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Relations Between Transpiration, Leaf Temperatures, and Some Environmental Factors

Ronald Kay Tew
Utah State University

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RELATIONS BETWEEN TRANSPIRATION, LEAF TEMPERATURES,

AND SOME ENVIRONMENTAL FACTORS

by

Ronald Kay Tew

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

of

MASTER OF SCIENCE

in

Soil Physics

UTAH STATE UNIVERSITY
Logan, Utah

1962

ACKNOWLEDGMENTS

I wish to express my appreciation to Dr. Sterling A. Taylor for his help and encouragement throughout this study. Also, the assistance of Dr. Gene Miller, Dr. Herman H. Wiebe, and Professor Gaylen Ashcroft has been of great value in furthering this project.

I am especially indebted to my wife who has been so patient and willing to help in every possible way. Without her cooperation this work could not have been carried on.

Appreciation is also extended to the Western Regional Research Project W-67 for their financial assistance which made it possible for me to continue my graduate work.

<div align="right">Ronald K. Tew</div>

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INTRODUCTION

Transpiration is the loss of water in vapor form from a plant. This is essentially the same process as evaporation except that it is modified by plant structure. Large quantities of water are removed from the soil, transferred through the conducting tissues of the plant, and dissipated into the air each day. As soon as the water is lost to the atmosphere, it becomes unavailable for human use.

Few people are aware of the actual magnitude of this process. Over 95 percent of the water absorbed by the plant is lost through transpiration, the other 5 percent being used in photosynthesis and as a plant constituent. Herbaceous plants may transpire several times their own volume of water in a single day. Many forests lose over 20 inches of water in a year. Such large quantities, when dissipated in vapor form, are sufficient to modify the climate in the surrounding area.

Insufficient research work has been done in the field of transpiration to thoroughly understand the significance of this process. This is evident from the many contradictions which are present in the work that has been done. Many of the conflicting ideas may have resulted from the lack of understanding of how environmental factors to which plants are exposed affect transpiration, or they may have resulted from inadequate equipment to satisfactorily study these factors.

With this in mind, an experiment was set up to gain basic information on the specific influence several environmental factors have on transpiration. The first part of the experiment was rather broad in scope. The influence that soil temperature, air temperature, relative

humidity, and wind have on transpiration rate, leaf temperature, and
stem temperature was studied with all but one of the environmental
factors being held constant. Leaf and stem temperatures were measured
throughout each experiment to see if the difference between leaf and
stem temperatures could be used as an indication of how rapidly
transpiration was taking place.

The second phase of the experiment was more specific, testing in
more detail how the interactions between soil temperature, relative hu-
midity, and air temperature affect transpiration rates under controlled
conditions. Three levels of each environmental factor were studied in
all possible combinations.

Also, preliminary testing was done on several research ideas. The
most fruitful of these appeared to be: (1) the use of fat solvents to
check stomatal opening under varying conditions of moisture, temperature,
and light; and (2) cetyl alcohol additions to the soil to reduce
transpiration.

REVIEW OF LITERATURE

Significance of Transpiration

The question of how important transpiration is to plants has been a
long debated question. Transpiration has been considered to be nothing
more than a necessary evil by Curtis (1926, 1936c), and Meyer et al.
(1960). Clements (1934), Wright (1939), and Freeland (1937) have indi-
cated that transpiration is one of the more important processes taking
place in the plant and that it is on a level comparable to photosynthe-
sis and respiration.

Benefits of transpiration

Some of the benefits ascribed to the process of transpiration are
as follows: translocation of water to all parts of the plant, translo-
cation of minerals, dissipation of radiant energy which cools the leaves,
reduction of plant disease, and action as a buffer in controlling plant
processes.

Translocation of water in plants. Maximov (1929) indicates that
transpiration is probably of major importance in translocating water to
the leaves. He states that there has to be a certain saturation of the
plant for functions like flowering and fruiting, and that optimum turgor
can be maintained by transpiration.

Meyer et al. (1960) state that although under conditions of high
transpiration, the movement of water in plants is more rapid than under
conditions of low transpiration, translocation of water continues even
though the transpiration rate is negligible. Sufficient water for

metabolic processes is supplied to the cells at night, after transpi-
ration has nearly ceased; however, metabolic processes have been slowed
down so that less water is necessary. It may be that water transported
through the plant by transpiration is not the water used in metabolic
processes; rather, it might pass out of the plant without entering into
such processes.

Absorption and translocation of minerals. At the present time, re-
searchers are nearly equally divided as to the part played by transpi-
ration in translocating minerals. The confusion that exists is probably
caused by the failure to eliminate all other factors in the metabolism
of the plant which might affect the absorption and translocation of
minerals.

Wright (1939) determined the effect of transpiration upon the
absorption of mineral salts by analyzing standardized culture solutions
in which plants had been growing under conditions of high and low
transpiration. The results of his experiment are shown in Table 1.

Table 1. Amount of mineral absorption with high transpiration and low
transpiration. (Wright, 1939, p. 173)

Treatment	Water Absorbed	Phosphorus Absorbed	Calcium Absorbed	Nitrates Absorbed	Potassium Absorbed
	cc	mg	mg	mg	mg
Jar 1 - High Trans.	330	13.6	25.0	41.4	35.6
Jar 2 - Low Trans.	150	8.6	15.0	41.0	27.8
Jar 2 - High Trans.	335	11.2	27.0	46.8	56.4
Jar 1 - Low Trans.	165	9.6	13.0	41.8	52.8

In all cases a higher rate of transpiration was accompanied by an in-
creased absorption of the various ions.

Another worker showing similar results states:

The data indicate that an increase in the absorption of
water results in an increase in mineral absorption, that
different mineral ions are not absorbed at the same rate,
and that the rate of absorption of each ion varies with
the kind of plant used. As to how transpiration acts in
increasing mineral absorption, whether by removing the
minerals that get into the xylem vessels of the root cells
or increasing the concentration at or near the surface of
the roots is still in the realm of speculation. (Freeland,
1937, p. 374)

Contrary to the preceding results, Meyer et al. (1960) indicate

that there appears to be no correlation between the rate of transpiration

and the rate of absorption of mineral salts. Also, there is no evidence

that inadequacies in the distribution of absorbed mineral salts through-

out the plant ever result from low transpiration.

The results of Broyer and Hoagland (1943, p. 263) are shown in

Table 2.

Table 2. Influence of transpiration and aeration of the culture medium
on absorption of salt by barley plants.

Experimental conditions	Total salt absorbed		Water absorbed
	K	Halide	
	meq	meq	ml
Low humidity, light; culture aerated	8.47	7.53	775
High humidity, light; culture aerated	8.20	7.30	225
High humidity, light; culture unaerated	3.84	3.00	175
High humidity, dark; culture aerated	7.26	6.12	75
High humidity, dark; culture unaerated	3.57	3.12	25

Their conclusion was that the supply of oxygen furnished to the roots

influenced the total absorption of the mobile ions, K and Br, to a

greater degree than did the atmospheric environment controlling the

absorption and transpiration of water.

Dissipation of radiant energy. Transpiration is an energy-consuming
process; therefore, it is naturally assumed that the evaporation of water
from the leaves would be effective in dissipating the energy being sup-
plied to them. However, Maximov (1929) indicates that too much im-
portance should not be attached to the value of cooling by transpiration
as plants could undoubtedly adapt themselves to endure higher temper-
atures.

> The dissipation of 0.65 g.-cal. of heat would require the
> evaporation of 0.0011 g. of water per square centimeter
> of leaf area per minute. This is equivalent to 6.6 g. of
> water per square decimeter of leaf area per hour, a rate
> of transpiration which is seldom attained by plants for
> any sustained period of time under natural conditions.
> (Meyer et al., 1960, p. 99)

Curtis (1936c) reported that the air is mostly transparent to infra-
red radiation, and that plants may lose or gain heat by radiation to or
from distant objects which may account for the cooling of leaves by
radiation more than by transpiration. The conclusion from these
statements seems to be that although transpiration may account for some
of the heat being dissipated, it plays no essential role because radi-
ation can be dissipated by physical means.

Shull (1930) found that probably 55 percent of the heat absorbed
by the leaf was dissipated by transpiration while only 45 percent was
dissipated by conduction, reradiation, and other means. He calculated
that the rate of temperature rise in a leaf in which no internal
transformation of energy was taking place would be about 35 C per minute
on the average. In case of heavy textured leaves, the temperature rise
with zero dissipation of absorbed energy would be less, and with thin
leaves would be more.

Wallace and Clum (1938) indicate that enough heat energy is supplied

to the leaf by the sun to burn it up if none were dissipated through radiation and cooling by transpiration. Clum (1926) found that leaves may be 13 C above air temperature in direct sunlight. If this temperature was added to a reasonable mid-summer temperature of 35 C, the leaf must then be at a temperature near 48 C. According to Wallace and Clum, this is so close to lethal that there can be little doubt that transpiration is significant in cooling the leaves.

Briggs and Shantz (1916) found the direct solar radiation received by the plants was not sufficient to account for observed transpiration during the midday hours. In some of the small grains the energy dissipated through transpiration was twice the amount received directly from the sun, indicating energy was also being supplied from other sources. Even on bright days, other sources of energy such as indirect radiation from the sky and surrounding objects contributes materially to the energy dissipated through transpiration. These statements are based on the assumption that the energy dissipated through transpiration is equal to the product of the transpiration in grams and the latent heat of vaporization of water.

Transpiration as a buffer. Clements (1934) states that because leaf temperatures vary when air temperature changes, it would seem obvious that the transpiration intensity fluctuates according to the fluctuation in light intensity. He supports the view that transpiration consumes a large amount of energy which cools the leaves, making possible a more uniform temperature. The cooling tends to act as a buffer in keeping temperature variations from becoming too great and markedly affecting the metabolic processes in the plant because of irregular rates of sunlight. This buffering action helps maintain favorable leaf

temperatures for photosynthesis to take place at a maximum rate. At 25
to 30 C, carbon dioxide is often a limiting factor to photosynthesis.
If temperatures were allowed to rise to 50 C, there would be a greater
deficiency of carbon dioxide because the solubility is decreased as
temperatures rise, and so it would definitely limit photosynthesis.

Detrimental effects of transpiration

Under conditions of deficient soil water or during periods of high
transpiration rates, even when the soil water supply is adequate, transpi-
ration results in a loss of water content in the plant and the turgidity
of the cells is reduced. Prolonged periods of drought conditions will
ultimately result in the desiccation of the plant with the consequent
death. If the plant is not desiccated to the death point, wilting alone
is enough to cause the stomata to close and reduce the intake of the
carbon dioxide necessary for photosynthesis.

It is probably true that lack of water in a plant caused by transpi-
ration is more often the limiting factor in plant growth than any other
single factor. Futhermore, deficiency of water caused by transpiration
is probably responsible for the death of more plants each year than any
other single cause.

> In the reforestation program now being carried on by various
> states and federal agencies, many millions of tree seedlings
> are planted each year. An extremely large number of these
> planted seedlings are killed the first year or two after
> planting. One of the major causes of the fatality is the
> inability of the seedlings to resist drought. (Schonmeyer,
> 1939, p. 447)

A logical question at this point is, why has transpiration not been
eliminated by natural selection if it is so harmful to the plant? The
fact is that many modifications have taken place which make it possible
for plants to adapt themselves to areas in which they could not exist

without these modifications. However, such processes as photosynthesis could not be carried on if transpiration were completely eliminated, because for photosynthesis, moist cells must be exposed to the air to absorb the carbon dioxide. Since these cells must be moist to absorb the carbon dioxide, it is inevitable that a certain amount of water loss is going to take place.

Environmental Factors Affecting Transpiration

Many environmental factors influence the rate at which transpiration proceeds. Solar radiation, the temperature of the air surrounding the leaf, relative humidity, wind velocity, and the availability of soil moisture all have a direct influence on transpiration rates.

Solar radiation

Solar radiation refers to the visible light and other forms of radiant energy reaching the earth from the sun. Indirect radiation from the sky and surrounding objects would have to be considered a part of the total radiation reaching the earth. Not all of this total radiant energy is available for use in the process of transpiration, however. A large portion of the energy is lost by conduction, convection, and reradiation.

The difference between the incoming and the outgoing radiation is called net radiation. This is the portion that supplies the necessary energy for transpiration. Tanner (1957, p. 221) states that "during the daytime, part of the net radiation usually goes into heating the air, (sensible heat), a small amount goes into heating the soil and vegetation, and the remainder goes into evapotranspiration." A difficult problem here is to find what portion of the total net radiation is used for evapotranspiration and what for heating the air and soil.

The study of how solar radiation affects transpiration has for the most part been confined to a consideration of the influence light has on the regulation of stomatal movement. Some investigators have found that light has a direct accelerating action on transpiration aside from the effect brought about by stomatal movement. According to Martin (1940, p. 351), this additional "accelerating effect of radiation on transpiration may be due to heating of the leaves and partly to a change in the permeability of the protoplasm." Also, light intensity affects leaf structure which significantly influences transpiration.

Influence of light on stomatal regulation. The stomata of most species open upon exposure to light and close in its absence. Most commonly, therefore, the stomata are open in the daytime and closed at night. This accounts, to a large extent, for the large difference in transpiration rates between day and night as is shown in Figure 1.

Time
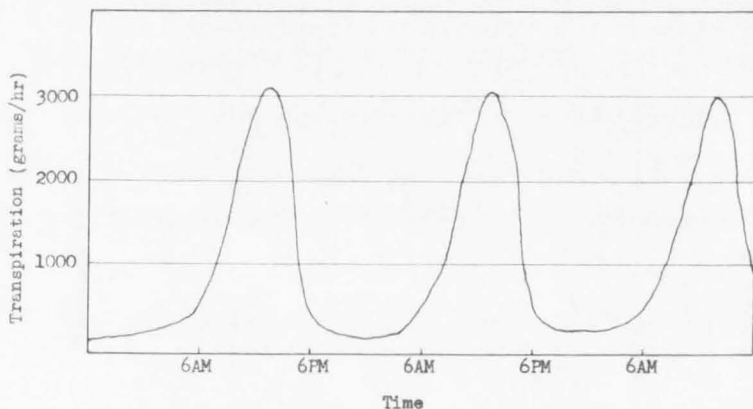
Figure 1. Daily periodicity of transpiration of alfalfa on three successive days under approximately standard-day conditions. Transpiration expressed as grams per hour per 6-foot-square plot of alfalfa. (Meyer et al., 1960, p. 94)

Although many theories have been proposed to give an adequate explanation of the influence light has on stomatal opening, the osmotic theory now seems to be most widely accepted. It is known that guard cells (cells surrounding stomata) contain chlorophyll in contrast to the ordinary epidermal cells. Also, these guard cells contain starch. The quantity present is not constant, however. The maximum starch occurs during the night, decreasing rapidly as daylight increases. The sugar content increases rapidly at this time, indicating the conversion from starch to sugar is taking place. Loftfield (1921) indicates that this conversion is an enzymatic process and should therefore follow the same law in regard to rate of reaction as any other chemical process.

As the starch is converted to sugar, an increase in the osmotic pressure of the guard cells increases their diffusion-pressure deficit relative to that of the adjacent cells. Water therefore moves into the guard cells, increasing their turgor, which in turn leads to a widening of the stomatal aperture. This would be the most simple explanation of how stomatal opening is influenced; however, the summary of Botany class notes[1] indicate that many factors may be involved in addition to starch conversion. Light may induce photosynthesis in the leaf mesophyll, which would reduce the carbon dioxide in the leaf mesophyll and guard cells, causing a higher pH; starch may then be converted to sugar raising the osmotic pressure, increasing the turgor of the cells, and causing opening. Whatever the case might be, transpiration increases because of decreased resistance as stomata open.

Leaf temperature. Bonner (1959, p. 449) indicates that "the rate of transpiration is in a great degree regulated by the temperature of the

[1]Botany 121, Utah State University, Winter Quarter, 1960.

leaf, which in turn determines the vapor pressure of water at the leaf
surface." If the vapor pressure of the leaf and the atmosphere is
known, then the vapor-pressure difference can be established. The vapor
pressure of the atmosphere can be easily determined if the air temper-
ature and humidity are known, but the vapor pressure of a leaf presents
a more difficult problem. It is difficult to obtain the leaf temper-
ature because of large and rapid changes that take place as is shown in
Figure 2.

Time (minutes)
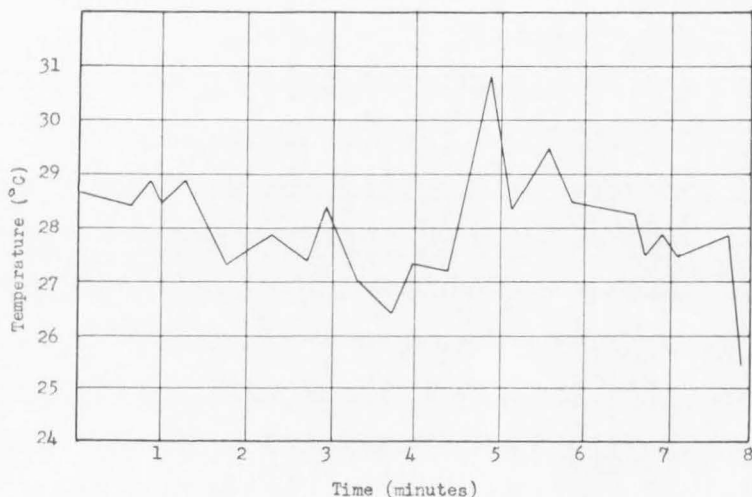
Figure 2. Curve showing rapidity of natural changes in temperature
of a leaf due to varying air currents. Air temperature immediately pre-
ceding these readings was 20.5 C, immediately afterwards, 19.7 C.
(Curtis, 1936b, p. 353)

Since the leaf has a small heat capacity and contains only a small
quantity of water, its temperature can rise or fall rapidly with chang-
ing environmental conditions. Curtis (1936a, p. 597) developed curves

showing the equivalent effects of raising the leaf temperature in terms
of lowering the relative humidity. These are shown in Figure 3.
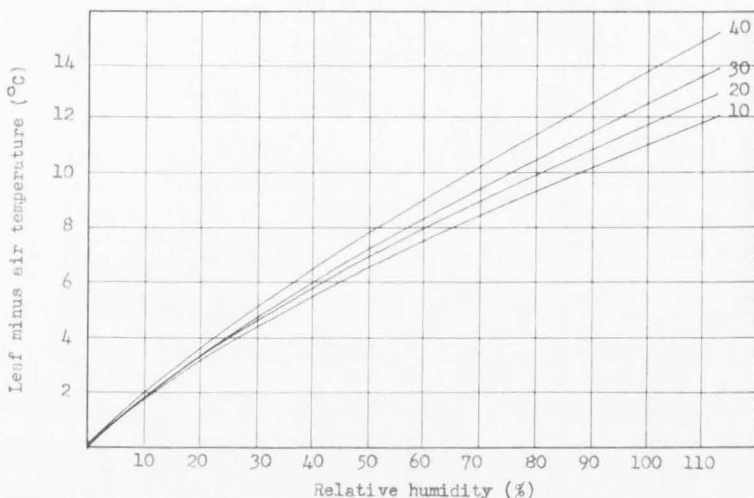
Figure 3. Effect on vapor-pressure gradient of raising leaf temper-
ature above air temperature in terms of lowering the relative humidity.
Leaf temperatures at start are at the four air temperatures 10, 20, 30,
and 40 C. Intercellular atmosphere of leaf remains saturated.

These curves give a picture of how leaf temperatures actually influence
the vapor-pressure gradient when there is a difference between leaf
and air temperature. An example of how they are used may increase the
clarity. With leaf and air temperatures both at 20 C and assuming 100
percent relative humidity in the intercellular spaces of the leaf and in
the atmosphere, the vapor pressure of the leaf and air will be equal to
17.36 mm of mercury. If the leaf temperature was increased 5 C, the
vapor pressure would then be equivalent to 23.52 mm of mercury. This
would increase the vapor-pressure gradient from leaf to air 6.16 mm which

would be equivalent to lowering the relative humidity of the air by 35.5 percent. The relative effect on the transpiration rate would be greater at higher air humidities than at low humidities because a small increase in leaf temperature at high humidities may double the vapor-pressure gradient while only causing a slight increase at lower humidities.

Protoplasmic changes. When temperatures are raised in the plant because of high intensities of solar radiation, the permeability of the protoplasm is directly affected. This influences the rate at which water is absorbed into the plant. Resistance to flow is decreased because the viscosity is reduced as the temperature rises. Protoplasm has a high percentage of water, and so it is apparent that resistance would be reduced and transpiration rates would increase.

In field experiments by Bloodworth et al. (1956), rapid changes in the rate of water movement resulted from a temporary cloud cover. The plant response to such conditions was found to be rapid and always resulted in slower rates of water movement. This may be because of rapid changes in plant temperatures that take place thus affecting the protoplasm.

Permeability to water might also be affected by the concentration of solutes in plant cells. The following observations were made while working with the hardening of plants to low water supplies:

> Plants having more concentrated sap transpired more rapidly than plants having less concentrated sap when the treatment resulting in increased concentration also resulted in a marked increase in permeability to water. This increased permeability to water more than offset the effect of high concentration on transpiration rates; therefore, hardened plants transpired from two to four times more rapidly than did the unhardened plants in spite of their higher osmotic concentration. (Boon-Long, 1941, p. 342)

Effect on leaf structure. The intensity of solar radiation in-
fluences leaf structure which affects transpiration rates. Even leaves
on the same plant might have different rates because of differences in
the structure of leaves that are shaded (lower leaves) and those in di-
rect sunlight (upper leaves).

> The sun leaves are usually narrower than the shade leaves in
> proportion to their length. Another difference between the
> sun leaves and the shade leaves of many species consists in
> the manner in which the margins of the former are recurved.
> In many instances the under leaf surfaces of sun leaves are
> strongly concave, while that of shade leaves is nearly plane.
> (Bergen, 1904, p. 228)

This could affect the angle the rays from the sun hit the leaf and there-
fore the heating which takes place. Table 3 shows how several different
plants had their sun leaves and shade leaves exposed to different
environmental conditions and how this affected transpiration rates.

Table 3. Transpiration from sun and shade leaves. (Bergen, 1904, p. 293)

| | Ratio | Loss of sun leaves | | |
| | | Loss of shade leaves | | |
	Olea	Pistacia	Q.Ilex	Rhamnus
I. Sun leaves in sun and shade leaves in shade.				
Maximum	3.04	4.60	10.70	7.00
Minimum	1.45	2.20	1.85	2.25
Average of all values obtained	2.10	3.70	6.35	5.91
II. Both kinds of leaves in full sunlight.				
Maximum	2.15	2.24	3.90	1.42
Minimum	1.17	1.00	0.96	0.52
Average of all values obtained	1.47	1.70	2.04	0.98
III. Both kinds of leaves in shade.				
Maximum	0.97	2.58	2.70	2.61
Minimum	0.81	0.68	0.93	1.17
Average of all values obtained	0.91	1.87	1.86	1.86

It can be seen that under nearly all conditions, sun leaves transpire

more rapidly than shade leaves.

Leaf structure might also be affected by species differences as can
be seen by the following statement:

> In some leaves, such as pine needles, the stomates are sunken
> in grooves or pits. This reduces transpiration because the
> pits become more or less saturated with water vapor, increasing
> the length of the diffusion path from intercellular spaces to
> outside air. Loblolly pine, for example, has only about half
> the transpiration rate per unit of leaf surface as deciduous
> species such as red oak. (Kramer and Kozlowski, 1960, p. 294)

Atmospheric temperature

Air temperatures are raised not only by solar radiation, but also
by radiation from all other objects in the universe. Winds sometimes
bring in heated air from desert areas. The sky should not be considered
as merely a source of energy loss, but also a source of energy gain be-
cause the earth receives energy from the sky during the day just as it
does from the sun; therefore, although solar radiation is the dominant
factor in controlling air temperature, other factors should be accounted
for when trying to determine potential transpiration rates.

The rate of transpiration becomes more rapid as air temperature
rises because the steepness of the vapor-pressure gradient from plant
tissue to air is increased. A significant part of the increase is caused
by the heating of the leaves above ambient temperature. Also as previous-
ly stated, protoplasmic changes occur because of variations in viscosity.

Relative humidity

As the air temperature changes, relative humidity, the ratio of the
actual vapor pressure of the air to the saturated vapor pressure at the
same temperature, also fluctuates. This may influence the vapor-pressure
gradient from plant tissue to air. The largest part of the gradient from

the soil to the air is normally found at the step from leaf to air. Most plants, including halophytes, rarely have a diffusion-pressure deficit in excess of 50 atmospheres, while the atmosphere usually greatly exceeds this as can be seen in Table 4. This shows that the bulk of the resistance to water loss, even at high humidities, is located in the loss from the leaf to the air.

Table 4. Relations between relative humidity and the diffusion-pressure deficit of the atmosphere. Air temperature is held constant at 20 C. (van der Homert, 1948, p. 148)

Relative humidity	D.P.D[a]
%	Atmospheres
99	13.4
97	40.6
90	140.5
80	297.5
50	924.2
10	3070.3

[a]Diffusion-pressure deficit.

Some workers have tried to state quantitatively the effect relative humidity has on transpiration. Thut (1938) stated that the water loss from plants is inversely related to the relative humidity. Bialoglowski (1935) found approximately a straight line relationship between transpiration and humidity at 30 C in the range between 60 and 95 percent relative humidity, with a very pronounced difference below 60 percent.

Influence of temperature. The strain under which an organism is placed in maintaining a water balance during temperature changes is more clearly shown by noting the vapor-pressure deficit than by recording the relative humidity. The vapor-pressure deficit undergoes a much greater variation than does the relative humidity during temperature changes. (Anderson, 1936, p. 280)

This can be seen by referring to Table 5. When the temperature rises from 20 to 30 C, assuming no change in the vapor pressure of the

Table 5. Relations between relative humidity and vapor pressure.
         (Anderson, 1936, p. 280)

Air temperature	Relative humidity	Vapor pressure	Vapor pressure deficit
C	%	mm Hg	mm Hg
20	70	12.28	5.26
30	38.6	12.28	19.54

atmosphere, a change less than 32 percent takes place in relative humidi-
ty, but more than 370 percent change in the vapor-pressure deficit takes
place. This indicates that the vapor-pressure deficit is a more sensi-
tive indicator of the water vapor conditions of the atmosphere and under-
goes greater variations for temperature changes than does the relative
humidity.

As has been stated by Meyer et al. (1960), Kramer and Kozlowski
(1960), Steward (1959), and Curtis (1936), a common mistake in the liter-
ature dealing with the effect relative humidity has on transpiration is
the claim that a rise in air temperature increases transpiration because
it lowers the relative humidity of the atmosphere. This change in rela-
tive humidity or vapor-pressure deficit of the atmosphere around the
leaf does not lower the vapor pressure of the atmosphere and has no
tendency to increase transpiration unless the leaf is also heated. The
heating of the leaf alone is responsible for increased transpiration,
because the total water content of the atmosphere does not change as the
temperature of the air changes.

Influence on radiation. Curtis (1936, p. 356) states that "a high
content of water vapor in the atmosphere is effective in absorbing infra-
red radiation, both from the sun and to the earth. This energy is

reradiated to the leaves, thus tending to raise their temperature." How-
ever, some of the heat gained by the leaf is dissipated by transfer to
the surrounding air, and hence leaf temperature depends greatly on the
rate of air movement over the leaf.

Wind velocity

> Although the amount of transpiration from a leaf is
> predominantly a function of the amount of energy received
> by the leaf, wind can influence the manner in which the
> leaf loses energy and thus can affect transpiration signifi-
> cantly. Wind influences transpiration by removal of the
> so-called 'layer' of saturated air from the surface of the
> leaf, and also by changing the temperature of the leaf.
> (Woolley, 1961, p. 112)

The cooling effect of wind decreases the steepness of the vapor-pressure
gradient and tends to reduce transpiration while removal of the saturated
air around the leaf increases transpiration. This makes it difficult to
determine exactly what net effect wind will have under any given con-
ditions.

Bange (1953) states that "in wind the transpiration rate should be
directly proportional to the stomatal aperture, at least if the wind is
strong enough to blow away all external diffusion resistances." Martin
and Clements (1935) indicate that winds of relatively low velocities are
able to increase the transpiration rate to a maximum. This can be seen
in Figure 4.

Meyer et al. (1960) indicate that the swaying of branches and shoots,
and fluttering of leaf blades in the wind also contribute to higher
rates of transpiration in moving than in quiet air. The bending and
moving may increase the rate of water loss in part by compressing the
intercellular spaces, thus forcing water vapor and other gases out
through the stomata.
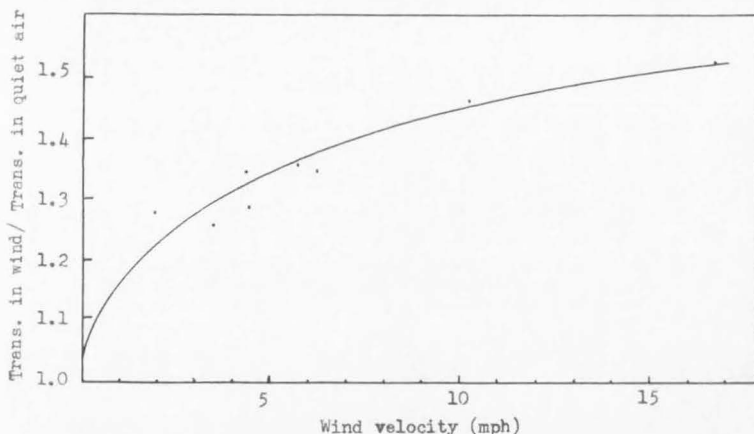
Figure 4. The effect of wind on the transpiration rate of sun-
flower plants. (Martin and Clements, 1935, p. 620)

The drying action of wind causes wilting of the leaves to occur
rapidly. Wallace and Clum (1938, p. 84) state that "when the wilting
is most severe, the leaves hang limply in a vertical position, and the
absorption of energy from the sun is greatly reduced. This drooping may
be of value in preventing excessive heating of the leaves."

Soil factors

Soil conditions influencing water availability also influence rates
of water loss. Some of the more important factors which affect the rate
of absorption follow: soil moisture availability, soil temperature,
soil aeration, and the concentration of solutes in the soil solution.
By affecting absorption, transpiration will likewise be affected.

Soil moisture availability. Schneider and Childers (1941, p. 565)
state that "a deficiency of water under natural and even cultural con-
ditions is probably responsible for poor growth and death of more plants

than disease, insects, or any other cause." Water loss from plant tissue by transpiration is not instantaneously replaced; therefore, wilting takes place if water cannot be supplied at a rate sufficient to replenish that lost from the plant. This frequently occurs if the soil moisture is somewhat deficient because of the increased resistance encountered in water movement.

When the water content of the leaf is reduced, the leaf turgor is reduced. This causes at least a partial closing of stomata even before apparent wilting takes place. The amount of resistance encountered in water movement increases, and thus influences the rate of transpiration. Kramer (1950, p. 280) stated that, "when wilted plants are watered they usually recover turgidity within a few hours, but the effects of wilting on internal processes and conditions do not disappear immediately." This is shown in Figure 5.
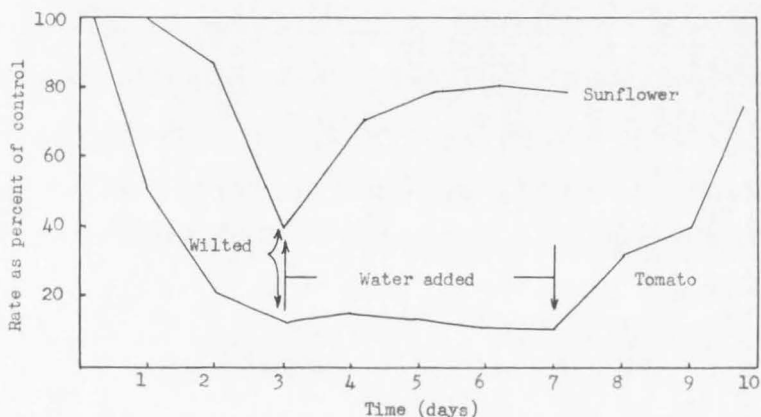

Figure 5. Effect of wilting and recovery rate of transpiration of sunflower and tomato. Rates of wilted plants are expressed as percentages of rates of well watered controls. The sunflowers were rewatered after 1 day in the wilted condition, but the tomatoes were kept wilted for over 4 days before rewatering. (Kramer, 1950, p. 281)

It took 3 or 4 days after the plants were rewatered to return to 70 or 80 percent of the normal transpiration rate before wilting. This indicates that wilting influences the internal processes of the plant.

It was shown by Martin (1940) that when plants were grown with a limited supply of available moisture, stomata were smaller and more numerous and the leaves were thinner. It appears that the leaf anatomy changed due to the failure of the cells to expand because of reduced turgor. Transpiration rates were affected when about two-thirds of the available moisture was removed from the soil. The stomata opening also appeared to be affected at this point.

There does not appear to be any set time that transpiration ceases when conditions cause the plant to dry out.

> There seems to be no reason why transpiration should not
> continue until, or beyond, the death of the plant, limited
> only by the energy available for evaporation, the resistance
> to water movement into, through, and out of the plant, and
> by the rate of flow of soil water to the roots. (Slatyer,
> 1957, p. 331)

Soil temperature. Rate of water flow to the roots is greatly affected by soil temperature. Vast changes in soil temperature take place throughout the year and also each day. High soil temperatures tend to increase water availability and low soil temperatures retard water availability.

As soil temperatures are lowered, root elongation is retarded which decreases the rate of penetration of roots into new regions of the soil. Water movement is retarded because of increased viscosity at lower temperatures. Also, cells in the plant roots become less permeable.

Cameron (1941, p. 24) while working with orange trees indicated that a marked reduction in rate of water loss occurred as the soil temperature was reduced from 90 to 43 F. This was particularly noticeable in

the daytime when transpiration rates were highest. The results of
Bialoglowski (1936) were somewhat different. He found that daily water
loss from leafy lemon cuttings under constant top conditions was unaf-
fected in the temperature range between 25 and 35 C. A marked reduction
in transpiration below 25 and above 35 C was observed as is shown in
Figure 6.
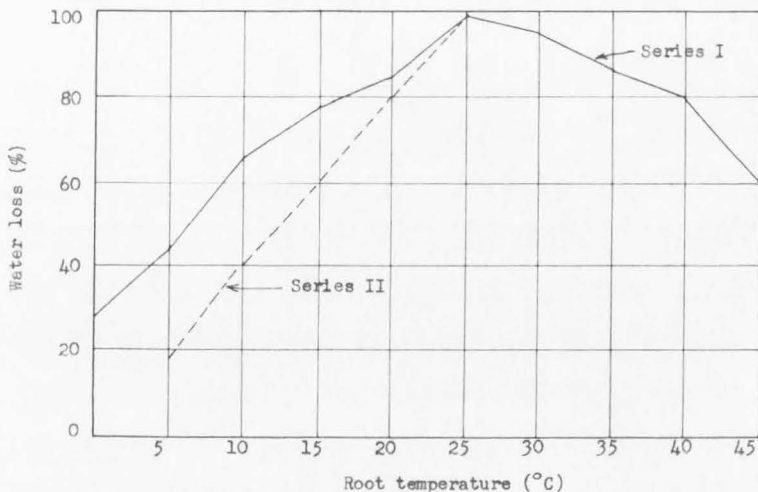
Figure 6. Effect of root temperature on the rate of transpiration
of rooted lemon cuttings. Water loss at the various root temperatures
is computed as percent loss at 25 C for the period of illumination.
(Bialoglowski, 1936, p. 97)

Neither Cameron (1941) nor Bialoglowski (1936) were able to detect any
influence of soil temperature on transpiration at night because of the
low rates of water loss.

Kramer (1942) observed that all plants are not affected to the same
degree. He found that as soil temperatures are reduced, absorption is

reduced, but species which normally grow in warm soil have their ab-
sorption rates reduced to a greater extent than the species which normal-
ly grow in cooler soils and during cooler seasons of the year.

Aeration. Deficient aeration often interferes with the absorption
of water. This may be brought about by compacting the soil or from
flooding for prolonged periods of time. It is not clearly understood
how poor aeration affects water absorption, but it might be caused by
reduced metabolic activity of the roots, or by physical changes in the
permeability of the roots.

Concentration of solutes. Meyer (1931) observed that the addition
of any type of salts to the soil decreased the transpiration rate of
cotton plants. This would apply equally well to other species. In
humid regions salt problems are rare, but in many arid regions of the
world where rainfall fails to leach the salt out of the soil, large
accumulations significantly decrease the rate of water absorption. This
affects transpiration rates and other plant processes.

Conclusion from Literature Review

Through the information presented, it is apparent that transpiration
is a complex process which is affected by many factors, and that there is
still a great deal of disagreement as to the importance of this process.

1. Solar radiation probably has more influence on transpiration
rates than other environmental factors because of the strong influence
it has on stomatal regulation, leaf temperature, leaf structure, and
protoplasmic changes in the plant.

2. Air temperature has a significant influence on the steepness of
the vapor-pressure gradient from plant tissue to air, and transpiration

rates depend primarily on this gradient.

3. Relative humidity has an indirect influence on the steepness of the vapor-pressure gradient. Also, radiation to and from the atmosphere is influenced by the amount of moisture present in the air.

4. Wind increases transpiration by removing the saturated air near the transpiring surfaces of the leaf, producing a steeper vapor-pressure gradient from plant tissue to the air.

5. Soil factors influence transpiration by affecting rates of water absorption. Absorption is affected by the amount of work that is required to remove soil moisture from the soil matrix, by the soil temperature, by soil aeration, and by the concentration of the solutes in the soil.

A process such as transpiration which influences the amount of available water for human consumption, and which is influenced by such a large number of environmental factors will surely tax the ingenuity of many investigators in trying to find methods whereby transpiration losses can be reduced.

METHODS AND MATERIALS

Measurement of Leaf Temperature

Some progress has been made in developing methods for measuring
leaf temperatures, but very little work has been done in recent years.
Early workers tried wrapping the leaf around a mercury thermometer to
determine the temperature. The development of thermocouples provided a
far more accurate method; however, thermocouples are cumbersome to work
with, and the leaf may be severely damaged when they are inserted.
Therefore, it is apparent that a new technique for measuring leaf
temperatures needed to be developed.

Throughout this experiment small thermistors were used and proved
to be very convenient and accurate. The most satisfactory type was
found to be the VECO 34-A1; however, lead wires are extremely fine and
difficult to work with. In order to connect additional wire to the
leads, the best method developed was to use a torch, silver solder, and
a good silver solder flux. Practice was required to perfect the tech-
nique before soldering the thermistor leads because of the cost involved
and the necessity of having good connections.

The procedure used in soldering additional wire on the leads was as
follows: (1) prepare the silver solder filings, (2) moisten the wire to
be attached to the thermistor lead so that a small amount of flux will
stick to it, (3) move the wire bearing the flux near the flame so that
the flux melts, (4) moisten the wire again and apply the silver solder
filings, and (5) melt the solder on the wire. It is now ready to attach

the thermistor lead. The solder is slightly melted again and the therm-
istor lead is quickly inserted into the melted solder. This is allowed
to cool and the flux is removed from the joint.

The thermistor leads and wires were cemented in $\frac{1}{2}$ inch plastic
tubing with Armstrong Adhesive (A-1). Only the thermistor bead was left
protruding. This eliminated the problem of the leads getting broken.
Each thermistor was calibrated to $\pm$ 0.1 C. With this type of equipment,
temperatures could be determined rapidly by placing the thermistor next
to any part of the plant. This made it possible to measure leaf and
stem temperatures without causing damage to the plant such as is the
case with thermocouples.

One problem encountered was the difficulty in finding a measuring
device which could be used without causing self-heating in the therm-
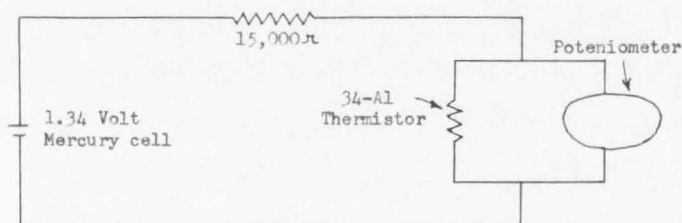istor. The circuit which was finally used is shown in Figure 7.

Figure 7. Circuit used with the VECO 34-Al thermistor to measure
leaf and stem temperature.

The 15,000 ohm resistor in the circuit prevented excessive amounts of
current from passing through the thermistor. A larger resistor would
reduce the sensitivity of the potentiometer, and a smaller resistor
would cause self-heating in the thermistor.

Measurement of Transpiration Rates

Transpiration rates were measured by the gravimetric or weighing method. In the first phase of the experiment, only one sunflower plant was used. The pot containing the plant was sealed in a plastic container so that the whole root system could be submerged in the constant temperature bath. A tube was inserted in the top where water was added and air supplied to the system during the experiment.

In the second phase of the experiment, 12 sunflower plants were used. Four plants were placed in each of three constant temperature baths. The plants were grown in paint-type cans fitted with friction lids. A hole was made in each lid and the space between the hole and the plant stem was filled with wax. Readings were taken in the morning and again at the end of the 8 hour experimental period. From these readings, the rate of water loss was determined. Since transpiration rate increases as plants become larger, the transpiration rate was checked under identical conditions at the beginning and again at the end of the experimental period to determine the change in transpiration rate that had taken place. A correction factor was determined by plotting time in days against the change in transpiration rate in grams on semi-log paper. The correction was applied to each of the readings involved.

Control and Measurement of Environmental Factors

The following factors were being controlled: soil moisture, soil temperature, air temperature, relative humidity, and wind. Soil moisture was maintained throughout the experiment at approximately field capacity.

Soil temperature was controlled by using constant temperature baths

in which the cans were nearly submerged. Each bath had a heating and
refrigerating unit which was controlled by a thermoregulator making it
possible to control the temperature very accurately. Temperatures were
checked several times each day to see that all controls were working
properly.

Wind velocities were obtained by using a large fan. Variation in
the speed to which the plants were exposed was controlled by the
distance the fan was placed from the plant. Wind speeds were measured
by using an anemometer.

Air temperature and relative humidity were controlled in the growth
chamber where there was a constant circulation of air to maintain a uni-
form set of conditions. Both were measured by using thermistors cali-
brated to ± 0.1 C. Wet bulb temperatures were obtained by wrapping a
wick, which was partially submerged in water, around a thermistor, and
putting a fan nearby to obtain the necessary air movement for maximum
wet bulb depression. Fluorescent lights of approximately 3,000 candle-
power provided a uniform lighting system which could be automatically
turned on and off at the desired time to provide day and night
conditions.

EXPERIMENTAL RESULTS AND DISCUSSION

Relations between Leaf Temperature and Transpiration Rates

The first phase of this research project was performed to see if the difference between leaf and stem temperature, the difference between leaf and air temperature, or the difference between an actively transpiring leaf and a dead non-transpiring leaf could be used as an indication of how rapidly transpiration was taking place. Also, several environmental factors were individually tested to see how each influenced the leaf temperatures and transpiration rates under greenhouse and controlled growth chamber conditions.

Greenhouse study

A typical example of how leaf temperatures of dead non-transpiring sunflower leaves and actively transpiring leaves compare with air temperature under steady greenhouse conditions in sunlight on two different days is shown in Table 6.

Table 6. Relations between the mean leaf and the mean air temperature of actively transpiring and dead non-transpiring leaves.

Date	Air temp.	R.H.	Trans. leaf temp.	Dry leaf temp.	Air temp. minus trans. leaf temp.	Air temp. minus dry leaf temp.
	C	%	C	C	C	C
Sept. 16	22.7	65	25	27.7	2.3	5.0
Sept. 19	22.0	68	24.3	27	2.3	5.0

All readings are the average over a 60 minute period between 1:30 and

2:30 PM. Air temperature and relative humidity were taken every 30
minutes. Leaf temperature was taken every 5 minutes. Indications are
that as long as relative humidity and air temperature remain relatively
constant, the differences between leaf and air temperature are steady.
However by referring to Table 7, it can be seen that the results are far
more variable if air temperature and relative humidity are fluctuating.

Table 7.   Fluctuations in leaf temperatures as relative humidity and air
temperature vary under greenhouse conditions.

Time	Air temp.	R.H.	Trans. leaf temp.	Dry leaf temp.	Temp. difference
PM	C	%	C	C	C
1:05	19.5	76	21.2	26.5	5.3
1:10			23.4	26.5	3.3
1:15			22.4	24.2	1.8
1:20	Fan & cooler turned off		22.5	25.4	2.9
1:25			24.9	30.4	5.5
1:30			26.4	33.4	7.0
1:35	24.3	55	27.3	33.6	6.3
1:40			28.2	33.0	4.8
1:45			28.0	34.7	6.7
1:50			28.0	33.4	5.4
1:55			27.8	32.9	5.1
2:00			27.5	36.0	8.5
2:05	26.7	44	29.0	35.7	6.7

Growth chamber study

Under controlled growth chamber conditions, it was found that,
unlike greenhouse conditions, the dry leaf temperature was essentially
the same as air temperature under all conditions which were being tested.
Therefore the dry leaf was discarded, and stem temperatures were measured
and compared with the temperatures of transpiring leaves.

The following conditions were established as a standard to be used
in the growth chamber: air temperature, 24 C; relative humidity, 50 per-
cent; wind velocity, below 1 mile per hour; soil temperature, 25 C; and

soil moisture, field capacity. All of the conditions were then held constant except the one that was being tested.

Air temperature. Leaf and stem temperatures and transpiration rates were measured at air temperatures of 20 C, 24 C, and 32 C. All readings were made during the same period of the day so that the periodicity of transpiration would affect the readings in the same way. Equal numbers of readings were not available each day because temperature and relative humidity changes occurred as the outside temperatures rose to a level where the cooling system no longer had ample capacity to maintain constant conditions in the growth chamber. Since it became hot earlier on some days fewer readings were obtained causing the number of readings to vary between 5 and 10.

The actual temperatures of the leaves and stems at various air temperatures were not of as much interest as the difference between the temperature of the plant tissues and the temperature of the surrounding air. Figure 8 shows the mean differences between leaf and air temperature, stem and air temperature, and leaf and stem temperature at three different air temperatures.

At the three air temperatures tested, the leaf temperature was between 0.5 and 2.5 C cooler than the air. The mean temperature difference between leaf and air at each interval tested in the growth chamber was practically the same, varying less than two degrees. This is opposite of the results under greenhouse conditions where the leaf was always somewhat warmer than the air and the variations were much greater. This could be due to the differences in light intensity and spectral distribution which caused a greater heating effect in the greenhouse.

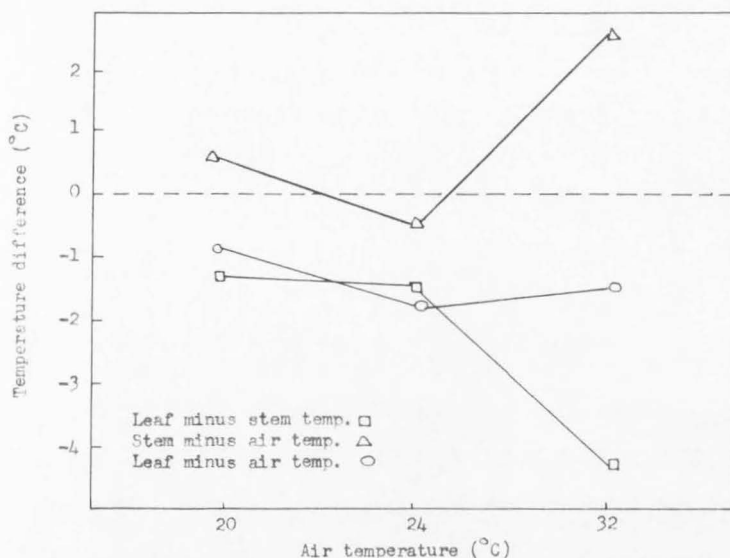The difference between the stem and air temperature was more erratic

Figure 8. Relations between stem, leaf, and air temperatures under different temperature conditions.

than between the leaf and air temperature. At 20 C and 24 C, the stem and the air were at about the same temperature, while at 32 C, the stem became somewhat warmer with a mean temperature of 2.68 C above air temperature.

Stem temperatures were found to be higher than the leaf temperatures under all conditions as can be seen in Figure 9. The mean differences between stem and leaf temperatures at 20, 24, and 32 C were 1.21, 1.32, and 4.31 C respectively while transpiration rates were 28 g/hr, 32 g/hr, and 44 g/hr.

Relative humidity. It was not possible to obtain large differences in relative humidity in the growth chamber. Therefore, the experiments
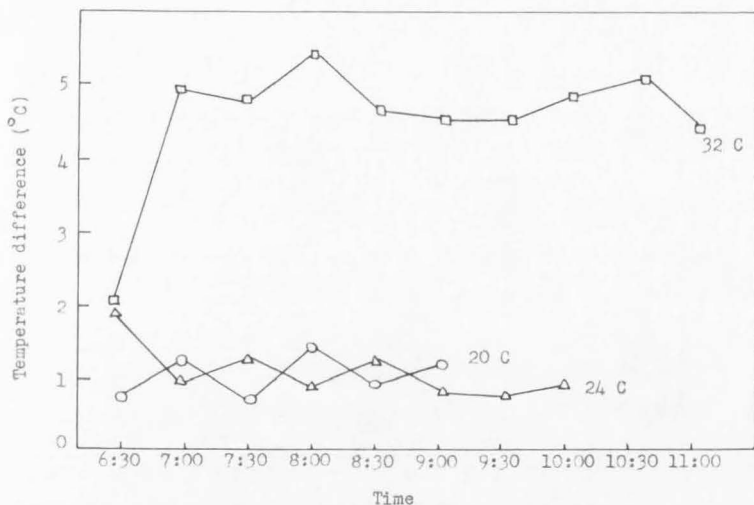
Figure 9. The difference between stem and leaf temperature when exposed to various air temperatures.

had to be made at 40, 50, and 60 percent relative humidity.

Figure 10 shows the mean differences between leaf and air temperature, stem and air temperature, and between leaf and stem temperature at three different relative humidities. At 40 and 50 percent, the air temperature was greater than the leaf temperature, but at 60 percent the leaf temperature was the greater. The mean temperature differences between leaf and air temperature at 40, 50, and 60 percent relative humidity were 1.51, 1.78, and 0.88 C respectively.

The difference between stem and air temperature fluctuated, but tended to become warmer as the relative humidity increased. Differences between leaf and stem temperature had the same trend as the transpiration rates at the different relative humidities. In all cases the stem was warmer than the leaf. These differences are not as
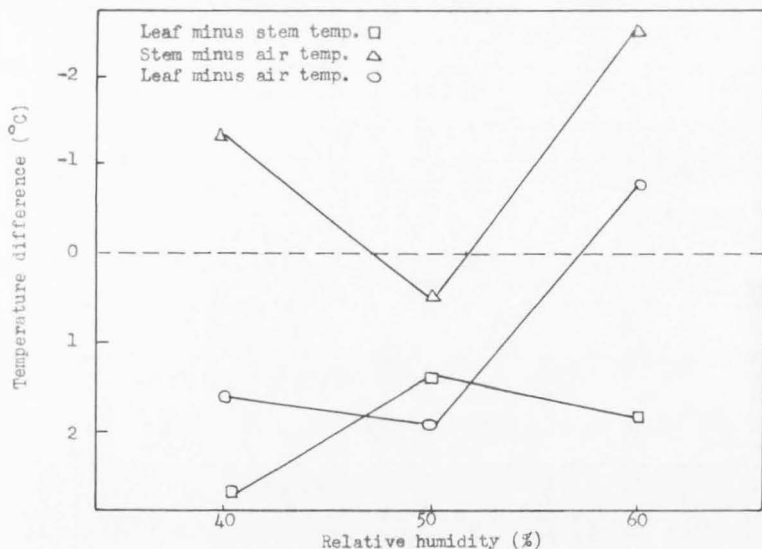
Figure 10. Relations between stem, leaf, and air temperatures under different relative humidity conditions.

consistent as might be expected when compared with the transpiration rates which increased 4 grams per hour for each 10 percent decrease in relative humidity. This indicated that in the range of 40 to 60 percent, a linear relationship might exist between relative humidity and transpiration rate.

Wind. The device used for measuring leaf temperatures would have to be modified to be used in winds greater than 4 or 5 miles per hour because of the fluttering of the leaves. In this experiment only two conditions were tested: wind at 4 miles per hour and slight air movement which resulted from circulation of air through the growth chamber. This circulation was not of sufficient magnitude to be registered by any of the anemometers used.

An analysis of variance was used to determine whether the variations among the temperature-difference means at different wind velocities were real. The variations among means were not significant at the 5 percent level on the difference between leaf and air temperature, and the difference between stem and leaf temperature; however, the difference between stem and air temperature was significant at the one percent level. Figure 11 shows the mean difference between leaf and air temperature, stem and air temperature, and stem and leaf temperature with a wind of 4 miles per hour and without measurable wind.
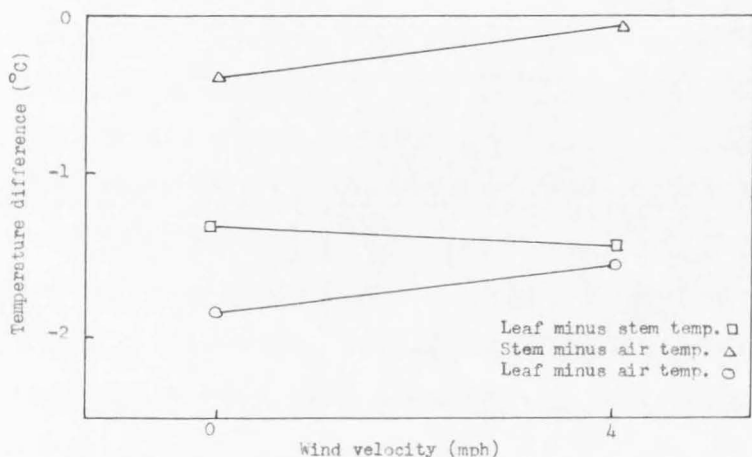

Figure 11. Relations between stem, leaf, and air temperatures when exposed to different wind conditions.

From the leaf and stem temperatures, the indication would be that wind has very little influence on the transpiration rate under growth chamber conditions. This was verified by transpiration measurements

since there was only a 3 g/hr. increase in the transpiration rate with
an increase in wind velocity to 4 miles per hour.

Soil temperature. High soil temperature along with high relative
humidity were the only two conditions in which the leaf temperature was
higher than the air temperature in the growth chamber. At low soil
temperature, the leaf, stem, and air temperature were essentially the
same. This is illustrated in Figure 12.
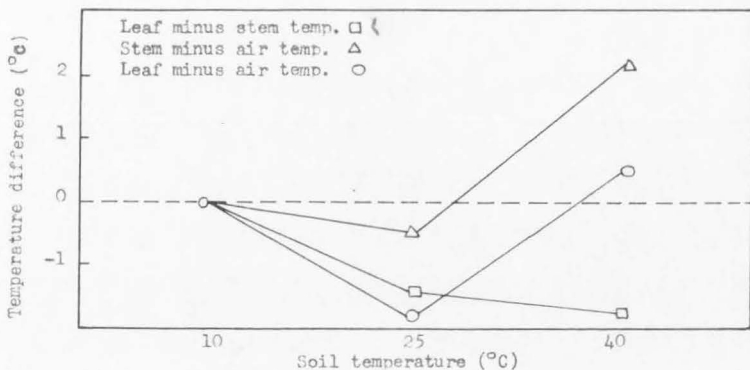
Figure 12. Relations between stem, leaf, and air temperatures
under various soil temperature conditions.

At 25 C, the leaf and stem were both cooler than the air, while at
40 C, both the stem and leaf were warmer than the air. It is possible
that the higher leaf temperature at higher soil temperature resulted
from translocated heat. Since the soil temperature was higher than the
room temperature, warm water was absorbed by the roots and translocated
through the plant causing the leaves to be heated. Since heat was
transported to the leaves from the soil, the leaves could attain a

higher temperature under the same light intensity than leaves which re-
ceived no transported heat. The mean differences between leaf and stem
temperature at 10, 25, and 40 C were .01, 1.32, and 1.70 C respectively.
The stem was warmer than the leaf at all three soil temperatures.

The transpiration rate was lower under low soil temperature con-
ditions than under any other conditions tested, although high relative
humidity also caused the transpiration rate to decrease to a low value.
As the soil temperature was increased from 10 to 40 C, there was an
accompanying increase in the transpiration rate. It appeared, however,
that the increase was not linear over the whole range. As was shown
above, the difference between stem and leaf temperature also increased
between 10 and 40 C with by far the largest increase occurring between
10 and 25 C.

Relations between Soil Temperature, Air Temperature, Relative Humidity, and Transpiration Rates

In the second phase of the experiment, the influence of soil temper-
ature, air temperature, and relative humidity on transpiration rates
was tested under controlled conditions. For the purpose of statistical
analysis, the variables relative humidity, soil temperature, and air
temperature were considered to be three factors with three levels in
each factor. A split-plot analysis of variance was used to test the
significance of each factor and the two and three factor interactions
with air temperature, soil temperature, and relative humidity being used
as whole-plot, split-plot, and split-split-plot respectively. The
results are shown in Table 8.

The variance analysis showed that there was no significant differ-
ence among the various levels of relative humidity. This may be

Table 8. Influence of soil temperature, air temperature, and relative
humidity on transpiration rate.

Soil temperature	Relative humidity		22	Air temperature 27	32	average
C	%		C	C	C	
10	35		13.7	13.3	12.3	13.1
	53		10.5	13.5	13.5	12.5
	65		13.2	13.3	19.2	15.2
		average	12.1	13.4	15.0	13.5
25	35		19.7	27.5	31.2	26.1
	53		23.0	27.5	28.5	26.3
	65		22.5	24.7	29.5	25.6
		average	21.7	26.6	29.7	26.0
40	35		20.5	26.7	32.0	26.4
	53		25.0	33.5	27.5	30.0
	65		23.2	21.2	33.7	26.0
		average	22.9	27.1	31.1	27.5

explained by the fact that there was not a wide enough range of relative
humidity to adequately test this condition without using larger plants
having higher transpiration rates. To detect the difference among
humidities, a replication experiment needs to be run in the future with
a wider range of values.

Soil temperature was a very important factor in controlling
transpiration rates. The main effects were significant at the 1 percent
level. At a soil temperature of 10 C, an increase in the air temperature
from 22 to 32 C caused a 24 percent increase in transpiration, although
this increase did not reach the level of statistical significance.
Increasing soil temperature from 10 to 40 C caused the transpiration
rates to double. At 40 C, a 10 degree increase in air temperature
brought a 29 percent increase in transpiration rate. On an absolute

basis, it appears that at low root temperatures the environmental factors
surrounding the leaves have relatively little influence on transpiration,
and it is likely that water intake by roots is the rate-limiting step.

In explaining the affect low soil temperature has on transpiration,
the following three factors need to be considered: root permeability,
root growth, and leaf surface area. It is common knowledge that cold
soil temperature decreases the permeability of roots and thus retards the
uptake of water. This could have easily been one of the major factors
involved in the low transpiration rates.

Root growth might also be affected by low soil temperatures; how-
ever, the root systems of the plants grown under 10, 25, and 40 C soil
temperatures were observed and there was no indication that the root
systems were significantly different. In all cases the roots grown
under the 10 C soil temperature appeared to be as large as the others.

In checking the leaf area of the various plants, it was found that
the plants grown under the 10 C soil temperature conditions had only 60
percent as much leaf area as the plants grown under 25 and 40 C. This
appears to be one important factor in causing lower transpiration rates
at 10 C than at 25 and 40 C.

At soil temperatures of 25 and 40 C, a significant increase in
transpiration could be observed as the air temperature was increased
from 22 to 32 C under all relative humidity conditions tested. The
maximum transpiration rate was achieved by the combination of the
highest levels of air and soil temperature. This is illustrated in
Figure 13. The relation between air temperature and transpiration rate
was nearly linear at all three soil temperatures. The difference be-
tween the transpiration rate at a soil temperature of 25 C and the rate
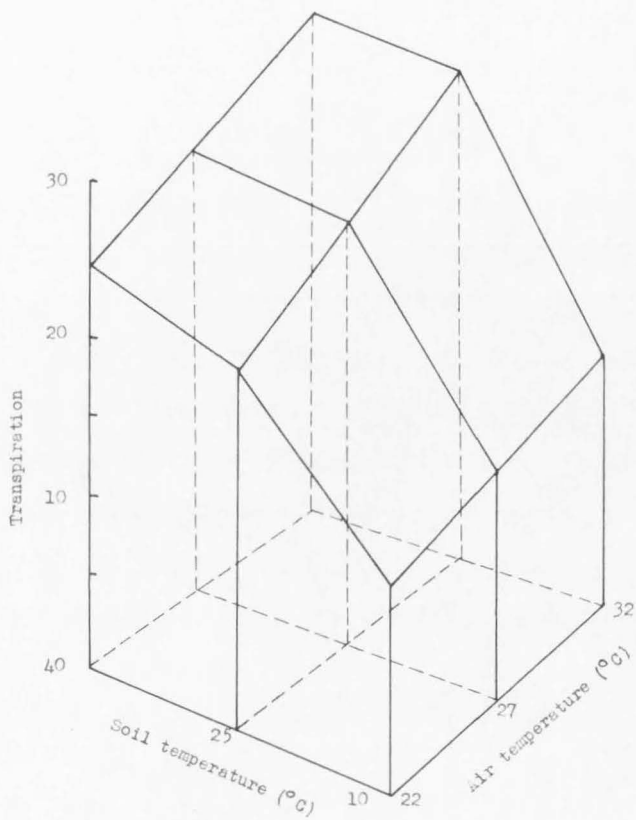at a soil temperature of 40 C under all conditions was very small.

Figure 13. Influence of soil temperature and air temperature on the rate of transpiration.

SUMMARY

Leaf temperatures were observed under greenhouse and growth chamber conditions. Large and rapid changes took place when plants were in direct sunlight, but the changes were much smaller under artificial conditions. Leaves were always warmer than the air under greenhouse conditions, but in the growth chambers the leaves were usually cooler than the air. This could be due to the differences in light intensity and spectral distribution which caused a greater heating effect in the greenhouse.

Under growth chamber conditions leaves were often 2 degrees cooler than the air. Only at the highest soil temperature, 40 C, in combination with the highest relative humidity studied, 65 percent, were the leaves found to be about 0.5 C warmer than the air. This may have resulted from translocated heat.

Stems were found to be warmer than leaves under all conditions tested in the growth chambers. It was not possible to find a consistant relationship between leaf and stem temperature that could be used as an indication of how rapidly transpiration was taking place; however, it is apparent from these studies that transpiration does have a significant cooling effect and may be important as a buffer in controlling extremes in plant temperatures.

Under growth chamber conditions, wind of four miles per hour had very little influence on the transpiration rates and leaf temperatures when compared with conditions where air movement was barely detectable.

Low soil temperatures had more influence on the transpiration rate

than any other factor studied. When the soil was at 10 C, other en-
vironmental factors had relatively little influence on transpiration.
This might have been caused by the decreased activity of soil water
slowing up the absorption process. Also, the leaf surface area was
significantly reduced by low soil temperature. Plants grown at 10 C
had 40 percent less leaf area than plants grown in soil temperatures
of 25 and 40 C.

Transpiration rates did not increase linearly as the soil temper-
ature was increased from 10 C to 25 and 40 C. By far the largest
increase came between 10 and 25 C with only small increases between
25 and 40 C.

Air temperature seemed to be the dominant factor in controlling
the transpiration rate except under low soil temperature conditions.
This might be expected because of the influence air temperature has on
the vapor-pressure gradient and leaf temperature. In the range of 35
to 65 percent, relative humidity had only a slight influence on trans-
piration rates under growth chamber conditions.

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APPENDIXES

APPENDIX A

Preliminary Testing on Stomatal Opening

The hypothesis that stomatal opening may be caused, at least in part, by the heating of the leaves above ambient temperature and may not be entirely a light effect was tested. The so-called injection method was used to qualitatively determine the degree of stomatal opening. This is based on the penetration of solvents of different surface tension and solubility characteristics. Ethyl alcohol, benezene, butyl alcohol, and xylene were the chemicals used. A certain amount of practice in using these chemicals is necessary under controlled conditions with each type of plant being studied, because a great deal of variation occurs among different plants in their response to the same chemicals. A typical example of how lilac leaves respond to the various chemicals can be seen in Table 9. This experiment was performed early in the morning just as the sun was rising so that all of the plant leaves would have retained their maximum turgor.

Table 9. The degree of stomatal opening under different conditions of light and soil moisture as determined by the injection method.

Treatment	Direct sunlight Well watered	Direct sunlight Water needed	Shade Well watered
Ethyl alcohol	Rapid penetration	No penetration	No penetration
Benezene	Rapid penetration	No penetration	Slow (15 sec)
Butyl alcohol	Rapid penetration	Slight (2 min)	Slow (15 sec)
Xylene	Rapid penetration	Rapid penetration	Rapid penetration

Heat was applied to leaves in which the stomata were partially or
totally closed, and then the stomatal opening was rechecked. A similar
experiment was also performed in a constant temperature room after the
plants had been in darkness over night.

With the technique used, it could not be conclusively demonstrated
in any of the tests that heat had an effect on stomatal opening. There
was some indication that this method of observing stomatal opening might
have some practical application in determining the appropriate time for
irrigation; however, no experiments were done in this area.

APPENDIX B

Cetyl Alcohol Additions to the Soil

Cetyl alcohol, which has been shown to reduce evaporation from lakes through formation of a surface monolayer, was mixed with the soil on one group of plants and the evapotranspiration rates were measured and compared with plants which were grown in untreated soil. Evapotranspiration rates were determined by weighing the plants in the morning and evening. Plants of a uniform size and transpiration rate were used. This experiment was carried on under greenhouse conditions for three weeks. As far as could be determined, there was no apparent change in evapotranspiration rates nor in the structure or growth of the plants.