cells.

As early as 1850, Lawes studied the effect of transpiration on salt uptake. Muenschen (1922) reported that several workers late in the 18th century and early in the 19th had studied the effect of transpiration on salt movement. Since then, the absorption of ions by plants has been a subject of investigation by many. It may be considered that the process of ion absorption consists of (a) a free space uptake by diffusion and exchange; (b) a metabolic uptake and accumulation; and (c) an uptake linked with water movement in transpiring plants. Of these three processes the first two are generally accepted by most investigators while the third one has been expressed by various divergent views.

In the 1920's the effect of aeration of the roots on the growth of plants received considerable attention (Allison and Shine, 1923). About twenty years later research workers began to study the relationship between respiration and the water uptake of plant tissues (Overbeek, 1942). Late in the thirties Rinders (1938) showed that the uptake of water is strictly an aerobic process, and concluded that the energy of respiration creates the conditions causing water uptake.

Jost (1916) found that an increase in water uptake was not proportional to the increase in suction tension in the xylem vessels. He observed that at increasing suction tension, the water uptake per unit pressure difference increased more than linearly. Recently, studies on water movement through decapitated plants have shown that the flux of water through the roots increased by either increasing the suction on the plant stump or by increasing the pressure on the solution surrounding the root. In both cases the relation between water flux and pressure gradient applied showed a non linear relation (Roberson, 1964; Lopushinsky, 1964).

The thermodynamics of irreversible process may explain the relation between the movement of water, solute, and the oxygen consumed in respiration of the root tissue. The application of this process to the simultaneous flow of these three compounds has not yet been made.

From literature it appears that respiration influences the uptake of water by plant roots (Ordin and Kramer, 1956; Lopushinsky, 1964). Many investigators have attributed the effect of various respiration inhibitors on the rate of water movement through the root to its direct effect on permeability of the cell membranes. However, no direct measurements of aerobic respiration and its effect on water uptake at different rates of transpiration have been examined.

The objective of this study is to find if this non-linearity between water movement and suction is the result of a mechanical linkage between the tissue and the pressure gradient or if there exists a respiration-linked deriving force on the water. This study also attempts to ascertain if the respirational energy contributes an independent force that causes water and solute to move across the plant roots to the xylem.

REVIEW OF LITERATURE

Processes of Water Uptake by Roots

The uptake of water and its movement through plants involves a number of physical and physiological processes. The atmospheric conditions around the plant specify the type and process of water intake by the roots.

Renner (1912, 1915) termed as "active absorption" that water uptake which develops appreciable positive pressure in the xylem (which occurs only in healthy, well aerated root systems) and depends directly or indirectly on conditions maintained by living, actively metabolizing, root cells. Renner used the term "passive absorption" for water that enters the root because of forces that develop in the shoots even if the roots were anesthetized or dead (Kramer, 1956; Slatyer, 1960).

In accordance with the suggestion of Thiman (1951), growth is considered in its simplest aspect, namely, as an irreversible increase in volume. Since under certain conditions irreversible increases in volume can be achieved without any concomitant increase in cellular protein or of cell wall components, the minimal and basic requirement for growth remains the absorption of water. Laties (1957) stated that,

> Although there is considerable diversity of opinion about the mechanism whereby higher plant cells increase in size, few would question this increase depend upon metabolic process. Metabolic water absorption may or may not be 'active' water absorption. The later term, which refers to the nonosmotic movement of water (Levitt, 1953), has a precise thermodynamic

> meaning—it is the movement of water against a water chemical potential gradient. Thus whether water enters the cell osmotically, as a consequence of the diminuation of wall pressure following enzymatic transformation of the cell wall, or whether water is actually secreted into the cell by a pumping mechanism that drives its energy from cellular respiration; the uptake in either case is metabolically induced. (Laties, 1957, p. 98)

Steward (1964) explained the growth of cells on the basis of active water uptake: that is, while the vacuole is being actively extended, it is not appropriate to explain its behavior in terms of simple equilibrium conditions for the growing cell will certainly not be in equilibrium with its surroundings. Under these circumstances a more active mechanism like that which accumulates salts seems more appropriate. He suggests that hormones cause growth and enlargement of cells by facilitating the uptake of water. Whether this occurs by making the cell wall more extensible or by a more active intervention in the actual entry of water molecules is not made clear.

Kramer (1956) mentioned that two general types of explanation have been offered for active water absorption. One is based on the assumption that roots behave like an osmometer, and water moves along an osmotic gradient from the dilute soil solution to the higher osmotic pressure in the xylem vessels. In the other type it is assumed that the living cells bordering the xylem bring about the secretion of water into the xylem vessels by a process other than osmosis.

Koslowski (1964) considered active water uptake as the nonosmotic water absorption. He cited several investigators who have maintained that a portion of water uptake by plant cells may be attributed to a nonosmotic, active process in which metabolic energy released somehow directly pumps water, Therefore, the concept of "active water absorption" has more than one explanation: i. e. nonosmotic water uptake (that is linked directly with energy of respiration), osmotic water uptake (coupling of water with ions actively transported), and metabolic water uptake. Slatyer (1960) reported that a controversy as to whether or not active absorption involves a nonosmotic mechanism has developed because some aspects of water absorption cannot adequately be explained on the basis of simple osmotic theory.

Through all this confusion, Spanner (1954) reported that in a general way the meaning of "active transport" is fairly clear. In his explanation, he stated that whenever movement of water occurs in a direction which we cannot explain as moving toward the attainment of equilibrium, we recognize a case of active transport. In the same report he added that an active movement can take place down a gradient of chemical potential or activity as well as up. In this report he introduced the thermodynamics of irreversible processes to explain the simultaneous movement of heat and water through biological membranes as one form of active transport of water.

Taylor (1963) suggested that active absorption may result from a significant linked transfer between water and solute, between two species of solutes, or between heat and water or solutes. He also attributed some active absorption to flow along a gradient of some form of matter or energy other than its own.

Kedem (1965) represented the metabolic reaction, solute flow, and water flow as coupled processes by the following equations:

$$\Delta\mu_w = R_{ww}J_w + R_{ws}J_s + R_{wr}J_r$$

$$\Delta\mu_s = R_{sw}J_w + R_{ss}J_s + R_{sr}J_r$$

$$A = R_{rw}J_w + R_{rs}J_s + R_{rr}J_r$$

where: J_s solute flux, J_w water flux, J_r metabolic reactions, $\Delta\mu_w$ water potential, $\Delta\mu_s$ solute potential, A the affinity of the chemical reactions are the driving forces that are the differences of the thermodynamic potentials on both sides of the membrane, and R_{ij} are the resistances to flow which are derivable from the phenomenological coefficient.

He visualized that active transport of water occurred whenever $R_{ij} \neq 0$, or in other words whenever there is coupling between a chemical reaction and flow of water.

Respiration and Uptake of Water by Plant Tissue

Extensive work has been done to study active water uptake by plant tissue and its relation to respiration and solute uptake. However, conclusion valid for segments of plant tissue do not necessarily hold true for intact plants. An excellent summary of the literature for internal water relations of higher plants is to be found in the review by Slatyer (1962).

Kramer (1956) stated that if the absorption of water occurs against a free energy or DPD gradient, energy to move the water must be supplied by respiration. After discussing some of the work done on this subject, he suggested that there seems to be little doubt that there is some kind of relationship between water uptake and respiration and added that the nature of the relationship is more debatable.

Steward _et al._ (1940) wrote that results of studies of salt and water uptake by discs of potato tissue "suggest that aerobic respiration, protein synthesis, water absorption and salt accumulation are all mutually dependent processes which occur in all cells that are not subject to equilibrium conditions."

Levitt (1947) calculated the energy required to maintain water uptake against a diffusion gradient and concluded that maintenance of a difference of more than one or two atmospheres would require an impossibly large expenditure of energy by the cell. Bennet-Clark (1948), Myers (1951), and Spanner (1952) criticized Levitt's conclusion because they felt he used too high a value for permeability. Slatyer (1960) stated that a lively controversy commenced on these issues. He indicated that Levitt (1953, 1954), Spanner (1954) and Stiles (1956) consider this aspect still open.

Mees and Weatherley (1957) suggested that decrease in water movement could be attributed to oxygen deficits rather than to the combined effect of carbon dioxide and lack of oxygen. They showed that the rate of water movement through tomato roots could be reduced to 90 percent by adding potassium cyanide to the root medium.

Glinka and Reinhold (1962) found that increasing the oxygen concentration to 40 percent increased the flux of water; also the presence of oxygen in the gas stream countered to a marked extent the inhibitory effects of carbon dioxide. They concluded that carbon dioxide acts rapidly to decrease and oxygen to increase the permeability of cells to water.

Bonner _et al._ (1953) found that the application of auxin indole acetic acid (IAA) to Jerusalem artichoke tuber tissue induces an uptake of water which is several times larger than water uptake by the same tissue in the absence of auxin; furthermore in the presence of auxin this tissue was able to take up water (at a reduced rate) from solutions of higher osmotic concentrations than that of the cell contents. They concluded that auxin-induced water uptake is dependent upon aerobic conditions and is abolished by the same low concentrations of dinitrophenol which inhibit oxidative phosphorylation.

On theoretical grounds nonosmotic water absorption against a diffusion gradient requires energy (Kozlowski, 1964). Kelly (1947) found that indole acetic acid (IAA) stimulates both water uptake and respiration. She concluded that water uptake is an aerobic process since it does not take place under anerobic conditions. Hackett and Thimann (1952) concluded that water uptake by potato tissue both in the presence and absence of externally added auxin is linked to the general aerobic metabolism.

Commoner et al. (1943) investigated the mechanism by which auxin increases water uptake. They attributed the effect to the absorption of salt by plant cells. Later studies by Overbeck (1944) and Levitt (1947) showed this hypothesis to be in error. They found no increase in osmotic potential of the cell sap and that the increase in water was due to cell enlargement.

Levitt (1948) concluded that 10^{-4} and 10^{-3} M KCN had no effect on auxin-induced water uptake, and the osmotic pressure at the end of the experiment is the same for slices aerated in indole acetic acid (IAA) as for slices aerated in distilled water, provided only the original water content is present. He concluded from that work that the results indicated that auxin-induced water uptake is not due to active absorption, to increased osmotic pressure, or to increased protoplasmic hydration. This was confirmed by Ketellapper (1953). Ketellapper found that IAA (1 mg/liter) showed a tendency to decrease the permeability to heavy water which increased by lowering the pH. He concluded that the relation between respiration and water uptake is not yet clear.

Hackett and Thiman (1950) found that water uptake by discs of potato tissue can be inhibited quantitatively by inhibitors of oxidative enzyme systems. Hacket *et al.* (1953) studied the terminal oxidase as mediating water uptake by plant tissue. They found that auxin-induced water uptake by slices of potato is shown to depend on oxygen tension and that the inhibition caused by carbon monoxide is largely reversed by light. They also found that copper-enzymes' poisons produce no inhibition. It was deduced then, that the water uptake process in potato tissue is controlled by cytochrome oxidase.

Pentinov and Grineva (1962) using carbon monoxide as an inhibitor of oxidase activity showed that in certain plants, the sunflower in particular, the activity of cytochrome oxidase system is largely responsible for water absorption while in others (corn) water uptake is not affected by inhibition of cytochrome oxidase.

In plants treated with a specific inhibitor of protein synthesis (chloramphenical), the process of absorption of water was not inhibited, and the data confirmed the viewpoint that a close relation exists between water absorption and general oxidative metabolism, while water uptake is independent of protein synthesis (Grineva, 1964).

Adding ATP (as a respiratory stimulator) had little effect or perhaps caused a slight decrease in the rate of water movement (Roberson, 1964). He also reported that respiration inhibitors, DNP and NaN_3 induced the rate of water movement at the different suction tension used, while the resistance of the root to water movement decreased when a combination of DNP and 1×15^{-2} M acetate buffer was used.

Lupushinsky (1964) also found that treatment of roots with 10^{-3} M sodium azide initially reduced the rate of water movement to about ten percent of the control rates. Longer exposure resulted in an increase in the rate.

Respiration and Uptake of Solute by Plant Tissues

The active uptake of salts or the interaction between solute uptake and respiration has been studied by several investigators. As this subject has been thoroughly reviewed by Laties (1957, 1959), Lundegardah (1955), Kramer (1956), Robertson (1956, 1960), Russell and Barber (1960), and Beevers (1960), only a brief discussion needs to be presented here.

Beevers (1960) reported that Steward emphasizes the stimulatory effect of adequate aeration on the ability of the tissues to accumulate salts. He also reported that the most revealing response is to the uncoupling agent DNP. It is observed from the literature that the effect of DNP on uptake processes is a function of several factors like pH, concentration, and time exposure of the plant to DNP. Also, some experiments concern the transport of salt to the vacuole, or accumulation in mitochondria, while others concern the transport of salt to the vessels. It was found that DNP at very low concentration causes an increase in the oxygen uptake and a decrease in salt uptake (Robertson et al., 1951; Noris and Treadwell, 1963). Van Andel (1953) found that the flux of salts from the tissue—the tissue secretion—as well as the transfer to the vessels of salt taken up from the medium—the uptake secretion—was inhibited by inhibitors such as KCN, DNP, and others. This indicates that both processes partially coincide. Their common part might be the transport of salt through the symplast. The water conductivity was also affected by the inhibitors in this study. Barber (1963) reported that concurrent transpiration and calcium uptake were prohibited by DNP, and the action of DNP was markedly pH dependent.

Arisz (1953) did not find any influence of DNP on the transport of chloride through the cytoplasm of Vallisenia, but the secretion of salts into the vacuole was inhibited. Working with intact plants, Barber and Koontz (1963) found that DNP initially decreased Ca accumulation, but after more than twelve hours, the amount of Ca that accumulated in the shoots was increased over the control. The uptake of calcium by excised barley roots appears to be largely non-metabolic. This was observed at both low temperature and with the application DNP (Moore et al., 1961). So, it seems no definite theory has been established. Biolo (1965) concluded that the degree of coupling of oxidation and phosphorylation necessary for the absorption of mineral nutrients by plant roots may differ depending on the particular element. His results confirmed those of Moore et al. (1961): the absorption of calcium by tomato roots took place to a considerable extent during the uncoupling of oxidation and phosphorylation.

Hodges and Hanson (1965) found that adding substrate or ATP increased the accumulation of calcium, while adding ADP or DNP decreased the uptake of calcium by maize nitochondria. They also found that ATP plus substrate mostly doubled the amount of uptake. In agreement with them, Soematowots and Jackson (1965) reported that the high energy compound ($\sim$P) content of roots treated with DNP and KBr was lower than that of those treated with DNP. Their interpretation was the ($\sim$P) was utilized for salt absorption.

On the other hand, Mengel (1963) found that the addition of ATP to the uptake solution decreases the uptake of Rb only when the oxidative respiration is not blocked. He concluded that the active Rb uptake is not primarily affected by a carrier phosphorylation and that the active ion transport of the respiratory enzymes. Jacoby (1965) confirmed this and further reported that externally added ATP inhibits sodium and potassium uptake by red beet tissue, though it did not inhibit chloride or bromide uptake.

Recently there has been presented a hypothesis that the uptake of salt is closely related to the protein synthesis and metabolism. Experiments with chloramphenicol proved that the uptake of salts by both roots and discs was decreased while the uptake of water was not affected (Bowling, 1963; Uhler and Russell, 1963).

Pressure Gradient Across the Root and Movement of Water, and Solute

As was mentioned earlier, some investigators believe that uptake of salts is an active process and water moves with it, while others believe that the uptake of solute is carried by water in the transpiration stream. Another group believes that salt uptake is active at first and later passive with water. In support of the osmotic theory, Eaton (1943) showed that the amount of exudation from detopped cotton plants is proportional to the difference between the osmotic potential of the xylem sap and the solution surrounding the roots.

Also, Arisz,*et al*. (1951) considered that water absorption follows the active transport and secretion of salts into the xylem. They concluded that important factors in the exudation are water conductivity of the protoplasm and salt secretion into the xylem, and both factors must have identical influence on the transport of water into the transpiration stream. Trubetskova (1965a) concluded that living cells secrete inorganic and organic substances into the root xylem vessels which create a definite osmotic potential within the vessel. As a result of the difference of the osmotic potential between the vessels and the water retaining forces of the external solution, there is an osmotic transport of water into the xylem vessels. He added the thought that the delivery of dissolved substances by the root and the delivery of water are closely interrelated.

Many experiments opposing the osmosis theory have been recorded. Overbeek (1942) concluded that the exudation from tomato roots was not only produced by osmotic water flow but that also there existed a component of exudation not driven by osmosis.

Brouwer (1954) studied the direct comparison of water and anion uptake in the same root. The results obtained showed that by increasing the suction tension in the xylem vessels, both water and anion uptake increased; but the anion uptake increased to a lesser degree than the uptake of water. By using respiration inhibitors in various concentrations, Brouwer found it possible to inhibit the anion uptake without reducint the water uptake. He considered that ions entered the xylem by a process dependent upon metabolism. Though he concluded that both processes, water uptake and anion uptake, are related to one another, there is no direct relation. Hylmo (1955) reviewed Brouwer's data on the zonal water and ion uptake. He concluded that the passive ion component is directly proportional to the water passage both when the same root zone was observed with different suction pressures and when different zones were compared with each other under the same suction pressures. He added that even the active ion component is partly dependent on the water flow. Brower (1956) confirmed his previous results. By applying sugar to the nutrient solution, he observed that the concentration of the transpiration stream was enhanced to about 200 percent of control, and in non-aerated solution or with the application of DNP the concentration decreased to about 25 percent of the control. Again he concluded that a dominant part of the ions in the transpiration stream arrived there by means of a process dependent on metabolism, and only a small percentage of the total ion transport seemed to be due to passive carrying along with the transpiration stream.

Honert et al. (1955) subjected corn plants to conditions of high transpiration in the sun and low transpiration in the dark and found no significant influence of transpiration on ion absorption. Here, however, they neglect the effect of temperature gradient which might cause considerable differences.

Mees and Weatherley (1957a, 1957b) measured the water flux caused by changing hydrostatic pressure on the culture medium and compared it with the change in flux caused by changing the osmotic potential. They proposed two permeability coefficients, one being an index of permeability due to gradients of hydraulic pressure and the other due to gradients of osmotic potential. The results obtained showed that the rate of water movement caused by a hydrostatic gradient is much greater than that caused by equivalent osmotic gradient. They attributed this to two reasons: first, that the osmotic permeability coefficient was increased considerably by the application of hydrostatic pressure; second, that there was a mass flow of water in addition to diffusional movement. Hylmo (1958) insisted on the theory of passive flow of ions in the transpiration stream. He wrote that further investigations are needed to show how great a part of the water-linked ion component is a passive mass movement of the solution through the root without involvement of the transported ions in the root metabolism. His experiment showed that the active accumulation is greatest in the root tip, and the ions associated with the transpiration stream are passed through the root without being involved in the metabolism of the root.

Lopushinsky and Kramer (1961) reported that at low rates of water movement, salt movement is primarily by active transport, while at higher rates of water movement, salt movement into the xylem probably occurs by both active transport and mass flow. They found that the amount of phosphorus and total salts moved under pressure differences did not increase in proportion to the increased rates of water movement. Also, the salt concentration of exudates obtained under pressure usually was less than the concentration of the external solutions, indicating the existance of a barrier in the roots which prevents free movement of ions into the xylem. Luposhinsky (1964) found that the rate of water movement through tomato roots increased with increasing the pressure differences on the solution from 0 to 40 lb/in^2 . The increase in flow was not a linear function of pressure difference except at pressures above 15 lb/in^2. He also observed that increasing pressure differences increased the amount of P^{32} , Ca^{45} , and total salts that moved into the root system. This increase was not in direct proportion to the increased rates of water movement. He stated that whether the increased rate of ion movement under pressure is the result of mass flow, increased diffusion, or increased active transport is not known. Roberson (1964) also reported non-linear relationship between the flux of water and the applied suction on the stump of detopped tomato plants.

Jensen (1962a, 1962b) showed that the root systems of tomato plants absorb water and nitrate at uniform rates when a constant vacuum (at the range 0-70 cm Hg) was established above the stump. He reported that the higher the degree of vacuum, the higher the rate of uptake was for water as well as for nitrate; but the relation between the rate of uptake of water and the rate of uptake of nitrate is not a simple linear function. He concluded that under the condition of the experiments (1962a), the passive uptake of nitrate amounts to at least 75 percent of the total uptake of nitrate. In 1964, Jensen repeated the same experiment but with different ions, potassium and calcium. He obtained results similar to those using nitrates.

Jackson and Weatherley (1962a) studied the effect of hydrostatic pressure gradient on the movement of potassium into a root. The results demonstrated that the application of pressure of two atmospheres caused an approximately fourfold increase in potassium flux from the root. They reported that this increase was independent of the presence of potassium in the external medium; therefore, it was attributable to an efflux of ions already stored in the root tissue. The effect was specifically a result of hydrostatic pressure, not a diffusion pressure deficit (DPD) difference across the cortex. They tentatively suggested that movement across the cortex to the xylem is a catenary process in which solute and water move independently at one stage and together as a solution at another stage. Repeating the same work with sodium and calcium (1962b), they found that a difference of two atmospheres pressure across the membrane resulted in a doubling of the sodium flux. Unlike the potassium flux, the sodium flux was dependent on a maintained supply of Na in the external medium. They stated that the Na flux resulting from a pressure difference appeared to be metabolism-facilitated. The story with calcium was different; metabolism-facilitated processes appeared to predominate in the flux through the xylem of Ricinus, but not in the flux through tomato roots. In another experiment using roots of Ricinus communis, transport of potassium to the vessels was found to be closely dependent on the supply of ion in the medium and was only a fraction of the total K taken up, while 99 percent of K absorbed was accumulated in the root tissues (Bowling and Weatherley, 1964). They did not apply suction on the stump; however they reported that potassium appeared to behave as Na did in the experiment of Jackson and Weatherley (1962b). Results were attributed to the difference in the salt status of plants. Again in 1965 Bowling and Weatherley published that in Ricinus communis plants the uptake of potassium was divisible into two components: (a) an accumulation by the cells of the root, and (b) a passage through the root to the shoot via the vessels. Moreover, these components were found to be entirely independent of one another. They added while (a) was unaffected by the water flux, (b) was entirely related to it and the ratio of the concentration of K^+ in the vessels to that in the medium was between 15 to 25. This ratio was similar in both intact and detopped exuding plants and remained constant in the face of wide changes in water flux. They concluded that there is no continuous mass-flow pathway between medium and xylem in these plants. Andreeva (1964) using sunflower and maize found no correlation between the absorption of nutrient substances and water. However, plants that were subjected to drying wind (5.6 m/sec) for a period of five to six hours showed a tenfold increase in the absorption of water and doubled the potassium uptake.

A comparison of the measured potential difference with the Nernst potentials for potassium and chloride suggested that the movement of K^+ into the sap is a passive process while the movement of Cl^- is an active process against the electrochemical potential gradient (Bowling and Spanswick, 1964).

Emmert (1964), in studies with decapitated roots of Phaseolus vulgaris, showed that exudate flow from the cut stem was altered by application of pressure to the surface of the ambient solution. Also, the ratio: Sr^{89}/Ca^{45} in the exudate to the ratio: Sr^{89}/Ca^{45} in the substrate decline as flow declined.

Rajan (1966) concluded that the evidence for the existance of a barrier—probably endodermis—preventing the passive diffusion of sulphate, and sensitivity of the transpiration stream concentration to root temperatures and sulphate concentrations favor the conclusion that the increased transport with increased transpiration was due to an active process.

Other Factors That Influence Water Uptake

Root permeability is one of the most important factors influencing water movement into plant roots. It is very hard to separate its function from other factors, and as mentioned before many investigators attributed the effect of respiratory inhibitors to their effect of permeability of the cell membranes. Recently Dainty (1963) reviewed the literature on water relations of plant cells. Lockhart (1965) and Thompson (1965) have revieewed the work on on cell extension and cellular membranes respectively. Richard et al. (1961) found that certain ring-substituted derivatives of carbonyl cyanide phenylhydrazone, which are among the most active known uncoupler of oxidative phosphorylation, caused an immediate striking decrease in the water permeability of roots at concentrations as low as 1 ppm. The decrease in the water uptake was accompanied by an increase in respiration. Woolley (1964) reported that one hour of treatment of maize roots with 3×10^{-5}M 2,4 dinitrophenol (DNP) at pH 4.5 decreased the permeability of the root, quadrupling the time needed for half equilibrium. The data were interpreted to mean that the resistance to equilibrium is uniformally distributed radially in a normal root but that most of the resistance of dinitrophenol treated root is near the surface. Later, Wooley (1965) stated that the root is fairly uniform in its resistance to water movement, in that the apparent diffusion coefficient within the epidermis is no less than one-third of the apparent diffusion coefficient in the root as a whole; and the apparent diffusion coefficient within the endodermis is no less than one-fifteenth of the coefficient at the root as a whole. Also, in the normal root, at least 70 percent, and probably about 83 percent, of the observed movement involves the protoplasm while in the inhibitor treated root the water movement is probably confined to the cell walls. He compared the equilibration of maize roots with tritiated water with the theoretical curves for the single cell, sheet, cylinder, and sphere and found that it followed the cylinder curve. This was interpreted to indicate that epidermis does not constitute a barrier to the entrance of water.

Kriedeman and Neales (1963) found that the incorporation of cetyl alcohol into the rooting medium of wheat plants at a concentration of five percent caused a significant reduction in transpiration in three of four experiments. Kuiper (1964) stated that alkenyl-succinic acids increase permeability of cells to water by the incorporation of the molecules into the lipid layer of the cytoplasmic membrane, thereby changing the membrane from a phase characterized by a high activation energy for water transport to a phase where only the effect of the viscosity of water is observable. Using the compound decenylsuccinic acid (DSA) at a concentration of 10^{-3}M with roots of beans, he reported that the rate of water movement increased to about 800 percent of the control when 60 cm Hg suction on the stump was used. Newman and Kramer (1966) have confirmed the increase in permeability using DSA at 10^{-3} M, but they found that 10^{-4} M DSA reduces the permeability; however both concentrations caused leakage of salts from the roots and cessation of root pressure exudation. They also found that roots of bean plants were killed when the roots were immersed in 10^{-3} M DSA, but the plant could survive by producing new roots. They suggested that DSA is acting as a metabolic inhibitor, and increase in water permeability is the result of injury to the roots.

Sayaev (1965) investigated the "free space" of root cells and its role in the absorption of water using the electron microscope. He found that the passive stream of water moved not only along extraordinary fine interfibrillar space of the cell wall, but also along the larger ultramicroscopic canals of cross section of the order of 300-500 A, penetrating the cell wall in a longitudinal direction and communicating with the intercellular space. He stated that the bulk of the stream of water passively entering the root evidently moves not through the protoplast of live cells, but through the free space of the cell membrane.

Temperature also influences the movement of water in the plant cell. It has more than one function. It causes changes in the viscosity of the protoplasm and water, the rate of metabolic mechanism; and when a temperature difference between two parts of the plant exists, water moves because of a force of thermal gradient.

The primary effect of low temperature on water absorption by plants appears to be to a reduction in the permeability of the tissue, directly through an effect on membrane permeability, and indirectly through increased viscosity of the protoplasm and water (Kramer, 1956). Some twenty years ago Kramer (1942) studied the effect of root temperature on the transpiration of cold season and warm season crops. It was demonstrated that the permeability of the roots of different species is affected differently by temperature.

Jensen and Taylor (1961) have observed that low temperatures decrease the amount of water that plants otherwise would absorb. They measured the rate of water movement through plants and found that the apparent activation energy for water movement through root systems was greater than that for the self-diffusion and viscosity properties of water alone. They reasoned that another mechanism, in addition to the purely physical process, was involved in water movement. Brouwer (1965) presented data on the effect of temperature on water movement in maize plants which indicates a combined action of suction tension, stomatal closure, viscosity and permeability. He reported that the complexity of the situation is because, in addition to influences of temperature on the conductivity of the tissue, there are also influences of suction tension and consequently of stomatal closure. Here, he neglected the influence of temperature potential gradient, which could be an effective factor. Campbell (1966) concluded that water moved as a result of a thermal gradient in both saturated and unsaturated potato tuber tissue while no thermo-osmosis was observed in saturated carrot tissue, saturated two percent agar, saturated gelatine, or frozen potato tuber tissue. Campbell also neglected other factors such as salt movement and the metabolic activity of the tissue cells.

Kuiper (1964) reported Q_{10} values as high as 3. 8 for water movement through bean roots. This value is well beyond the range of values generally attributed to physical processes. Trubetskova (1965b) studied the effect of temperature on active and passive absorption of water by the root system of plants. He reported that within the temperature limits of 10-30 C, the temperature coefficient (Q_{10}) for active absorption of water was above two and reached five to seven, indicating the biological nature of the process, which is probably caused by respiration; and Q_{10} for passive transpiration was 1. 0 to 1. 3 indicating the physical nature of this phenomenon. In another experiment on active transport on intact guttating plants in which transpiration was blocked by maintenance of the above ground organs in humid atmosphere, the measured Q_{10} was also above 2. 0 (5-7); and it was the same when the plant was detopped. Rajan (1966) obtained similar results.

THEORY

The treatment of simultaneous fluxes of solute and solvent has been greatly facilitated by the development of thermodynamic methods for dealing with non-equilibrium states. These methods have been termed the thermodynamics of irreversible processes. First developed by Onsager, irreversible thermodynamics has been treated by deGrott (1951). Its utility and importance in the analysis of biological systems was pointed out by Spanner (1954) and Kedem and Katchalsky (1958) who developed equations of particular application to biological systems.

The occurrence of an irreversible process within a system leads to an increase of entropy; the rate of increase of entropy per unit volume in an isothermal system (Guggenheim, 1959) is shown in the following equation:

$$\frac{d_i s}{dt} = \frac{I}{T} \sum_{i=1}^{n} J_i X_i \qquad (1)$$

where

$\frac{d_i s}{dt}$ is the rate of entropy production inside the system

T is the absolute temperature

J_i flux of the component i

X_i affinity or force that causes the flux of i

If a series of fluxes of components J_1, J_2, ----J_n are occurring simultaneously under the influence of forces X_1, X_2 ----X_n, then the application of Onsager's theory of irreversible processes

(Onsager, 1931a, 1931b) gives the following series of equations:

$$J_1 = L_{11}X_1 + L_{12}X_2 + L_{13}X_3 ---- + L_{1n}X_n$$

$$J_2 = L_{21}X_1 + L_{22}X_2 + L_{23}X_3 ---- + L_{2n}X_n \qquad (2)$$

$$J_n = L_{n1}X_1 + L_{n2}X_2 + L_{n3}X_3 ---- + L_{nn}X_n$$

Phenomenological coefficients such as L_{11} and L_{22} relate flows and forces directly, where no interaction between flows occurs. Phenomenological coefficients such as L_{12} and L_{13} take into consideration the interaction between fluxes of different components.

Taylor (1963) stated that the thermodynamic theory of irreversible process consists of finding the appropriate conjugated fluxes and affinities. However, the experimental limitations of the problem and measurements that can be made should indicate the choice of the fluxes and/or the affinities.

In applying the irreversible thermodynamics to the process of active transport, one finds there are three fluxes: J_w the flux of water, J_s the flux of solute, J_o the flux (or consumption) of oxygen. These fluxes are related to the affinities as shown in the following equations:

$$J_w = L_{ww}X_w + L_{ws}X_s + L_{wo}X_o$$

$$J_s = L_{sw}X_w + L_{ss}X_s + L_{so}X_o \qquad (3)$$

$$J_o = L_{ow}X_w + L_{os}X_o + L_{oo}X_o$$

Kedem and Katchalsky (1961) showed that the affinities are the gradients of chemical potential or

$$X_i = - \frac{d\mu i}{d\ x}$$

Thus, the phenomenological equation (3) for a root membrane of unit thickness can be expressed as:

$$\begin{aligned} J_w &= L_{ww}\,\Delta\mu_w + L_{ws}\,\Delta\mu_s + L_{wo}\,\Delta\mu_o \\ J_s &= L_{sw}\,\Delta\mu_w + L_{ss}\,\Delta\mu_s + L_{so}\,\Delta\mu_o \\ J_o &= L_{ow}\,\Delta\mu_w + L_{os}\,\Delta\mu_s + L_{oo}\,\Delta\mu_o \end{aligned} \qquad (4)$$

From classical thermodynamics, and the Gibbs-Duhem equation, under isothermal condition it may be shown (Taylor, 1963; Katchalsky and Curran, 1965) that:

$$\Delta\mu_w = \bar{V}_w\,(p_1 - p_2)\,, \qquad (5)$$

$$\Delta\mu_s = RT\,\ln \frac{C^1_s}{C^2_s}\,, \text{ and} \qquad (6)$$

$$\Delta\mu_o = RT\,\ln \frac{C_o}{C^2_o} \qquad (7)$$

where:

$\Delta\mu_w$ is the chemical potential difference of water across the membrane

$\bar{V}_w$ is the partial specific volume of water

p_1 is the pressure on the exudate

p_2 is the pressure on the external solution

$\Delta\mu_s$ is the chemical potential difference of solute, between exudate and external solution

R the gas constant

T absolute temperature in ^{o}K

C^1_s concentration of solute in exudate

C_s^2 concentration of solute in external solution

$\Delta\mu_o$ is the chemical potential difference of oxygen, between exudate and external solution

C_o^1 concentration of oxygen in exudate

C_o^2 concentration of oxygen in external solution

Our problem is to solve for the phenomenological coefficients in equation (4) and to find if the respiration induces a flux of water and/or solute. Further, we must examine whether the water carries the solute with it or if the solute potential difference causes a flux of water. Using the appropriate experimental data for the amount of flux and that of driving forces in equation (4), we find that there are three equations and nine unknowns. For this reason the irreversible thermodynamic equations had been used as the model for multiple regression analysis.

In multiple regression a variable y is dependent upon more than one independent variables, x_1, x_2, x_3 -----x_n. Applying this to our case, where there are three fluxes y_w, y_s, and y_o each of which is dependent on three forces x_w, x_s, and x_o , we have the following equation:

$$\begin{aligned} y_w &= a_1 + b_1 x_w + b_2 x_s + b_3 x_o \\ y_s &= a_2 + b_4 x_w + b_5 x_s + b_6 x_o \\ y_o &= a_3 + b_7 x_w + b_8 x_s + b_9 x_o \end{aligned} \tag{8}$$

The series of equations (8) is analogous to that of equation (3), with the difference of the constant a_i (i = 1, 2, 3). From equation (4), if all the forces are equal to zero, then there is no flux; this agrees with the physical facts of the problem. But, in equation (8) when all the forces are equal to zero, the flux would still be equal to a_i, which is the height of the hyper plane in four dimensional space. So, a_i indicates that there might be flux even when all the forces are equal to zero. Since physically there must not be any flux when there are no forces, then a_i different from zero seems to be an absurd result. Ezekiel and Fox (1959, p. 63-64) state:

> The value for a is the height of the line when x = o. In this example, it indicates a flow of 9.5 units might be expected at Newgate even when there is no flow at all at Libby. Since Libby is downstream from Newgate, this seems to be an absurd result. The statistic a therefore has no meaning of and by itself in this particular example, beyond placing the height of line as a whole for the range within which it does have meaning.
>
> The statistic b, on the other hand, is always meaningful. It indicates the difference in y for any difference of 1 unit in x, on the average of all observations, and within the range covered.

So neglecting a, or assume it is zero, we have for example:

$$y_w = b_1 x_w + b_2 x_s + b_3 x_o$$

and from equation (3)

$$J_w = L_{ww} x_w + L_{ws} x_s + L_{wo} x_o$$

If we assume term by term correspondence then:

$$b_1 = L_{ww}, \; b_2 = L_{ws}, \text{ and } b_3 = L_{wo}$$

$$b_4 = L_{sw}, \; b_5 = L_{ss}, \; b_6 = L_{so},$$

$$b_7 = L_{ow}, \; b_8 = L_{os}, \; b_9 = L_{oo}.$$

Hence, the net regression coefficients will be treated as the phenomenological coefficients in this study.

MATERIALS AND METHODS

Experimental Materials

Helianthus annuus (Russian Mammoth Sunflower) seeds were germinated on cheese cloth or on Brillite. One week after germination, the seedlings (two to three inches tall) were transferred to 1 liter culture chambers filled with Hoglands solution full strength. This was made up after Hogland and Arnon (1950) except that iron was given as chelate 138. The solutions were aerated continuously through sintered stone aerating blocks from a compressed air system. Two to three weeks later the plants were transferred to 3.5 liter wide mouth (3.5 inch in diameter) containers. The plants were supported in the top of the container by an esterfoam disk. The Hogland solution was changed every week and aerated as described above.

Apparatus and Preliminary Experiments

The apparatus, Figure 1, consists of:

1. Root chamber; that is a 2.0 liter wide mouth thermos jug fitted with tinned mason lid. In the lid five holes were drilled and a 15 cm length of pyrex glass tubing (5.0 mm) was centered and fixed by silastic cement in each hole. The center tube was used to connect the stump of the plant to a 100 ml pipette equipped with two valves that

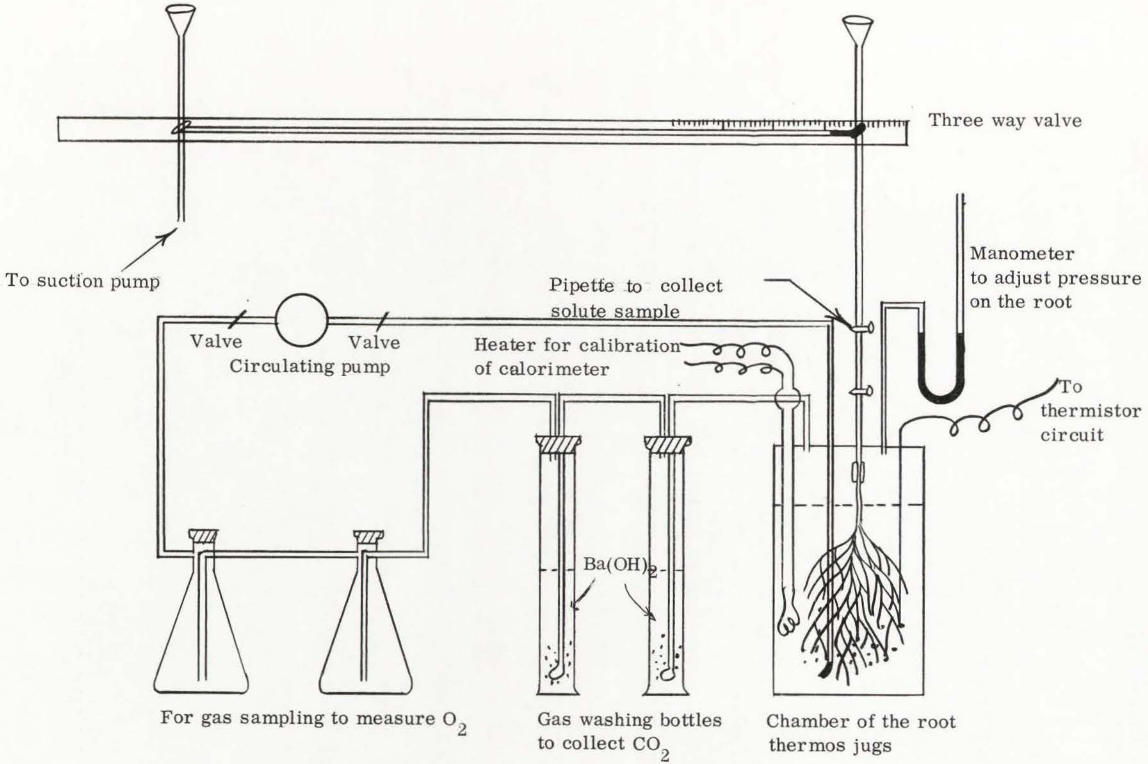

Figure 1. Apparatus proposed to measure water movement, oxygen consumption, salt movement, and heat evolved by plant roots.

were used to collect the exudate sample. Of the other four tubes two were used for aeration, inlet and outlet. One of the remaining two was connected to a mercury manometer to detect changes in pressure that might develop in the root chamber; the other was blocked with a rubber stopper having a thermistor (Victory Engineering Corporation 32A11, Springfield, New Jersey) in it with its wires connected to a Wheatstone bridge and recorder, to detect the change in temperature caused by heat evolved in respiration.

2. A suction pump to supply the suction over the stump was attached by a 1/4 inch T tube to a Mercury Cartesian Diver manostate to keep a constant amount of suction on the stump. The suction was detected by a mercury manometer. The exudate was forced to pass through a 1 mm bore capillary tube. The capillary tubing was selected from standard glass stock and was examined for irregularities in the diameter of the bore. It was found to be accurate to witnin 5 percent. The capillary tube was attached to the surface of a 1-meter ruler. At each end of the capillary tube a three way stopcock was attached to facilitate filling the system with water and to introduce a droplet of mercury for detecting and measuring the rate of movement of water through the tube. The free end of the capillary tube was attached to the pipette by 1/4 inch unflexible polyethylene tubing to avoid collapse when high suction was applied. The other junctions were made by 1/4 inch Tygon tubing.

3. The pressure side of a small diaphragm circulating pump (Dyna Pump, Standard Scientific Supply, New York City) was attached to the air inlet tube of the root chamber, and the section side was attached

to one side of the gas sampling flask. The other side of the gas sampling flask was attached to two drying towers filled with silica gel. The drying tower was attached to two gas washing bottles (extra course, Van Waters and Rogers, Inc. , Salt Lake City, Utah) which were in turn attached to the air outlet of the root chamber.

A preliminary experiment was conducted to investigate the possibility of measuring the heat of respiration and correlating it with the uptake of water at different rates of suction on the stump of the root.

The amount of heat evolved by respiration was too small to detect with the thermister. This problem was aggravated by the loss in heat as a result of evaporation from the root chamber, and some compensatory gain in heat from the circulatory (air) pump after it became warm. Although the apparatus was put in a room with constant temperature, it was impossible for it to reach equilibrium in the time available to take measurements within one root. Because of these difficulties in measuring heat of respiration, it was necessary to measure respiration by the amount of oxygen consumed and carbon dioxide produced.

Experimental Procedure

Plants six to seven weeks old were detopped within on inch of the top of the root. Then the root (about 30-35 cm net length and weight 90-120 g) was transferred to the root chamber in 1400 ml half strength Hogland solution. The cut stem was sealed to the center tube in the lid with gum rubber tubing, sealed with paraffin wax. The lid was closed tightly and sealed on all sides with about 1/2 inch paraffin wax. Air which had been passed through soda lime to absorb carbon dioxide was bubbled in the root chamber through sintered stone aerating block connected to the air inlet of the chamber until the paraffin wax was solidified. The tube above the stump was washed three to four times with deionized water (using a syringe with a fine long polyethylene tube instead of the needle). As soon as this tube was filled with deionized water it was connected to the pipette, and the time for the solute movement was recorded. Then the root chamber was connected to the gas circulatory system and time was recorded. A mercury droplet was then introduced into the capillary tube, and its rate of movement was recorded. Readings were taken every 15 or 20 min, and a new mercury droplet was introduced as necessary. After 50-60 min the circulatory pump was turned off, and the time again recorded. Also, at the same time or after 1 min both the lower and upper valves of the pipette were shut, and the pipette was disconnected. The solution above the stump was collected (by the syringe) in a 12 ml vial, and the solution in the pipette was added to it.

Again air was bubbled into the root chamber until the gas washing bottles were prepared. The same procedure was repeated by applying suction of 10 cm Hg on the stump for 50-60 min, then repeated for 20, 30, and 45 cm Hg.

Analytical

Measurement of exudate

At the end of all the experiments the capillary tube volume was calibrated and used for calculating the rate of exudate J_w.

Measurement of oxygen consumed

A Beckman GC-2 gas chromatograph with dual column attachment in combination with a Bristol recorder was used for O_2 analysis. A six-foot molecular sieve (13x) column was used for the separation of N_2 and O_2 in the sample. The analysis of the gas sample was carried out at 40 C with helium as a carrier gas flowing at the rate of 0.33 liters/min and with filament current of 260 ma.

At the beginning of a run, immediately after the circulatory pump was turned on, a 100 µl gas sample from the gas sampling flask was withdrawn by means of hypodermic syringe (250 µl capacity) and was injected into the gas chromatograph for oxygen analysis. The same procedure was repeated at the end of a run, just before the circulatory pump was turned off. Peak heights that appeared on the recorder chart were used as the indication of the quantity of oxygen in the sample. Calibration was used to calculate the amount of oxygen in the samples. With a known quantity of air circulating in the close system, the amount of oxygen was calculated, and the difference between the amount at the beginning and that at the end of a run was the amount of oxygen consumed by the root during that period.

Measurement of carbon dioxide produced

The air coming out of the root chamber was passed through 0.2 N $Ba(OH)_2$ solution in the gas washing bottles. The CO_2 given off by respiration was then precipitated in the $Ba(OH)_2$ solution as $BaCO_3$ with a partial neutralization of the $Ba(OH)_2$. At the end of the run the gas washing bottles were disconnected, and the residual $Ba(OH)_2$ was titrated by HCl, and the CO_2 evolved was calculated using the equation:

$$\text{Milligrams of } CO_2 = V \times N \times 22.0 \text{ (the normal weight of } CO_2\text{)}$$

where:

V = the difference between blank and experimental titration in milliliters

N = the normality of HCl used for titration

This weight of CO_2 was converted to volume using the ideal gas equation at the pressure and temperature of the experiment.

Measurement of osmotic pressure

A vapor pressure osmometer model 301A (Hewlett-Packard, Avondale, Pa., 19311) was used for solute analysis. An aqueous thermistor probe (part No. 301-131) was used. The thermistors are small (0.043 inch) beads mounted on fine (0.004 inch) wire. Solutions with concentrations between 0.005 and 0.1 M are optimal, and the model 301A is designed to read to ± 0.001 C or better.

The collected samples were all adjusted to a volume of 12.0 ml using deionized water. Syringes were washed three to four times with solution before a sample was withdrawn. The syringes were put in the sample chamber for 10-15 min to achieve temperature equilibrium with the sample. Then the solution thermistor was washed with eight to ten drops of solution, and the last drop was allowed to hang on the thermistor. At that time a stop watch was started. At the end of 2 min the needle was centered with ΔR decale dials and a reading was taken. Subsequently, readings for three to four drops of each sample were taken and averaged.

The concentration of the sample for every run was determined by the use of a calibration curve. The calibration curve was made by the use of KCl solution (using deionized water) at the range of 0.001-0.050 M.

The concentration of the exudate was calculated by the equations:

$$V_1 = J_w \times t$$

and

$$V_1 \times N_1 = V_2 \times N_2$$

where:

V_1 is the total volume of exudate at period t

J_w is the rate of flux of exudate

N_1 is the (normality) concentration of exudate

V_2 is the volume of the sample (12.0 ml)

N_2 is the concentration of the sample

The flux of solute J_s was calculated by the equation

$$J_s = \frac{V_1 \times N_1}{t}$$

Experimental Treatments

The same experimental procedure was followed for all five treatments as described before the control except that the root pressure was measured for each root before it was subjected to treatment.

After the first run without applying any suction, the root was transferred to another root chamber containing 1400 ml of Hogland half strength plus treatments with final concentrations as follows:

1. 5×10^{-4}M decenylsuccinic acid
2. 1×10^{-3}M sodium oxide
3. 1×10^{-3}M 2,4 dinitrophenol
4. 5×10^{-4}M adenosine triphosphate (disodium salt)
5. 1 mg/liter indol acetic acid

In case of decenylsuccinic no buffer was added, and the pH of the solution was always 3.9-4.0. In the rest of the treatment and control a buffer (disodium phosphate and citric acid) was added and the pH was adjusted for 4.5.

The root was left for equilibrium in the treatment solution for 2 hr after which the flow of water, solute, and oxygen consumption were measured at the experimental suction (0, 10, 20, 30, and 45 cm Hg).

Experimental Data and Analysis

The basic data consist of the flux of water J_w, and the flux of solute J_s from the external through the plant root system and out the decapitated stem. The consumption of oxygen within the nutrient solution will be assumed to represent the flux of oxygen into the root system. The forces that cause these fluxes are the difference in suction (Δp) on the water across the roots, the difference in solute concentration between the solution and exudate, and the difference in oxygen concentration and exudate as given in Appendix I. In some of the experiments where there was a leak of air bubbles from the stump junction, and in others where there was leak of air in the air circulating system, the data have been disregarded.

The forces have been calculated from the thermodynamic relations given in equations (5), (6), and (7). The oxygen concentration in the external solution was calculated from its solubility under the condition of the experiment. The concentration in the xylem sap was calculated according to the Warburg equation given by Goddard and Bonner (1960) which is:

$$C_x = C_o - \frac{a}{2D} (Hx - x^2)$$

where:

C_x is the p_{O_2} in atmospheres at x

C_o is the external p_{O_2} in atmospheres

D is the diffusion constant

a is respiratory rate in ml O_2/mg of tissue sec

H is thickness of tissue in centimeters

x is distance from the surface in centimeters ($x \cong \frac{H}{2}$)

Goddard and Bonner also stated that for the respiratory rate of 100μl O_2 per gram weight per hour, from the equation the limiting thickness at which p_{O_2} just falls to zero at the center of the tissue is 0.507 cm, and if the respiratory rate is ten times as great, the limiting thickness would be 0.16 cm. A sample of calculation for fluxes and forces is to be found in Appendix I.

In this study the phenomenological coefficients of irreversible thermodynamics were calculated by the use of multiple regression (using equations (8) and (9)). These coefficients appear in Tables 1a, 2a, and 3a. Also in these tables the multiple correlation coefficients are presented.

In addition to the measures of the importance of all of the independent variables combined (by the multiple correlation coefficients, R), the importance of each of the individual variables (the forces) taken separately, while simultaneously allowing for the variation associated with remaining independent variables, may be compared by the measurement of the standard partial regression coefficients (or β coefficients). This comparison is made by expressing each force in terms of its own standard deviation.

In Tables 1b, 2b, and 3b the standard partial regression coefficients (or β coefficients) are tabulated for the corresponding net regression coefficients for all the treatments.

According to irreversible thermodynamic phenomena, calculations of the phenomenological coefficients might help in discovering the effect of forces on fluxes. For example, the ratio of L_{ws}:L_{sw} would indicate whether the amount of water moved by solute potential is equal, less than, or more than the amount

Table 1a. The phenomenological coefficients (net regression coefficients) for the relations between water flux and changes in pressure, solute potential, and oxygen potential, with the multiple correlation coefficients

Treatment	L_{ww} μmole min^{-1} cm^{-1} x 10^2	L_{ws} μmole min^{-1} cm^{-1}	L_{wo} μmole min^{-1} cm^{-1}	R
Control	- 7.50	-0.20	- 21.80	0.691
DSA	-16.44	+0.20	+199.40	0.918
NaN_3	-14.50	-0.15	+ 6.01	0.977
DNP	-17.00	+0.32	-144.20	0.741
ATP	- 3.83	-0.30	+ 2.23	0.794
IAA	- 3.15	+0.25	- 19.61	0.772

Table 1b. The standard partial regression coefficients (β) for the relations between water flux and changes in pressure, solute potential and oxygen potential

Treatment	L_{ww}	L_{ws}	L_{wo}
Control	0.631	0.122	0.178
DSA	0.838	0.078	0.322
NaN_3	0.847	0.279	0.022
DNP	0.991	0.115	0.323
ATP	0.567	0.292	0.037
IAA	0.775	0.422	0.606

Table 2a. The phenomenological coefficients (net regression coefficients) for the relations between solute flux and changes in pressure, solute potential, and oxygen potential, with the multiple correlation coefficients

Treatment	L_{sw} μmole min^{-1} cm^{-1}	L_{ss} μmole min^{-1} cm^{-1} x 10^{-4}	L_{so} μmole min^{-1} cm^{-1} x 10^{-3}	R
Control	-0.19	+4.02	- 2.45	0.537
DSA	-0.39	+3.73	+47.90	0.932
NaN_3	-0.84	+2.70	- 5.96	0.960
DNP	-0.67	+1.13	-62.30	0.694
ATP	-0.17	+2.35	- 5.42	0.614
IAA	-0.09	+2.55	- 5.29	0.470

Table 2b. The standard partial regression coefficients (β) for the relations between solute flux and changes in pressure, solute potential and oxygen potential

Treatment	L_{sw}	L_{ss}	L_{so}
Control	0.701	1.081	0.087
DSA	1.081	0.784	0.416
NaN_3	1.023	0.161	0.047
DNP	0.943	0.099	0.334
ATP	0.615	0.567	0.221
IAA	0.290	0.102	0.764

Table 3a. The phenomenological coefficients (net regression coefficients) for the relations between oxygen flux and changes in pressure, solute potential, and oxygen potential, with the multiple correlation coefficients

Treatment	L_{ow} μ mole min^{-1} cm^{-1}	L_{os} μ mole min^{-1} cm^{-1} x 10^{-4}	L_{oo} μ mole min^{-1} cm^{-1} x 10^{-2}	R
Control	- 1.18	+11.80	- 9.28	0.834
DSA	- 0.31	+ 3.26	- 1.86	0.837
NaN_3	+ 0.05	- 2.36	- 11.24	0.812
DNP	- 0.12	+ 1.01	- 14.99	0.836
ATP	- 0.46	+ 2.46	- 10.89	0.880
IAA	- 0.83	+ 10.47	- 21.77	0.958

Table 3b. The standard partial regression coefficients (β) for the relations between oxygen flux and changes in pressure, solute potential, and oxygen potential

Treatment	L_{ow}	L_{os}	L_{oo}
Control	1.296	0.948	0.983
DSA	0.008	0.821	0.194
NaN_3	0.048	0.120	0.754
DNP	0.193	0.102	0.935
ATP	0.290	0.102	0.764
IAA	0.314	0.271	1.036

of solute moved by water potential gradient. The ratios of the linked transfer or drag coefficients are given in Table 4.

Table 4. The ratio of the phenomenological coefficients for different treatments

Treatment	L_{sw}/L_{sw}	L_{wo}/L_{ow}	L_{so}/L_{os}
Control	+ 1.03	+ 18.5	- 2.10
DSA	- 0.51	- 650	+ 147.0
NaN_3	+ 1.25	+ 120	+ 25.0
DNP	- 0.48	+ 1220	- 614.0
ATP	+ 1.78	- 4.84	- 22.0
IAA	- 2.91	+ 23.66	- 5.0

Summary curves which compare the relative influence of suction applied on the stump of the root for different treatments (with decenylsuccinic acid that causes changes in permeability of the membranes, respiratory inhibitors, and respiratory stimulators) on the flux as a percentage of the flux before applying suction are given for water flux (Figure 2), solute flux (Figure 3), and oxygen flux (Figure 4). As the amount of suction increased, the flux of water increased at different rates for different treatments. In the solute flux the rate for control treatment decreased with increasing suction, but it increased at different pattern for the other treatments. Oxygen

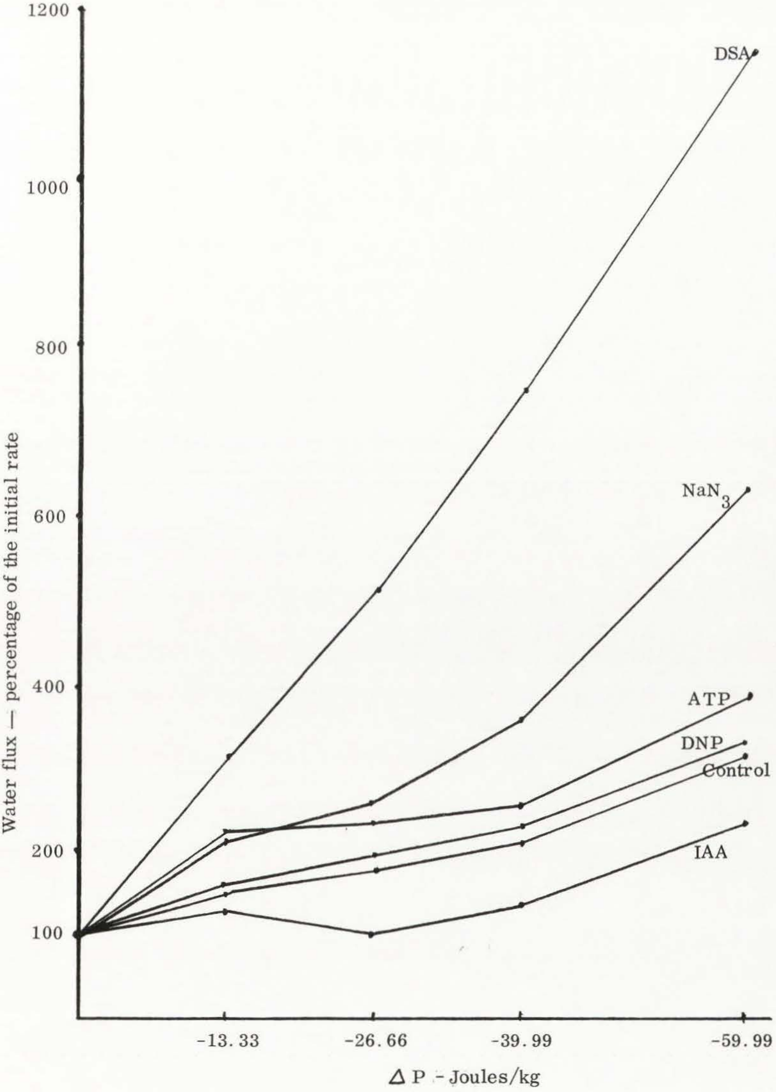

Figure 2. Water flux as percentage of the initial rate in relation to the suction applied.

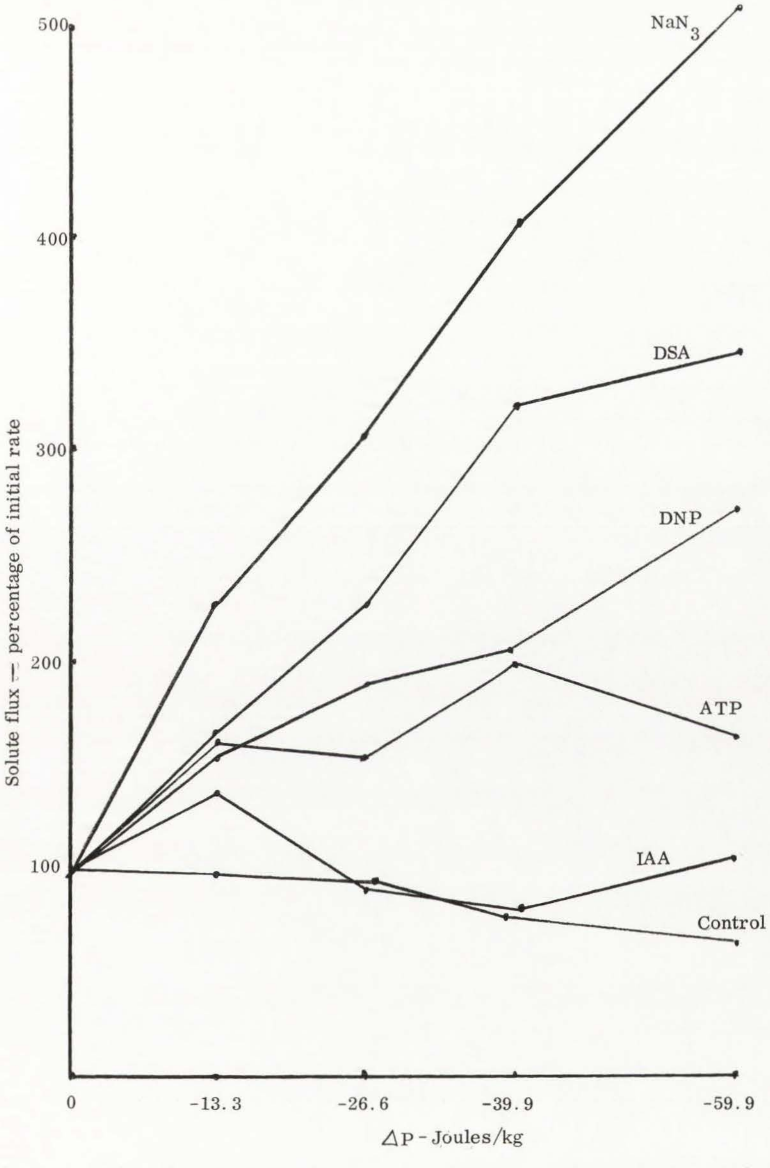

Figure 3. Solute flux as percentage of the initial rate in relation to suction applied.

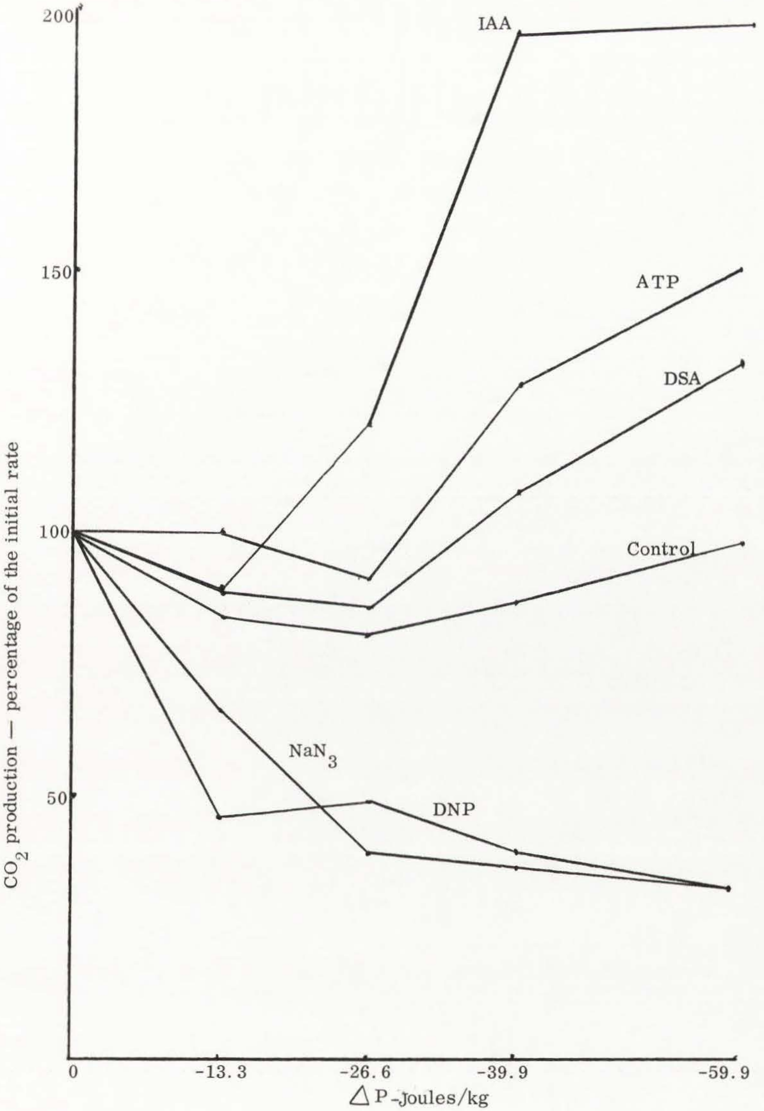

Figure 4. Carbon dioxide production as percentage of the initial rate in relation to suction applied.

flux increased with increasing suction for the control treatment, decenylsuccinic acid (DSA), adenosine triphosphate (ATP), and indole acetic acid (IAA), while it decreased with increasing suction for both of 2,4-dinitrophenol (DNP) and sodium azide (NaN_3).

A four dimensional graphical presentation for the relation between the fluxes and the three forces producing it is not possible. However, the relationship between the flux of water and the difference in pressure gradient for different treatment are presented in Figures 5 to 10. The regression line has been plotted by calculating the flux of water at two levels of suction applied (-39.99 cm Hg) while the other two forces were held constant and was chosen to be the average of each over the whole range for the solute potential gradient and oxygen potential gradient. The regression line fit the experimental points quite satisfactorily in cases where the variable pressure difference was the most important factor in the flux, while it was far from it when the other forces were the important variables. In all treatment, as the suction increased the water flux increased, the relationship appeared to be linear only in the case of DSA.

The flux of the solute in response to a pressure gradient is presented in Figures 11 to 16. (The pattern of the graph of the solute flux was analogous to that of the water flux.) In the case of the control the regression line appears to be in the opposite direction from the experimental points which means that forces other than the pressure gradient are predominant in determining the solute flux. This agrees with the data of Table 2b, where the relatively large value for L_{ss} in the

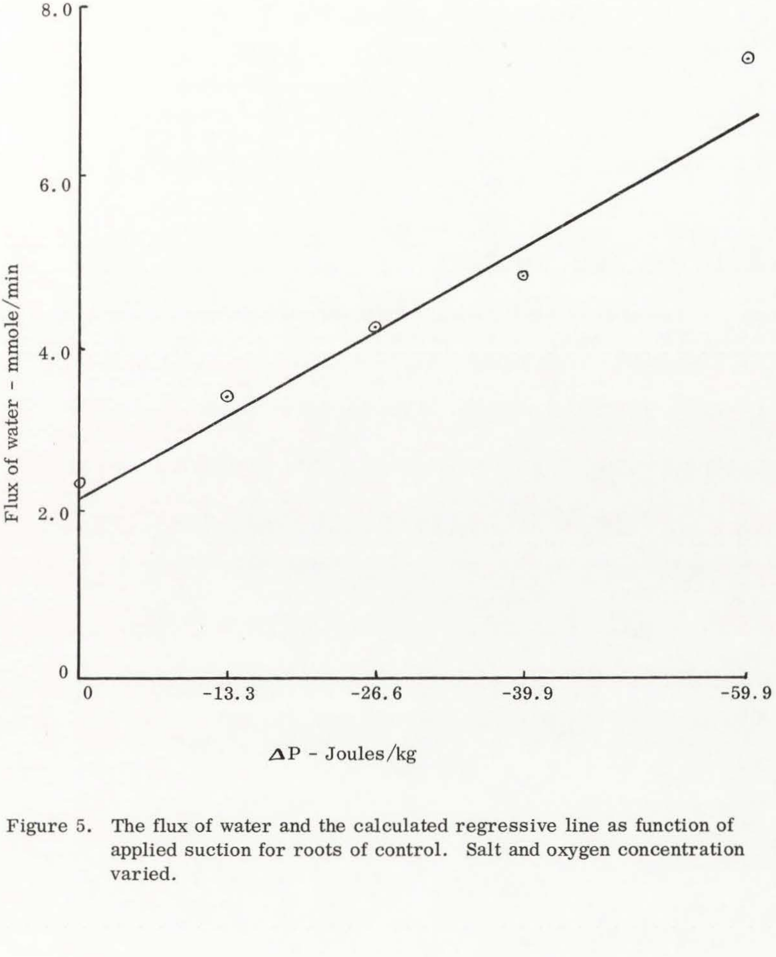

Figure 5. The flux of water and the calculated regressive line as function of applied suction for roots of control. Salt and oxygen concentration varied.

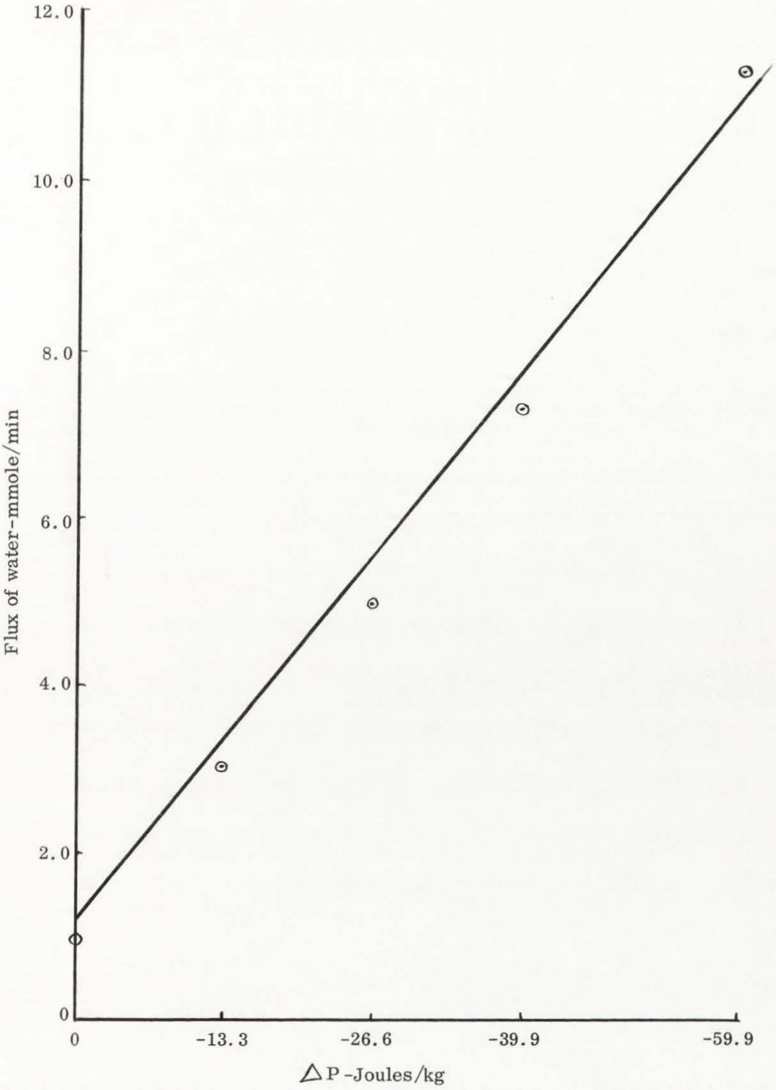

Figure 6. The flux of water and the calculated regression line as function of applied suction for roots treated with DSA 5 x 10^{-4} M. Salt and oxygen concentration varied.

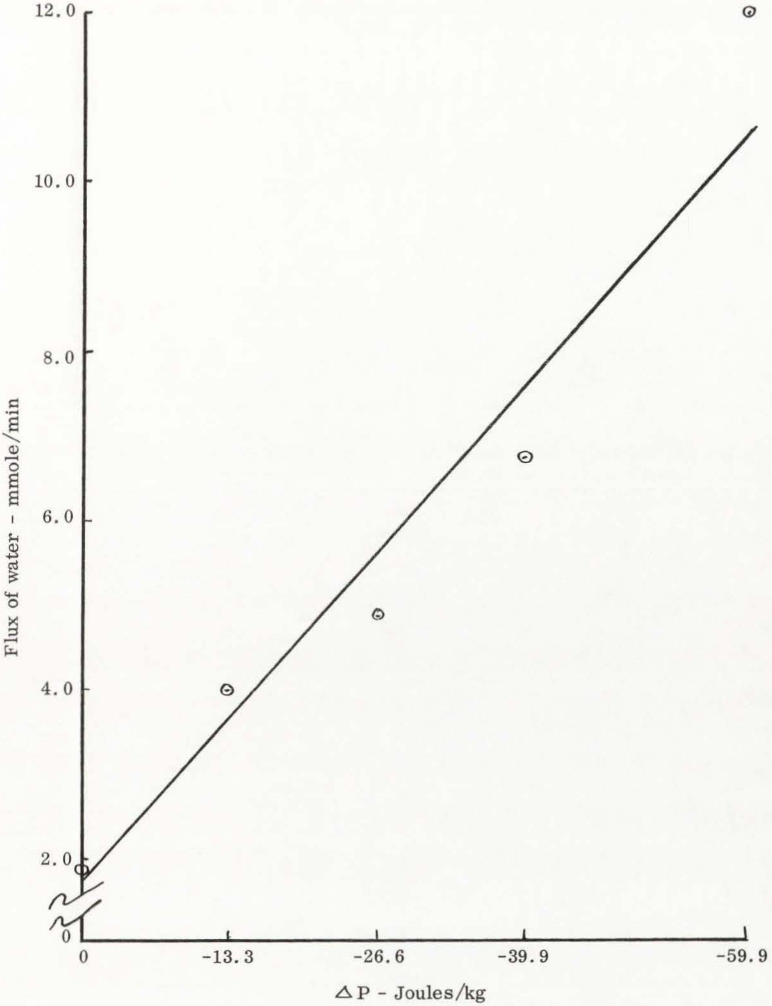

Figure 7. The flux of water and the calculated regression line as function of applied suction for roots treated with NaN_3 1×10^{-3} M. Salt and oxygen concentration varied.

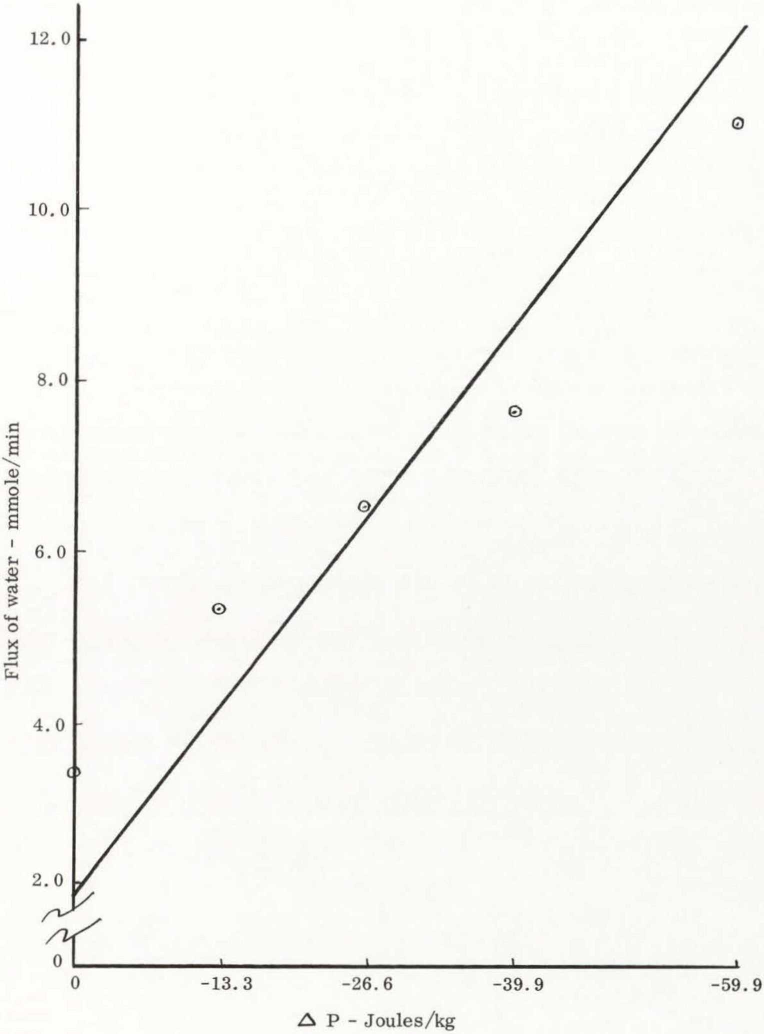

Figure 8. The flux of water and the calculated regression line as function of applied suction for roots treated with DNP 1×10^{-3} M. Salt and oxygen concentration varied.

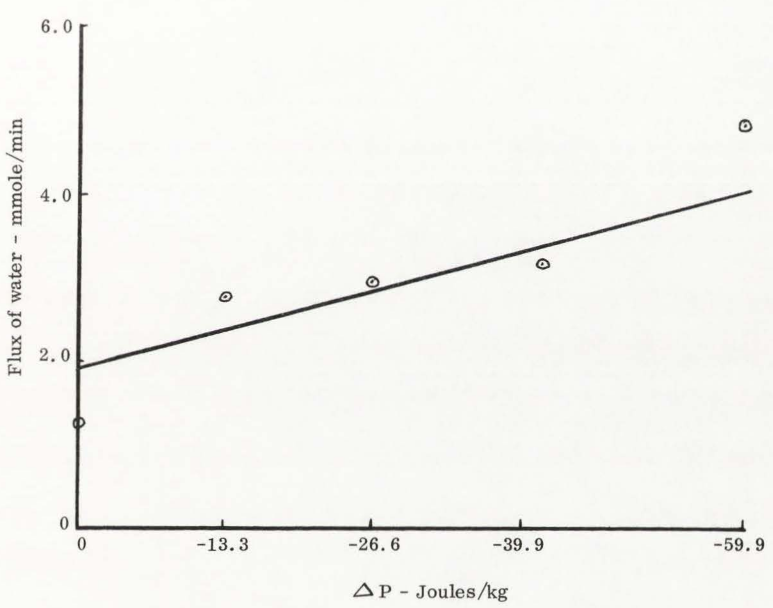

Figure 9. The flux of water and the calculated regression line as function of applied suction for roots treated with ATP 5×10^{-4} M. Salt and oxygen concentration varied.

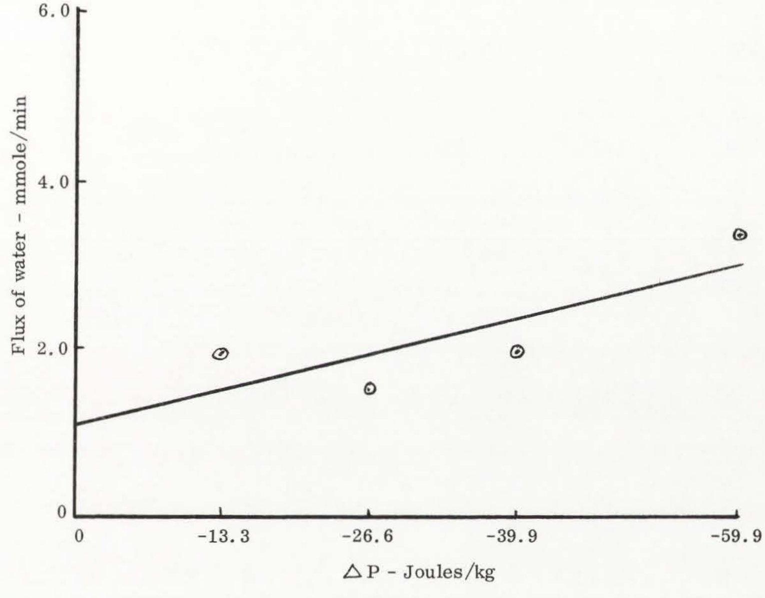

Figure 10. The flux of water and the calculated regression line as a function of applied suction for roots treated with IAA 1 mg/liter. Salt and oxygen concentrations varied.

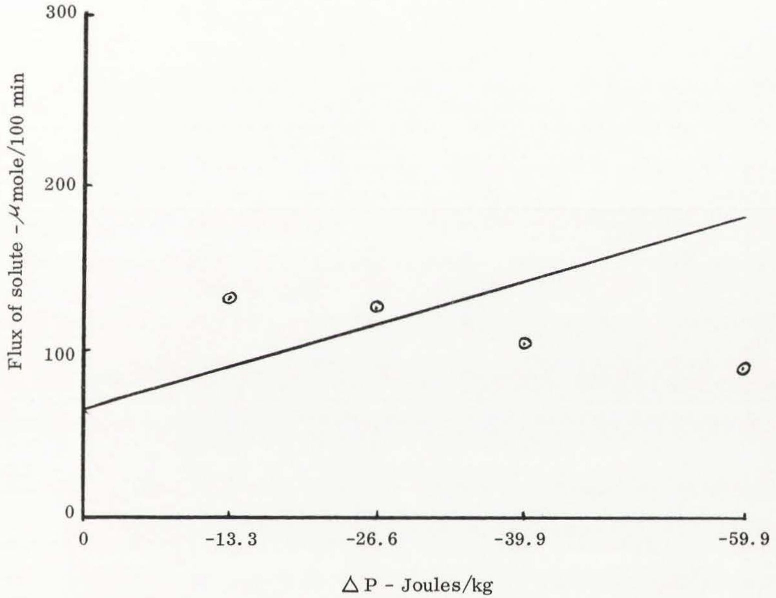

Figure 11. The flux of solute and the calculated mean regression line as a function of applied suction for control plant. Salt and oxygen concentration varied.

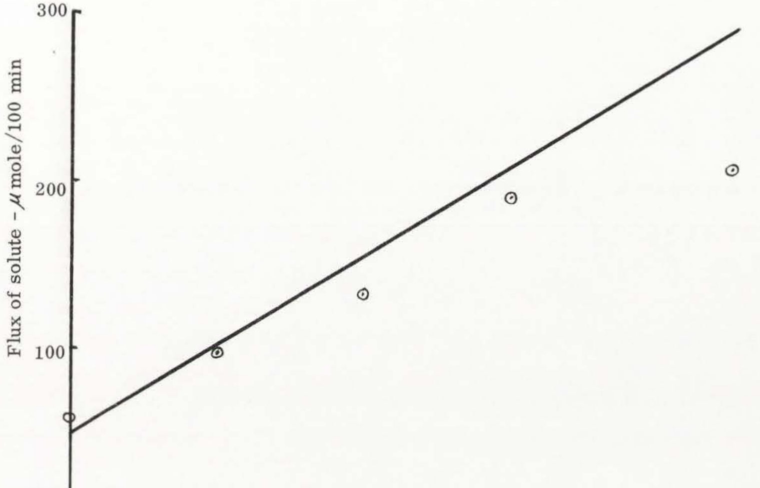

Figure 12. The flux of solute and the calculated mean regression line as function of applied suction for roots treated with 5×10^{-4} M DSA. Salt and oxygen concentration varied.

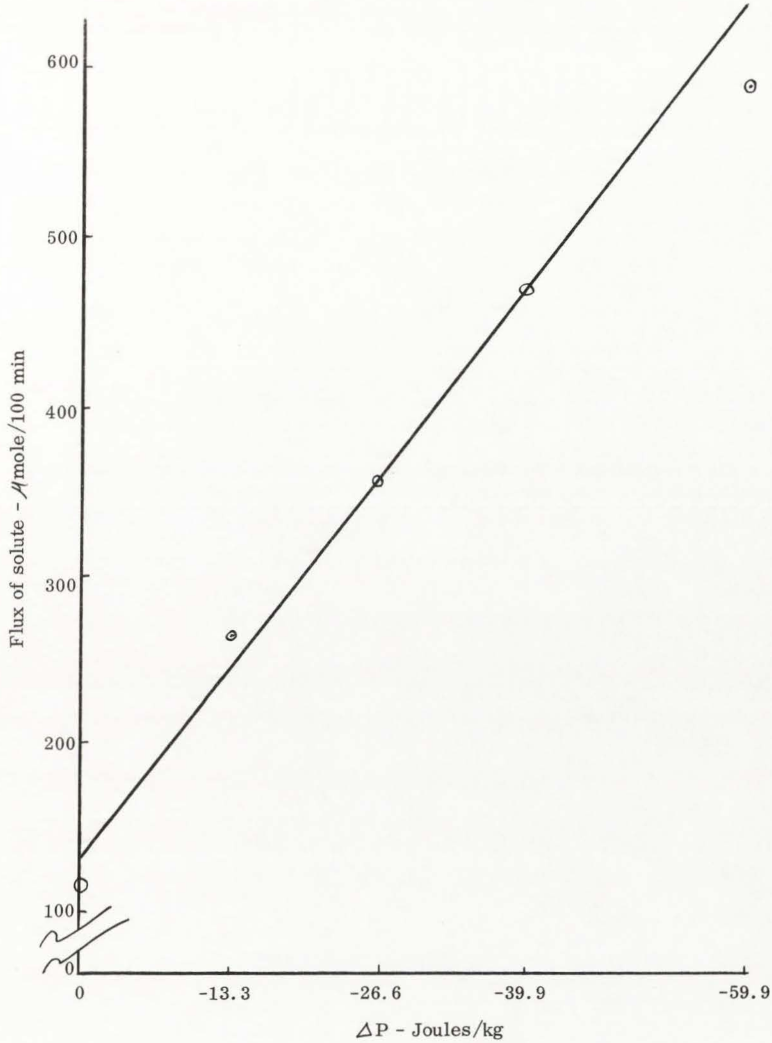

Figure 13. The flux of solute and the calculated mean regression line as a function of applied suction for roots treated with 1 x 10^{-3} M NaN_3. Salt and oxygen concentration varied.

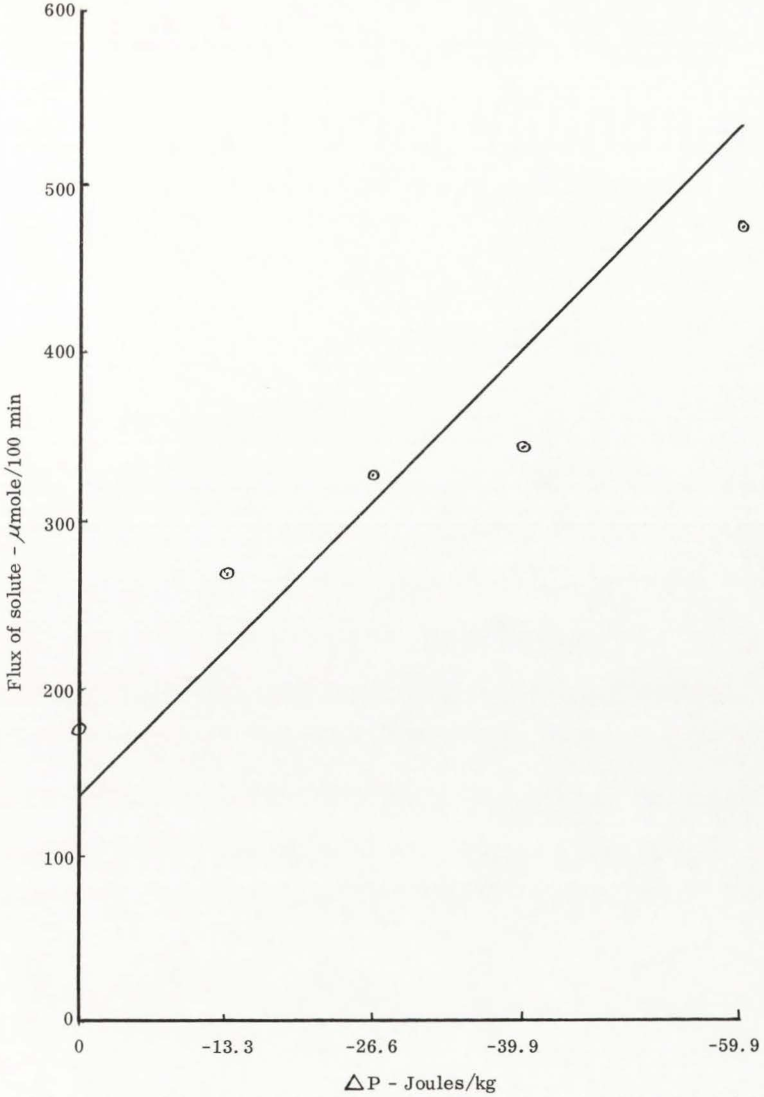

Figure 14. The flux of solute and the calculated mean regression line as function of the applied suction for roots treated with 1×10^{-3} M DNP. Salt and oxygen concentration varied.

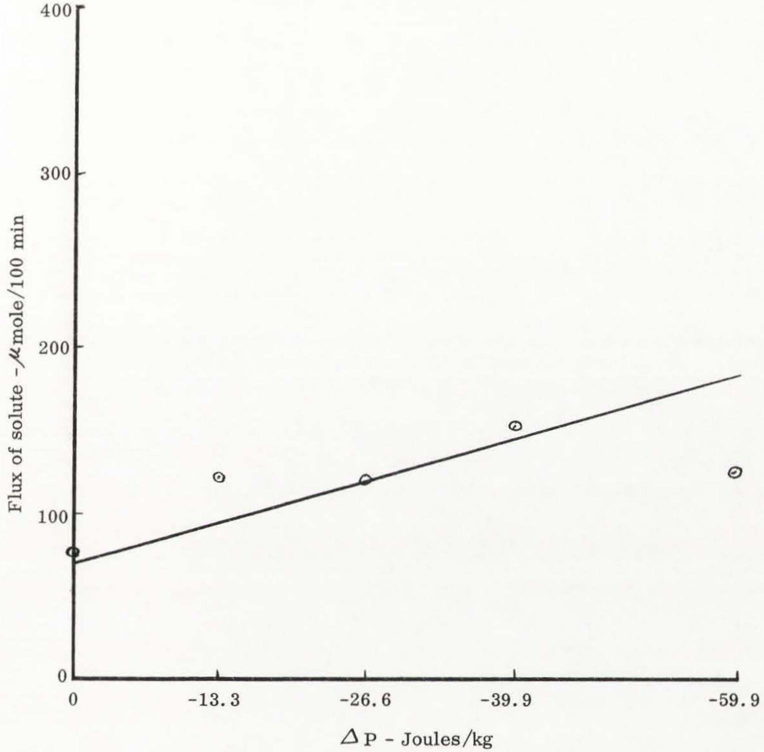

Figure 15. The flux of solute and the calculated mean regression line as function of applied suction for roots treated with 5×10^{-4} M ATP. Salt and oxygen concentration varied.

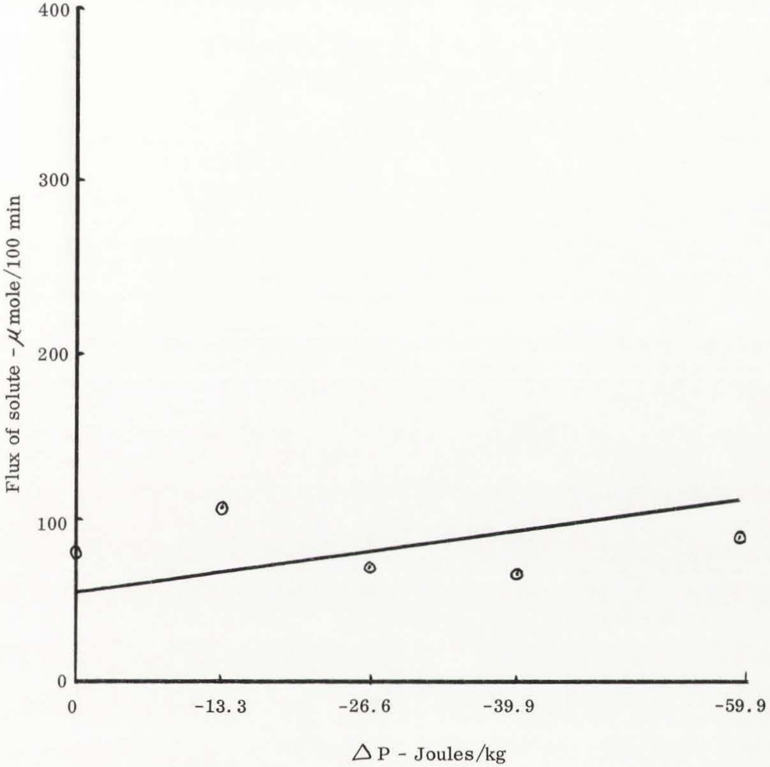

Figure 16. The flux of solute and the calculated mean regression line as function of applied suction for roots treated with 1 mg/liter IAA. Salt and oxygen concentration varied.

case of control indicates that the most important variable determining solute flux is the solute potential.

On the other hand, when roots were treated with DSA, the pressure gradient was the most important variable determining solute flux as can be seen by the value 1.081 for L_{sw} in Table 2b as compared to 0.784 for L_{ss} and 0.418 for L_{so}. As the suction increased the solute flux increased as shown in Figure 12. The failure of the simple regression line to fall above the experimental points indicates that the other two forces probably had significant influence.

The solute flux increased almost directly with suction (Figure 13) for roots treated with NaN_3. This is shown by the data in Table 2b where $L_{sw} = 1.023$ is dominant with respect to $L_{ss} = 0.161$ and $L_{so} = 0.047$.

With DNP treatment the flux of solute in response to water potential has become almost exactly parallel to the flux of water by increasing the suction as may be seen by comparing Figures 8 and 14. In these cases the water transfer coefficient $L_{ww} = 0.991$ (Table 1b) and the solute water interaction coefficient $L_{sw} = 0.943$ (Table 2b) are dominant but the failure of the simple regression to fit the determined points is the influence of relatively large respiration coefficients $L_{wo} = 0.323$ and $L_{so} = 0.334$ respectively.

Adding ATP or IAA to the nutrient solution caused fluctuation in the solute flux with suction that were similar to those in the water flux vs suction up to the level of -39.99 joules/kg as can be seen by comparing Figures 9 and 15 and 10 and 16. This correspondence is somewhat unexpected in view of the wide variation in coefficients as may be shown by comparing Tables 1b and 2b.

Oxygen fluxes (or respiration rates) as a function of suction are presented in Figures 17-19. The flux of oxygen for increasing suction showed an initial decrease followed by an increase, with a minimum at -26.66 joules/kg suction for control, and ATP treatment, and at -13.33 joules/kg suction for DSA and IAA treatments as shown in Figures 17 and 19. The simple regression line indicates that for the control treatment the suction was not the only important variable; the value of the coefficients L_{ow}, L_{os} and L_{oo} (Table 3b) suggests that the other two forces have about the same effect as suction. Respiratory inhibitors, NaN_3 and DNP, showed a decrease in respiration as the suction increased (Figure 18).

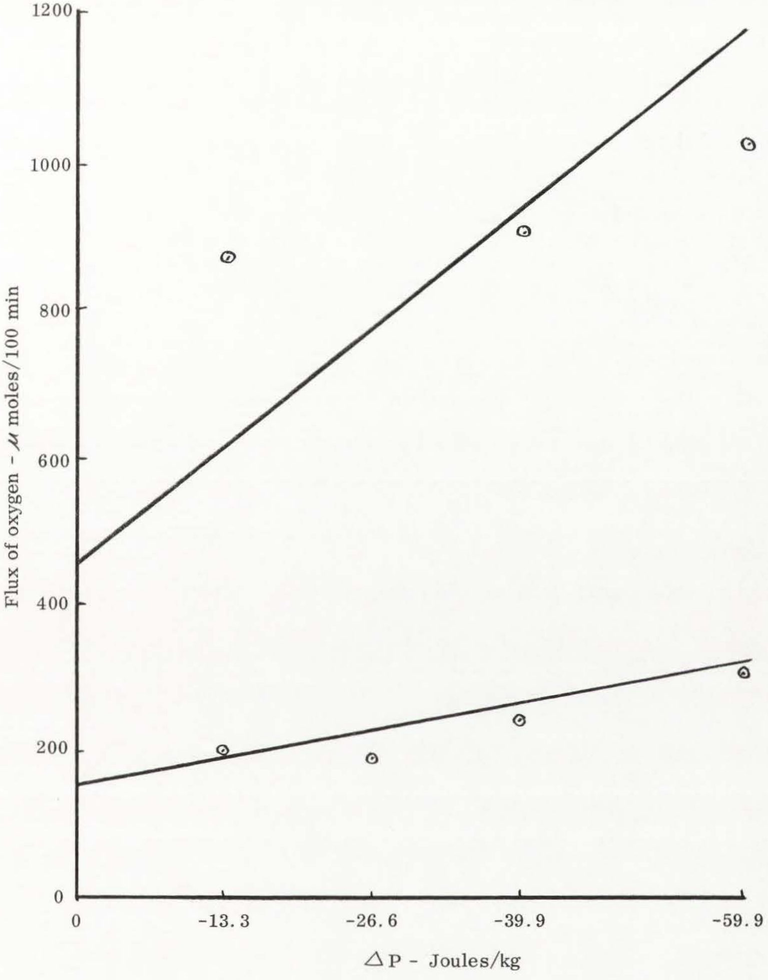

Figure 17. The flux of oxygen and the calculated regression lines as function of applied suction for control and roots treated with DSA. Salt and oxygen concentrations varied.

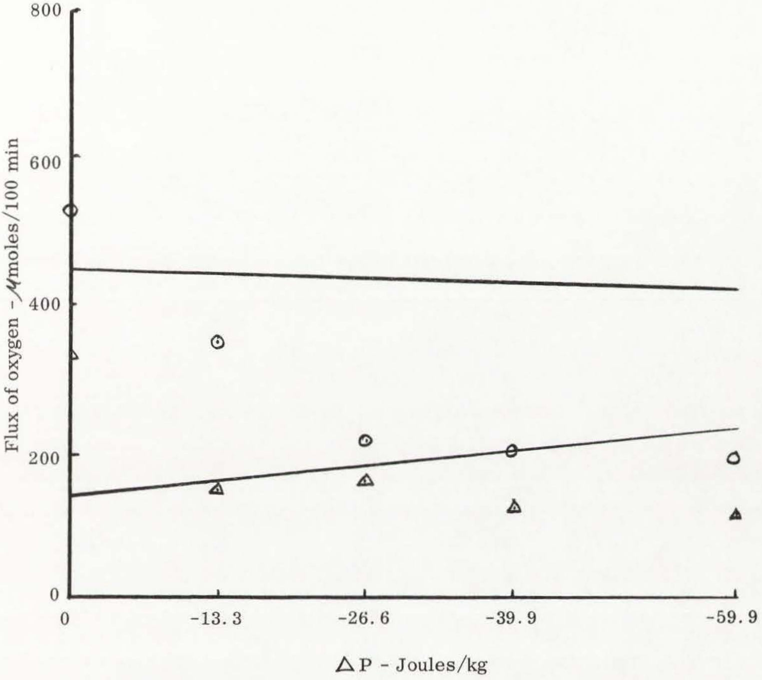

Figure 18. The flux of oxygen and the calculated regression lines as function of applied suction for roots treated with NaN_3 and DNP. Salt and oxygen concentrations varied.

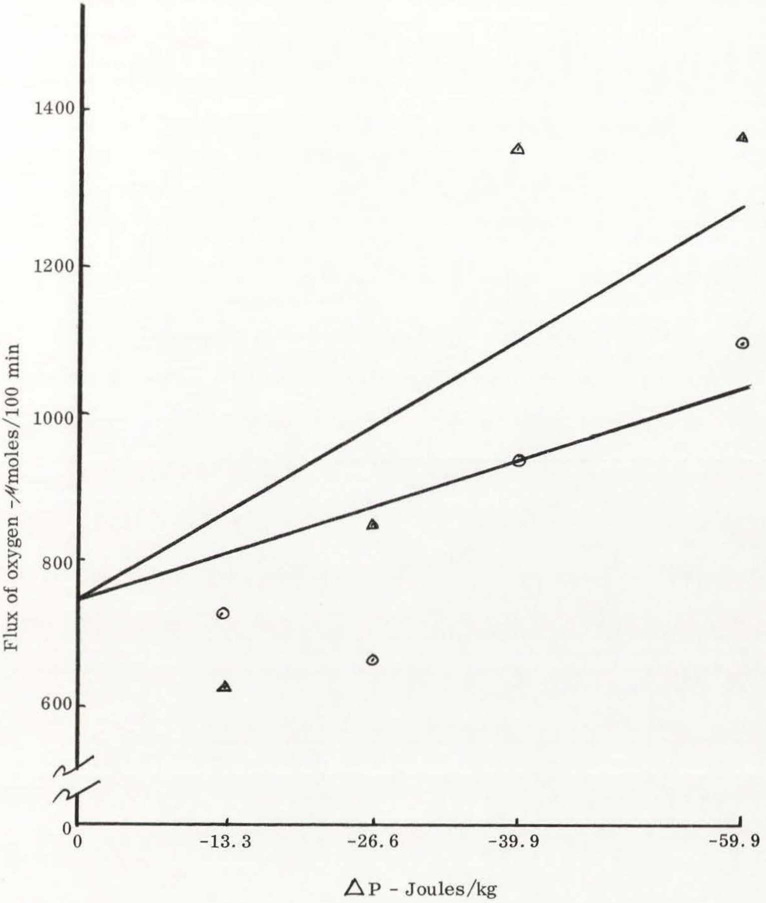

Figure 19. The flux of oxygen and the calculated regression lines as function of applied suction for roots treated with ATP and IAA. Salt and oxygen concentrations varied.

DISCUSSION

Water Flux

The flux of water through sunflower root systems was increased by increasing suction for all the treatments. As was expected under control conditions, the increase in flux was not linearly related to suction though the pressure potential gradient appeared to be the most important force in water movement through the root as indicated by the dominance of the L_{ww} (β) coefficients (Table 1b) over both the L_{ws} and L_{wo} coefficients. The phenomenological coefficient for respiration L_{wo} as shown in Table 1a is about a hundred times as great as the solute potential gradient. The standard regression coefficient, which takes into account both the magnitude of the coefficient and the gradient, however, indicates that these two forces have about equal effect, or perhaps the oxygen potential has a slightly higher effect on the flux of water through control plants.

Adding decenylsuccinic acid (DSA) to the ambient solution proved that permeability of the membrane is the most important factor. DSA increased the permeability of the root system to water as shown by the increase of L_{ww} (Table 1a) from -7.50 for control to -16.44 for DSA. However, DNP was even more effective $L_{ww} = 17.00$ and NaN_3 had almost as much effect ($L_{ww} = 14.50$) while both ATP and IAA decrease the hydraulic transfer coefficient. Taking all the three forces into account, the multiple correlation coefficient (R) for DSA treatment showed that the relation between water flux and pressure difference, solute concentration difference, and oxygen consumption rate is highly significant for straight line with R = 0.918, compared by R = 0.691 for control treatment when the same three forces were taken into account. It is evident from the comparison of the standard partial regression coefficient for DSA treatment that the respirational force contributes about four times as much as the solute force, but somewhat less than one-third as much as a pressure difference to the flow of water through the root system.

In this study, respiratory inhibitors both increased the hydraulic conductivity of the root system as shown by the larger values of L_{ww} (Table 1a). In the case of sodium azide (NaN_3), it was found that the flux of water increased according to the linear equation (4) with R = 0.977. The standard partial regression (β) coefficients suggest that the permeability factor was the most important ($L_{ww} = 0.847$) followed by the solute potential ($L_{ws} = 0.279$), and the oxygen potential gradient ($L_{wo} = 0.022$) has very little effect. This result might be attributed to injury of the root by 1×10^{-3} M NaN_3 + buffer treatment; the decrease in rate of respiration as shown by decreased oxygen flux and the increase in solute flux (Appendix, Table 7) with suction confirm this suggestion.

It is apparent from Figure 8 that in roots treated by 1×10^{-3} M DNP + buffer (pH = 4.5), the flux of water increased with suction but the simple relation was not linear. The inclusion of both solute gradients and respiration effects were not enough to satisfactorily linearize the relation as shown by the unsatisfactory multiple regression coefficient, R = 0.741. In this case the pressure potential gradient was the most important (Table 1b, $L_{ww} = 0.991$). It had about three times the effect of oxygen potential gradient ($L_{wo} = 0.323$) which had about twice the effect of the solute potential ($L_{ws} = 0.115$). Here all three forces have an influence on the water flux while the oxygen potential was ruled out in case of NaN_3. However, in both cases the solute flux increased vigorously as the suction increased (Appendix Table 7 and 8), which indicates that the roots might have been injured by these two treatments. when compared to the decrease in solute flux with increasing suction for control (Table 5) and the slight increase with increasing suction for DSA, ATP, and IAA treatments (Appendix Tables 6, 9, 10 respectively). This will be discussed further in the section of solute flux.

From Figure 2, it is shown that the flux of water for roots treated with adenosine triphosphate (ATP) had a pattern similar to those treated with indole acetic acid (IAA). In both cases, it was somewhat similar to the control, with the difference that for ATP the flux increased for the first level of applied suction and then was constant for the next two levels and increased again at the highest level while the control was more nearly linear throughout (Figure 9). This may be attributed to the effect of the phosphorylation process on the uptake of solute and confirmed by the standard partial regression (β) coefficient where the importance of the pressure gradient was less than twice as much as the solute potential gradient (Table 1b).

Also, for ATP, the (β) coefficient indicated that the oxygen potential gradient effect on water flux was negligible, though from Appendix Table 9 we can see that the respiration rate of roots under this treatment increased as the pressure gradient increased.

IAA is a well known respiratory stimulator (Kelly, 1947; Kazlowski, 1964). The data in Figure 10 show that the flux increased for the first increment in pressure difference and then decreased at the level of -26.66 joules/kg followed by successive increases for the next two levels. This might be attributed to the effect of IAA on the plasticity of the membrane which could cause water to accumulate into the cells at the particular pressure value; then as higher suctions were applied, the cells would release this water, and it would move toward the xylem. This might explain why the flux of water varied with different pressure gradients until the pressure gradient was more than the increase in plasticity.

For the indole acetic acid (IAA) treatment, the standard partial regression coefficients (Table 1b) indicate that the pressure potential gradient effect was almost equal to the oxygen potential gradient. This would be in accord with the foregoing explanation of the effect of respiration on the plasticity of the cell membranes. This also confirms the conclusion of Hacket and Thimann (1953) and Ketellaper (1953) that the effect of auxin on water uptake is not caused by the formation of osmotically active substances in the cell.

From Table 1a it is evident that ATP and IAA decreased the permeability of the root system to about one-half the value it had in the control. Also, considering all the three forces, the multiple correlation coefficient R is about the same for these two treatments and is not as significant as that for the DSA treatment. This indicates that the linear equations (4) are not suitable for application to most systems treated with these materials. This comparison was made because the respiration rate pattern for the DSA treatments (Figure 4) was approximately the same as for ATP and IAA treatments, and falls between them and the control. This is not in agreement with the ideas of Newman and Kramer (1966) who suggested that DSA may function as a metabolic inhibitor because of the similiarity between the effects of sodium azide (NaN_3) and 10^{-4} M DSA. It is true that if one compares the curve for water flux of the roots treated with DSA and those treated with NaN_3 that he might conclude that DSA is a metabolic inhibitor; but from measurements of respiration (Figure 4) and the results of solute potential (in other words the concentration of the exudate) and how it varies with the change in pressure gradient (Table 6) compared to the results of solute potential of ATP and IAA (Tables 9 and 10), one cannot conclude that DSA is a metabolic inhibitor. Our results are in agreement with Kuiper (1964) who suggested that 10^{-3} M DSA caused an increase in the permeability of bean roots without harming the tissue.

From this discussion it may be concluded that the nonlinearity of the relationship between water flux and pressure gradient is mainly because solute concentration gradients and respiration take place in plants treated with DSA and NaN_3, whereas this would not account for the nonlinearity in the case of control plants or those treated with DNP, ATP or IAA. Also, it can be concluded that a respiration stimulator decreases the pearmeability of the membrane from the results of the ATP and IAA treatments. If the respiration has an effect on the uptake of water it should be by the effect of the respirational energy coupled with the flux of water itself as shown by DSA, DNP, and IAA. Results of DSA treatment indicate that the nonlinearity is due almost exclusively to respiration since the effect of salt was negligible, and the combined linear equation fits the data with a high correlation. These results might answer Barr's (1966) question about this subject. He found that the nutrient solutions had lower water potentials than the leaves even though the plants were measurably transpiring. He stated that it would be necessary to examine further the nature of root pressure before deciding whether the inverted gradients reported are due to a truly active transport of water or to coupling of water movement perhaps with ion movement. These results, however, are opposed to the suggestion of Lopushinsky (1965) and Ordin and Kramer (1956) that the effect of respiratory inhibitor is on the permeability of the membranes of the root.

Also, it can be concluded that the solute potential gradient has a small but important effect on the flux of water through roots under pressure gradient differences, particularly in roots treated with NaN_3, ATP and IAA.

Solute Flux

Changes in the flux of solute through the root with a change in pressure gradient were often quite different, for the various treatments, than were the changes in the flux of water.

In the control roots, the flux of solute decreased as the pressure gradient increased (Figure 3 and Appendix Table 5). This could be associated with the storage of nutrients in the roots, such that stored nutrients appeared in the first application of suction. This is in agreement with the results found by Jackson and Weatherely (1962a) in which application of pressure of 2 atm caused approximately a fourfold increase in potassium outflow, independent of the presence of potassium in the external medium. This outflow was attributed to ions already stored in the root tissue. Results on controls (Appendix Table 5) also indicate that there is no passive movement of solute dissolved in the water and passing through free space in sunflower roots since there seems to be a negative correlation between water flux and solute flux. This result seems to be at variance with those obtained by Hylmo (1955) with peas and by Brower (1954) with broad beans, and Jensen (1962a) with nitrate in tomato roots; but they are in agreement with the results of Honert (1955) with maize plants. In all of the roots of the control treatment the solute potential difference decreased as the pressure gradient increased and always had a negative sign at the highest level of pressure difference. The negative sign arises because the concentration in the exudate was less than that in the bathing solution. This suggests a sieve effect of the membrane on the solute in the control root systems. Figure 11 and Table 2b show that the pressure gradient was not the important factor in solute flux, but the solute potential gradient was the most important factor. However, the multiple regression coefficient ($R = 0.537$) proved that the linear model equation (4) is a rather poor model for indicating solute movement thus suggesting that either factors other than water flux, solute gradient or respiration are involved, or else these factors act in a complicated non linear way.

Roots treated with DSA . showed an increase in the flux of solute but a decrease in solute potential difference as the pressure gradient was increased (Figure 3 and Appendix Table 6). However, in this experiment, the exudate concentration was always higher than the concentration of the ambient solution even at the highest pressure gradient. This can be attributed to the effect of DSA on the permeability of the membrane, while the root is still alive. The standard partial regression coefficients indicate that the most important force was the pressure gradient followed by the solute potential gradient and the oxygen potential gradient. The multiple correlation coefficient proved the existance of a highly significant relationship between solute flux and the forces, thus suggesting that the linear model equation (4) was adequate to explain the solute transfer in root systems treated in this manner. Thus the non linearity of the control plants is somehow related to the action of DSA.

The multiple correlation coefficient for roots treated with sodium azide proved a highly significant relation between solute flux and the forces, but this fact does not mean much because as mentioned previously this treatment could have injured the root. Appendix Table 7 and Figure 3 show evidence that the solute flux increased linearly as a function of the pressure gradient. Also, the concentration of the exudate increased continuously, while respiration dropped down which indicates again the injury of the root. It was fortunate that this happened to show that the treatment of DSA did not cause such an injury to the root.

The solute flux behaved exactly as water flux for the roots treated with DNP. As the pressure gradient increased, the flux increased but not linearly. The regression line in Figure 14 is parallel to the experimental graph. The presence of the first half of the graph above the regression line and the second half under it may be because of two reasons: (a) the decrease in the amount present in the storage, (b) and when the DNP was absorbed inside the tissue, it caused more internal cells to release their stored solids. It has been found that DNP uncouples phosphorylation (Beevers, 1960), but in these studies the accumulation of the nutrients in the tissue was measured without applying suction. It is also possible that the root was injured by the DNP treatment, and the ruptured membrane allowed the solute to pass through. This might explain the observation of faint yellow color in the exudate (DNP solution is yellow in color) at -26.66 joules/kg pressure gradient. The yellowish color in the exudate increased at higher pressure differences. This supports the observation of Barber and Koontz (1963) who found DNP in the shoots of barley seedlings and reported that longer exposure to DNP resulted in increased accumulation of calcium in the shoots.

Adding ATP to the culture solution caused an increase in the flux of solute with pressure difference. Even though the solute potential difference decreased (Table 9), it was never negative as occurred in the control. The (β) coefficients indicate that the pressure potential difference and the solute potential difference exerted approximately equal influence.

This might be because the added ATP moved into the tissue and caused an increase in the uptake of the solute. This evidence confirmed the work of Hodges and Hanson (1965) that the uptake of calcium by maize mitochondria increased by adding ATP to the solution. At the same time the results are in conflict with Mengel's (1963) statement that addition of ATP to the uptake solution decreased the uptake of Rb^+. It may be concluded that ATP is required for uptake of nutrients.

For roots treated with IAA the most important force that caused the solute flux was the oxygen potential gradient (Table 2b). From Figure 16 it is evident that as the pressure difference increased, the flux of solute first increased and later decreased. The pattern of the curve is similar to that for the control treatment. This treatment compared with the treatment of ATP suggests that ATP acts as a carrier for the uptake of solute while IAA simply influences the plasticity of the membrane and causes an increase in volume of the cell by the uptake of water. These results are in agreement with Hackett and Thimann (1952), and Ketellaper (1953) who found that the increase water uptake (due to IAA treatment) was accompanied by a decrease in the osmotic potential of the cell sap.

Flux of Oxygen (The Respiration Rate)

Most of the oxygen effects have been discussed in the preceeding two sections, but there are some others that need to be clarified.

From the results of J_o as function of the forces (Table 3a, 3b) it may be observed that for control, DSA, and respiratory stimulators, as the pressure gradient increased the uptake of oxygen increased, while the opposite occurred for respiratory inhibitors (Figure 4).

In this study the correlation between the flux of oxygen and the three forces was highly significant for the control and all the treatments as indicated by the large multiple correlation coefficient (Table 3a).

For the control root systems all the three forces were equally important. The importance of the pressure gradient is explained by the fact that oxygen must enter all living cells in a dissolved state (Giese, 1962); hence it moves with water. Also, the solute uptake requires oxygen. Finally oxygen would move along an oxygen potential difference; this might explain the equality between the effect of the three forces on oxygen flux.

Adding DSA ., as mentioned before, did not kill the root tissues. The increase in oxygen uptake by increasing the pressure gradient is the result of exposing more oxygen to the inner cells, and from Table 3b, it is evident that the most important factor is the pressure gradient followed by the solute potential gradient, where the oxygen potential gradient had quite a small effect.

Respiratory inhibitors caused inverse relation between the flux of oxygen and the pressure gradient difference. For both DNP and NaN_3 the increase in pressure gradient did not increase oxygen uptake appreciably because in addition to exposing the oxygen to the cells inside the tissue, the inhibitor was also exposed at the same time. The inhibition of oxygen absorption in the growth zone of lupine roots by adding NaN_3 had been observed by Potapove and Salamatove (1964) who found that NaN_3 inhibited oxygen absorption

Oxygen uptake increased as a function of pressure gradient with the addition of ATP and IAA. The increase by adding IAA was more than by ATP because IAA is a respiratory stimulator. Because the permeability of the membrane did not increase, with these treatments, it appears that the most important factor in oxygen flux is the oxygen potential gradient (Table 3b).

The Phenomenological Coefficients

From Table 1a one can see that calculated values for the permeability coefficient L_{ww} are all negative. This is because of the direction of the pressure gradient (suction was applied on the stump). L_{ww} values indicate the change in the permeability of the membranes with different treatments. It is recognized that the respiratory inhibitors have increased the permeability of the membranes but this could be caused by injury to the tissues as discussed before. The treatment with ATP and IAA decreased the permeability of the root to water, though the respiration increased. This excludes the idea that the respiration effect on water movement is by changing the permeability.

The direct transfer coefficients L_{ss} and L_{oo} (Tables 2a, 3a) are also consistent in the sign for all treatments. The positive sign of L_{ss} indicates that the flow of solute is taking place against concentration gradient, which is true for active uptake of solute, whereas the negative sign of L_{oo} indicates the flow of oxygen in the direction of low concentration of oxygen.

The values for L_{wo}, L_{ws}, L_{so} are inconsistent in sign for different treatments. This might be because of the flow of solute from storage inside the root and the effect of the treatment on the release of solute from storage and because of the effect of different treatments by enhancing or reducing respiration. By the same reasoning we find the ratios $L_{ws}:L_{sw}$, $L_{wo}:L_{ow}$, and $L_{so}:L_{os}$ (Table 4) are contrary to the Onsager theory.

CONCLUSIONS

1. The nonlinearity of the flux of water through the root systems of sunflower is due to causes associated with the membrane (mainly the permeability of the membrane).

2. There exists a respiration linked force that causes water movement through the roots of sunflower.

3. Respiratory inhibitors increase while respiratory stimulators decrease the permeability of the membrane.

4. The uptake of water due to solute potential difference, under transpiring condition, is small but important.

5. The uptake of solute in normal root systems is by an active process from solution to the xylem; it then moves passively to the leaves.

6. An increase in passive water uptake might cause an increase of respiration of the root tissue by exposing more oxygen to the internal part of the root tissue.

7. Decenylsuccinic acid does not appear to be a metabolic inhibitor for sunflower roots.

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APPENDICIES

Appendix I

Experimental Results

i. $\Delta\mu_w = \mu_w^1 - \mu_w^2 = \overline{V}_w (P_1 - P_2)$

$$= (1)\ (66 - 76) = 10 \text{ cm Hg}$$

$$\Delta\mu_w = (-10 \text{ cm Hg})\ \left(\frac{101.317 \text{ joule/kg}}{76 \text{ cm Hg}}\right) = 13.33 \text{ joule/kg}$$

ii. Sample calculation of $\Delta\mu_s$:

$$\Delta\mu_s = R\ T \ln \frac{C_s^1}{C_s^2}$$

For the concentration of exudate $C_s^1 = 8.4$ mmole/liter and

the concentration of ambient solution $C_s^2 = 16.9$ mole/liter

at room temperature T = 298 K,

$$\Delta\mu_s = (8.3144 \text{ joules}/^{\circ}\text{K mole})\ (298^{\circ}\text{K})\ (2.303)\ (\log 16.9 - \log 8.4)$$

$$= (5706.12)\ (1.2279 - 0.92428) \text{ joules/mole}$$

$$\Delta\mu_s = 1732.3 \text{ joules/mole} = 23236 \text{ joules/kg*}$$

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*In converting from joule/mole to joule/kg, the equivalent weight of KNO_3 was used. The exact composition of the exudate was not determined; therefore, an average equivalent weight was chosen arbitrarily. Since the calibration curve of the vapor pressure osmometer was obtained with KNO_3, this was a convenient and also a reasonable choice.

iii. Sample calculation of $\Delta\mu_o$:

The respiration rate at 0.0 suction for root #28 (control) was 0.515 mg CO_3/min. The specific respiration rate (for 130.5 g wet weight) mole O_2/g hr $= \frac{(0.515)(60)}{(44)(130.5)(1000)}$

$= 5.381 \times 10^{-6}$ mole O_2/g hr

$= (5.381 \times 10^{-6})\ (22.414)\ (10^{6})$ liter O_2/g hr

$= 120.6$ liter O_2/g hr

The specific rate of 120.6 liters/g wet weight hr is close to what Goddard and Bonner (1960) have presented. They stated that for the respiratory rate of 100 liter O_2/g wet weight hr the limiting thickness at which p_{O_2} just falls to zero at the center is 0.507 cm. Using Warburg's equation they reported:

$$H^2 = \frac{8D}{a}\ (C_o - C_x)$$

or for atmospheric conditions where C_x is zero in the center

$$H^2 = K\ C_o$$

and p_{O_2} or $C_o = 0.208$ and tissue thickness is 0.507 cm. Thus,

$$K = \frac{(0.507)^2}{0.208} \quad - 1.2067$$

Assuming the average thickness of the sunflower root to be about 2 mm (0.2 cm), we can calculate the oxygen concentration at the center of the root. When

$C_o = 0.208$ atm

$$0.04 \text{ cm}^2 = (1.2067)\,(0.208 - C_x)$$

$$C_x = \frac{0.211}{1.2067} = 0.175.$$

At the end of an experimental run, the oxygen concentration above the ambient solution falls down because of respiration. This can be calculated as follows:

Total volume of air in the system = 1400 ml

Oxygen concentration of the air = 0.208

Volume of O_2 at the beginning of a run = 1400 x 0.208 = 291.2 ml

Volume of O_2 consumed at a run = 19.78 ml

Volume of O_2 at the end of the run = 291.2 - 19.78 = 271.42 ml.

Thus, the oxygen concentration of the air at the end of the run is 0.194, and

$$0.04 \text{ cm}^2 = (1.2067)\,(0.194 - C_x)$$

$$C_x = \frac{0.194}{1.2067} = 0.161$$

The solubility of oxygen in water can be calculated from Henry's law (Moore, 1963)

$$x_B = p_B/K_B$$

where: x_B is the mole fraction

p_B is the partial pressure of the gas

K_B is Henry's law constant (for O_2 at 25 C, K is 4.58×10^4).

For $p_{O_2} = 0.208$ atm, and 1.0 liter H_2O

$$x_{O_2} = \frac{p_{O_2}}{K_{O_2}} = \frac{0.208}{4.58 \times 10^4} = 4.54 \times 10^{-6}$$

$$n_{O_2} = (55.5)(4.54 \times 10^{-6}) = 2.525 \times 10^{-4} \text{ mole}$$

and $C_o^2 = 2.525 \times 10^{-4}$ mole/liter.

For $p_{O_2} = 0.175$ atm, and 1.0 liter H_2O

$$n_{O_2} = 2.124 \times 10^{-4} \text{ mole}$$

and $C_o^1 = 2.124 \times 10^{-4}$ mole/liter.

So at the beginning of a run:

$$\Delta \mu_o = RT \frac{C_o^1}{C_o^2}$$

$$\Delta \mu_o = (8.3144 \text{ joule/mole})(2.303)(\log 2.124 \times 10^{-4} - \log 2.525)$$

$$\Delta \mu_o = (5706.12)(-0.07511) = -428.58 \text{ joule/mole}$$

$$= -26788 \text{ joule/kg.}$$

At the end of a run:

$$p_{O_2}^{ext} = 0.194 \text{ atm}, \ C_o^2 = 2.367 \times 10^{-4} \text{ mole/liter}$$

$$p_{O_2}^{int} = 0.161 \text{ atm}, \ C_o^1 = 1.954 \times 10^{-4} \text{ mole/liter}$$

and $\Delta \mu_o = -28914$ joule/kg.

Thus the average $\Delta \mu_o = -27851$ joule/kg.

Table 5. The fluxes of water J_w, solute J_s, and oxygen J_o, due to forces of water potential $\Delta\mu_w$, solute potential $\Delta\mu_s$, and oxygen potential $\Delta\mu_o$, for control.

J_w mole/100 min x 10^5	$\Delta\mu_w$ Joule/kg	$\Delta\mu_s$ Joule/kg	$\Delta\mu_o$ Joule/kg	J_s mole/ 100 min	J_o mole/ 100 min
3.833	00.00	23236	-27851	116	1271
5.911	-13.33	20614	-27186	224	1057
6.539	-26.66	21208	-27186	187	794
7.305	-39.99	9260	-26998	146	714
10.039	-59.99	-15942	-27266	93	915
1.217	00.00	30775	-27526	70	852
1.511	-13.33	25517	-27112	49	705
2.194	-26.66	14258	-27186	51	754
2.44	-39.99	7095	-27112	46	767
4.655	-59.99	-6062	-27112	59	861
1.878	00.00	38934	-27357	220	995
2.983	-13.33	33477	-27357	123	870
3.872	-26.66	29163	-27357	140	964
4.622	-39.99	17213	-27357	117	1227
7.400	-59.99	-803	-27357	109	1285

Table 6. The fluxes of water J_w, solute J_s, and oxygen J_o, due to forces of water potential $\Delta\mu_w$, solute potential $\Delta\mu_s$, and oxygen potential $\Delta\mu_o$, for roots treated with decenylsuccinic acid treatment.

J_w mole/100 min x 10^5	$\Delta\mu_w$ Joule/kg	$\Delta\mu_s$ Joule/kg	$\Delta\mu_o$ Joule/kg	J_s mole/ 100 min	J_o mole/ 100 min
0.967	00.00	18223	-27039	27	134
2.278	-13.33	4530	-26927	42	223
3.228	-26.66	4530	-26927	59	192
4.233	-39.99	2166	-26998	72	214
6.222	-59.99	1531	-27039	95	281
1.272	00.00	57501	-27039	115	299
3.311	-13.33	31119	-26857	135	214
5.744	-26.66	20312	-26927	170	205
8.233	-39.99	18009	-26927	226	250
12.022	-59.99	10485	-26857	264	277
1.022	00.00	49955	-26998	73	321
3.283	-13.33	24139	-26927	109	214
4.689	-26.66	25379	-26998	161	205
6.778	-39.99	30232	-26927	270	277
10.077	-59.99	19119	-26998	256	393
0.644	00.00	25731	-26998	22	138
3.339	-13.33	21116	-26857	101	143
6.322	-26.66	10210	-26857	138	161
9.972	-39.99	3873	-26857	184	227
16.716	-59.99	-10960	-26857	192	227

Table 7. The fluxes of water J_w, solute J_s, and oxygen J_o, due to forces of water potential $\Delta\mu_w$, solute potential $\Delta\mu_s$, and oxygen potential $\Delta\mu_o$, for roots treated with sodium azide treatment.

J_w mole/100 min x 10^5	$\Delta\mu_w$ Joule/kg	$\Delta\mu_s$ Joule/kg	$\Delta\mu_o$ Joule/kg	J_s mole/ 100 min	J_o mole/ 100 min
1.505	00.00	29130	-27266	61	839
4.489	-13.33	45095	-27186	295	393
6.200	-26.66	41941	-26998	371	254
8.005	-39.99	44077	-26857	509	165
12.550	-59.99	41436	-26857	738	210
1.650	00.00	42829	-27112	150	736
4.172	-13.33	39446	-27112	232	660
4.211	-26.66	52052	-26927	340	281
6.478	-39.99	48133	-26927	463	245
11.622	-59.99	30453	-26857	491	205
1.211	00.00	49442	-27039	91	294
2.455	-13.33	59139	-26998	246	187
3.467	-26.66	58840	-26857	344	138
4.855	-39.99	58840	-26857	483	178
11.116	-59.99	38130	-26857	592	196
3.267	00.00	35558	-27186	161	299
4.983	-13.33	39875	-27857	280	187
5.772	-26.66	43219	-27857	359	183
7.911	-39.99	37219	-27857	410	214
12.833	-59.99	17473	-27857	527	111

Table 8. The fluxes of water J_w, solute J_s, and oxygen J_o, due to forces of water potential $\Delta \psi_w$, solute potential $\Delta \psi_s$, and oxygen potential $\Delta \psi_o$, for roots treated with 2,4 dinitrophenol

J_w mole/100 min x 10^5	$\Delta \psi_w$ Joule/kg	$\Delta \psi_s$ Joule/kg	$\Delta \psi_o$ Joule/kg	J_s mole/ 100 min	J_o mole/ 100 min
4.867	00.00	28418	-26998	194	272
5.722	-13.33	22685	-26857	191	85
5.900	-26.66	37564	-26857	310	111
4.372	-39.99	33813	-26857	204	134
8.650	-59.99	17213	-26857	470	111
4.155	00.00	39875	-27112	233	651
7.105	-13.33	38574	-26998	383	268
9.644	-26.66	31977	-26857	427	232
12.316	-39.99	31839	-26857	543	134
16.211	-59.99	32114	-26857	720	111
2.289	00.00	45003	-26998	150	129
3.611	-13.33	43311	-26857	224	103
4.011	-26.66	42339	-26788	242	94
5.350	-39.99	32780	-26857	242	85
6.144	-59.99	25425	-26788	223	62
2.072	00.00	42140	-26998	124	317
4.772	-13.33	39553	-26857	265	174
6.428	-26.66	35803	-26857	319	232
8.416	-39.99	36638	-26857	428	187
12.844	-59.99	25425	-26857	467	169

Table 9. The fluxes of water J_w, solute J_s, and oxygen J_o, due to forces of water potential $\Delta\psi_w$, solute potential $\Delta\psi_s$, oxygen potential $\Delta\psi_o$ for roots treated with Adinosine triphosphate

J_w mole/100 min x 10^5	$\Delta\psi_w$ Joule/kg	$\Delta\psi_s$ Joule/kg	$\Delta\psi_o$ Joule/kg	J_s mole/ 100 min	J_o mole/ 100 min
1.650	00.00	25379	-27357	57	897
4.244	-13.33	25900	-27186	150	959
3.472	-26.66	27407	-27039	127	691
4.128	-39.99	24859	-27112	139	1004
6.233	-59.99	19080	-27112	177	928
1.561	00.00	52817	-27357	122	946
2.478	-13.33	45799	-27449	157	910
2.850	-26.66	44429	-27526	173	986
2.922	-39.99	40281	-27604	299	1383
3.805	-59.99	26244	-27851	134	1704
0.805	00.00	41903	-27112	45	567
3.133	-13.33	23228	-27039	101	473
3.911	-26.66	19700	-27112	113	562
3.589	-39.99	19907	-27357	104	830
4.461	-59.99	12850	-27526	105	1218
0.989	00.00	54310	-27039	81	495
1.205	-13.33	46074	-27039	77	549
1.405	-26.66	28532	-27266	53	410
2.094	-39.99	19287	-27039	60	504
4.561	-59.99	1485	-26998	75	522

Table 10. The fluxes of water J_w, solute J_s, and oxygen J_o, due to forces of water potential $\Delta\mu_w$, solute potential $\Delta\mu_s$, oxygen potential $\Delta\mu_o$ for roots treated with Indole acetic acid

J_w mole/100 min x 10^5	$\Delta\mu_w$ Joule/kg	$\Delta\mu_s$ Joule/kg	$\Delta\mu_o$ Joule/kg	J_s mole/ 100 min	J_o mole/ 100 min
o.778	0000	47904	-27112	49	567
1.283	-13.33	42646	-27039	70	522
1.544	-26.66	35306	-27039	68	491
1.889	-39.99	36216	-27186	85	950
2.994	-59.99	25149	-26998	96	535
2.167	0000	39661	-27266	108	821
2.505	-13.33	43189	-27186	104	714
1.450	-26.66	39783	-27112	72	1191
1.894	-39.99	9261	-27605	38	1753
3.833	-59.99	3383	-27851	64	2191

Appendix II

The following propositions were defined in open public meeting:

A. The uptake of water by plants (under normal conditions) due to salt concentration is negligible.

B. Knowledge of the interaction between simultaneous movement of solute, heat and water can be directly applied to reclamation of saline soils.

C. It is possible to produce fruits commercially from trees grown in the Sinai sandy soil of Egypt.

D. U. S. Universities can unify standards about the rights and responsibilities of students on their campuses.