Plant Water Potential Gradients Measured in the Field by Freezing Point

By

J. W. CARY and H. D. FISHER

Snake River Conservation Research Center, Kimberly, Idaho — 83341

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Abstract

A portable freezing point meter was used in the field to measure the water potential gradients in sunflower (*Helianthus annuus*), beans (*Phaseolus vulgaris*), corn (*Zea mays*), wheat (*Triticum aestivum*), pumpkin (*Cucurbita pepo*), potato (*Solanum tuberosum*), alfalfa (*Medicago sativa*), and sugarbeets (*Beta vulgaris*). The measurements were made between daybreak and sunrise, and again during the middle of the afternoon on days when the potential evapotranspiration varied between 6.5 and 8.0 mm of water.

The gradients varied from a maximum of 0.2 bar per cm in a wheat, down to an undetectable value for pumpkin. Although most of the soil in the root zone was kept at potentials above –1 bar, the bulk of the root tissue had water potentials of –5 to –10 bars. Differences in water potential between shaded and unshaded leaves, and between leaf tissue and guttation fluid suggested a similar drop of several bars between xylem elements and the surrounding leaf tissue in some plant species. The implications of such drops are discussed with respect to plant water transport equations and pressure cell potential measurements.

Introduction

Water potential in plants is important because of its influence on growth and development (21). Water potential and potential gradients also influence the water flow through plants which is a key link in the hydrologic cycle. Although the importance of plant water potential has been recognized for many years, experimental problems have made measurements difficult until the recent development of the vapor pressure psychrometer, the pressure cell, and the portable freezing point meter.

Most of the published data concerning water potentials have been taken from plants grown in greenhouses or environmental control chambers. Although many investigators are ultimately interested in the behavior of plants in their natural field environment, only a few measurements of water potential under natural conditions have been reported (10, 11, 13, 15, 16, 25). Moreover there is evidence that the water relations of plants grown under artificial conditions are significantly different from those grown in their natural environment. For example, working in an artificial environment, it was found (5) that sunflower (*Helianthus annuus*) leaves stopped growing when the water potential dropped below –3.5 bars, yet most potential measurements reported by persons studying plants under field conditions are less than –5 bars and the plants grow well.

Water potential gradients in plants under field conditions are of particular interest because the various components of the gradients act as driving forces for water flow in plants. The gradients are also important because the drop in potential between the soil and any group of plant cells determines the upper limit for water potential in the cells. Since with few exceptions (10, 25) almost no information is available on water potential gradients in plants under natural field conditions, a study was undertaken to gain some insight into how the gradients in different plants respond to the environment.

For field studies, the pressure chamber (4) and freezing point meter (6) are presently the most suitable methods for measuring plant water potentials because they are portable, measurements take only 3 or 4 minutes, and neither require ambient temperature control. Results obtained with the pressure chambers may or may not agree closely with results obtained with the vapor pressure psychrometer, which is probably the most accurate method for measuring plant water potential under laboratory conditions (4, 9, 14). In a previous study (6), the potential measurements made with a psychrometer and freezing point meter were compared and found to have an average random difference of 2.6 bars over the range of –5 to –30 bars. The correlation coefficient between the two methods for nine different

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species of plants was 0.8. Since, depending on plant species, the average variation between random, but supposedly similar, plant samples from the field falls between 1.5 and 2.3 bars (unpublished data), it was decided that the freezing point meter could be used satisfactorily for the study reported here, though some measurements were made with the pressure chamber for comparison purposes.

Procedure

Water potential measurements were made on a variety of plants growing in the field. The plants included: Sunflower (*Helianthus annuus* L.), beans (*Phaseolus vulgaris* L.), corn (*Zea mays* L.), wheat (*Triticum aestivum* L.), pumpkin (*Cucurbita pepo*), potato (*Solanum tuberosum* L.), alfalfa (*Medicago sativa* L.), and sugarbeets (*Beta vulgaris* L.). The water potential measurements were made with the freezing point meter. The meter was a modification of the unit previously described (6). It was powered by a 12-volt car battery, with the temperature of the freezing chamber controlled automatically by a separate circuit, diagrams of which are available from the authors upon request. The theory, as well as detailed instructions for assembly and operation, are being published elsewhere. (Measurement of Plant and Soil Water Stress, Utah State Univ. Exp. Sta. Bull., Herman Wiebe, ed., scheduled for printing March 1971).

Above-ground plant samples consisted of leaf tissue taken as near the petiole and main rib as possible without including large veins. The above-ground measurements were made in random order with respect to location on the plant. The potential of each sample was measured before another was taken. After completing the above-ground measurements, segments of roots were dug up and placed in the freezing point meter. The measurements were made both in the morning between daylight and sunrise, and during the early part of the afternoon. In all cases, clear weather prevailed, and days were selected in which the potential evapotranspiration varied between 6.5 and 8.0 mm H_2O. The soil water potential in the 15- to 40-cm depth was always within the tensiometer range (–0.1 to –0.9 bar) with the one exception noted for wild sunflower.

Results

Figure 1 shows water potential measurements on potato and bean vines. Measurements on a potato vine in which the leaves were all exposed to the sun are shown by the dots. Another potato vine, in which 3 of the leaves were shaded by the plant canopy, is shown by the crosses. The leaves exposed to a full radiation load had lower water potentials, as has been noted by others (11, 15, 19). While the bean vine was exposed to the same radiation load and had similar water potentials, it was not nearly as sensitive to changes in shading of the leaves, nor was there a large nighttime rise in water potential in the vine. Beans have a rather limited root system and are always troubled with root rot in southern Idaho. Beans are also unique in their leaf movement, for as the water stress in the plant increases, the leaves tend to turn their edges to the sun, reducing the radiation load (12).

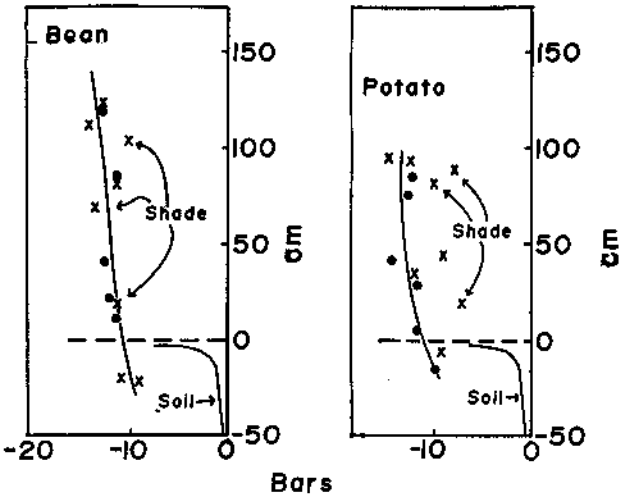

Figure 1. *Plant water potential in potatoes and beans as a function of the steam length from the soil surface which is taken as zero.* Data for potatoes are for 2 different plants, both sampled during midafternoon; for bean (●) sunrise, (×) afternoon.

Typical water potential gradients in corn are shown in Figure 2. Two plants growing on the south end of the field so that they were exposed to a full radiation load show a reasonably similar and smooth water potential pattern (shown by triangles and dots). However, a plant sampled at the same time just down the row gave the erratic water potential pattern shown by the crosses. Some leaves on this plant were exposed to a full radiation load as indicated by the four low potential points. Other leaves were receiving various degrees of shading from the surrounding canopy, thus accounting, in part, for the higher water potentials observed on lower portions of the plant. Shading in such a canopy is quite transient due to sun and shadow movements, and so makes the potential measurements more difficult to interpret. The plant in the row was presumably growing at a lower soil temperature than the plants on the end of the row where part of the soil surface was exposed to full sun intensity. This may have also affected the water potential levels in the plants.

Figure 3 shows the water potential patterns in corn plants measured between daylight and sunrise on three different mornings on the south edge of the field. The

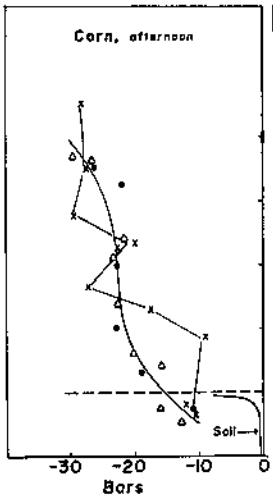

Figure 2

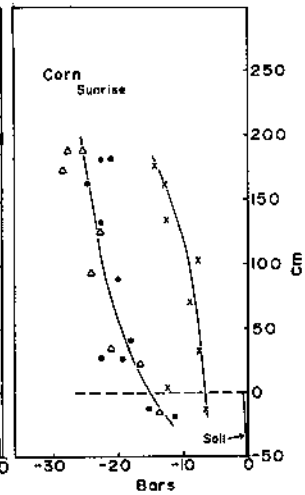

Figure 3

Figure 2. *Plant water potential in corn as a function of the stem length from the soil surface which is taken as zero.* (△), (●) full sun, (×) part shade.

Figure 3. *Plant water potential in corn at sunrise as a function of stem length from the soil surface which is taken as zero.* The lower potential curve was from plants immediately following a 24-hour irrigation, while the higher potential curve was from a plant one day after irrigation ended. Symbols see Figure 2.

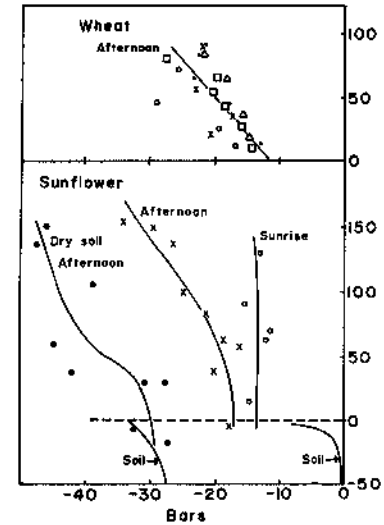

Figure 4. *Plant water potential in sunflower and wheat as a function of stem length from the soil surface which is taken as zero.* The various data point symbols for wheat represent individual plants sampled during midafternoon.

two plants (dots and triangles) represented on the lower curve had been irrigated throughout the previous day and night so that the soil was very moist. Data points in the upper curve were measured 24 hours after the cessation of an irrigation and indicated a reasonable rise from the previous afternoon's water potential (15). The apparent adverse effect of irrigation on the water potential on the lower curve may have been due to a decrease in root permeability brought about by lower soil temperatures or aeration. This type of response to irrigation was also occasionally noted with other crop plants, though it did not persist for more than a day.

The upper curve in Figure 3 shows a normal pattern for plant moisture stress at sunrise. It was interesting that guttation sometimes occurred in corn under these water potential conditions (1). In general, the guttation developed during cool nights when the soil was moist. The expelled fluid had an osmotic potential greater than –2 bars, yet samples from the corn leaves never indicated a water potential greater than –6 bars.

The two upper curves in Figure 4 show the daily water potential response in a wild sunflower growing in moist soil. The lower curve shows the afternoon potential pattern for a wild sunflower existing on a soil with an average maximum water potential of –30 bars in the root zone. All leaf measurements were taken on tissue exposed to the sun, so there was no obvious explanation for the erratic behavior of the water potential distribution. During the afternoon, when leaves were removed from the sunflowers, plant sap flowed from the cut petiole within a few minutes, indicating positive pres-

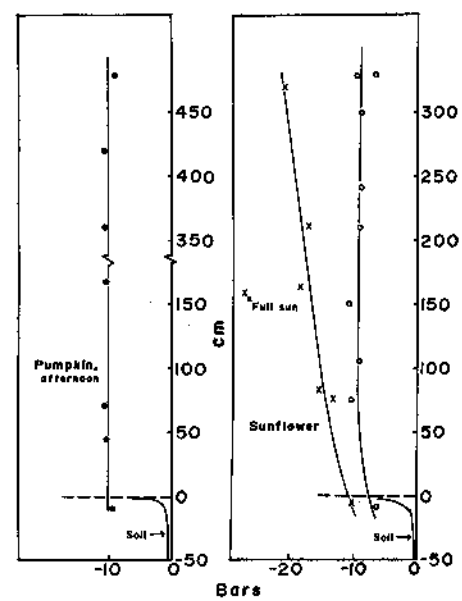

Figure 5. *Plant water potential of sunflower and pumpkin as a function of stem length from the soil surface which is taken as zero.* Sunflower: (○) sunrise; (×) afternoon.

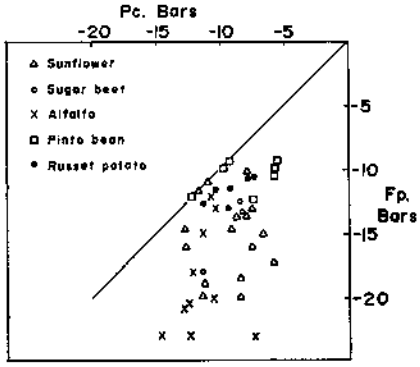

Figure 6: *A comparison of water potential measurements made with the pressure chamber* (Pc) *and freezing point meter* (Fp).

sures still existed in the tissue. This was true even of the plants existing on the very dry soil.

The potential gradients which developed in the sunflower plants were never as steep as those which commonly developed in wheat plants during the afternoon, even when growing in moist soil (17) (Figure 4). The wheat also occasionally guttated in the early morning after a cool night and, like the corn, the leaf water potential was generally between –5 and –10 bars, while the guttation fluid was higher than –2 bars.

Figure 5 shows a sharp contrast to the steep afternoon water potential gradient developed by wheat. The pumpkin, exposed to a full radiation load in midafternoon, developed no measurable water potential gradient. At the same time, a tall domestic sunflower standing nearby did show a definite gradient of water potential (Figure 5), even though its leaves were turned such that, with one exception, they were receiving only a partial radiation load from the sun. The "sunrise" curve in Figure 5 shows the water potential distribution in the sunflower the following morning at sunrise with the expected nighttime increase in water potential (15).

A comparison between the potential measurements made with the pressure chamber and the freezing point meter are shown in Figure 6. Leaf tissues run in the freezing point meter were subsamples of the portion of plant placed in the pressure chamber. Similar measurements and results have been reported using the pressure cell and vapor pressure psychrometer on twigs and leaves from trees (25). If each plant had been in equilibrium and if both the pressure chamber and the freezing point meter measured only total water potential, all points would fall on the 1 : 1 line. Obviously, some of these conditions were not fulfilled and the implications concerning the plant potential measurements will be discussed.

Discussion

Plant water transport equations are useful in the interpretation of the experimental results. It can be shown from the theory of thermodynamics of irreversible processes that the liquid phase flux may be approximately described as:

$$J_\lambda = -\frac{1}{R_\lambda}\left[\frac{d\Phi}{dz} - \gamma\frac{1}{\varrho_\lambda g}\frac{d\Pi}{dz}\right] \qquad [1]$$

where J_λ is flux of water including solutes, R_λ is the reciprocal of the hydraulic conductivity, Φ is hydraulic head, γ is the osmotic efficiency or reflection coefficient, ϱ_λ the density of the liquid, g the acceleration of gravity, Π the osmotic pressure, and z the position in the gravitational field. Equation 1 assumes one effective osmotic component, one directional flow, and no significant effects from thermal or electrical gradients. It is the simplest relation that can be used to describe flow in the paths between the soil and the root xylem, and from the xylem into surrounding cells. Flow through the xylem is thought to be reasonably free of semipermeable barriers, $\gamma = 0$, so that equation 1 becomes for this case:

$$J_\lambda = -\frac{1}{R_\lambda}\frac{d\Phi}{dz}. \qquad [2]$$

It also follows from the theory of irreversible thermodynamics that water vapor transport between the air water interfaces inside the leaf tissue and the atmosphere outside may be described as:

$$J_w = -\frac{r}{p}\left[\frac{L_{wq}}{H} - L_{ww}\varrho_w\right]\frac{dp}{dz} = -\frac{1}{R_v}\frac{dp}{dz}. \qquad [3]$$

where J_w is flux of pure water, r the universal gas constant, p the vapor pressure at the level z, H the heat of vaporization, L phenomenological coefficients, and R_v a resistance or proportionality constant for water vapor flux inside the leaf. This relation includes the influences of thermal gradients which are important in vapor transport.

All the plants studied showed a strikingly lower water potential in the root tissue than in the soil surrounding the roots. This potential drop was from 5 to 10 bars, and persisted even during the relatively low transpiration period at night. This is not surprising in principle, for a growing plant is never an equilibrium system and potential gradients will always exist (5, 19, 22, 23). The large potential drop cannot necessarily be interpreted as a large value of R_λ in the roots since the flow per unit surface area, the reflection coefficient, and osmotic potential gradient are not known (equation 1). Neither do these data necessarily indicate that all of the water in the roots has a potential 5 or more bars below that of the soil water. The potential measured by freezing point is thought to consist of the sum, $\varrho_\lambda g\Delta\Phi + \Delta\Pi$ (as in equation 1) pertaining to the liquid adsorbed in and

around the cell wall tissue when the elevation component in the gravitational field can be neglected. The pressure chamber, of course, does not measure $\Delta\Pi$ potential components and is thought to give more nearly $\varrho_l\, g\Delta\Phi$ of the liquid in the xylem tissue when the elevation component can be neglected. In any case, the water enters the younger, more permeable, root tips from the soil, flows through developing xylem, and gradually into the surrounding masses of root cells where its potential was measured by freezing point. Since the solution flows through the xylem (by equation 2) and then along a continuous water film without semipermeable membranes into the surrounding cell wall regions where equation 1 begins to apply due to the increasing value of γ, it follows that the potential of water in the root xylem and absorbing tips must lie between the soil water potential and the water potential in the bulk of the root tissue.

While the potential gradients generally tend to approach zero over the dark period, exceptions do occur (Figures 1 and 3). In the case of corn, root permeability was evidently decreased by irrigation, and in the case of beans, root rot was possibly a factor, although on some nights during the growing season the water potential in the bean plants did increase to –5 or –6 bars.

There was a wide range of water potential gradients in the various plants during the afternoon. While values of 0.5×10^{-3} bar/cm are considered representative (21), values observed in this study ranged up to nearly 0.2 bar/cm in wheat. Within limits, an increasing water potential gradient does not necessarily mean a large difference in evapotranspiration. It does, however, follow an increasing deficit in the water potential of the leaves and this may influence the plant's growth.

Shading leaves of some plants results in a significantly higher water potential, while in other plants shading is not so important. In cases where shading of leaves causes a higher water potential with respect to the unshaded leaves in either direction along the stem, it follows from equations 1 and 2 that the water potential can be considerably higher in the xylem elements throughout the plant than in the leaf tissue (18, 19, 25). This may be analogous to the difference in water potential between the root tissue and the soil surrounding the plant roots. In the case of leaves, transport described by equations 1 and 3 may both be involved. Since there is a continuous gas phase throughout most leaves which is subject to continuously changing temperatures as the radiation and sensible heat balance on the leaf surface changes under field conditions, there may be some evaporation, diffusion, and recondensation within the leaf (equation 3). Such vapor flow will not necessarily be in the same direction as the total water potential gradient. It is even possible that some viscous or mass transport of water vapor occurs inside leaves due to changing ambient pressures associated with convective and turbulent fluxes in the air masses around the leaves. Equation 3 does not include such transport, but can be modified to do so. Probably, though, liquid phase transfer (equation 1) is predominant. The water potential drop between the xylem and bulk of leaf tissue could be caused by a flow path with a large R_l or by a small value for γ. In the case of a small value of γ, the water flow path might be rather unselective so far as solutes were concerned, yet the solutes could be reabsorbed by specific areas of the cells independently of the water before they diffuse into the vessels. This sort of action is known to occur with potassium uptake by guard cells (20), and possibly in the absorption of the contents from ruptured cells (2). Guttation of a –1 or –2 bar fluid by leaves with a tissue potential of –5 bars could also be favored by a low γ value. If γ decreases as the temperature falls on a cool night, the cell wall turgor pressure could cause some net outflow of solution responding to the hydraulic head term in equation 1. Such outflow could help displace some of the higher potential xylem fluid from the end of the vessels. As the temperature rises, γ could increase, stopping outflow, and the solutes could be reabsorbed by the cells before appearing at the leaf margins. It has been noted that the amount of water adsorbed by leaf tissue may decrease as the temperature decreases (8, 24), which could indicate a temperature-sensitive reflection coefficient. It appears that γ may also change with light intensity and CO_2 concentration, at least in the case of guard cells (20). In any event, we do not propose that changes in osmotic efficiency of the leaf cells are responsible for guttation, but rather that a time variable γ could favor guttation and account for the difference in water potential between the leaf tissue and droplets which form on the leaf margins.

The potential drop between the xylem and the leaf cells may also be related to the discrepancy between the pressure cell and freezing point measurements, *i.e.*, the pressure cell tends to measure the water potential in the xylem elements, while the freezing point meter and the psychrometer tend to measure the potential of water held in cell walls and intracellular spaces. It is interesting that the only points that fell on the 1 : 1 line in Figure 6 were those of the bean and sunflower. The bean showed a relatively insensitive response to shading (Figure 1), indicating that the water potential in the leaf tissue stayed reasonably near that in the conductive tissue. While many of the measurements made with the sunflower were not near the 1 : 1 line in Figure 6, there are some data in the literature (4) indicating that under some conditions a reasonable correlation between psychrometer and pressure cell readings may be observed. On the other hand, it is hard to reconcile the good agreement between the pressure cell and psychrometer reported for corn (9) with our observations of the erratic potential pattern developed by corn from shading in the plant canopy (Figure 2). Of course, using the pressure

cell on soft tissue plants such as those studied here may result in several problems (14), such as crushing the conductive tissue in the pressure seal, and mixing of the phloem sap with the xylem fluid. When the pressure cell shows lower potentials than the psychrometer (14), the discrepancy probably does not arise from a difference in xylem water pressure and leaf cell water potential, but from a large pressure drop in the tissue surrounded by the seal (3), or from the previous rupture of water columns in xylem elements (7) which may refill under the positive pressures inside the chamber before the fluid appears at the point of observation.

Measurements of plant water potential made under natural field conditions may show considerable variability due to natural differences in internal water transport which are compounded by changes in the radiation load from the sun. However, if enough measurements are made with due regard to conditions at the time, meaningful patterns of plant water potential can be developed. These patterns indicate that there is a significant decrease in potential between the soil and bulk of the root tissue. In some plants there may also be a significant decrease in water potential between the xylem elements and the bulk of the leaf tissue. This particular property can cause large differences in the plant water potential distributions. For example, in wheat the difference between xylem and leaf tissue potential may be 5 bars or more. Thus, the wheat plant may guttate a fluid with potential of around −1 bar, even though the average water potential in the surrounding leaf tissue may be less than −5 bars. Pumpkin, on the other hand, showed almost no potential gradient through the aerial portions of the plant. The other plants tested were intermediate to these extremes.

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