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Physical Aspects of the Internal Water Relations of Plant Leaves^{1, 2}

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Under equilibrium conditions, the state of the water in plant leaf cells may be written in terms of the various components of the potential energy

$$\Psi = \Psi_{\pi} + \Psi_p + \Psi_m \quad \text{I}$$

where Ψ is the total water potential, Ψ_{π} is the osmotic potential component, Ψ_p the pressure potential component (turgor pressure), and Ψ_m is the component due to adsorption forces such as those in the cell wall. The partition of energy between the osmotic and the adsorption components is somewhat arbitrary since some of the water in the leaf tissue may be subject to both osmotic effects and adsorption forces, particularly at low leaf-water content. In the vacuole the osmotic component is the more important. Therefore, the adsorption potential is usually neglected and equation I reduces to the more familiar

$$\text{DPD} = \text{CP} - \text{TP} \quad \text{II}$$

where the diffusion pressure deficit (DPD) is a measure of the total potential, CP represents the osmotic pressure, and TP the turgor pressure. If the potentials in equation I are expressed in terms of energy per unit volume, then they have the dimensions of pressure which are commonly used in equation

II. However, the sign of the total water potential is opposite from that of the DPD.

If the cell solution were to behave ideally, the osmotic pressure would be directly proportional to the solute concentration. There would exist, then, a simple relation between osmotic potential and cell water content:

$$\Psi_{\pi} = \Psi^{\circ}_{\pi} / \theta \quad \text{III}$$

where Ψ°_{π} is the osmotic pressure at full turgor and θ is the relative water content of the cell. θ is the ratio of the water content of the cell to that water content it has when in equilibrium with free water at the same temperature and pressure. If the amount of bound water is appreciable, then this amount should be subtracted from θ . Slavik (10) found as much as 30% bound water in his experiments.

The osmotic and pressure components of the potential are not independent. Because of the elastic nature of the cell wall, changes in turgor pressure cause changes in cell volume due to changes in cell water content. This, in turn, changes the cell concentration. If it is assumed that the relation between the turgor pressure and the cell volume is linear (3, 7), then $\Psi_p = c(\theta - \theta_0) / \theta_0$ where θ_0 is the relative water content at which the turgor potential becomes zero and c is the modulus of elasticity. Equation I then becomes

$$\Psi = \Psi^{\circ}_{\pi} / \theta + c(\theta - \theta_0) / \theta_0 + \Psi_m(\theta) \quad \text{IV}$$

giving us a relation between the water potential and the relative water content of the cell. $\Psi_m(\theta)$ represents the relation between water content and matrix

¹ Revised manuscript received January 11, 1965.

² This work was supported in part by the Meteorology Department, United States Army Electronic Research and Development Activity, Fort Huachuca, Arizona.

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potential. Growth can be expected to cause some departure from the expressions used in deriving equation IV, but to the extent that the assumptions are valid, equation IV gives a unique relation between the total water potential and the relative water content of the leaf.

Haines (6) has questioned the assumption of a linear relation between the cell dimensions and the turgor pressure. However, his conclusions were based in part upon a misstatement of Hooke's law. Nevertheless, there is evidence, such as the data of Tamiya (11) for *Nitella* [cited by Bennet-Clark (1)], that suggests that the relation between turgor pressure and cell volume may be highly nonlinear.

In practice, it is much easier to make the measurements needed to test equation IV on tissue rather than single cells. The assumptions necessary to derive IV might be met more nearly by a large group of cells than by a single cell. The purpose of this paper is to examine the relation between the total potential, its various components, and the relative water content of plant leaves; to determine the applicability of equation IV; and to provide, if possible, a sound basis for the present empirical use of water content to estimate water potential.

Materials and Methods

Plants studied were cotton (*Gossypium hirsutum*, var. Acala), pepper (*Capsicum frutescense* L., var. California Wonder), sunflower (*Helianthus annuus* L.), and birdsfoot trefoil (*Lotus corniculatus* L.). The plants were grown in a greenhouse at $25 \pm 5^\circ$. In order to obtain different values of water potential, water was withheld from the plants until their leaves wilted to the desired extent. Mature unshaded leaves were sampled periodically and their water potential and osmotic potential were determined with a thermocouple psychrometer (4). The relative water content of another portion of each leaf (other leaflets from the same trifoliolates of trefoil) was determined by the method of Weatherly (12).

In 1 series of experiments, the area of individual leaf disks (or whole leaflets in the case of trefoil) was measured as a function of water content. The area was determined optically by means of a Weston Model 603 light meter and the water content determined by weighing. The disks were brought to full turgidity and were then measured as they were allowed to dry. Duplicate measurements gave very good agreement except at relative water content less than about 0.3, where wrinkling of the disk became a problem.

Results and Analysis

If equation III is valid, the change in the log of the relative water content should equal the change in the log of the osmotic potential. Figure 1 shows that this occurs for the 4 species. Because of the

scatter of the data in figure 1, corrections for bound water of less than 10% would not be noticeable. Since the water potential is assumed to be zero at a relative water content of 1.0, the turgor pressure equals the osmotic pressure at this water content. The osmotic potential at this point is designated Ψ_π^0 and for the 4 species studied is approximately -11.5 bars for cotton, -10.5 bars for sunflower, -11.5 bars for trefoil, and -11 bars for pepper. Ψ_π^0 depends upon the solute content of the cells and is strongly influenced by the conditions under which

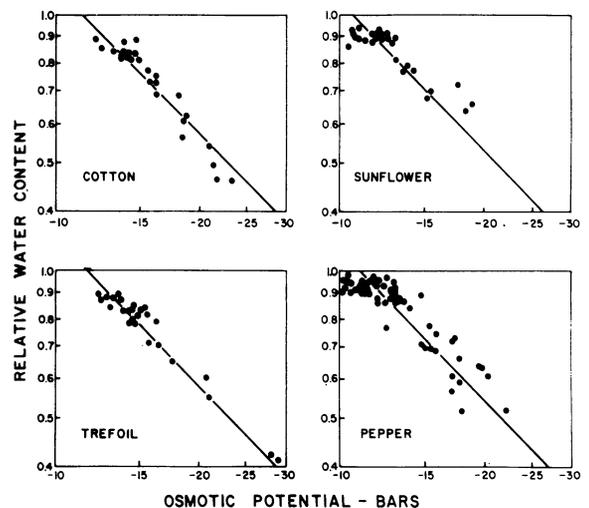


FIG. 1. Relative water content as a function of the average osmotic potential in the plant leaf. The straight lines represent the relation expected if the solutes behave ideally and there is no bound water.

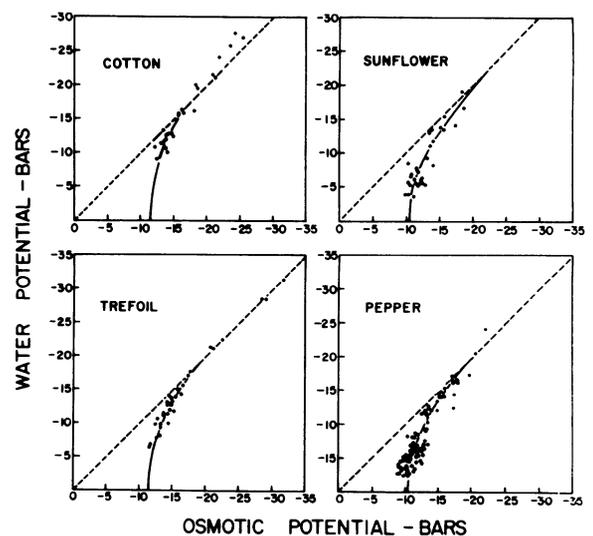


FIG. 2. Average water potential plotted as a function of average osmotic potential in the plant leaf. The difference between the smooth curves through the data and the dashed lines with a slope of unity gives the pressure (turgor) potential.

the plants are grown, particularly the concentration and composition of the soil solution (2).

In figure 2, the water potential is plotted as a function of the corresponding osmotic potential. The smooth curves were drawn through the data points in such a way as to intersect the abscissa at the value of Ψ°_{π} determined from figure 1. The dashed line in each graph represents the locus of points of equal osmotic and total water potential, i.e., zero turgor pressure. Except in the case of the cotton, the turgor pressure decreases with decreasing osmotic potential, eventually becoming zero. In the case of cotton, the last few data points lie above the dashed line in the region corresponding to a negative turgor pressure. Although Slatyer (9) has also reported negative turgor potentials for cotton, their existence is questionable. Judging from the water content measurements, the osmotic potential values for the cotton in the region of -25 bars may be too low. The water potential at zero turgor pressure is estimated from the point of intersection of the smooth curves with the dashed lines in figure 2. These values are for cotton, -19 bars; sunflower, -22.4 bars; trefoil, -20.3 bars; and pepper, -22 bars.

The horizontal or vertical distance from the smooth curve to the dashed line in each graph in figure 2 gives the turgor pressure. From this figure it is not difficult to construct a curve relating turgor pressure to water potential. The turgor pressure thus estimated is plotted as a function of the corresponding relative water content in figure 3. If the water content is taken as a measure of average cell

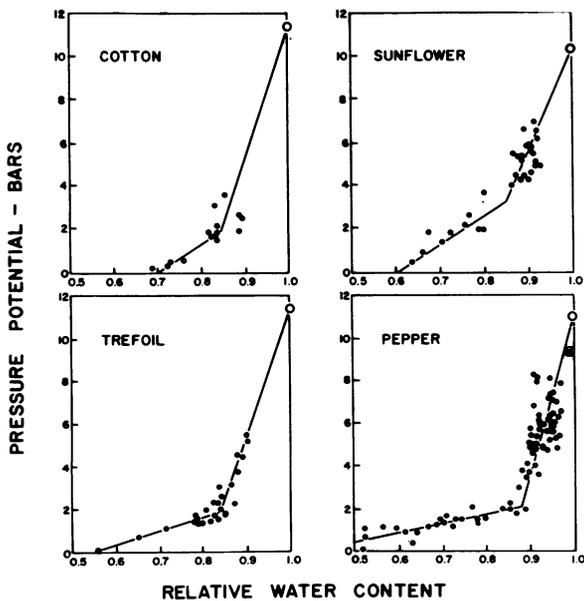


FIG. 3. Pressure potential of the plant leaf as a function of the relative water content. The pressure potential at a relative water content of unity was taken numerically equal to the osmotic potential at this water content in figure 1.

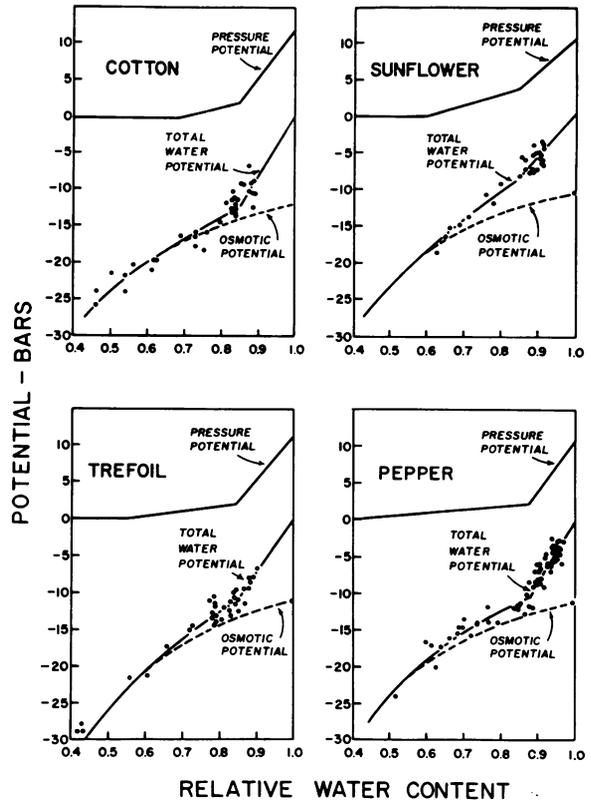


FIG. 4. The osmotic, pressure, and total water potential of the plant leaf as a function of the relative water content. The circles represent the experimentally determined values for the total water potential. The dashed line is the theoretically predicted osmotic potential. The osmotic and pressure potential components are added to give the calculated relation between total water potential and relative water content indicated by the smooth curve.

size, it is obvious that cell size is not a simple linear function of turgor pressure. However, the data can be represented reasonably well by 2 straight-line segments. One of the line segments is drawn so as to pass through the point of maximum turgor pressure corresponding to Ψ°_{π} , as determined from figure 1, when $\theta = 1$. It appears that Hooke's law is obeyed reasonably well if a distinction is made between a condition of high turgor pressure and one of low turgor pressure and with a different modulus of elasticity for each range. The change in the elasticity occurs at about 2 bars for cotton, trefoil, and pepper, and at about 3.5 bars for sunflower.

The data are plotted in a more conventional fashion in figure 4, in which the water potential is plotted as a function of relative water content. The results are typical of others in the literature in that a smooth curve drawn through the data would tend to show a point of inflection in the region of -10 to -15 bars. The dashed line in each of the graphs in figure 4 is the osmotic potential calculated from

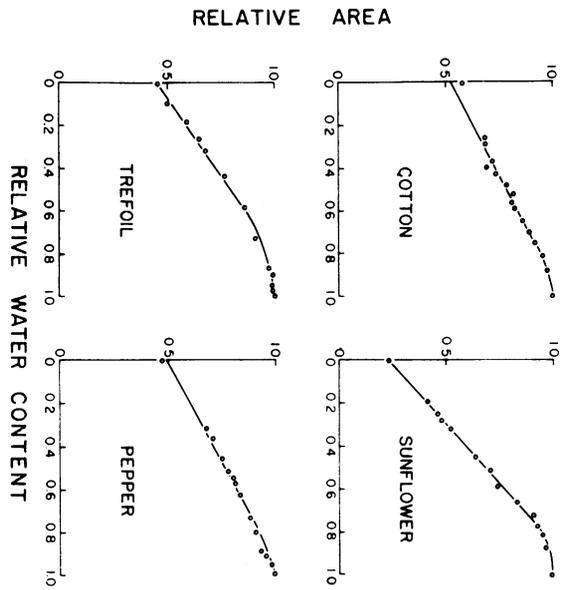


FIG. 5. Relative area of leaf disks as a function of relative water content.

equation III using the value for Ψ°_{π} estimated from figure 1. The pressure potential is given by the solid straight line segments along or above the \times axis. This component of the potential is presumed zero at a relative water content less than about 0.5 and then becomes positive with increasing water content. The solid curve represents the sum of the 2 components as represented in equation IV. Specification of a value for the osmotic potential at full turgor, and 2 values for the modulus of elasticity and their range of appli-

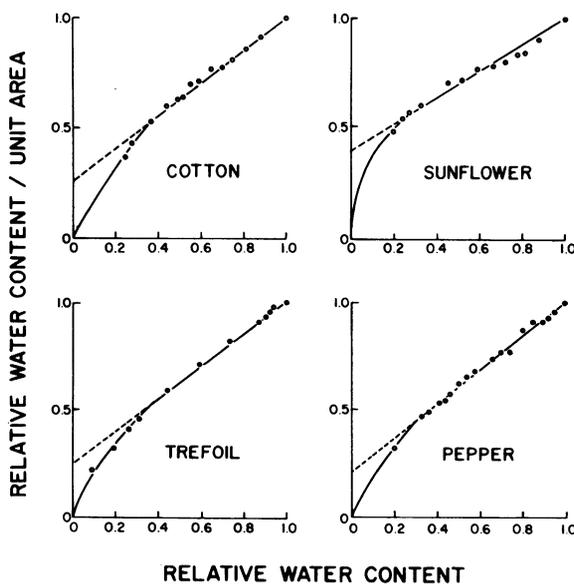


FIG. 6. Relative water content per unit area as a function of the relative water content. This ratio gives a measure of leaf thickness.

cability is sufficient to obtain a relation between water potential and relative water content which fits the experimental data well within the experimental error.

Because of the anisotropic nature of a plant leaf, it might well be expected that the elastic properties of the leaf would be different along different axes. To investigate this, the areas of individual leaf disks were measured as a function of relative water content. The results of these measurements are given in figure 5, where the relative area is plotted as a function of relative water content. Dividing the relative water content by the relative area gives a measure of the leaf thickness. This ratio is plotted as a function of relative water content in figure 6. The data fall on a straight line above a water content of about 0.4 but tend to curve toward the origin at lower water contents. That the data points do not all lie on a straight line passing through the origin can be explained by assuming that the water that is bound in the cell walls does not contribute to the expansion of the leaf. The straight-line portion of the curve is displaced upward because of this water. On extrapolating the curves in figure 6 back to zero water content, the quantity of water involved can be estimated. This turns out to be about 15% for cotton and approximately 10% for the other 3 species, relative to the fully turgid condition.

The relative diameter and relative thickness are plotted in figure 7 as a function of turgor pressure.

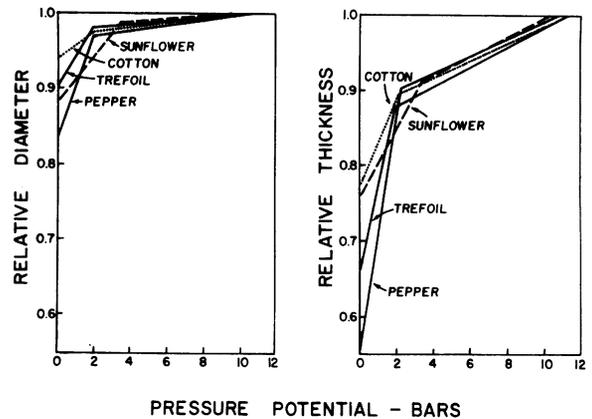


FIG. 7. Relative diameter and relative thickness of leaf disks as a function of the pressure potential. The slopes of these lines are proportional to the moduli of elasticity.

Most of the increase in volume with increasing turgor pressure occurs in the leaf thickness with only a relatively small increase occurring in the lateral dimensions of the leaf. All 4 species studied exhibited very nearly the same moduli of elasticity in the high turgor pressure range, with more variation between species in the low pressure range. Values for the elastic moduli taken from the slopes of the

Table I. *Moduli of Elasticity*

Species	Turgor pressure range	Bulk modulus	In plane of leaf	Perpendicular to plane of leaf
	bars	dynes/cm ²	dynes/cm ²	dynes/cm ²
Cotton	>2	6.0 × 10 ⁷	42.0 × 10 ⁷	8.1 × 10 ⁷
	<2	1.5 × 10 ⁷	5.0 × 10 ⁷	2.0 × 10 ⁷
Sunflower	>3.4	4.7 × 10 ⁷	46.5 × 10 ⁷	7.9 × 10 ⁷
	<3.4	1.4 × 10 ⁷	3.3 × 10 ⁷	2.3 × 10 ⁷
Trefoil	>2	6.0 × 10 ⁷	48.0 × 10 ⁷	7.7 × 10 ⁷
	<2	0.63 × 10 ⁷	2.6 × 10 ⁷	0.85 × 10 ⁷
Pepper	>2	7.1 × 10 ⁷	35.5 × 10 ⁷	9.9 × 10 ⁷
	<2	0.44 × 10 ⁷	1.6 × 10 ⁷	0.59 × 10 ⁷

lines in figures 3 and 7 are given in table I. Ordinarily the elastic modulus is defined in terms of the increase in a dimension relative to that dimension when there is zero stress. However, it is much more difficult to fix precisely the point of zero turgor than the point of maximum turgor. For this reason, the moduli in table I were calculated with respect to a relative water content of 1.0. Strictly speaking, a linear relation between stress and elongation in 1 dimension will not result in a linear relation between stress and volume change. However, if the relative change in volume is small as is the case at high turgor pressure, the relation will be very nearly linear. In the low turgor pressure range, the data do not justify a more precise formulation of the relation between stress and strain.

Discussion

Further refinement and improvement of equation IV so far as plant leaves are concerned will require data with less scatter. This can probably be accomplished, in part, by achieving much greater uniformity in the material samples. Even so, the present data indicate that equation IV is sufficiently accurate to be very useful.

Rawlins (8) has recently shown that a low rate of water vapor exchange between the plant material and the sample chamber can cause systematic errors in measurements made by the thermocouple psychrometer. The direction of these errors depends upon whether there are extraneous absorbing surfaces in the chamber or not. Were it not for such surfaces, which act as sinks for water vapor, an empty sample chamber should approach saturation. In our experiments, this was never quite achieved. A precise estimate of this error for our data cannot be given, but it is believed to be less than 2 bars. Such an error would lead to errors in some of the numbers calculated, e.g., Ψ°_{π} , but should not alter the general conclusions.

Some interesting conclusions concerning the phenomenon of wilting can be drawn from the data. It has been generally assumed (9) that the permanent wilting point corresponds to zero turgor pressure in the plant leaf. The data of these and other experi-

ments (4) indicate that visible wilting symptoms occur at a turgor pressure of 2 or 3 bars. Therefore, the visible wilting associated with the permanent wilting point is due to a marked change in the elastic properties of the cell when the turgor pressure drops below a critical value, rather than the complete absence of turgor per se. This is quite logical from a purely physical standpoint. Disregarding the support given to the leaf blade by the veins, the bending of a leaf is analogous to the bending of a beam. The extent to which the leaf will flex under its own weight should be inversely proportional to the appropriate modulus of elasticity and to the cube of the blade thickness. When the turgor pressure is above 2 bars, the thickness is relatively constant and little variation in flexure with varying turgor pressure is to be expected. When the turgor pressure is reduced below the critical pressure of about 2 bars, the elastic modulus decreases markedly, allowing the leaf to sag. As the turgor pressure is further reduced, the reduction in leaf thickness tends to permit further bending. The cotton leaf is relatively rigid and is well supported by the veins so that it exhibits only modest wilting symptoms. The pepper, which on the other hand is quite elastic and undergoes a considerable change in thickness, shows extreme wilting symptoms as the turgor pressure approaches zero. It is not unreasonable to expect a similar effect in the petiole. The critical turgor pressure at which this change in elasticity is observed corresponds to a water potential of about -11 to -13 bars. This is in very good agreement with the traditionally accepted permanent wilting point, which has been found to be reasonably well correlated with a soil-water potential of -15 bars.

The values for the elastic moduli for the leaves given in table I are of the same order of magnitude as those reported for epidermal root cells of wheat by Frey-Wyssling (5). He obtained a value of 27.5×10^7 dynes/cm² for fully elongated cells.

Summary

Relations between the water potential, osmotic potential, pressure potential, and relative water con-

tent have been derived on the basis of 2 simple assumptions. Measurements of these quantities were made on leaves of cotton, sunflower, pepper, and birdsfoot trefoil to test the validity of these relations. Within the precision of the data, the assumption that the osmotic potential is inversely proportional to the relative water content of the leaf was satisfied. The turgor pressure was not related to water content in a simple linear fashion but the data could be represented adequately by 2 straight-line segments. A marked change in the modulus of elasticity of the leaves occurs at a turgor pressure of about 2 bars, corresponding to a water potential of about -12 bars. The so-called permanent wilting phenomenon is explained in terms of the variation in elastic modulus. The major change in leaf dimensions with changing water content occurred in the leaf thickness with only a modest variation in the leaf area.

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