

# Influence of Temperature Gradients on Leaf Water Potential<sup>1</sup>

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## ABSTRACT

Water potential was monitored at nine locations along single maize (*Zea mays L.*) leaf blades with aluminum block *in situ* thermocouple hygrometers. Water potential showed a continuous decrease toward the tip, with a 2- to 4-bar difference between leaf base and tip under both moist and dry soil conditions. The water potential difference between the soil and the leaf base was about 4 bars. Water potentials decreased during the day and during a drying cycle, and increased at night and after irrigation. Heating a band of a leaf to 40 C or cooling it to 7 C had no influence on the water potential of the affected portion when this was corrected for hygrometer output over standard calibrating solutions at the respective temperatures. Heating or cooling a portion of a leaf had neither short nor long term effects on water potential of more distal leaf portions continuously monitored by hygrometers in dew point readout. Water potential fluctuated with an amplitude of about 1.5 bars and an irregular period of 10 to 30 minutes. Measurements with silver foil *in situ* psychrometers gave similar results.

Temperature gradients and fluctuations are a fact of life for plants. Temperature influences psychrometric water potential determinations, and temperature correction factors have been published (2, 10). We are not aware of studies in which water potentials were measured in parts of the same plant intentionally subjected to wide temperature differences. Here we report such studies on maize, the leaves of which are long enough to permit different temperature regimes on an individual leaf. Our experiments show that temperature gradients have little influence on the water potential of the affected or of other plant parts.

## MATERIALS AND METHODS

Maize plants (*Zea mays L.*) were grown in soil, three plants/18-liter can, and were used when they were 9 to 12 weeks old and beginning to tassel. During the summer, they were grown in a glasshouse and during the winter in a growth cabinet with about 290  $\mu\text{einsteins m}^{-2} \text{sec}^{-1}$  illumination (quantum sensor L1 190, Lambda Instruments, Lincoln, Neb.) from both fluorescent and incandescent lights, 16-hr photoperiod, and a 30 C:25 C day-night temperature regime. The experiments were done in a growth room with 140  $\mu\text{einsteins}$  illumination; 12-hr photoperiod, 26 C:20 C day-night temperature regime.

The treatments involved subjecting four regions of an intact, attached leaf to different temperatures as follows: base: ambient temperature; midbase: 18 cm, ambient, heated or cooled; midtip: 18 cm, ambient, heated or cooled; tip: ambient temperature. The midbase and midtip portions were enclosed in a Styrofoam picnic chest with an added vertical partition and a transparent plastic top. The chest was cut horizontally and the leaf with attached hygrometers was inserted between the two halves.

Leaf water potential was monitored with silver foil hygrometers (4) in earlier experiments and aluminum block hygrometers (3, 6; L51, Wescor Inc., Logan, Utah) in later experiments. Both types of hygrometers were calibrated in both the psychrometric and dew point readout (HR33 microvoltmeter, Wescor Inc.) over standard solutions at temperatures ranging from 5 to 45 C. The cooling coefficient for the dew point readout was also corrected for temperature.

Different schedules can be used to read the hydrometers. For earlier experiments, we read the psychrometric value immediately after 10-sec cooling, followed by 2-min dew point equilibration and reading, followed without additional cooling by the psychrometric reading. Both schedules gave similar readings on calibrating solutions, but the delayed reading time schedule consistently gave higher water potentials on dryer leaves when stomates would be closed. Our interpretation is that condensing water on the junction temporarily lowers humidity within the chamber and that with prolonged time in the dew point mode, during which water neither condenses on nor evaporates from the junction, the humidity in the chamber more nearly approaches that of the mesophyll. With a leaf resistance of 80  $\text{cm sec}^{-1}$  and a hygrometer chamber depth of 2 mm, a 2-min delay is sufficient to reduce the difference in humidity between chamber and mesophyll to 0.1% of the difference occurring immediately after the 10-sec cooling period. The data reported in Figures 1 and 2 are averaged dew point and psychrometric determinations by the delayed schedule. The dew point mode can also continuously monitor the water potential for periods extending to many hours (Fig. 3).

The mounting procedure differed in some details from that described elsewhere. The leaf was gently washed with distilled H<sub>2</sub>O and a sponge 1 hr before the hygrometers were attached. Prior to attachment, a rubber washer (cut from 0.2 mm sheet rubber-dental dam) was cemented inside the leaf slit of the aluminum block to provide a base, or back stop, to press the leaf firmly but gently against the hygrometer unit. The aluminum block hygrometer housings, mounted on wooden dowels on a Styrofoam block base, were then assembled along both sides of the leaf with care to avoid leaf twisting or injury. Then the hygrometer cylinders themselves, each with a Parafilm gasket lightly coated on both surfaces with petrolatum, were inserted in the aluminum blocks, seated firmly against the leaf (with the rubber washer on the other side of the leaf), and secured with the setscrew. Reading could be made within 1 hr but often required 5 hr to equilibrate. With this procedure, we were able to mount and obtain satisfactory readings from as many as eight out of 10 hygrometers.

The rubber back stop can be criticized because it insulates the leaf from the aluminum block, possibly resulting in temperature gradients. Such temperature gradients can be detected by non-zero voltages prior to cooling the junction; these were less than 0.3  $\mu\text{v}$  in our system, equivalent to less than 1 bar. An alternate method of mounting the leaf directly against the aluminum block resulted in two problems: only a fraction of the units sealed, and the leaf often slipped within the unit. Both problems were aggravated by the need to mount a number of units on a single leaf.

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Heat conduction along hygrometer lead wires caused erroneous readings when chamber temperatures differed substantially from external temperatures. This problem was alleviated by enclosing at least 20 cm of lead wire inside the chamber.

The hygrometers were left in place for as long as 10 days. They apparently caused little injury to the leaf, as the location in which they had been mounted was generally not discernible after hygrometer removal, and the leaf remained apparently healthy for another week or more.

Water potential of soil core samples was measured in a Wescor

C-52 sample chamber. Leaf resistances (5) (Lambda Instruments) and xylem pressure potential (9) were measured on leaves of the other plants in the same container. The xylem pressure potential was measured on leaf strips, about 0.8 cm wide, cut and torn from the edge of leaves near the tip.

**RESULTS**

The data from 10 experiments with maize and two with amaryllis (*Hippeastrum vittatum* Herb.) agreed. Successive readings taken within 5 min on an individual hygrometer nearly always agreed within 0.2 bar. On the other hand, readings on adjacent hygrometers at the same temperature and within 5 cm of one another differed by 12% on the average. The data points plotted on Figure 1 illustrate the variability encountered throughout the study; because plant size and the times required to reach wilting differed in the experiments they can not be readily averaged. Instead, data from individual representative experiments are reported. The lines showing water potential changes (Figs. 1 and 2) were drawn by visual inspection.

Water potentials decreased during the day and rose somewhat at night. They continued to decrease during a drying cycle and rose after irrigation on the 8th day (Figs. 1 and 2). The failure of the tip portion to recover completely after irrigation (Fig. 2, days 8 and 9) is explained by progressive necrosis of the tip, which, in this particular experiment, reached the most distal hygrometer on the 8th day. When a leaf or leaf area became necrotic, the water potential consistently dropped precipitously.

Water potentials generally decreased from the leaf base to the tip by about 3 bars. We found no evidence that this difference changed as the soil dried. The soil, roots, and stem accounted for about half of the total soil to leaf tip water potential gradient.

Warming or cooling a portion of the leaf had no effect on the water potential of the affected portion (Fig. 1). This remained the mean of the water potentials of adjacent proximal and distal leaf portions kept at ambient temperatures. It also fell each day regardless of the heating-cooling sequence.

Heating or cooling a band of the leaf, or both concurrently on adjacent bands, had no discernible effect on more distal portions of the leaf, or for that matter, on more basal portions of the leaf or the rest of the plant. This is apparent for the tip portions of the leaf (Figs. 1 and 3). Water potentials of other leaves on the same plant, not shown here, likewise showed no response to localized heating or cooling of a single leaf.

To check for any transient responses associated with heating

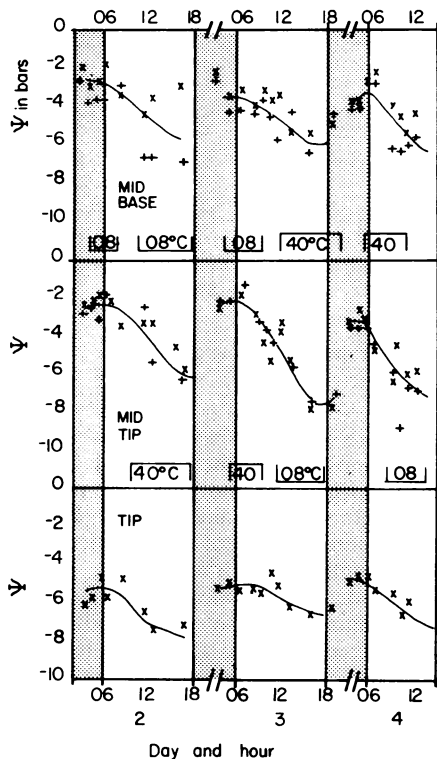


FIG. 1. Water potentials of various portions of a maize leaf through 3 days. The midbase and midtip portions were heated to 40 C or cooled to 8 C at various times as indicated by the bar symbols. The x and + symbols are data from different, adjacent hygrometers. The lines were drawn by visual inspection. Shaded portions indicate darkness.

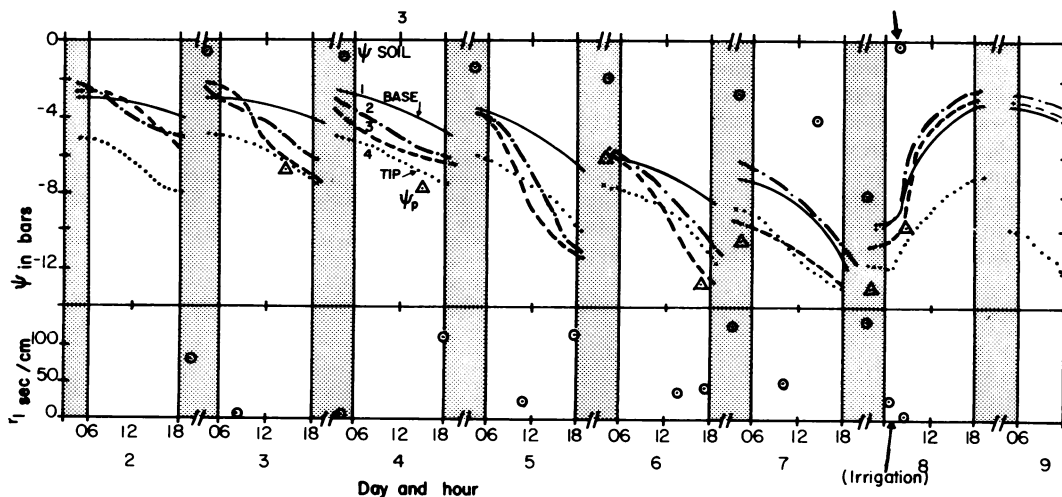


FIG. 2. Water potentials at different positions of a maize leaf through a drying cycle. Soil water potential: O; leaf pressure chamber readings: Δ; and leaf diffusive resistance readings: O (bottom graph) are also shown. Leaf portions are coded: 1: base —; 2: midbase - - - -; 3: midtip ·····; 4: tip ······. The plant was irrigated at 7:00 AM hr on day 8.

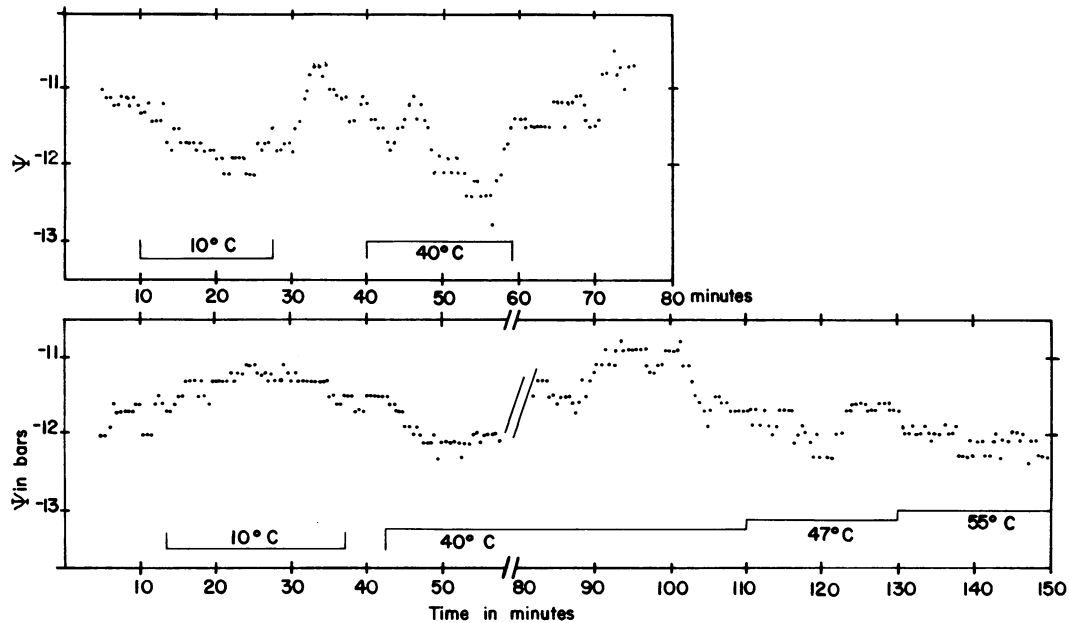


FIG. 3. Water potentials of two maize leaf tips while the midportions were subjected to warming or cooling as indicated. Water potential was about  $-14$  bars 24 hr later in the lower leaf tip.

or cooling an intermediate band, we continuously monitored the tip in the dew point readout (Fig. 3). There was considerable fluctuation in water potential, perhaps associated with stomatal oscillations (1); but this fluctuation was not correlated with heating or cooling the midleaf portion. At the conclusion of one experiment, we heated the midportion of the leaf to  $55^{\circ}\text{C}$ , again without effect on the distal leaf water potential. Although this drastic treatment killed all tissue of the heated portion except the midvein and several lateral veins, the distal portion remained alive and green for another week.

Data taken with silver foil hygrometers were similar to those taken with aluminum block hygrometers. The silver foil units, however, showed greater variability in readings, probably due to lower temperature uniformity in the hygrometer leaf system and larger zero offset values. We were also less successful in sealing them to the leaves for prolonged periods.

### DISCUSSION

Temperature gradients evidently have little if any influence on water potential throughout the plant. This may be explained by the fact that all parts of the plant are in liquid phase contact, with water movement along pressure gradients. When no membranes are traversed, liquid water or solution flow in tubes is from high to low pressure (or when xylem pressures are negative, from less negative to more negative pressures). Temperature has no effect on this flow, except for minor influence on viscosity. This is easily demonstrated in plumbing systems, in which cold water flows through and is heated in a water heater, then flows out into cold pipes.

Our experiment does not give information regarding the influ-

ence of temperature gradients on water movement across membranes (7, 8). In moving into the root, water traverses at least two membranes during radial movement from surface to xylem. The feeder roots are small, so any radial temperature gradients are negligible. Where water moves by diffusion in plants, the temperature is essentially uniform.

These results indicate that the temperature at which water potential is determined hygrometrically is not important as long as the readings are corrected to a common temperature.

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