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19 May 1972

Silver-Foil Psychrometer for Measuring Leaf Water Potential in situ

Abstract. *The water potential of leaves in situ can be measured without temperature control with a miniature, single-junction psychrometer constructed from silver foil and attached to the leaf with a silver-impregnated, conductive coating. The temperature of the psychrometer has been found to stay within 0.025°C of the temperature of a simulated leaf when the latter temperature was changing at a rate of 1°C per minute. Leaf water potentials can be measured with a precision of ± 1 bar, or better.*

Although the psychrometric method of measuring the water potential of leaves (chemical potential of water in leaves) in situ is theoretically sound (*1*), it is subject to errors introduced by temperature fluctuations. As a result, most leaf water potentials are measured on detached leaves in constant temperature baths (*2*). In the past, measurements of the water potential of leaves in situ also required precise temperature control (*3*). This requirement for temperature control has precluded routine measurements of the leaf water potential in situ.

For measuring leaf water potential it is essential that either the psychrometer chamber be at the temperature of the leaf, or the temperature difference between the two be known. Rawlins and Dalton (*4*) met this requirement for soil psychrometers used in situ by embedding the psychrometer within the sample. Wiebe *et al.* (*5*) used this same technique satisfactorily for measuring the water potential of stems, but it is not possible at present to embed a psychrometer within a thin leaf.

Two publications describe psychrometers designed to overcome this temperature problem. Calissendorf (*6*) added a second set of thermocouple junctions to measure the temperature difference between the leaf and the psychrometer chamber. Neumann and Thurtell (*7*) clamped the leaf between metal heat sinks to assure uniform temperature. In this report, we describe a leaf psychrometer that overcomes temperature-induced errors in water potential measurements by being small enough and constructed of metal with sufficiently high thermal conductivity to follow the normal temperature fluctuations of an exposed leaf.

The psychrometer, illustrated in Fig. 1, consists of a silver-foil (*8*) disk, 50 μm thick and 13 mm in diameter, in which an indentation 1 mm deep and 5 mm in diameter has been formed to serve as the psychrometer chamber.

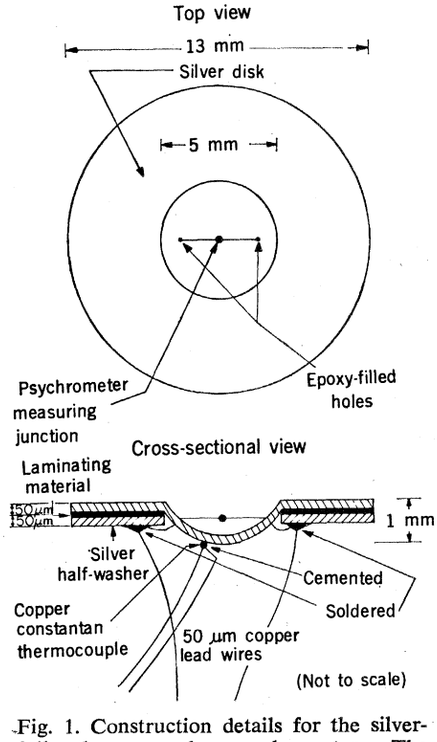

Fig. 1. Construction details for the silver-foil thermocouple psychrometer. The measuring thermocouple is constructed from 25-μm Chromel and constantan wire. The junction is approximately 0.2 mm in diameter (*14*).

The indentation is formed by placing the silver disk on a lead surface, positioning a steel die over it, and tapping the die with a hammer. To the back of the washer-shaped lip of the psychrometer, two half-washers of silver foil 50 μm thick are bonded with thermosetting, electrical insulating adhesive film (*9*). The film permits good thermal contact between the half-washers and the psychrometer chamber while serving as an electrical insulator. Each half-washer serves as a reference junction for the pair of thermocouple and lead wires soldered to it. Two small holes are drilled through the psychrometer chamber opposite each other for passage of the thermocouple wires. The holes are sealed with epoxy and each thermocouple wire is positioned in the center of the hole before the epoxy solidifies. A copper-constantan thermocouple is cemented to the back of the psychrometer chamber for monitoring the chamber temperature.

The psychrometer, insulated on the back with about 2.5 cm of foamed plastic, is cemented to a leaf by coating the lip of the psychrometer, which is 4 mm wide, with a silver-impregnated, water-based conductive coating (*10*), and pressing it against the abaxial side of the leaf. Tests conducted by Hoffman and Herkelrath (*11*) showed that the coating is not visibly harmful to leaves and remains attached for several weeks. Subsequent tests on citrus leaves, which have no stomates in the adaxial epidermis, also showed no visible damage. To prevent the silver coating from shorting out the psychrometer by coming in contact with the half-washer reference junctions, the edge of the psychrometer is coated with an epoxy sealant. Until the coating dries, the psychrometer is supported and a small weight is placed on top of the leaf to prevent its curling. The conductive coating can be removed from the psychrometer without damage with solvent (*12*).

The capability of the psychrometer to follow changes in simulated leaf temperature was measured in the laboratory by attaching a psychrometer, well insulated on its back side, to a copper plate with the conductive coating. The copper plate simulated a leaf of uniform temperature. The temperature of the plate was changed by heating or cooling a copper rod soldered to it. A thermocouple, attached to the plate, monitored the plate temperature. The temperature of the psychrometer chamber was monitored with both the

measuring junction of the psychrometer and the thermocouple attached to the back of the psychrometer chamber. When the plate temperature was changed at a rate of 1°C per minute, the psychrometer temperature lagged about 0.025°C. This temperature differential would induce an error in the measurement of leaf water potential of about ± 1 bar (*4*).

Psychrometers were calibrated over disks of filter paper saturated with KCl solutions having osmotic potentials of − 2, − 5, − 13.5, − 25 bars. The psychrometers were calibrated in a constant temperature bath and read automatically with a scanning device (*13*). A cooling current of 4 ma was used for 30 seconds. The average linear calibration equation at 25°C was $\Psi = 0.83 - 2.26\ V$, where Ψ is the water potential in bars, and V is the thermocouple output in microvolts. The correlation coefficient was 0.999.

The influence of temperature on the psychrometer calibration equation was also determined during calibration by recording the psychrometer output at intervals of about 5°C between 10° and 35°C, for three temperature scans —two ascending and one descending. From these calibration data, an equation was derived relating psychrometer output (V) and leaf temperature (T) to water potential (Ψ). The equation can be written as

$$\Psi = \frac{I + SV}{1 + S(0.338 - 0.133T)}$$

where I and S are the intercept and slope of the psychrometer's linear calibration equation at 25°C.

Examples of leaf water potential measurements made in situ with this silver-foil psychrometer, as well as the ambient temperatures during the measurements, are given in Fig. 2. All the water potentials reported have been corrected for temperature to 25°C. Figure 2A shows the diurnal fluctuations of water potential in a mature sunflower leaf for a plant growing wild on our laboratory grounds. The water potential ranged from about − 11 bars in the early afternoon to about − 3 bars at night. Since this mature plant was rooted in a large volume of soil and the weather was mild, the daily variations in water potential remained about the same for the days reported.

The results of a test of the psychrometer for lower and wider-ranging plant water potentials are given in Fig. 2B. Here, the water potential of a mature tomato leaf is given throughout parts

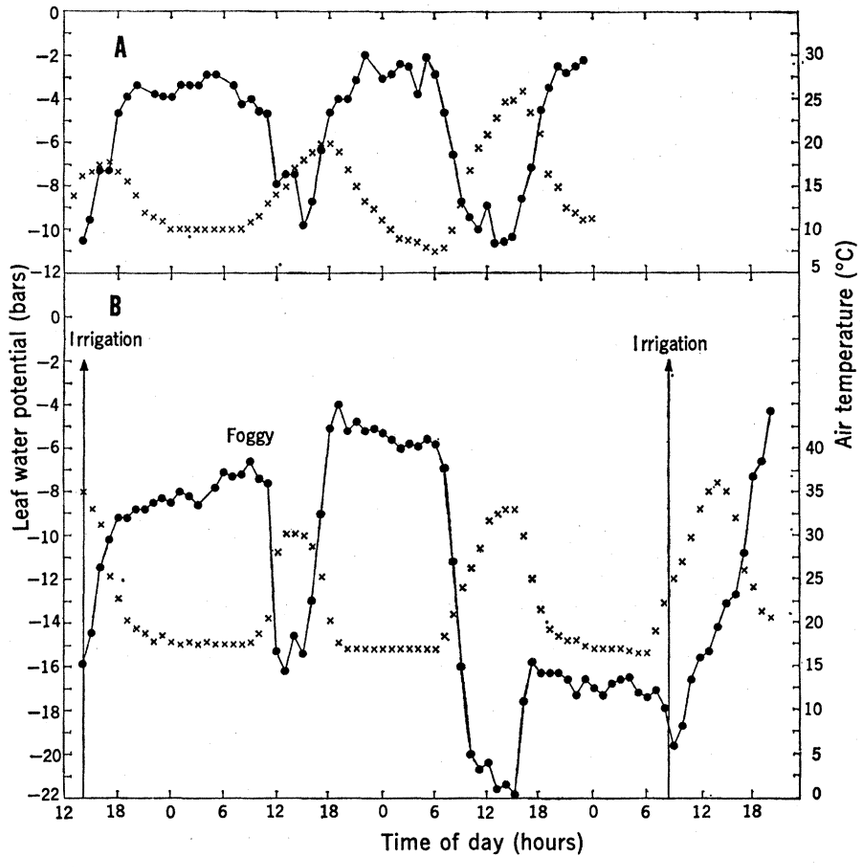

Fig. 2. Hourly averages of water potential for leaves in situ. (A) Measurements at 15-minute intervals for a sunflower leaf and (B) measurements at 10-minute intervals for a tomato leaf; ●, water potential; X, air temperature.

of two irrigation cycles. The potted tomato plant was located in a greenhouse in which the air temperature was maintained at about 17°C at night, but was allowed to vary with weather conditions during the day. The water potential of the tomato leaf was about − 16 bars when the plant was irrigated at 1400 hours the first day. During the first night, the leaf's water potential rose all night long as the plant took up the irrigation water. The morning of the second day was foggy until about 1100 hours, and the leaf's water potential did not drop appreciably until then. The second evening after irrigation, the water potential rose even higher than during the previous night, probably because of the time lag in water uptake. During the latter part of the night, however, the water potential dropped steadily from a peak of about − 4 bars in the evening, which indicated the beginning of leaf dehydration as water was extracted from the soil. During the third day, the water potential dropped to − 21 bars and the leaf wilted. The water potential recovered to only about − 16 bars that evening and steadily decreased during the night. On the morning of the fourth day, the plant was again irrigated, and the leaf water potential rose steadily all day despite the normal high stress during midday. By evening, the water potential had risen to about − 5 bars.

The abrupt reversal of the direction of the water potential change following the second irrigation demonstrates that the psychrometer responded to the water status of the leaf independently of temperature. The fact that measured leaf water potentials are in phase with evaporative demand, as indicated by ambient temperature, implies that little lag exists in the measurements.

These examples demonstrate that the temperature difference between the silver-foil psychrometer and the leaf to which it is attached is sufficiently small to permit measurements of leaf water potential in situ. The way now appears open for routine measurements of leaf water potential on intact plants in the field.

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Thermal Panting in Dogs: The Lateral Nasal Gland, a Source of Water for Evaporative Cooling

Abstract. *Two lateral nasal glands appear to provide a large part of the water for evaporative cooling in the panting dog; their function is analogous to that of sweat glands in man. Each gland drains through a single duct which opens about 2 centimeters inside the opening of the nostril. This location may be essential to avoid desiccation of the nasal mucosa during thermal panting. The rate of secretion from one gland increased from 0 to an average of 9.6 g (gland · hour)$^{-1}$ as air temperature was increased from 10° to 50°C. Evaporation of the fluid from the paired glands could account for between 19 and 36 percent of the increase in respiratory evaporation associated with thermal panting. The fluid secreted by the gland was hypoosmotic to plasma.*

Schmidt-Nielsen *et al.* found that, during normal open-mouth thermal panting in the dog, most of the air enters the nose and leaves the mouth (*1*). The nasal passages are, therefore, the primary site of evaporation. The authors suggested that a large serous type gland which is found in the nasal cavities might be a major source of the water for evaporation. This gland was first described by Steno in 1664 (*2*). It is found in a variety of animals which utilize thermal panting for evaporative cooling (dog, cat, pig, sheep, goat, and small antelopes) (*3*). In such typical "sweaters" as man, horse, and cattle, the gland is either absent or of microscopic proportions (*3*). We wanted to know whether these glands are an important source of water for evaporation during thermal panting.

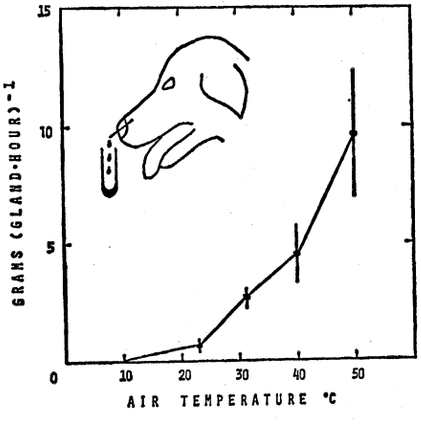

Fig. 1. Weight of fluid collected from one chronically cannulated lateral nasal gland as a function of air temperature. Each point is an average weight of nine measurements from three dogs. Each vertical bar is twice the standard error of the mean.

There are two glands, one in each maxillary recess. Each gland empties through a single duct (*4*) which opens about 2 cm inside the nostril (*5*, *6*). One gland was chronically cannulated under general pentobarbital anesthesia in each of three 25-kg dogs. An incision was made slightly lateral to the nasal septum, and the lateral wall of the nose was reflected to expose the orifice of the duct to the lateral nasal gland. A PE 60 cannula was sutured into the orifice. The cannula extended approximately 2 cm anterior to the orifice of the duct so that it was just visible through the external nares. The wound was then closed.

The rate of secretion from these glands increased markedly with increasing ambient temperature (Fig. 1). No secretion was observed at 10°C. The gland began to secrete as air temperature was increased from 20° to 30°C, and an average of 9.6 g (gland · hr)$^{-1}$ was collected at 50°C.

In order to evaluate the importance of this secretion for evaporative cooling, we compared the rate of secretion from both glands with the increment in respiratory evaporation associated with thermal panting. We trained the dogs to wear ventilated masks and determined the amount of water added to the air flowing through the mask (*7*). Saliva was observed dripping from the tongue of two dogs at high air temperatures, but not from the third (Fig. 2). This water would appear as respiratory evaporation in our collection system, even though it played no role in evaporative cooling. To correct this error, we collected the saliva which dripped from the tongue of each dog in separate experiments at each temperature. This drooling was copious in two dogs and as much as 100 g · hr^{-1} was collected at 50°C (Fig. 2).

The mean value for salivary dripping from each dog at each temperature was subtracted from the observed respiratory water loss in the previous experiments to obtain respiratory evaporation. To check the validity of this correction, we investigated the heat balance of the animal. In the steady state, heat production must equal heat loss. The three avenues of heat loss are evaporation, conduction, and radiation. We selected a steady-state situation in which air and wall temperatures were approximately the same as the body temperature of the dog, thereby nearly eliminating conduction and radiation as means of heat dissipation. Heat loss by evaporation, therefore, equaled heat production. When the ambient temperature was 40.0°C and rectal temperature was 39.1°C, the heat production equaled 2.70 kcal (kg hr)$^{-1}$ and calculated evaporative heat loss equaled 2.90 kcal (kg hr)$^{-1}$. Thus we have

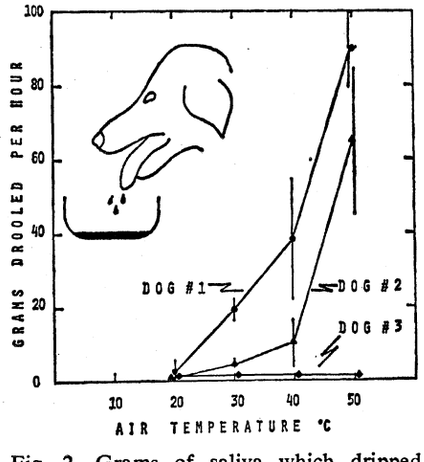

Fig. 2. Grams of saliva which dripped from the tongue as a function of air temperature. This was extremely variable from dog to dog, and none was collected from dog 3 (even at 50°C). Each point represents the mean of six to eight measurements, and each vertical bar represents twice the standard error.