UNIVERSITY OF MANITOBA

THE EFFECT OF WATER STRESS ON THE PHOTOSYNTHESIS OF THE POTATO (SOLANUM TUBEROSUM L.)

by

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ABSTRACT

EFFECT OF WATER STRESS ON THE PHOTOSYNTHESIS OF THE POTATO

Leaf water potentials, soil water potentials, and net photosynthesis rates were determined on potato plants grown in containers in growth chambers under two light intensities. Measurements were taken as the soil moisture decreased from field capacity to the wilting point. Leaf water potentials were measured by the thermocouple psychrometer technique. Soil water potentials were determined from the water retention curve and from thermocouple psychrometers. The water retention curve gave a better estimate of soil water potential than the thermocouple psychrometers. Net photosynthesis rates were determined by use of an infrared carbon dioxide gas analyzer.

Net photosynthesis rate was severely reduced by increasing water stress. Net photosynthesis rate began to decline as soon as soil moisture content dropped below field capacity. Rates at field capacity or 0 bars soil water potential was 10 mg CO_2 hr^{-1} dm^{-2} for the low light intensity and 17 mg CO_2 hr^{-1} dm^{-2} for the high light intensity. Leaf water potentials were -3 to -4 bars at this level. At leaf water potentials of -8 to -10 bars and soil water potentials of -7.5 to -9 bars net photosynthesis

had essentially stopped. These results are similar to those obtained by Boyer (1970 b) for soybean, sunflower and corn except potato was far more sensitive to water stress. The sharp reduction in net photosynthesis rate as soon as the plant is subjected to water stress explains why the potato responds so well to irrigation.

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INTRODUCTION

Plant growth is limited by water stress. Although this limitation has been observed since man began irrigating crops in ancient Egypt, the effect of water stress on plant growth is still not completely understood. Because water affects many of the processes associated with photosynthesis, and since net photosynthesis rate is a measure of dry matter production, water stress would be expected to have a great influence on growth.

The potato is the most important commercial vegetable crop in Manitoba, the 1970 acreage being approximately 33,000 acres. Because it is a root crop and because of the increase in mechanized harvesting the potato is usually grown on coarse textured soils. These soils have a low moisture holding capacity and therefore water stresses develop very quickly. Hence in Manitoba, potatoes frequently grow under conditions of water stress. There is a considerable acreage of coarse textured soils in Manitoba which are suitable for potato production. The acreage of these soils which can be irrigated is increasing through development of new water resevoirs (eg. Shellmouth Dam.)

For this reason potato growers have become interested in irrigation and in the past few years several growers have begun to irrigate their potatoes. In view of these developments and because the potato responds so well to irrigation, this project on the effect of water stress on growth of the potatoes was initiated. It is hoped that the information derived from this project will benefit potato production in Manitoba.

LITERATURE REVIEW

Introduction

Water stress has long been known to affect plant growth and the use of irrigation to overcome this stress and to ensure growth to maturity is well documented (Singh, 1969). The affect of water stress on photosynthesis has also been studied by many workers.

Although much has been learned, the relationship between photosynthesis and water stress is not completely understood. It is the aim of this project to study net photosynthesis rate of potatoes as it is affected by water stress.

Definition of Pertinent Terms

Water Potential

Water potential refers to the energy of water. The total potential (or energy per unit quantity) of water is defined as the mechanical work required to transfer a unit quantity of water from a standard reference state, where potential is taken as zero, to the situation where the potential has the defined value. A pool of pure water at an elevation which can be arbitrarily specified and which experiences a gas pressure of one standard atmosphere has been adopted as this reference state (Rose, 1966). This energy per unit quantity of water in the soil is affected mainly by the moisture content. Other factors affecting water potential are the soil water's position in the earth's gravitational field, the gas pressure acting on it and its chemical constitution. Spatial differences in energy per unit quantity of soil water are the cause of movement of such moisture from regions of higher specific energy to regions of low specific energy. Because the specific energy of water in unsaturated soil and in plant tissue is lower than that of a free water surface, water potential is usually a negative number.

Photosynthesis

Photosynthesis as defined by Barnhart (1947) is "a process of green plants by which carbohydrates are formed from carbon dioxide and water under the influence of light." Arditti and Dunn (1968) define photosynthesis as "the utilization of radiant energy to synthesize chemical compounds." In plant physiology and biochemistry, photosynthesis classically refers to the synthesis of carbohydrates from carbon dioxide and water in the presence of light according to the equation:

$$6CO_2 + 6H_2O \xrightarrow[\text{Chlorophyll}]{\text{light}} C_6H_{12}O_6 + 6O_2 \text{ -------------} (1)$$

Growth is determined by net photosynthesis rate. For purposes of this thesis net photosynthesis rate will be regarded as net assimilation of carbon dioxide.

Plant water stress

Water stress is the term used to define the internal water balance of a plant (Kramer, 1963). Water stress is measured by diffusion pressure deficit, water potential or plant water suction. The greater the suction the greater is the water stress. Tissue water balance depends on the rates of absorption and loss. Water is taken up by the roots and utilized in various plant processes and lost from the plant by transpiration. Transpiration is affected by leaf area and structure, extent of stomatal opening, and environmental factors. Absorption on the other hand is affected by the rate of water loss, the extent and efficiency of the root system, hydraulic properties of the soil, and environmental factors. Plants undergo water stress if transpiration rate exceeds absorption rate. Under conditions of low soil moisture content, absorption rate is very small, and the result is a high plant water stress. However, plant water stress can develop at relatively high soil moisture content if transpiration rate is excessively large. For this reason soil moisture stress is not always a good indicator of plant water stress. Since plant water stress has a direct influence on plant growth, it is more important to measure leaf water stress.

Thermocouple psychrometer

The thermocouple psychrometer is a device used to determine water potential by measuring relative humidity by use of a thermocouple. The theoretical basis for its use is the relation between water potential in a solution and the relative vapor pressure in an atmosphere in equilibrium with the solution.

$$\psi = (RT/M)\ (\ln p/p^0) \text{------------------------------} (2)$$

ψ = water potential

R = ideal gas constant

T = absolute temperature

M = molar volume of water

p/p^0 = relative humidity (expressed as a fraction)

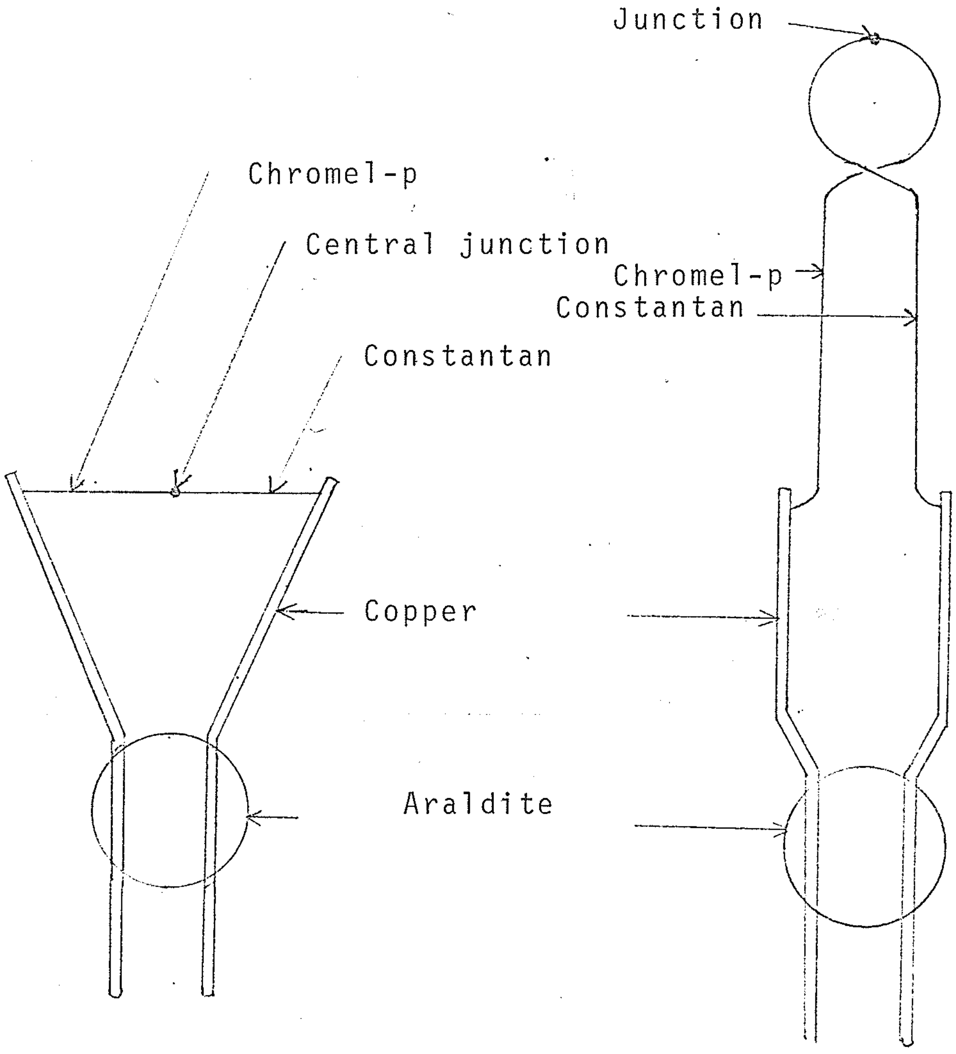
Thus by knowing relative humidity over a solution one can determine its water potential.

Types of Thermocouple Psychrometers

As stated previously, a thermocouple psychrometer measures relative humidity. There are two types of thermocouple psychrometers 1) the Spanner or peltier cooled variety and 2) the Richards or droplet thermocouple psychrometer (Fig.1).

Spanner thermocouple psychrometer

The Spanner thermocouple psychrometer (Spanner, 1951)



Spanner

Richards

Fig. 1. Spanner and Richards type thermocouple psychrometers. Redrawn after Lang and Trickett (1965).

involves the use of a fine thermocouple wire which is cooled below the dew point by passing a current through it. Water condenses on the thermocouple junction maintaining it at the dew point temperature. This cooling effect is called Peltier cooling. The way this system operates is as follows:

1) the thermocouple assembly with the sample is placed in a controlled temperature water bath ($\pm$ .001° C)

2) the system is allowed to come to equilibrium, i.e. the water vapor pressure above the sample reaches a constant value.

3) once the system is equilibrated, the galvanometer is zeroed.

4) a current is passed through the thermocouple which condenses a droplet of water on the junction.

5) the temperature (emf) of the thermocouple is then read on the galvanometer.

By knowing ambient and dew point temperatures relative humidity can be calculated and potential can be determined by equation 1. Rather than calculate relative humidity each time, a calibration curve for water potential-emf output is determined over known solutions of KCl (Fig. 2). Hence all that is necessary is to determine emf output of the thermocouple psychrometer to determine potential.

One limitation is that the Spanner thermocouple psychrometer requires very sensitive temperature control ($\pm$ .001° C).

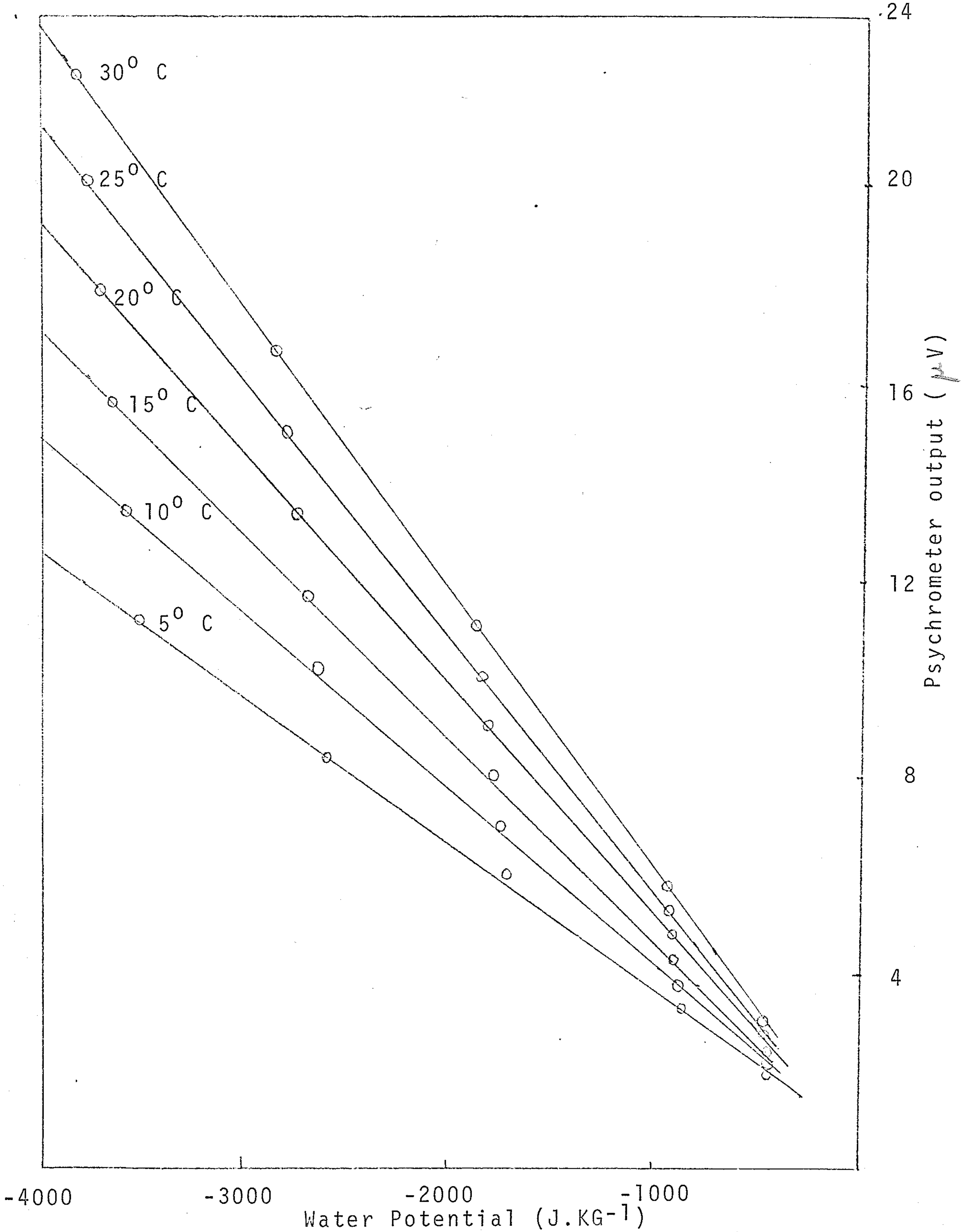


Fig. 2. Calibration curve of a thermocouple psychrometer. Redrawn from Lang and Barrs (1965).

A change of relative humidity from 100 to 99% will change the water potential from 0 to -15 bars at 25° C. In a closed psychrometer chamber a small change in temperature will create a large change in relative humidity and hence in potential. Because extremely small voltages are measured (10 μV range) very sensitive equipment is required. Another limitation of the system is that the Peltier cooling effect lowers the temperature very little. Chromel-p and constantan thermocouple can be cooled a maximum of 1.5° C. As a result, most thermocouple psychrometers of the Spanner type are not effective for measuring potentials below -50 bars.

Richards thermocouple psychrometer

The Richards' thermocouple psychrometer is similar in design to Spanner's except a ring is soldered near the junction (Fig. 1). A small water drop is placed in the ring and allowed to evaporate to produce dew point temperature. The thermocouple psychrometer is sealed in the chamber with the sample, placed in the water bath and allowed to equilibrate. A reading is usually obtained in 10 to 30 minutes if the vapor condition of the sample is steady. Potential can be determined by equation 1 or a calibration curve. As with the Spanner thermocouple psychrometer a calibration curve of water potential vs. emf output is prepared over known NaCl or KCl solutions.

This type of thermocouple psychrometer requires precise temperature control and precise emf measurement. Relative humidity can be measured at very low potentials because the droplet of water placed on the thermocouple can lower the dew point temperature more than Peltier cooling. Water evaporates from the junction to produce dew point temperature. This small addition of water vapor to the sample may give a higher reading. Boyer (1971) compared the Spanner and Richards thermocouple psychrometers and found the Spanner water potential value to be lower than the Richards reading.

Measurement of leaf water potential

Leaf water potential has been measured on the intact plant and on excised tissue. Boyer (1971) and Lang (1965) compared both techniques and found little difference between them.

Excised-tissue method

Ehlig (1962) measured leaf water potential of pepper, cotton and birdsfoot trefoil. Sections of leaves were excised and placed around the inside of the chamber where they were allowed to equilibrate for 2 to 6 hours. Using a Richards type thermocouple psychrometer, Ehlig found that leaf water potential in birdsfoot trefoil ranged from -8.6

bars to -48.8 bars. The -8.6 bar reading was obtained when plants were well watered and the -48.8 bar reading was obtained when plants were severely wilted.

Box (1965) used a Peltier type thermocouple psychrometer to measure leaf water potential of cotton. Twenty leaf discs, 1 cm. in diameter were excised from a cotton plant and placed in a brass chamber which was then connected to the thermocouple psychrometer. Then, the whole apparatus was enclosed in a stainless steel test tube and placed in a controlled temperature bath. The leaf discs were allowed to equilibrate until water potential in the vapor phase reached a constant value. This usually required about 2 hours. Box found leaf water potentials of -40 and -65 bars at relative water contents of 94 and 53 percent, respectively.

Yang and de Jong (1968) studied leaf water potentials in wheat plants using a Spanner type thermocouple psychrometer. Wheat leaves 4 cm. in length were inserted into a stainless steel enclosure with the thermocouple psychrometer and placed in a 25° C water bath which was controlled to $\pm$ $.001^{\circ}$ C. The samples were allowed to equilibrate which usually required 5 hours. Leaf water potentials from -10 bars to -40 bars were recorded.

Intact-leaf method

Lambert and Van Schilfgaarde (1965) used a Spanner type thermocouple psychrometer to measure water potential on an intact leaf of a red kidney bean plant. The whole leaf was sealed in a teflon coated acrylic chamber. The entire system was enclosed in a water bath to control temperature. Equilibration times varied with solutions and leaves. Leaf samples were allowed to equilibrate for 30 hours before measurements were made. By passing the plant through an irrigation cycle, different leaf water potential measurements were obtained. Leaf water potentials varied from -3 to -16 bars.

Lang and Barrs (1965) developed a system similar to that of Lambert and Van Schilfgaarde (1965). They constructed a stainless steel chamber and surrounded it with a water jacket which was finally covered with foamed polyurethane insulation. They trimmed the leaves of cotton to 80 by 41 mm. 16 hours before enclosing the leaf in the chamber. A leaf near the intact leaf was removed and leaf water potential was measured by a Spanner type thermocouple psychrometer. Values obtained from both excised and intact leaves were in close agreement. The leaf water potentials of cotton could not be compared to other data as there were none available. Leaf water potential decreased as soil moisture decreased in the soil.

Manohar (1966) developed a small chamber, Spanner type thermocouple psychrometer to measure water potential in plant tissue. The thermocouple psychrometer chamber consisted of a silver cylinder (.06 $cm.^3$) with the base consisting of the sample. This apparatus was sealed and placed in a constant temperature bath.

Hoffman and Splinter (1968) used a system in which a thermocouple psychrometer chamber was glued to the underside of a tobacco leaf. The whole apparatus was placed in a controlled temperature water bath. Leaf water potentials decreased as soil moisture decreased. Leaf water potentials were .75 to 3.5 bars lower than soil water potentials. Because the results obtained were in agreement with those expected, it was concluded that the system worked.

An isopiestic thermocouple psychrometer developed by Boyer (1966) was used to measure leaf water potential of sunflower tissue. This thermocouple psychrometer was similar to a Richards thermocouple psychrometer except that rather than placing a drop of water on the junction, a solution of a known concentration of sucrose was placed on the junction. Two consecutive measurements were made, one with water on the junction and one with a solution close to the potential of the leaf. Thermocouple output was plotted as a function of potential of the water or solution on the thermocouple and the line was extrapolated to zero output. The potential at zero output was taken as the potential of the leaf tissue. To test the accuracy of this method sunflower tissue was equilibrated over a known solution and then placed in the thermocouple psychrometer chamber. Measured values were very close to the known potentials.

Water potential measurements were made on both detached and intact leaves. Detaching leaves from the plant had no effect on water potential measurement. Hence Boyer concluded that detached tissue could be used to determine leaf water potential of intact leaves.

Measurement of soil water potential

Determination of soil water potential by thermocouple psychrometery was attempted by Korven and Taylor (1968). They used a Spanner type thermocouple psychrometer (Fig. 3) which required the use of a temperature controlled water bath for the sample. The soil sample chamber was connected to the thermocouple psychrometer chamber and the whole assembly was immersed in the water bath. When the samples had come to equilibrium, water potential was recorded. They concluded that the thermocouple psychrometer can be used

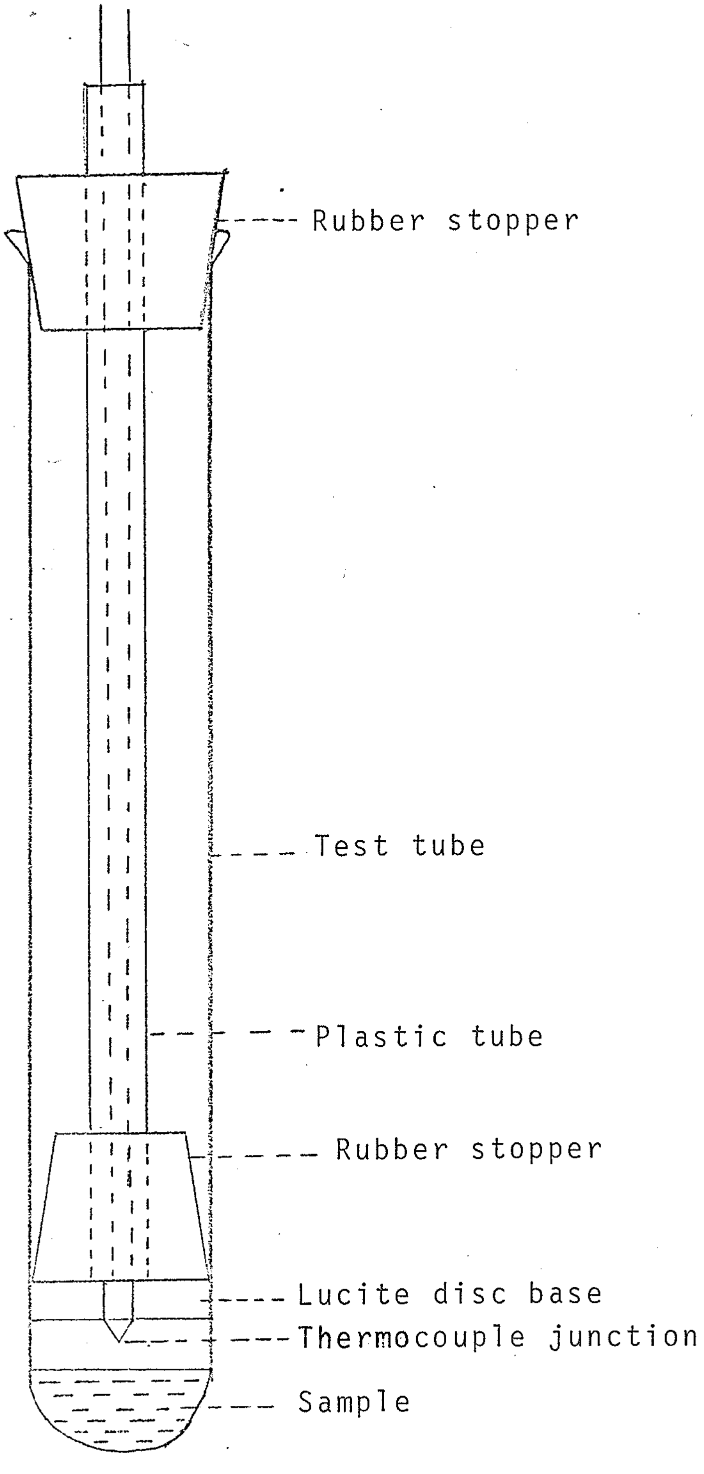


Fig. 3. Sketch of thermocouple psychrometer apparatus used by Korven and Taylor (1959).

to determine relative activity of soil water and sulphuric acid solutions with the same accuracy.

Richards and Ogata (1961) conducted thermocouple psychrometer measurements with a Richards thermocouple psychromenter on soil samples equilibrated on the pressure membrane. They measured total suction, matric suction, and solute suction. It was found that total suction as measured by the thermocouple psychrometer was equal to the sum of matric suction and solute suction. Matric suction was measured by the pressure membrane and solute suction was measured by the thermocouple psychrometer. From this it was concluded that the thermocouple psychrometer measured total water potential of soil.

Rawlins and Dalton (1967) developed a thermocouple psychrometer which did not require precise temperature control. "If a chamber were sealed so that water vapor could neither enter nor leave, the error in water potential resulting from changes in temperature of the chamber would be about 1 bar per 0.01^{o} C at 25^{o} C. If, on the other hand, vapor were free to move to and from the chamber from a sample, the error would be less." These authors enclosed the thermocouple assembly in a ceramic chamber (Fig. 4). The soil thermocouple psychrometers were embedded in the soil

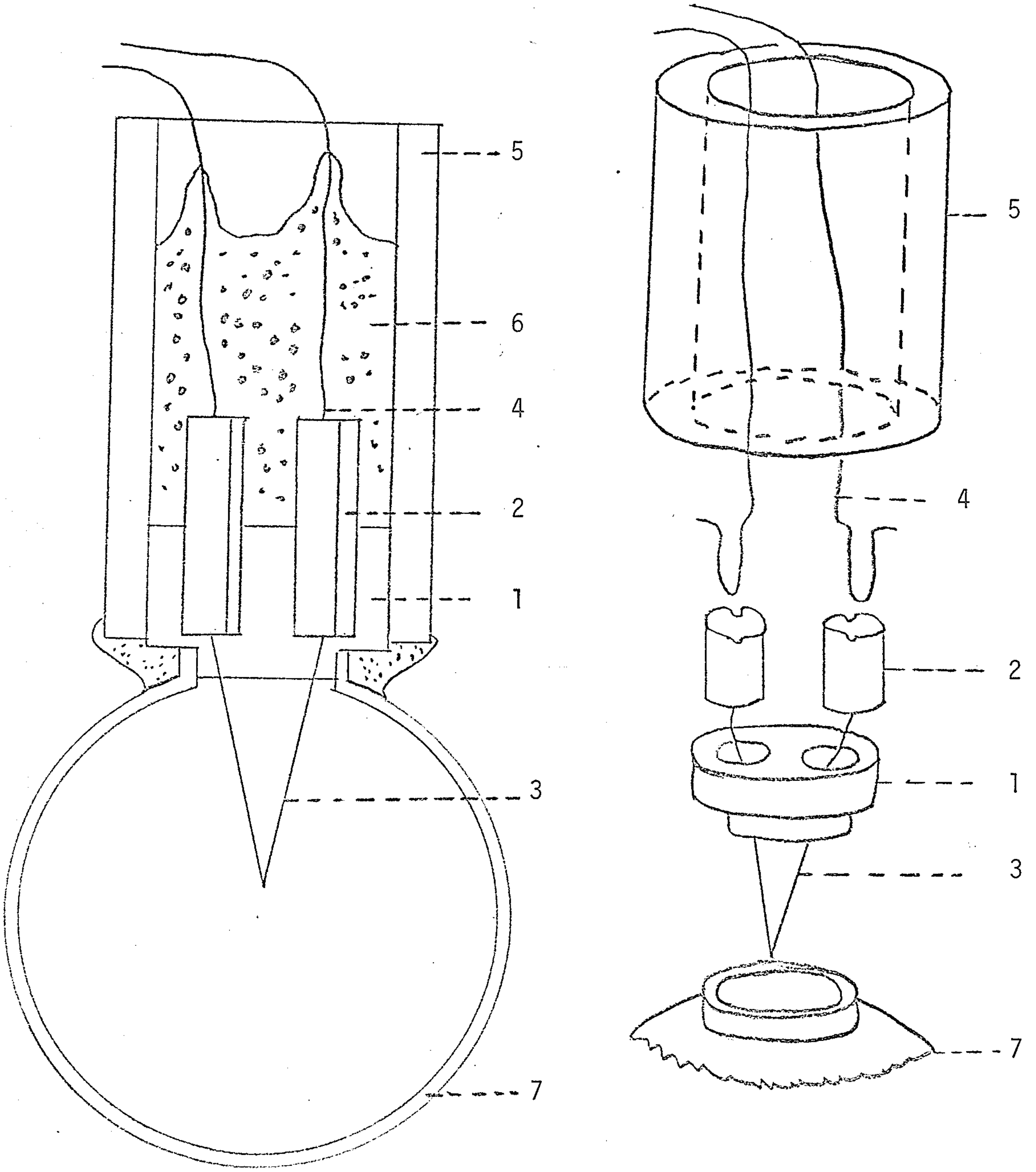


Fig. 4. Sketch of thermocouple psychrometer used to measure soil water potential in situ. Redrawn from Rawlins and Dalton (1967). Legend: 1, Teflon insert 2, copper heat sinks 3, thermocouple 4, copper lead wire 5, acrylic tubing 6, epoxy resin 7, ceramic bulb.

and then the soil was allowed to pass through an irrigation cycle. Water potential was measured concurrently by tensiometers. There was a discrepancy between the two systems but the discrepancy was constant indicating some error in one of the systems. Water potentials measured by tensiometer were higher than those measured by the thermocouple psychrometer. Although soil temperatures fluctuated, variation of thermocouple psychrometer water potential measurement was only ±0.5 bars. The system requires no temperature control and hence can be used in the field.

Lang (1968) used a Spanner type thermocouple psychrometer covered with a stainless steel gauze cage to measure soil water potential. Nine thermocouple psychrometers were embedded in a 16 liter pot of soil containing a cotton plant. The whole system was enclosed in a controlled temperature water bath. The pot was watered then allowed to dry. Water potential decreased with decreasing soil moisture. Soil water potential decreased more during the day than the night. Since the soil water potentials decreased with time and environmental stress it was concluded the system worked.

Recent developments in thermocouple psychrometers

From the literature cited most authors found that constant temperature baths were required for meaningful measurement. Since temperature control is difficult and expensive some researchers have tried to develop new techniques which require little temperature control. Wescor Inc.* now supplies commercially a thermocouple psychrometer which can measure soil or liquid samples without precise temperature control. Their design is similar to that of Rawlins and Dalton (1967). These thermocouples are enclosed in ceramic bulbs and have accuracies of ± 0.5 bars. Wescor Inc. also now make a sample chamber psychrometer which can be used for measuring potential of almost any material provided it can fit in the small chamber and potential values are not lower than -50 bars. Research is currently continuing but at present accuracy of measurement is still limited to ± 0.1 bar.

Millar, Lang, and Gardner (1970) are using a four terminal thermocouple psychrometer in which one pair of leads applies a cooling current and the other two leads measure the temperature of the junction. This system requires less temperature control and also removes the heating error from the Peltier effect.

Calissendorff and Gardner (1971) have built a thermocouple psychrometer chamber with several thermocouples inside. The additional thermocouples sense the temperature difference between the psychrometer junction and the sample.

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*Wescor Inc., Logan, Utah

This system has been used successfully on corn plants grown in the field.

Measurement of Net Photosynthesis

The technique of measuring net photosynthesis rate by measuring carbon dioxide assimilation began in approximately 1945. Researchers have used whole plants, a few leaves, a single leaf, part of a leaf and detached leaves. The recent trend has been to use a single attached leaf or, where the species has permitted, several leaves. Some workers have used several plants. For example, Musgrave and Moss (1961) used a chamber 9 feet long, 5 feet wide and 12 feet high on corn plants in the field. Boyer (1970), Hesketh (1963) and Chapman and Loomis (1953) used small chambers which enclosed one leaf or part of a leaf depending on the species. Tregunna, Krotkov and Nelson (1966) detached the leaf and placed it in a small chamber for net photosynthesis measurement.

The apparatus used in making measurements is essentially the same in all instances. Gas is passed through the chamber and by some means net carbon dioxide assimilated is measured. There are two systems, an open and closed system. The open system involves passing a known concentration of CO_2 over the leaf which in turn passes through an apparatus which measures CO_2 concentration. By knowing the amount of

CO_2 delivered and the amount of CO_2 leaving the assimilation chamber, net CO_2 uptake can be determined. Chapman and Loomis (1953) used an open system where CO_2 was collected in KOH solution.

Most of the recent researchers have used a closed system. In this system air is recirculated. The rate of decrease in CO_2 concentration with time is used to calculate net photosynthesis rate. Conversely an increase in CO_2 concentration can be used to calculate respiration rate. Boyer (1970), Bate (1969), and Lister, Krotkov and Nelson (1961) among others have used a closed system to measure rate of net photosynthesis.

Problems associated with photosynthesis measurement

When using an assimilation chamber it is important to remember that the leaf is thrust into a new environment. Therefore one should try to maintain conditions in the assimilation chamber similar to the environment in which the plant is growing. Avery (1967) conducted tests on perspex chambers to determine how they affected temperatures of the leaf. His data indicated that the temperature inside the assimilation chamber was 10° C higher than the ambient air when sunlight intensity was 64,800 lumens/m^2. Leaves which were shaded usually had temperatures 2-3° C higher than ambient air temperature. Since these temperature differences significantly affect rate of photosynthesis several attempts have been made to prevent an increase in temperature in the assimilation chamber. Air flow worked very well provided flow rates were sufficiently high. A cooling coil was inserted in the chamber and met with limited success (Avery 1967). Boyer (1970) used a chamber with one side constructed of metal which housed cooling coils.

Maintaining constant humidity in the chamber is also a problem where certain carbon dioxide infrared gas analyzers are used. Water vapor and carbon dioxide both absorb infrared light. To rectify this problem calcium chloride tubes are placed in the line to remove water vapor. As a result transpiration rate may be considerably higher than that of leaves outside the chamber. Models in which water vapor does not interfere with CO_2 analysis are now available and their use will provide values more representative of those occurring under "natural" conditions.

Water Stress Effect

Water stress or internal water balance is one of the most important factors in controlling physiological processes. The major functions of water in plants include:

1) water is a major constituent of active tissue
2) water is a reagent for metabolic cycles
3) water acts as a solvent
4) water provides turgidity for cell enlargement.