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Title THE EFFECT OF SOIL MOISTURE SUCTION AND SOIL TEMPERATURE ON TRANSPIRATION, PHOTOSYNTHESIS AND RESPIRATION OF MONTEREY PINE (PINUS RADIATA D. DON)

Abstract approved

Dr. T. Youngberg

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A special apparatus was developed in which the soil moisture levels of several soil cells could be maintained independently by various osmotic solutions at a selected temperature. The effect of four soil moisture suctions and four soil temperatures on the rates of transpiration, photosynthesis and respiration of monterey pine seedlings was studied. Transpiration was determined by a constant water level device which recorded the total amount of water used by the plant. Leaf resistances to CO₂ and water vapour were calculated.

In general, the rates of photosynthesis, respiration and transpiration decreased with increasing soil moisture suction. Photosynthesis and transpiration decreased sharply from 0.35 bars to 0.70 bars soil moisture suctions.

The rates of transpiration increased faster than the rate of
photosynthesis with increasing soil temperature. The rates of respiration fluctuated with soil temperature.

Where the ratio of transpiration to photosynthesis is constant as between 60° F and 80° F at all soil moisture suctions except 0.35 bars, the same process was assumed to be limiting (probably stomatal control). At 0.35 bars soil moisture suction, physiological and viscosity factors are to be considered.

The activity of the root is temperature dependent and suction dependent. At high suctions, the temperature effect is small, at low suction the temperature effect is large.

At suctions higher than 0.70 bars, the diffusion process is stomatal controlled.
The Effect of Soil Moisture Suction and Soil Temperature on Transpiration, Photosynthesis and Respiration in Monterey Pine (*Pinus radiata* D. Don)

by

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THE EFFECT OF SOIL MOISTURE SUCTION AND SOIL TEMPERATURE ON TRANSPIRATION, PHOTOSYNTHESIS AND RESPIRATION IN MONTEREY PINE (PINUS RADIATA D. DON)

INTRODUCTION

Over a period of time, the relative success or failure of a plant in a specific environment is a function of the relative magnitudes of such major life processes as transpiration, photosynthesis and respiration. Plant growth is contingent upon the balance between the rates of carbohydrate production by photosynthesis, the use of these materials in respiration and the rate of conversion of photosynthate into new tissues.

The more important environmental factors governing these biological processes are light, temperature, soil moisture, mineral nutrition and CO$_2$ level. The first four are of greatest interest to the forester because they may be manipulated by appropriate stand treatments or by selection of species in sites where most of the environmental factors are particularly suitable for certain specific requirements. The only way in which environmental factors such as water and temperature can affect growth is by affecting internal processes and conditions of plants. Thus it is necessary to study the effects of water deficits on physiological and biochemical processes in order to understand why they reduce plant yields.
Many studies have been made on the effects of soil water suction on transpiration, photosynthesis and respiration. The techniques that were used, however, have left much to be desired. An experimental evaluation requires the ability to control the soil moisture content at a constant value. In most of the studies, soil moisture was controlled by discontinuing the watering of potted seedlings and checked by a continual weighing of the potted seedlings or by determining moisture contents gravimetrically (1, 4, 10, 29, 30, 32, 40, 41, 53). In the interpretation of results of plant growth versus soil moisture regime studies, the essentiality of thorough root penetration throughout the entire soil volume that is being studied should be acknowledged by all investigators. In other words, a meaningful relation between plant response and soil moisture conditions is possible only for that part of the soil mass that is sufficiently close to the root as to function as a source of water for the root. Uncertainties concerning the relation between this "active soil volume" and the total soil volume under study may well account for some of the seemingly contradictory results to be found in the literature.

In studying the effects of water deficits on plant processes under non-steady state conditions, the internal water balance of plants ought to be determined in order to have some quantitative measure of the extent of the water deficits existing in plants. In
most studies that have been reported, plant water stress per se was not measured but rather it was assumed that as soil water stress increased, there was a concomitant increase in plant water stress (1, 10, 40, 41). It should be realized that plant water stress depends on the relative rates of water absorption and water loss and not on the rate of water absorption alone. This balance between water absorbed and water loss depends on soil, plant and climatic factors. It has been suggested (4) that only measurements of the physical status of the plant water (a diffusion pressure deficit (DPD) or leaf water potential) enable a meaningful interpretation of the effect of soil moisture stress on physiological processes under a non-steady state condition.

This experiment was formulated on the basic premise that in view of the points noted above, the soil water stress and plant water stress were measured or controlled in manners which made proper interpretation of the results either impossible or doubtful. The objective of this study is to relate the rates of transpiration, photosynthesis and respiration of monterey pine seedlings to soil water suction and soil temperature. The effect of the interaction of these two parameters has long been neglected in studies of this type. A determination of the diffusion resistances in the pathway of the evaporating water and in the pathway of CO₂ moving into or out of the stomata at different soil moisture suctions and soil temperatures will aid the interpretation of the results.
LITERATURE REVIEW

Effect of Water Suction on Plant Growth

Stomatal Opening

Stomatal opening seems to be one of the most sensitive plant processes with respect to internal water deficits. Kramer (20) pointed out that a slight decrease in leaf turgidity sometimes is accompanied by increased opening of stomates, but further reduction nearly always is accompanied by decrease in stomatal aperture. Milthorpe and Spencer (31) indicated that the rate and direction of change in the water content of the adjacent cells was more important than the magnitude of the water deficit of the whole leaf in affecting stomatal movement. Premature closure of stomates is undesirable because, in at least some species, it cuts off the supply of CO₂ for photosynthesis.

Transpiration

Less than 5% of all the water absorbed by plant roots plays a permanent role in the development of the plant and its metabolic processes (20). The water is mainly lost in the form of vapor or leaf transpiration. The greatest amount of water is lost through the stomates. Some takes place through the cuticle. Transpiration
takes place by the movement of water from leaf veinlets into surface layers of outer cell walls and evaporation of water from surface layers into the atmosphere as cuticular transpiration, or from mesophyll walls into intercellular spaces and then outward diffusion through stomates.

The concept of a continuous water system from the soil through the plant to the atmosphere permits the expression of water transport through the whole system as a series of equalities (13).

\[
\text{Transpiration} = \frac{P_1 - P_0}{R_{\text{soil}}} = \frac{P_2 - P_1}{R_{\text{root}}} = \frac{P_3 - P_2}{R_{\text{xylem}}} = \frac{P_4 - P_3}{R_{\text{leaf}}} = \frac{P_5 - P_4}{R_{\text{vapor}}} \tag{1}
\]

The resistances (R) or the water potential gradients (P5 - P0) of the series are affected by environmental or plant factors thus changing the rate of transpiration.

Transpiration rate may be reduced by drought as well as by flooding (18). However, drought seems to be by far the more important factor in the transpiration decrease.

One of the controversial issues in transpirational studies is ascertaining of the point when the rate starts to decrease. Most people now agree that the rate decreases with decreasing soil moisture (4, 8, 10, 29, 30, 43, 50, 52), although Veihmeyer and Hendrickson (49, 50) claim that the rate of water extraction from soil by plants is not influenced by the water content so long as it is
above the permanent wilting point. Thus transpiration is little affected between low and high soil moisture.

Satoo (39) reported a slight decrease at first but once a certain point, specific to a given species, was reached the decrease became sudden. Slatyer (43) noted a very low level of transpiration in privet and tomato following such a sudden decrease. At very high soil moisture stresses, this level was about 5% of maximum. Brix (4) did not observe any appreciable change in transpiration of tomato and loblolly pine seedlings until the fifth day after the soil had been watered to field capacity. He did not measure the soil water stress. Loustalot (29) measured transpiration and net photosynthetic rates of pecan while soil moisture was gradually depleted to below the wilting point. Transpiration showed the first sign of decline in the afternoon when the soil moisture content was 18%. Martin (30) obtained a decrease in transpiration in sunflower only after two-thirds of the available water was removed.

Photosynthesis

The rate of photosynthesis rarely is limited by lack of water as a reagent, but it often is limited because dehydration of protoplasm reduces its photosynthetic capacity (20, 25) and because stomatal closure reduces the supply of carbon dioxide to the chloroplasts.

It is common knowledge that a decrease in the photosynthetic
rate occurs as soil moisture stress increases. Many researchers have reported steady decreases in rate of photosynthesis with decrease in soil moisture content. Verduin and Loomis (52) and Schneider and Childers (41) have reported large decreases in photosynthesis in wilting leaves. On the other hand, Upchurch et al. (48) found no reduction in photosynthesis of ladino clover until the readily available soil moisture was almost entirely depleted, although the rate fell rapidly when wilting occurred. Loustalot (29) reported that the photosynthetic rate of pecan leaves was reduced to two-thirds, and eventually to 11% of the maximum rate after five days of root submersion. Clark (6) observed that the maximum photosynthetic rate in balsam fir and white fir did not occur when the soil was wettest but occurred after much water loss had taken place. The increased rates of photosynthesis were attributed to improved aeration, to increased stomatal opening or both. It seems fairly well established (11), however, that photosynthesis is relatively less affected by stomatal closure than transpiration because the resistance to $CO_2$ diffusion lies both in the stomates and in the mesophyll. Negisi and Satoo (32) and Satoo and Negisi (40) measured net photosynthesis in *Pinus densiflora* and *Cryptomeria japonica* while the water was depleted from the soil (field capacity 64%, PWP 33%). The maximum net photosynthetic rate occurred at about 50% soil moisture and thereafter fell to zero when the soil was near
the wilting point. The decrease was attributed to stomatal closure and the direct effects of leaf water deficits.

**Respiration**

The literature relating soil moisture stress to respiration is very scanty! In addition, there is a certain disagreement about the dependence of respiration on soil moisture. Schneider and Childers (41) found that while photosynthesis of apple trees in drying soil was decreasing, respiration was increasing. Upchurch et al. (48) found small increases in respiration of wilting ladino clover. The leaves of *Pinus nigra austriaca* dried gradually in the laboratory respired slowly at first but when the water content had declined to 68%, the production of CO₂ was increased (36). The leaves of tobacco (14) if removed from the plant showed increased respiration upon wilting, but after water loss was large, respiration was decreased. A comparison of the respiration of barley seedlings in soils of different moisture content showed that those seedlings with the greater soil moisture had the least respiration and that the rate of this process increased as the soil moisture content was reduced (15). Brix (4) reported a rather "unique" trend in the respiratory rate of loblolly pine. The rate dropped sharply at the onset of drought but then increased again only to decrease after a very high diffusion pressure deficit developed. However, he reported a steady decrease in
respiration rates with decreasing soil moisture in tomato. Parker (33) observed very irregular respiratory rates in the needles of Austrian pine left to dry out, but the general trend of the curves was downward with decreasing moisture of the needles.

**Effect of Soil Temperature on Plant Growth**

There is a scarcity of literature on subjects relating soil temperature per se to photosynthesis and respiration rates in plants, although much work has been reported with regards to transpiration and soil temperature.

In explaining the effect of low soil temperature on plant growth, many factors ought to be considered: root permeability, root growth, leaf surface area, retention and movement of water in the soil.

Low temperatures retard the elongation of roots. This would be most important in soils with moisture contents below field capacity since it is here that moisture availability depends on the extension of the root tips into contact with the water films surrounding hitherto untouched soil particles. The permeability of the cells decreases with temperature. The viscosities of the protoplasm and of the colloidal gels in the cell walls are much higher at low temperatures. The increased viscosity probably retards the movement of water across the mass of living cells lying between the soil and the xylem of the roots. Lowering the soil temperature decreases
the rate of movement of water from the soil to the absorbing surfaces of the roots. Kramer (23) points out that the viscosity of water increases as the temperature decreases, being twice as high at 0°C as at 25°C. This not only slows down the rate of movement from soil to roots but must considerably decrease the rate of movement through the root cells themselves.

Cameron (5) reported that higher leaf water deficits in orange were obtained at low soil temperatures than at high soil temperatures both in the field and in the air-conditioned chamber. Kramer (24) found that watermelons and cotton absorbed only 20% as much water at 10°C as at 25°C. Loblolly and slash pine absorbed only 4% as much water at 10°C as at 25°C, while a comparable figure for white and red pine was 60%. Tew et al. (47) concluded that lessened water uptake may limit the transpiration rate at low soil temperatures. They observed a greater transpiration at a soil temperature of 40°C than at 25°C. This was attributed to the fact that at a soil temperature of 40°C, the leaf and stem were both warmer than the air. With 25°C soil the leaf was cooler than the air presumably as a result of transpiration. Clements and Martin (7) reported that: (1) transpiration of sunflower plants varied little with soil temperature between 55°F and 100°F, but dropped rapidly below 55°F, was reduced to half at 38°F and approached zero at 32°F, (2) stomata did not begin to close until the temperature
dropped to $40^\circ F$ but were nearly completely closed at $37^\circ F$. (3) the plants recovered rapidly from the wilted condition when the soil temperature was raised. It is common knowledge that cold adapted trees often show maximum photosynthesis at low temperatures (34).

A pertinent question to ask in evaluating the effect of soil temperature on plant growth is, "To what extent does soil temperature affect plant temperature?" Tew et al. (47) claimed that soil temperature had a marked influence on stem and leaf temperatures. They conjectured that the higher leaf temperature at higher soil temperatures resulted from translocated heat. Warm water absorbed by the roots could have caused the temperature of the stem and leaves to rise. Cox (8) obtained small increases in leaf temperatures with increases in soil temperatures. Ansaris and Loomis (2) and Salisbury et al. (38) reported that leaf temperatures are determined by air movement, air temperature, radiation, and leaf mass, with a smaller effect assignable to differences in transpiration.

It is generally accepted that the principal effect of low temperature on plants is that of decreased water absorption. This is attributed to the combined effects of decreased permeability of the root membranes and increased viscosity of water resulting in increased resistance to water movement across the living cells of the roots. The effects of low temperature in decreasing root extension, root respiration and active absorption are said to be of
secondary importance.

**Diffusion Resistance to Carbon Dioxide and Water Vapour**

The concept of a continuous water system from the soil through the plant to the atmosphere has often been used. This concept permits the evaluation of plant responses to changes in the water status in terms of Van den Honert's (13) catenary process. The rate of water movement through the entire system is effectively controlled at the point of the greatest resistance. He expressed water transport through the whole system as a series of equalities:

$$T = \frac{P_1 - P_0}{R_{\text{soil}}} = \frac{P_2 - P_1}{R_{\text{root}}} = \frac{P_3 - P_2}{R_{\text{xylem}}} = \frac{P_4 - P_3}{R_{\text{leaf}}} = \frac{P_5 - P_4}{R_{\text{vapour}}}$$

The resistances (R) and the water potential gradients (P₅-P₀) of the series are subject to the influence of environmental factors which in turn change the rate of transpiration.

It is agreed by many investigators that over the entire range of available soil moisture, the main resistance to transpiration is in the gaseous phase from the evaporating surfaces of the mesophyll cells through the stomata to the ambient air (3, 8, 11, 42). This short review will therefore only be concerned with the vapour resistance of the above equation.

Water vapour encounters several different resistances in its
outward diffusion. These are the 1. resistance encountered by water molecules passing from cell surfaces through the intercellular spaces to the stomata (the intercellular space resistance), 2. the stomatal resistance from the inner end of the stomatal tube to the outer end (effective length) (35), 3. the external resistance from the stomata to the ambient air, and 4. the resistance encountered by water molecules diffusing across the cell walls of the mesophyll cells to the evaporating surfaces, the so-called mesophyll resistance.

In the diffusion of \( \text{CO}_2 \) from the external air towards the reaction center in the chloroplasts resistances are also successively encountered in the external air, in the stomata, in the intercellular spaces and in the dissolved state in the mesophyll cells (11).

Bange (3) characterized the external resistance by the so-called micro- and macro vapour cups existing over the individual stomata and whole leaf. Wind reduces the external resistance by blowing away the vapour cups. The stomata have little influence on the transpiration rate until they are nearly closed in an environment with calm air because of high external resistance. But when appreciable wind is present, the external resistance is low and stomatal control is apparently effective throughout the range of stomatal apertures. However, Penman and Schofield (35) regarded the stomates as having little control of \( \text{CO}_2 \) diffusion unless they are closed.
The resistance of the mesophyll is considered to be negligible when adequate water is available to the plant. It has, however, been postulated that as the soil dries out and soil moisture stress increases the resistance of the mesophyll increases to a point where it can no longer be ignored.

Stomata must be open for the inward diffusion of carbon dioxide in amounts large enough to support photosynthesis and plant growth. At the same time transpirational loss occurs. Several investigators contend that stomatal resistance is the main resistance, others suspect the presence of other significant resistances to transpiration. Shimshi (42) demonstrated that corn seedlings grown at lower soil water potentials would transpire at a lower rate than those grown at a high water potential but having equivalent stomatal resistance. Cox (8) working with white clover arrived at the same conclusion. He showed that mesophyl resistance increases and can thus markedly reduce transpiration in the absence of stomatal closures. Penman and Schofield (35) considered the major resistance to CO₂ diffusion to be within the mesophyll cells rather than in the gaseous diffusion pathway to these cells. Gaastra (11) obtained quantitative measurements of the several components of the total diffusion and concluded that mesophyll resistance may be an important rate limiting factor in photosynthesis. The experiments of Gaastra did not include a variable to account for differences in
water supply to plant roots.

Pisek and Winkler (36) measured the photosynthetic rate and stomatal aperture in leaves which were continuously losing water. Stomatal opening was reported to parallel the photosynthetic rate. Gaastra (11) observed from the data of Pisek and Winkler (36) that in the stomatal opening phase, the photosynthetic rate was 2.4 to 3.5 times that in the closing phase. He suggested that the water loss brought about a greater increase in mesophyll than in stomatal resistance.
MATERIALS, METHODS AND APPARATUS

Controls of Soil Moisture and Temperature

A technique for controlling soil water content during plant growth has long been sought after by many investigators. In the osmotic control method developed by Zur (54), a thin layer of soil is encased in a membrane which is permeable only to water but not the solute. This soil cell is then immersed in an osmotic solution containing Carbowax 6000, a polyethylene glycol with a molecular weight of 6000. Cox (8) has summarized Zur's findings with this method: that good control of soil moisture was only possible provided that the soil cell was kept very thin, that growing plants were kept small (to keep the transpirational demand low) and that the osmotic concentrations were kept low. With some modifications of Zur's method, Cox (8) has used the method successfully for measuring transpiration rates of clover.

Figures 1 and 2 show the special apparatus developed in which the soil moisture levels of several soil slabs could be maintained independently by various osmotic solutions at a selected temperature. This apparatus is similar to the one developed by Cox (8) but was modified a great deal. It consists of four independent osmotic chambers, each of which is surrounded by a water jacket, the four
Figure 1. A picture of apparatus used showing four independent osmotic chambers each of which is surrounded by a water jacket, the four water jackets being connected in a series. The soil cells can be seen standing in the osmotic solution and burettes for transpiration measurements are shown in the background.
Figure 2. A close-up picture showing one osmotic chamber surrounded by a water jacket, the bubbling device and burette for transpiration measurements and four soil cells inserted in the osmotic chamber.
water jackets being connected in a series as shown in the figure. Water is pumped into the water jackets from the temperature-controlled water source and then recycled to the same source. This gave a positive temperature control of the osmotic solutions and/or the soil.

The osmotic solutions were stirred by a propellor connected to a shaft which protruded through the wall of the osmotic chamber. Leakage around the shafts was prevented with O-ring seals. The shafts were driven by a geared-down electric motor through a chain drive.

Soil boxes or cells (11 1/2" x 4 1/8" x 3/8") were constructed of lucite and possessed removable sides (Figure 3). Each cell was filled and evenly packed (to a bulk density of about 1) with a mixture of Apt and Shanahan soil series. The mixture was made of the two soils in the ratio of three parts of Apt soil (clay loam with 8% organic matter) to one part of Shanahan (loamy fine sand) to give a clay loam texture. A mechanical analysis of the mixture showed sand, 39%; silt, 30%; and clay, 31%. The success of a plant in an enclosed environment of this soil cell requires that aeration be good, or rather that water-logging due to low infiltration rates be precluded. The admixture of the loamy fine sand made this possible.

Four concentrations of carbowax 6000 which correspond to 0.35, 0.70, 1.5 and 2.5 bars osmotic pressures were used in the
Figure 3. A picture of four soil cells; nos. 42 and 53 have removable sides intact. Next to no. 53 is a soil cell with one side removed to expose soil and root. The last cell is enclosed in a Visking membrane bag.
experiment. These osmotic pressures were not calculated but were obtained from Zur's (54) work. A graph of concentration of carbowax 6000 and the corresponding osmotic pressure is given in Appendix III.

**Transpiration Measurements**

Each osmotic chamber is connected to a constant water level device. The constant water level devices operate on the same principle as a mariotte bottle and maintained the osmotic chambers at the same pressure throughout the experiment. These devices in the form of burettes are graduated thus making it possible to accurately measure the volume of water necessary to maintain the volume of the osmotic chamber constant over a period of time. As water is transpired by the plants, water is moved from the osmotic solution across the membrane to replace the water being used by the plant in the soil. The constant water level devices thus indicate the amount of water necessary to maintain the level or volume of the osmotic chamber constant and consequently the amount of water being transpired. If the volume of the osmotic chamber is not maintained constant then the concentration of the osmotic solution will increase as water moves from the osmotic solution into the soil with a concomitant increase in soil moisture stress.
Photosynthesis and Respiration Measurements

The $\text{CO}_2$ exchange of the plants was measured with a Beckman Model IR215 infrared gas analyzer connected to a Heath recorder. Closed systems similar to those used by Krueger (26) or Lister et al. (28) for the measurement of changes in carbon dioxide concentrations were used in this study. The detailed description of these systems may be found in the above papers. Appendix IV shows a sketch of the arrangement used in this study. During measurement the entire top of each plant was enclosed in a cuvette made of plexiglass (Figure 4). The gas analyzer was connected to the plant chamber or cuvette in a closed system through which the air was circulated by a peristaltic type pump. The rate of net photosynthesis was established by measuring the decline in $\text{CO}_2$ level in the cuvette within a five minute period from an initial $\text{CO}_2$ concentration of 375 ppm. The rate of respiration was measured similarly by recording the increase in $\text{CO}_2$ concentration over a five-minute period in the dark (Figure 5) from a $\text{CO}_2$ level reached by photosynthesis to a higher level. The photosynthetic and respiratory rates were measured at the different soil moisture suctions and different soil temperatures and the rates were expressed as $\text{cm}^3 \text{CO}_2$ per $\text{cm}^2$ leaf surface area per second. Light intensity was maintained constant at the tops of the plants at 2000 f. c.
Figure 4. The cuvette encloses the entire top of each set of four seedlings during measurement of photosynthesis. Tygon tubings lead from the cuvette to the gas analyzer. Note the air-tight seal made with modelling clay between cuvette and bottom plate.
Figure 5. Black polyethylene bag provides darkness for respiratory measurements.
Measurement of Diffusion Resistances

No attempt will be made here to review the methods that are available in measuring the diffusion resistances to CO₂ and water vapour in plants. Suffice it to say that many methods are available.

In the method used for this study, the data needed for the calculation of the stomatal diffusion resistance are derived from the continuously measured transpiration rates and leaf temperatures, simultaneously with the continuously measured photosynthetic rates. The procedure outlined by Gaastra (11) is reported below.

Brown and Escombe used Fick's diffusion law for the calculation of the rate of diffusion in stomatal tube

\[ Q = \frac{D(C_0 - C_1)A}{L} \]

\( Q \) = diffusion rate \((\text{cm}^3/\text{sec})\)
\( D \) = diffusion constant \((\text{cm}^2/\text{sec})\)
\( C \) = concentration \((\text{cm}^3/\text{cm}^3)\)
\( A \) = cross sectional area \((\text{cm}^2)\)
\( L \) = length of diffusion path \((\text{cm})\)

The diffusion resistance can be defined as

\[ r = \frac{1}{D.A.} \]

\( r \) = diffusion resistance \(\text{sec/cm}\)
For steady-state conditions the rate of photosynthesis, $P$, which under all conditions is proportional to the rate of $CO_2$ diffusion, may be expressed as follows:

$$P = \frac{[CO_2_a] - [CO_2]_{surf}}{r_a, CO_2} = \frac{[CO_2]_{surf} - [CO_2]_{int}}{r_s, CO_2} = \frac{[CO_2]_a - [CO_2]_{int}}{r_a, CO_2 + r_s, CO_2}$$

$$P = \text{rate of photosynthesis (cm}^3\text{CO}_2/\text{cm}^2/\text{sec})$$

$[CO_2_a] = \text{concentration of CO}_2 \text{ in the external air}$

$[CO_2]_{surf} = \text{concentration of CO}_2 \text{ at the leaf surface}$

$[CO_2]_{int} = \text{concentration of CO}_2 \text{ in the intercellular spaces}$

$r_a, CO_2 = \text{diffusion resistance of CO}_2 \text{ in air}$

$r_s, CO_2 = \text{diffusion resistance of CO}_2 \text{ in stomates.}$

Accordingly the rate of transpiration, $T$, can be expressed as:

$$T = \frac{[H_2O]_{int} - [H_2O]_{surf}}{r_s, H_2O} = \frac{[H_2O]_{surf} - [H_2O]_a}{r_a, H_2O} = \frac{[H_2O]_{int} - [H_2O]_a}{r_s, H_2O + r_a, H_2O}$$

$$T = \text{rate of transpiration (cm}^3\text{H}_2\text{O/ cm}^2/\text{sec})$$
\[ T = \text{transpiration rate (cm}^3/\text{cm}^2/\text{sec}) \]
\[ [H_2O] = \text{concentration of water vapour (cm}^3/\text{cm}^3) \]

From simultaneous measurements of rates of transpiration (T) and photosynthesis (P), and the concentration of CO\(_2\) and H\(_2\)O, the diffusion resistance of any part of the diffusion path can be obtained. The total resistance in the pathway of the evaporating water is calculated from:

\[
(r_s + r_a) \cdot H_2O = \frac{[H_2O]_{\text{int}} - [H_2O]_a}{T} \tag{5}
\]

\(H_2O_{\text{int}}\) can be related to the relative turgidity of the leaf.

For most practical applications this relative humidity can be assumed to be equal to 100%.

The air resistance or boundary layer resistance, \(r_a, H_2O\)' can be obtained by determining the evaporation rate from a moist piece of blotting paper of the same size and shape as the leaf and exposed to identical environmental conditions. For such a leaf model, \([H_2O]_{\text{surf}}\) can be derived from the measured surface temperature.

\[
r_a, H_2O = \frac{[H_2O]_{\text{surf}} - [H_2O]_a}{E} \tag{6}
\]

\(E = \text{evaporation rate (cm}^3/\text{cm}^2/\text{sec})\)
The stomatal diffusion resistance for CO₂ can then be calculated according to the relationship:

\[
\frac{D_{H₂O}}{D_{CO₂}} = \frac{r_{s, (CO₂)}}{D_{CO₂}} \left[ (r_a + r_s)_{H₂O} - r_a, H₂O \right]
\]  

(7)

When \(D_{H₂O}\) and \(D_{CO₂}\) are the diffusion constants of water vapour and CO₂ in air respectively. The values 0.14 and 0.24 were used respectively for \(D_{CO₂}\) and \(D_{H₂O}\).

In these calculations the resistance in the intercellular spaces is not considered separately. It is assumed that this resistance is usually low compared to other resistances.

The magnitude of the mesophyl resistance particularly when dealing with the effect of water stress on \(P\) and \(T\) can be evaluated using the equation:

\[
P = \frac{[CO₂]_a - [CO₂]_{chl}}{(r_a + r_s + r_{me}, CO₂)}
\]

(8)

Where \([CO₂]_{chl}\) = concentration of CO₂ in the chloroplasts.

This equation can be used if the CO₂ concentration in the chloroplast can be determined. Gaastra (11) uses data to suggest that this concentration is approximately equal to zero under conditions where CO₂ is limiting. Since the value of \(r_a, H₂O\) is known from the evaporation experiments with leaf models, \(r_a, CO₂\) can be calculated according to:
\[ r_{a, CO_2} = \frac{D_{H_2O}}{D_{CO_2}} \cdot r_{a, H_2O} \]  

The value of \( r_{s, CO_2} \) has already been determined and \( r_{me, CO_2} \) can then be obtained by subtracting \( (r_a + r_s) \), \( CO_2 \) from the sum of the resistances.

**Growth Chamber**

All of the experiments were performed in a room with temperature and humidity controls. Air temperatures were maintained within \( \pm 1^\circ F \) of 70\(^\circ\) F. Relative humidity was maintained within \( \pm 1\% \) of 50\%.

Air movement in the growth chamber was maintained at a constant speed by drawing air over the plants with an electric fan. The actual wind speeds were not measured but were maintained at a constant rate below leaf flutter.

**Experimental Procedures**

The soil-filled cells were watered to about field capacity and three pregerminated seeds of monterey pine were then planted in each soil cell. Only the healthiest seedling was retained in each cell after a month and these were grown for a total period of about six months in a green house at a day temperature controlled to 75 \( \pm 5 \)\(^\circ\) F and night temperature to 70\(^\circ\) F. When the seedlings were
about six months old and the roots had adequately permeated the soil mass (Figures 3 and 6) the removable sides of the soil cell were replaced with the Visking membrane in the form of a bag (Figure 3) with the bottom sealed off with paper clips. The soil was wetted to beyond field capacity before the membrane was put on. It is essential to have good contact between the membrane and the soil and this was taken into consideration in the construction of the soil cells. The latter fitted quite snugly into the membrane bag.

Each osmotic chamber was brought to volume with its corresponding solution of carbowax 6000. The cells were suspended in the osmotic solutions in a manner which excluded air bubbles in the osmotic chambers as the air bubbles might affect transpiration measurements. The burettes were then filled with water. Two days were allowed for the system to come into equilibrium and to check for leaks in the system. A soft synthetic material put around the plant system and covering the soil surface prevented evaporation from the soil. When the system was in a state of semi-equilibrium, the bottom plate of the cuvette was put on and all the four slits made on this plate through which the plant stems were introduced into the cuvette were sealed off with modelling clay.

Equilibrium had been reached by the third day. The water level in the burette was recorded at 8:00 a.m. The plants were allowed to transpire for nine hours and the final burette reading was taken at
Figure 6. The root systems of four seedlings which quite adequately permeated the soil volume.
5:00 p.m. Starting at 1:00 p.m. on the same day, photosynthesis and respiration measurements were made. Also the leaf temperatures were recorded using a radiation thermometer. All these measurements took place at the same starting soil temperature of 50°F. The same set of measurements was repeated on the following day under the same environmental conditions just as a check on the first set of readings. Then the temperature of the water jacket and hence the soil was changed to 60°F. One day was allowed for the soil to reach equilibrium with this new temperature and transpiration, and photosynthesis and respiration measurements were also made. This procedure was followed for 70°F and 80°F soil temperatures. The above measurements were taken at all possible combinations of the four levels of osmotic pressures and four soil temperatures. Measurements were taken on a set of four seedlings at these combinations (Figure 4). A total of 16 soil cells was used in the experiments. Air temperature, relative humidity, and light intensity were maintained constant during all tests.

The plants were then harvested and the area of the needles was estimated according to a procedure discussed below. The soil cells were removed from the osmotic solutions, at which time soil samples for moisture determinations were taken from each cell as a check on the osmotic control of moisture content.
Estimation of Leaf Surface Area

The majority of needles on young Monterey pine seedlings are juvenile with only about 10% of the needles appearing in fascicles of three. For this reason, Kozlowski and Shumacher's (18) method could not be employed in estimating foliar surface. Instead a rather simple method was devised.

This method utilizes the assumption that the outline of any cross section along the length of any needle is triangular. This assumption seems valid as cross sections of the needles examined in the laboratory showed triangular nature.

To calculate the foliar surface, it is necessary that lengths and average "diameters" (base of triangle) of the needles be determined. The Monterey pine needles were divided into fifteen length classes, viz: 9.5, 9.0, 8.5, 8.0 . . . . 0.5 cm and the number of needles in each class was obtained. The average "diameter" (or length of the base of the triangular needle) of each length class was estimated using a microscope with a scale attached. The height of the triangle was also estimated. The cross sectional area of each needle could then be calculated and this multiplied by the length of the needle gave the area of each needle. The latter was then summed over all the length classes to give an aggregate foliar surface area of each seedling.
EXPERIMENTAL RESULTS AND DISCUSSION

Although two separate runs of this experiment were made, the results of only the first run are reported. This is because leakages developed in the membrane on a few of the soil cells and thus rendered the osmotic control of soil moisture rather unsatisfactory.

Due to the paucity of the data (Table 1), no statistical analysis was done on the data collected. Ideally the experiment should have been replicated at least once but time did not permit this.

Transpiration

Figures 7 and 8 depict the results of the transpiration measurement of 23-week old monterey pine seedlings as affected by soil temperature and soil moisture suction. There was a definite decrease in transpiration from the high to low soil moisture in accordance with most other studies reported (4, 10, 32, 53). Figure 7 shows quite clearly that even in the so-called wet range of soil moisture, a very pronounced decrease in transpiration occurred. At a soil temperature of 80°F, the transpiration rate was decreased by more than 50% in going from a soil moisture stress of 0.35 bars to 1.50 bars. At 50°F, the effect of increasing soil dryness was overshadowed by a low soil temperature. Only very small changes in transpiration occurred between 0.35 bars and 2.50 bars. The relationship of
Figure 7. Transpiration of 23-week old monterey pine seedlings at 2000 f. c. and 27° C as a function of soil moisture suction with temperature as a parameter.
Figure 8. Transpiration of 23-week old monterey pine seedlings at 2000 f. c. and 27° C as a function of soil temperature with soil moisture suction as a parameter.
transpiration and soil moisture suction was a linear one at 50°C in contrast to the curvilinear relationship observed at higher temperatures.

Table 1. Data showing the measured rates of transpiration, net photosynthesis and respiration of monterey pine seedlings at four soil temperatures and four soil moisture suctions.

<table>
<thead>
<tr>
<th>Soil Moisture Suction</th>
<th>Transpiration</th>
<th>Net photosynthesis</th>
<th>Respiration</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperature</td>
<td>Bars cm³/cm²/sec x 10⁻⁵</td>
<td>cm³/cm²/sec x 10⁻⁵</td>
<td>cm³/cm²/sec x 10⁻⁵</td>
</tr>
<tr>
<td>50°C</td>
<td>0.35</td>
<td>0.172</td>
<td>2.90</td>
</tr>
<tr>
<td></td>
<td>0.70</td>
<td>0.164</td>
<td>2.56</td>
</tr>
<tr>
<td></td>
<td>1.50</td>
<td>0.150</td>
<td>2.00</td>
</tr>
<tr>
<td></td>
<td>2.50</td>
<td>0.139</td>
<td>1.66</td>
</tr>
<tr>
<td>60°C</td>
<td>0.35</td>
<td>0.381</td>
<td>3.46</td>
</tr>
<tr>
<td></td>
<td>0.70</td>
<td>0.330</td>
<td>2.70</td>
</tr>
<tr>
<td></td>
<td>1.50</td>
<td>0.264</td>
<td>2.30</td>
</tr>
<tr>
<td></td>
<td>2.50</td>
<td>0.197</td>
<td>1.99</td>
</tr>
<tr>
<td>70°C</td>
<td>0.35</td>
<td>0.520</td>
<td>4.06</td>
</tr>
<tr>
<td></td>
<td>0.70</td>
<td>0.392</td>
<td>3.03</td>
</tr>
<tr>
<td></td>
<td>1.50</td>
<td>0.278</td>
<td>2.44</td>
</tr>
<tr>
<td></td>
<td>2.50</td>
<td>0.217</td>
<td>2.23</td>
</tr>
<tr>
<td>80°C</td>
<td>0.35</td>
<td>0.606</td>
<td>4.28</td>
</tr>
<tr>
<td></td>
<td>0.70</td>
<td>0.450</td>
<td>3.22</td>
</tr>
<tr>
<td></td>
<td>1.50</td>
<td>0.300</td>
<td>2.64</td>
</tr>
<tr>
<td></td>
<td>2.50</td>
<td>0.236</td>
<td>2.36</td>
</tr>
</tbody>
</table>
The plot of transpiration versus soil temperature in Figure 8 shows a steady increase in transpiration with increase in temperature. The steepness of the curves decreased with increasing soil moisture stresses. There was more than a 200% increase in transpiration in going from 50°F to 80°F at 0.35 bars whereas it was only about 50% for 2.50 bars of moisture suction. The transpiration rate was strikingly low at 50°F soil temperature on all soil moisture suctions but increased sharply at 60°F.

In explaining the effect of low soil temperature on transpiration, it is pertinent to consider root permeability, root growth, leaf surface area and retention and movement of water in the soil due to viscosity changes. Kuiper (27) has attributed non-linear effects of soil temperature on transpiration to a combination of physiological and viscosity factors. Figure 9 shows that root growth, and thus root permeability, is certainly a factor to be considered. There was a progressive decrease in the number of new roots developed from 0.35 bars to 2.50 bars after running the plants through all the four temperatures. Increased root growth implies more water absorbing surface with its concomitant increase in transpiration. The dormancy of the seedlings which was also broken seemed to increase leaf surface area.

The linear effect of soil moisture suction on transpiration at 50°F is definitely a viscosity effect. The latter tended to overshadow
Figure 9. Four soil cells enclosed in Visking membranes and removed from the osmotic solution at the end of the experimental run of 12 days showing new root developments during this period. Soil moisture suction increases from left to right, viz: 0.35, 0.70, 1.50 and 2.50 bars.
the effect of soil moisture suction.

Photosynthesis

With decreasing soil moisture, the photosynthetic rates decreased (Figure 10). The photosynthetic rates decreased steadily with the decreasing soil moisture, very rapidly at first, but less pronounced at the higher suction used. There was a sharp decline from 0.35 bars to 0.70 bars soil moisture suction. Like the transpiration rates, this demonstrates that photosynthesis decreases in the wet range of soil moisture which is in agreement with some reported studies (4, 10, 53).

Figure 11 shows a plot of photosynthesis versus soil temperature. With a probable exception of the curve at 0.35 bars, the curves all have essentially the same slope. Moreover, the relationship between photosynthesis and soil temperature seems linear.

The decrease in photosynthesis with increased soil dryness is accounted for by a decrease in stomatal opening caused by increased leaf water deficit. One of the most sensitive plant processes to leaf water deficit or drought is the stomatal opening. The sharp drop in the rates of photosynthesis from 0.35 bars to 0.70 bars will seem to bear this out. Premature closure of stomates means a reduction in CO₂ availability to the plants and hence, in photosynthesis.

The linearity of the photosynthesis versus soil temperature
Figure 10. Net photosynthesis of 23-week old monterey pine seedlings at 2000 f. c. and 27° C as a function of soil moisture suction with soil temperature as a parameter.
Figure 11. Net photosynthesis of 23-week old monterey pine seedlings at 2000 f.c. and 27° C as a function of soil temperature with soil moisture suction as a parameter.
The curve seems to support Kuiper's (27) finding that such linear relationship can be linked to viscosity effects. The seemingly non-linear nature of the curve at 0.35 bar may suggest a combination of physiological and viscosity factors. It is at this soil moisture suction that a majority of new roots developed within the experimental period.

Respiration

In general the respiratory rates of the young monterey pine seedlings decreased with increasing soil moisture suction (Figure 12). Contrary to the results obtained by Schneider and Childers (41) in apple trees, there was no increase in the respiratory rate at the onset of drought. The rate decreased steadily resembling the results obtained by Brix (4) in the tomato plant or in the loblolly pine before very high diffusion pressure deficits were reached. The decrease in the respiratory rates was relatively smaller than that in the photosynthetic rates with regards to soil moisture suction. At 0.35 bar soil moisture suction and 50° F soil temperature, the respiratory rate reached about 50% of the photosynthetic rate. At other suctions and identical temperature, the proportion did not change appreciably.

There is much disagreement and uncertainty in the literature concerning the dependence of respiration on soil moisture stresses. This result supports the notion that, at least within the soil moisture
Figure 12. Respiration of 23-week old monterey pine seedlings at 2000 f.c. and 27° C as a function of soil moisture suction with soil temperature as a parameter.
levels studied, the rate of respiration decreases steadily with soil dryness (4, 15, 32, 48, 53).

Figure 13 shows the dependence of respiration on soil temperature. There seems to be no clear-cut trend in this relationship. Removing the points obtained at 60°F, the relationship can be represented by straight, more or less, flat lines. Unfortunately, it was not possible, within the time limit, to obtain a few replicates which might ascertain a definite trend in the above relationship. From the data available, it is evident that the respiration rate fluctuated with increased soil temperature. It is not apparent what might be responsible for the trend obtained. One might conjecture that root respiration with increase in soil temperature might have something to do with it. The differences in leaf temperature with increasing soil temperature and soil moisture suctions were negligible.

Resistances in the Path of CO$_2$ and Water Vapour

The leaf resistances for CO$_2$ and water vapour were calculated according to Gaastra's (11) method using the simultaneously measured rates of photosynthesis, transpiration and leaf temperature. In these calculations, the assumption is made that the vapour pressure within the plant leaf is a function of temperature alone and that CO$_2$ concentration in the chloroplasts is approximately zero under
Figure 13. Respiration of 23-week old monterey pine seedlings at 2000 f. c. and 27°C as a function of soil temperature with soil moisture suction as a parameter.
conditions of CO$_2$ limitation or high light intensity. However, there is a serious doubt cast on the latter assumption under the conditions of light, $3.42 \times 10^{-4}$ erg sec$^{-1}$ cm$^{-2}$, and the CO$_2$ concentration, 375 ppm used in this experiment. An example of these calculations is given in Appendix II.

Subtracting the boundary layer resistance, 0.0632 sec cm$^{-1}$, from the total resistance gives the corresponding leaf resistances. Results of these calculations are shown in Table 2. These results show the combined effect that soil moisture suction and soil temperature have on leaf resistances. Figures 14-17 depict the results graphically.

The maximum diffusion rates to CO$_2$ and water vapour through the stomata were obtained at the highest soil water potential used and there was a progressive decrease with increasing soil moisture stress. There was about a 300% increase in stomatal resistance to both CO$_2$ and water vapour in going from 0.35 bars to 2.50 bars of soil moisture suction. In plots of stomatal resistances to both CO$_2$ and water vapour against soil temperature (Figures 15 and 17), the highest resistances were obtained at 50$^\circ$ F and this decreased very sharply at all suctions from 50$^\circ$ F to 60$^\circ$ F. The highest drop occurred at 0.35 bars. From 60$^\circ$ F to 80$^\circ$ F, the drop in stomatal resistance became gradual. Table 2 suggests that the stomata are quite wide open at 80$^\circ$ F as compared to 50$^\circ$ F even at the highest
Figure 14. Stomatal diffusion resistance to water vapour as a function of soil moisture suction with soil temperature as a parameter.
Figure 15. Stomatal diffusion resistance to water vapour as a function of soil temperature with soil moisture suction as a parameter.
Figure 16. Stomatal diffusion resistance to CO$_2$ as a function of soil moisture suction with soil temperature as a parameter.
Figure 17. Stomatal resistance to CO₂ as a function of soil temperature with soil moisture suction as a parameter.
suction investigated. It thus appears that the viscosity effects of soil temperature on water transport within the soil-water-plant system produces an end result very similar to that of increased soil moisture stress.

Table 2. Data showing the diffusion resistances in the paths of \( \text{CO}_2 \) and water vapour at four soil temperatures and four soil moisture suctions.

<table>
<thead>
<tr>
<th>Soil Temperature</th>
<th>Soil Moisture Suction-Bars</th>
<th>( r_s, H_2O ) sec cm (^{-1} )</th>
<th>( r_s, \text{CO}_2 ) sec cm (^{-1} )</th>
<th>( r_{me}, \text{CO}_2 ) sec cm (^{-1} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>50°C F</td>
<td>0.35</td>
<td>5.58</td>
<td>9.56</td>
<td>-1.00</td>
</tr>
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<td></td>
<td>0.70</td>
<td>6.19</td>
<td>10.61</td>
<td>-1.03</td>
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<td></td>
<td>1.50</td>
<td>7.17</td>
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<td>2.50</td>
<td>8.14</td>
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<td>0.754</td>
</tr>
<tr>
<td>60°C F</td>
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<td>2.66</td>
<td>4.51</td>
<td>2.81</td>
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<td></td>
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<td>2.50</td>
<td>6.03</td>
<td>10.34</td>
<td>2.71</td>
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<tr>
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<td>3.51</td>
<td>2.50</td>
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<td>5.75</td>
<td>9.85</td>
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<td>80°C F</td>
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<td>5.55</td>
<td>9.51</td>
<td>1.65</td>
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</tbody>
</table>
Table 2 shows the values of mesophyll resistances computed according to Gaastra's (11) method. These values are not in agreement with reports by Cox (8) and Fry (10). There was no trend in the relationship with soil moisture stress or soil temperature. Cox (8) reported that mesophyl resistance increased with soil moisture suction and that at high soil moisture stresses, mesophyl resistance significantly affected transpiration. No such conclusions could be drawn from this study. The validity of Gaastra's (11) method in calculating mesophyl resistance seems questionable, when applied to this experiment.

**Analysis**

A measure of efficiency of water use in photosynthesis is given by the ratio between transpiration and photosynthesis, a low value indicating more economical use of water. These ratios are shown in Table 3 and Figure 18 shows a plot of these ratios against soil temperature. From the table, it can be seen that the most economical use of water is at the lowest soil temperature investigated. A ratio of 0.59 at 0.35 bars and 50° F compared to 1.42 at 80° F and same suction signifies a "wastage" of water at the higher temperature. On the other hand, the water economy did not change appreciably between 60° F and 80° F at the 0.70, 1.50 and 2.50 bars respectively. However, the most economical use of soil moisture
Figure 18. Ratio of transpiration to photosynthesis as a function of soil temperature with soil moisture suction as a parameter.
is not necessarily the best for the plant especially if the soil moisture status is adequate.

Table 3. Ratios of transpiration to photosynthesis calculated for the different combinations of soil moisture and soil temperature.

<table>
<thead>
<tr>
<th>Soil Moisture Suction-Bars</th>
<th>Transpiration/Photosynthesis</th>
<th>Soil Temperature degrees F</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>50</td>
</tr>
<tr>
<td>0.35</td>
<td></td>
<td>0.59</td>
</tr>
<tr>
<td>0.70</td>
<td></td>
<td>0.64</td>
</tr>
<tr>
<td>1.50</td>
<td></td>
<td>0.75</td>
</tr>
<tr>
<td>2.50</td>
<td></td>
<td>0.84</td>
</tr>
</tbody>
</table>

Figure 18 shows a more or less exponential increase in ratio between transpiration and photosynthesis at 0.35 bar soil moisture suction. The ratio increased sharply between 50° F and 60° F at all suctions but these increases became almost negligible between 60° F and 80° F at 0.70, 1.50 and 2.50 bars soil moisture suctions. This seems to suggest that at these suctions and soil temperatures, both transpiration and photosynthesis were limited by the same factor, probably stomatal resistance. This is borne out by Figures 15 and 17. Here the slopes of the $r_s$, $CO_2$ and $r_s$, $H_2O$ versus soil temperature curves became almost negligible and were more or less
parallel to one another.

The curve obtained at 0.35 bar soil moisture suctions and the sharp increases between 50° F and 60° F can be attributed to physiological and viscosity factors. Based on the assumption that stomatal resistance was equally limiting CO₂ and water vapour transfer, certain computations were carried out (Tables 4, 5, 6 and 7). All the observed photosynthesis data obtained at 80° F were set as maximum values, 100%, and the percentages of the observed data for the remaining soil temperatures based on the maximised values obtained at 80° F were calculated. These values (Table 4) were used to adjust the transpiration rates (Table 5). The values thus obtained for transpiration were higher than the observed value. This suggests that more corrections have to be made. The calculated transpiration rates were then adjusted for the viscosity of water with the viscosity of water at 80° F as a reference. Table 6 shows the obtained values of transpiration corrected for stomatal resistance and viscosity of water. Corrections for a decrease in viscosity with temperature increase were not made for 1.50 and 2.50 bars suctions and 60° F and 70° F because as Figure 18 suggested, stomatal resistance was probably most dominant here. These corrected values were still higher than the observed values. Table 7 shows the numbers in percentages by which these values should be reduced to give the observed transpiration rates. It seems quite logical to account
Table 4. Net photosynthesis as percentages of the maximum obtained at soil temperature of 80° F.

<table>
<thead>
<tr>
<th>Soil Moisture Suction-Bars</th>
<th>Soil Temperature degrees F</th>
<th>Net photosynthesis as percentages of the maximum obtained at 80° F</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>50</td>
<td>60</td>
</tr>
<tr>
<td>0.35</td>
<td>68</td>
<td>81</td>
</tr>
<tr>
<td>0.70</td>
<td>80</td>
<td>84</td>
</tr>
<tr>
<td>1.50</td>
<td>76</td>
<td>87</td>
</tr>
<tr>
<td>2.50</td>
<td>70</td>
<td>84</td>
</tr>
</tbody>
</table>

Table 5. Observed transpiration rates adjusted for stomatal resistance by values calculated in Table 4.

<table>
<thead>
<tr>
<th>Soil Moisture Suction-Bars</th>
<th>Soil Temperature degrees F</th>
<th>Observed transpiration rate (cm³ cm⁻² sec⁻¹ x 10⁻⁵) adjusted for stomatal resistance by values in Table 4</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>50</td>
<td>60</td>
</tr>
<tr>
<td>0.35</td>
<td>0.412</td>
<td>0.491</td>
</tr>
<tr>
<td>0.70</td>
<td>0.360</td>
<td>0.378</td>
</tr>
<tr>
<td>1.50</td>
<td>0.228</td>
<td>0.261</td>
</tr>
<tr>
<td>2.50</td>
<td>0.165</td>
<td>0.198</td>
</tr>
</tbody>
</table>
Table 6. Adjusted transpiration rate of Table 5 further adjusted for viscosity of water with viscosity of water at 80° F as a base (\( \frac{\gamma_{50}}{\gamma_{80}} = 0.67, \frac{\gamma_{60}}{\gamma_{80}} = 0.78, \frac{\gamma_{70}}{\gamma_{80}} = 0.90 \))

<table>
<thead>
<tr>
<th>Soil Moisture Suction-Bars</th>
<th>50</th>
<th>60</th>
<th>70</th>
<th>80</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.35</td>
<td>0.276</td>
<td>0.383</td>
<td>0.518</td>
<td>0.606</td>
</tr>
<tr>
<td>0.70</td>
<td>0.241</td>
<td>0.295</td>
<td>0.381</td>
<td>0.450</td>
</tr>
<tr>
<td>1.50</td>
<td>0.153</td>
<td>--</td>
<td>--</td>
<td>0.300</td>
</tr>
<tr>
<td>2.50</td>
<td>0.111</td>
<td>--</td>
<td>--</td>
<td>0.236</td>
</tr>
</tbody>
</table>

Table 7. Percentages by which the adjusted or calculated transpiration rates should be multiplied to obtain the observed transpiration rates.

<table>
<thead>
<tr>
<th>Soil Moisture Suction-Bars</th>
<th>50</th>
<th>60</th>
<th>70</th>
<th>80</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.35</td>
<td>62</td>
<td>99</td>
<td>101</td>
<td>100</td>
</tr>
<tr>
<td>0.70</td>
<td>68</td>
<td>112</td>
<td>103</td>
<td>100</td>
</tr>
<tr>
<td>1.50</td>
<td>98</td>
<td>--</td>
<td>--</td>
<td>100</td>
</tr>
<tr>
<td>2.50</td>
<td>125</td>
<td>--</td>
<td>--</td>
<td>100</td>
</tr>
</tbody>
</table>
for this by the increased root growth with increased soil temperature obtained during the course of the experiment (Figure 9). In order to obtain the observed transpiration rate at, say 50° F and 0.35 bars suction, the calculated value of 0.312 cm³ cm⁻² sec⁻¹ should be reduced to 62% of this value. This is to say that the transpiration rate at 80° F of 0.606 cm³ cm⁻² sec⁻¹ could have been reduced to 62% of this value had it not been for the increased root development at this temperature. These correction factors for root growth increase with increasing soil moisture stress and soil temperature. Clearly these corrections are quite valid as one would expect root growth to increase with soil temperature. These simple calculations lend support to the suggestions that stomatal diffusive resistance, viscosity of water and root growth are major factors to be considered in explaining some of the results obtained in this experiment.
SUMMARY AND CONCLUSIONS

Many studies have been made on the effects of soil water suction on transpiration, photosynthesis and respiration. The techniques that were used, however, have left much to be desired. An experimental evaluation requires the ability to control the soil moisture content at a constant value.

A special apparatus was developed in which the soil moisture levels of several soil cells could be maintained independently by various osmotic solutions at a selected temperature. The effect of four soil moisture suctions and four soil temperatures on the rates of transpiration, photosynthesis and respiration was studied. Carbowax 6000 was used as the osmotic solution and soil temperature was controlled with a water bath. Transpiration was determined by a constant water level device which recorded the total amount of water used by the plant. Photosynthesis and respiration were measured using an infra-red gas analyzer. A determination of stomatal resistances to CO$_2$ and water vapour was also made.

In general with increasing soil moisture suction, the photosynthetic, respiratory and transpiration rates also decreased. Even in the so-called wet range of soil moisture, photosynthesis and transpiration decreased sharply from 0.35 bars to 0.70 bars soil moisture suctions. This is a direct consequence of the
sensitivity of stomates to soil water suction.

The rates of transpiration increased faster than the rate of photosynthesis (see ratios Table 3) with increasing soil temperature. The rates increased most at 0.35 bars soil moisture suction and at all suctions from 50° F to 60° F.

Where the ratio of transpiration to photosynthesis is constant as between 60° F and 80° F at all soil moisture suctions except 0.35 bars, the same process is limiting (probably stomatal control). At 0.35 bars soil moisture suction, physiological and viscosity effects of soil temperature are to be considered.

There is no reason to believe that the plant changed above ground due to the environmental conditions of the experiment. Therefore the activity of the root is temperature dependent and suction dependent. At high suctions, the temperature effect is small, at low suction the temperature effect is large.

At suctions higher than 0.70 bars, the diffusion process is stomatal controlled.
BIBLIOGRAPHY


APPENDICES
Figure 19. Osmotic pressure of carbowax 6000 solutions (After Zur, 1961).
APPENDIX II

Example of Calculations of Diffusion Resistances in the Path of CO₂ and Water Vapour

\[(r_s + r_a)_{H_2O} = \frac{[H_2O]_{int} - [H_2O]_a}{T}\]  \hspace{1cm} (5)

The following data were obtained for a soil temperature of 50°F and soil moisture stress of 0.35 bars.

Transpiration \(T\) = \(10^{-5} \times 0.172 \text{ grams } H_2O/cm^2/sec\).

Leaf Temperature = 21.5°C

Saturation water vapor density at 21.5°C

\[e_s = 0.01888 \times 10^{-3} \frac{gm}{cm^3}\]

Air Temperature = 70°F or 21.1°C

\[e_a = e_s (R.H) = (0.01834 \times 10^{-3})(0.50) = 0.00917 \times 10^{-3} \frac{gm}{cm^3}\]

\[(r_s + r_a)_{H_2O} = \left(\frac{0.01888 - 0.00917}{10^{-5} \times 0.172}\right) \times 10^{-3} \frac{gm \cdot cm^{-3}}{gm \cdot cm^{-2} \cdot sec^{-1}} = 5.54 \text{ sec cm}^{-1}\]

\[r_a, H_2O = 0.0632 \text{ sec cm}^{-1}\]

\[r_s, H_2O = 5.58 \text{ sec cm}^{-1}\]
\[ r_{a, H_2O} = \frac{[H_2O]_{surf} - [H_2O]_a}{E} \]  

Evaporation \( E = 10^{-4} \times 0.7564 \text{ gm cm}^{-2} \text{ sec}^{-1} \)

Temperature of blotting paper = 21.5°C

Saturation water vapour density at 21.5°C =

\[ 0.01888 \times 10^{-3} \text{ gm cm}^{-3} \]

\[ [H_2O]_a = 0.00917 \times 10^{-3} \text{ gm cm}^{-3} \]

\[ r_{a, H_2O} = \frac{0.01888 - 0.00917}{2 \times 10^{-4} \times 0.7564} \times 10^{-3} \text{ gm cm}^{-3} \]

\[ = 0.0632 \text{ sec cm}^{-1} \]

\[ r_{s, CO_2} = \frac{D_{H_2O}}{D_{CO_2}} \left[ (r_a + r_s)_{H_2O} - r_{a, H_2O} \right] \]

\[ = \frac{0.24}{0.14} \left[ 5.642 - 0.0632 \right] \]

\[ = 1.714 \times 5.579 \]

\[ = 9.562 \text{ sec cm}^{-1} \]

Calculation of mesophyll resistance

\[ P = \frac{[CO_2]_a - [CO_2]_{Chl}}{(r_a + r_s + r_{me})_{CO_2}} \]
Data Collected:

\[ r_{a, CO_2} = \frac{D_{H_2O}}{D_{CO_2}} \cdot r_{a, H_2O} \]

\[ = \frac{.24}{14} \times .0632 \text{ sec cm}^{-1} = 1.714 \times .0632 \]

\[ = .1083 \text{ sec cm}^{-1} \]

\[ r_{s, CO_2} = 9.5620 \text{ sec cm}^{-1} \]

\[ P = 2.90 \times 10^{-5} \text{ cm}^3 \text{ cm}^{-2} \text{ sec}^{-1} \]

\[ [CO_2]_a = .375 \times 10^{-3} \text{ cm}^3 \text{ CO}_2/\text{cm}^3 \text{ air} \]

\[ [CO_2]_{ch} = 0 \]

From Eq. (8):

\[ 2.90 \times 10^{-5} \text{ cm}^3 \text{ cm}^{-2} \text{ sec}^{-1} = \frac{.375 \times 10^{-3}}{\left(9.562 + .1083 + r_{me, CO_2}\right)} \]

\[ \left(9.562 + .1083 + r_{me, CO_2}\right) = 12.93 \text{ sec cm}^{-1} \]

\[ r_{me, CO_2} = 3.26 \text{ sec cm}^{-1} \]
Figure 20. Moisture release curve of Apt-Shanahan soil used in this study.
Figure 21. A schematic drawing of the apparatus used.