Relations Between Transpiration, Leaf Temperatures, and Some Environmental Factors

Ronald Kay Tew

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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

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Logan, Utah

1962
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Ronald K. Tew
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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 humidity, 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 indicated that transpiration is one of the more important processes taking place in the plant and that it is on a level comparable to photosynthesis 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, translocation 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 transpiration 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, researchers are nearly equally divided as to the part played by transpiration 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>
<thead>
<tr>
<th>Treatment</th>
<th>Water Absorbed</th>
<th>Water Absorbed</th>
<th>Calcium Absorbed</th>
<th>Nitrate Absorbed</th>
<th>Potassium Absorbed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jar 1 - High Trans.</td>
<td>330 cc</td>
<td>13.6 mg</td>
<td>25.0 mg</td>
<td>41.4 mg</td>
<td>35.6 mg</td>
</tr>
<tr>
<td>Jar 2 - Low Trans.</td>
<td>150 cc</td>
<td>8.6 mg</td>
<td>15.0 mg</td>
<td>41.0 mg</td>
<td>27.8 mg</td>
</tr>
<tr>
<td>Jar 2 - High Trans.</td>
<td>335 cc</td>
<td>11.2 mg</td>
<td>27.0 mg</td>
<td>46.8 mg</td>
<td>56.4 mg</td>
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<tr>
<td>Jar 1 - Low Trans.</td>
<td>165 cc</td>
<td>9.6 mg</td>
<td>13.0 mg</td>
<td>41.8 mg</td>
<td>52.8 mg</td>
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</tbody>
</table>

In all cases a higher rate of transpiration was accompanied by an increased 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 throughout the plant ever result from low transpiration.

The results of Broyer and Hoagland (1943, p. 263) are shown in Table 2.

<table>
<thead>
<tr>
<th>Experimental conditions</th>
<th>Total salt absorbed</th>
<th>Water absorbed</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>K</td>
<td>Halide</td>
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<tr>
<td>Low humidity, light; culture aerated</td>
<td>8.47</td>
<td>7.53</td>
</tr>
<tr>
<td>High humidity, light; culture aerated</td>
<td>8.20</td>
<td>7.30</td>
</tr>
<tr>
<td>High humidity, light; culture unaerated</td>
<td>3.84</td>
<td>3.00</td>
</tr>
<tr>
<td>High humidity, dark; culture aerated</td>
<td>7.26</td>
<td>6.12</td>
</tr>
<tr>
<td>High humidity, dark; culture unaerated</td>
<td>3.57</td>
<td>3.12</td>
</tr>
</tbody>
</table>

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 supplied to them. However, Maximov (1929) indicates that too much importance should not be attached to the value of cooling by transpiration as plants could undoubtedly adapt themselves to endure higher temperatures.

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 6.5 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 infrared 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 radiation 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, transpiration 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 transpiration is more often the limiting factor in plant growth than any other single factor. Furthermore, 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. (Schormeyer, 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.

![Graph showing 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.](image)

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 notes¹ 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

¹Botany 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 temperature and humidity are known, but the vapor pressure of a leaf presents a more difficult problem. It is difficult to obtain the leaf temperature because of large and rapid changes that take place as is shown in Figure 2.

Figure 2. Curve showing rapidity of natural changes in temperature of a leaf due to varying air currents. Air temperature immediately preceding 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 changing 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 temperature 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 influences 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 direct 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 therefore 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 nine 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 because 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 previously 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 Hornert, 1948, p. 118)

<table>
<thead>
<tr>
<th>Relative humidity</th>
<th>D.P.Da</th>
</tr>
</thead>
<tbody>
<tr>
<td>%</td>
<td>Atmospheres</td>
</tr>
<tr>
<td>99</td>
<td>13.4</td>
</tr>
<tr>
<td>97</td>
<td>40.6</td>
</tr>
<tr>
<td>90</td>
<td>140.5</td>
</tr>
<tr>
<td>80</td>
<td>297.5</td>
</tr>
<tr>
<td>50</td>
<td>924.2</td>
</tr>
<tr>
<td>10</td>
<td>3070.3</td>
</tr>
</tbody>
</table>

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. Bialogowski (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)

<table>
<thead>
<tr>
<th>Air temperature</th>
<th>Relative humidity</th>
<th>Vapor pressure</th>
<th>Vapor pressure deficit</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>3%</td>
<td>12.28 mm Hg</td>
<td>5.26 mm Hg</td>
</tr>
<tr>
<td>20</td>
<td>70</td>
<td>12.28 mm Hg</td>
<td>19.54</td>
</tr>
<tr>
<td>30</td>
<td>38.6</td>
<td>12.28 mm Hg</td>
<td></td>
</tr>
</tbody>
</table>

atmosphere, a change less than 32 percent takes place in relative humidity, but more than 370 percent change in the vapor-pressure deficit takes place. This indicates that the vapor-pressure deficit is a more sensitive indicator of the water vapor conditions of the atmosphere and undergoes 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 literature 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 relative 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 infrared radiation, both from the sun and to the earth. This energy is
reradiated to the leaves, thus tending to raise their temperature." However, 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 significantly. 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 conditions.

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.
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 conditions 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 unaffected 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)](image)

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 absorption rates reduced to a greater extent than the species which normally 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-Al; 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 technique 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 thermistor 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 \( \frac{1}{4} \) 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 thermistor. 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.](image)

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 uniform set of conditions. Both were measured by using thermistors calibrated 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 candlepower 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.

<table>
<thead>
<tr>
<th>Date</th>
<th>Air temp.</th>
<th>R.H.</th>
<th>Trans. leaf temp.</th>
<th>Dry leaf temp.</th>
<th>Air temp. minus trans.</th>
<th>Air temp. minus dry leaf temp.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>C</td>
<td>%</td>
<td>C</td>
<td>C</td>
<td>C</td>
<td>C</td>
</tr>
<tr>
<td>Sept. 16</td>
<td>22.7</td>
<td>65</td>
<td>25</td>
<td>27.7</td>
<td>2.3</td>
<td>5.0</td>
</tr>
<tr>
<td>Sept. 19</td>
<td>22.0</td>
<td>68</td>
<td>24.3</td>
<td>27</td>
<td>2.3</td>
<td>5.0</td>
</tr>
</tbody>
</table>

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.

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

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 percent; 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
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.

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 0.38 °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
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.

Figure 10. Relations between stem, leaf, and air temperatures under different relative humidity conditions.
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.

![Graph showing temperature differences](image)

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](image_url)

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 received no transported heat. The mean differences between leaf and stem temperature at 10, 25, and 40 °C were 0.01, 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 conditions 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 temperature, 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 B.

The variance analysis showed that there was no significant difference among the various levels of relative humidity. This may be
Table 8. Influence of soil temperature, air temperature, and relative humidity on transpiration rate.

<table>
<thead>
<tr>
<th>Soil temperature</th>
<th>Relative humidity</th>
<th>Air temperature 22</th>
<th>Air temperature 27</th>
<th>Air temperature 32</th>
<th>average</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>%</td>
<td>C</td>
<td>C</td>
<td>C</td>
<td></td>
</tr>
<tr>
<td>10</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>35</td>
<td>13.7</td>
<td>13.3</td>
<td>12.3</td>
<td>13.1</td>
<td></td>
</tr>
<tr>
<td>53</td>
<td>10.5</td>
<td>13.5</td>
<td>13.5</td>
<td>13.5</td>
<td></td>
</tr>
<tr>
<td>65</td>
<td>13.2</td>
<td>13.3</td>
<td>19.2</td>
<td>15.2</td>
<td></td>
</tr>
<tr>
<td>average</td>
<td>12.1</td>
<td>13.4</td>
<td>15.0</td>
<td>13.5</td>
<td></td>
</tr>
<tr>
<td>25</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>35</td>
<td>19.7</td>
<td>27.5</td>
<td>31.2</td>
<td>26.1</td>
<td></td>
</tr>
<tr>
<td>53</td>
<td>23.0</td>
<td>27.5</td>
<td>28.5</td>
<td>26.3</td>
<td></td>
</tr>
<tr>
<td>65</td>
<td>22.5</td>
<td>24.7</td>
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</tr>
<tr>
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<td>26.6</td>
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</tr>
<tr>
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<tr>
<td>35</td>
<td>20.5</td>
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<td>32.0</td>
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</tr>
<tr>
<td>53</td>
<td>25.0</td>
<td>33.5</td>
<td>27.5</td>
<td>30.0</td>
<td></td>
</tr>
<tr>
<td>65</td>
<td>23.2</td>
<td>21.2</td>
<td>33.7</td>
<td>26.0</td>
<td></td>
</tr>
<tr>
<td>average</td>
<td>22.9</td>
<td>27.1</td>
<td>31.1</td>
<td>27.5</td>
<td></td>
</tr>
</tbody>
</table>

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; however, 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 between 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.
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 consistent 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 environmental 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 temperature 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 transpiration rates under growth chamber conditions.
LITERATURE CITED


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, benzene, 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>
<thead>
<tr>
<th>Treatment</th>
<th>Direct sunlight</th>
<th>Direct sunlight</th>
<th>Shade</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Well watered</td>
<td>Water needed</td>
<td></td>
</tr>
<tr>
<td>Ethyl alcohol</td>
<td>Rapid penetration</td>
<td>No penetration</td>
<td>No penetration</td>
</tr>
<tr>
<td>Benzene</td>
<td>Rapid penetration</td>
<td>No penetration</td>
<td>Slow (15 sec)</td>
</tr>
<tr>
<td>Butyl alcohol</td>
<td>Rapid penetration</td>
<td>Slight (2 min)</td>
<td>Slow (15 sec)</td>
</tr>
<tr>
<td>Xylene</td>
<td>Rapid penetration</td>
<td>Rapid penetration</td>
<td>Rapid penetration</td>
</tr>
</tbody>
</table>
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.
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 evaportranspiration rates were measured and compared with plants which were grown in untreated soil. Evaportranspiration 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 evaportranspiration rates nor in the structure or growth of the plants.