Terminology of Cell-Water Relations

Abstract. *Use of the term "water potential" in place of "diffusion pressure deficit" would improve communication between botanists and scientists in other fields because the concept of potential is familiar to most scientists. Water potential, expressed as* Ψ_w, *is the difference in free energy or chemical potential per unit molal volume between pure water and water in cells at the same temperature. The potential of pure water is set at zero; hence the potential of water in cells and solutions is less than zero, or negative. The water potential of a cell is numerically equal to its diffusion pressure deficit, but has a negative sign.*

Communication in the field of plant- and soil-water relations has been hindered by lack of a standardized terminology acceptable and meaningful to all scientists in that field and in related areas of the biological and physical sciences. Of the many available terms describing the water-absorbing capacity of plants and the energy status of water in plants and soils, *water potential* seems most satisfactory because it is consistent with modern concepts of thermodynamics. It is hoped that an explanation of the derivation of the term *water potential* and of its relationship to other terms currently in wide use will hasten its acceptance as the basis for a standard terminology in plant- and soil-water relations.

Among the numerous terms introduced by botanists to describe the free-energy status of water in cells and plant tissue are *suction force, water absorbing power, Hydratur*, and *diffusion pressure deficit.* Only the term *diffusion pressure deficit* (DPD) attained wide usage in the United States. Meyer (*1–3*) stated that the DPD of a cell or tissue can be regarded as a measure of the pressure with which water will diffuse into it if the cell or tissue is immersed in pure water. The DPD terminology has been useful for many years, but, as pointed out by Slatyer and Taylor (*4*), the time has come when it should be abandoned in favor of the more basic terminology used in physical chemistry and thermodynamics. The term *diffusion pressure* is rarely used today in physical sciences.

Water potential refers to the same property of water as DPD, but is a more meaningful name for it. The term *potential* is widely used in the physical sciences and in soil science and is familiar to workers in many fields. Furthermore, use of the *water potential* terminology encourages isolation and evaluation of the various components, osmotic, matric, and pressure, which affect the total potential of water in various parts of the system.

To explain the concept of *potential*, we will start with the general concept of free energy, or Gibbs free energy. The "free energy" in a system is an expression of the capacity of the system or a component of the system to do work. The free energy of a substance depends on the mean free energy per particle and on the concentration of particles, that is, the mole fraction of the substance under consideration. The free energy of water in a system can be expressed as the chemical potential of the water, which is equal to its partial molal Gibbs free energy.

The net potential of the water in the system (μ_w) is equal to the chemical potential of pure, free water ($\mu_w{}^\circ$) adjusted for the effects of those forces in the system which change its chemical potential. If the effects of these forces are expressed through their influence on vapor pressure, the chemical potential of water in the system may be described as the algebraic sum of the components of

$$\mu_w = \mu_w{}^\circ + RT \ln e/e^\circ \tag{1}$$

where R = the ideal gas constant (erg/mole per degree), T = the absolute temperature (degrees K), e = the vapor pressure of water in the system at temperature T, and e° = the vapor pressure of pure free water at the same temperature. The units of $RT \ln e/e^\circ$ are thus: (erg/mole per degree) × (degrees), or erg/mole, the same as those of μ_w and $\mu_w{}^\circ$.

Absolute values of chemical potential are not easily measured, but differences in chemical potential can be measured. The standard reference from which to measure the difference conventionally is taken to be the chemical potential of pure free water. Hence, Eq. 1 becomes

$$\mu_w - \mu_w{}^\circ = RT \ln e/e^\circ \tag{2}$$

When e/e° is less than 1, $\ln e/e^\circ$ is a negative number, hence the potential of the system is less than that of pure free water and is expressed as a negative number.

The expression of chemical potential in energy units, that is, ergs per mole, is inconvenient in discussion of cell-water relations. In cells we ordinarily deal with pressures, namely osmotic pressures and turgor pressures. Consequently, it is more convenient to convert from energy units to pressure units by dividing both sides of Eq. 2 by the partial molal volume of water, V_w, as follows:

$$\frac{\mu_w - \mu_w{}^\circ}{\bar{V}_w} = \frac{RT \ln e/e^\circ}{\bar{V}_w} \tag{3}$$

The units of Eq. 3 are:

$$\frac{\text{erg/mole}}{\text{cm}^3\text{/mole}} = \frac{\text{erg}}{\text{cm}^3} = \frac{\text{dyne/cm}}{\text{cm}^3} = \text{dyne/cm}^2$$

Dynes per square centimeter are more conveniently expressed as bars or atmospheres, which are related as follows: 1 bar = 0.987 atm = 10^6 dyne/cm^2 or erg/cm^3.

By definition, Eq. 3 describes the *water potential*, designated by the symbol Ψ_w, of a system. Thus,

$$\Psi_w = \frac{\mu_w - \mu_w{}^\circ}{\bar{V}_w} = \frac{RT \ln e/e^\circ}{\bar{V}_w} \tag{4}$$

This equation indicates that Ψ_w is equivalent to the difference in free energy per unit molal volume of water between water in the system and pure free water, and is related to the vapor pressures of water in the system and of pure water at the reference temperature.

The potential of water in any system is affected by factors which change the free energy or chemical activity of water molecules. Water potential is decreased by the addition of solutes, by matric forces which adsorb or bind water, by negative pressures such as those in the xylem of transpiring plants, and by reduction in temperature; the potential is increased by the wall pressure of partly or fully turgid cells and by increase in temperature.

For a plant cell under isothermal conditions, we can summarize the above factors as follows:

$$\Psi_{\text{cell}} = \Psi_s + \Psi_p + \Psi_m \tag{5}$$

where Ψ_{cell} is the water potential of the cell, and the other terms express the contributions to Ψ_{cell} by solutes (Ψ_s), pressure (Ψ_p), and matric forces (Ψ_m). Ψ_s and Ψ_m are negative, Ψ_s expressing the effect of solutes in the cell solution, and Ψ_m the effect of water-binding colloids and surfaces in the cell. Ψ_p is positive unless there is a negative wall pressure, a rare occurrence. The sum of the three terms is a negative number except in fully turgid cells, when it becomes zero.

Except in very dry tissue or in cells

with small vacuoles, Ψ_m is small relative to Ψ_p and Ψ_s. If we disregard Ψ_m, Eq. 5 becomes:

$$\Psi_{cell} = \Psi_s + \Psi_p \qquad (6)$$

It will be recalled that DPD was defined by Meyer (*2*) as:

$$DPD = OP - TP \qquad (7)$$

To compare the terms of Eq. 6 and Eq. 7, we express the potentials in Eq. 6 as their algebraically equivalent pressures: $\Psi_s = -OP$, $\Psi_p = TP$, and $\Psi_{cell} = -(OP - TP)$. Thus, it can be seen that Ψ_{cell} or Ψ_w and DPD are numerically equal but are opposite in sign, that is,

$$\Psi_w = -DPD \qquad (8)$$

The change from DPD to Ψ_w is relatively simple except for the fact that Ψ_w is a negative number and must be thought of as becoming lower with increasing water stress. Thus, water potential (Ψ_w) increases in magnitude but decreases in absolute value (becomes more negative) as water stress increases. The same situation occurs in reading temperatures below zero on a thermometer. For example, −5°C is a higher temperature than −10°C and −5 bars is a higher potential than −10 bars.

The potential terminology can be applied to soil water. Total potential of soil water includes: osmotic potential (Ψ_s), gravitational potential (Ψ_g), matric or capillary potential (Ψ_m), and potential caused by external gas pressure (Ψ_p).

$$\Psi_{soil} = \Psi_s + \Psi_g + \Psi_m + \Psi_p \qquad (9)$$

However, the *total soil-moisture stress* of certain investigators (*5*) refers only to the matric and osmotic forces, hence:

$$\Psi_{soil} = \Psi_m + \Psi_s = -TSMS \qquad (10)$$

The total free energy level or water potential of plant tissue or soil can be determined by measuring its vapor pressure (*6*). Measurements made on soil with pressure plates or pressure membranes indicate only the matric or capillary potential (Ψ_m) of the soil water.

In summary, terms such as DPD and Ψ_w are merely names applied for convenience to the basic property of water known as its chemical potential, which is an expression of its free energy status. Ψ_w can be regarded as a measure of the driving force which causes water to move into any system (*7*), such as plant tissue or soil, or from one part of the system to another.

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References and Notes

1. B. S. Meyer, *Botan. Rev.* **4**, 531 (1938).
2. ———, *Plant Physiol.* **20**, 142 (1945).
3. ———and D. B. Anderson, *Plant Physiology* (Van Nostrand, New York, 1939).
4. R. O. Slatyer and S. A. Taylor, *Nature* **187**, 922 (1960).
5. C. H. Wadleigh and A. D. Ayers, *Plant Physiol.* **20**, 106 (1945).
6. J. S. Boyer and E. B. Knipling, *Proc. Natl. Acad. Sci. U.S.* **54**, 1044 (1965); G. A. Richards and G. Ogata, *Science* **128**, 1089 (1958).
7. R. O. Slatyer and W. R. Gardner, in *The State and Movement of Water in Living Organisms*, G. E. Fogg, Ed. (Cambridge Univ. Press, New York, 1964), pp. 113–129.

8. The assistance of Dr. R. O. Slatyer of Commonwealth Scientific and Industrial Research Organization, Canberra, Australia, in developing a better understanding of cell water terminology is acknowledged.

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Infrared Study of the Hydroxyl Bands in Clinoamphiboles

Abstract. *Sharp single peaks in the fundamental and first-overtone bands of the O-H stretching vibration in pure Mg^{2+} and Fe^{2+} amphiboles split into a maximum of four sharp peaks, corresponding to hydroxyl groups linked to 3 Fe, 2 Fe + Mg, 2 Mg + Fe, and 3 Mg, in mixed Fe^{2+}-Mg^{2+} amphiboles. Within any one solid-solution series, the frequencies of these peaks can be correlated with the electronegativity of ions in the* M_1 *and* M_3 *positions, and differences between series can be correlated with the size of ions in the* M_4 *position. The O-H vector lies approximately normal to z in the (010) plane. The distribution of Fe^{2+} and Mg^{2+} ions between the* (M_1,M_3) *and* (M_2M_4) *positions in the cummingtonite-grunerite series, and between the* (M_1,M_3) *and* M_2 *positions in the tremolite-ferroactinolite series, has also been estimated.*

The observation (*1*) of possible overtones of the O-H stretching vibration as strongly polarized bands in the near-infrared spectra of certain amphiboles led us to investigate both the fundamental and first-overtone regions of this vibration. Minerals of the tremolite-ferroactinolite $[Ca_2(Mg,Fe)_5Si_8O_{22}(OH)_2]$ and cummingtonite-grunerite $[(Mg,Fe)_7Si_8O_{22}(OH)_2]$ series were chosen initially because of their simple chemistry.

The fundamental band (3600 to 3700 cm^{-1}) was recorded on a Perkin-Elmer model 337 spectrophotometer modified for ordinate and abcissa expansions, the KBr disc method being used. Spectra of the polarized first-overtone bands at 7050 to 7200 cm^{-1} were recorded on a Cary model 14 spectrophotometer with orientated thin (30 μ) sections by means of a polarizing-microscope technique (*2*). This technique was developed further to enable the indicatrix orientation to be determined over the whole wavelength range from 4000 to 22,000 Å. Measurements were made at room temperature on five members of the cummingtonite-grunerite series with 35 to 98 percent Fe^{2+}, and on four members of the tremolite-ferroactinolite series with 0 to 48 percent Fe^{2+} (all percentages mentioned in this report are 100 $Fe^{2+}/(Fe^{2+} + Mg^{2+})$.

The fundamental band (Fig. 1) shows a single sharp peak (*A*) in iron-free tremolite. Additional peaks (*B, C, D*) appear at lower frequencies as the ferroactinolite content increases, and peak *A* simultaneously decreases in intensity. There is no significant wavelength shift of individual peaks with Fe^{2+} concentration analogous to that observed in the electronic spectra (*1*). The fundamental band in grunerite with 98 percent Fe^{2+} consists of a single sharp peak (*D′*) with a small pip (*C′*) on the high-frequency side. With increasing Mg content, *C′* first grows, and then *B′* and *A′* appear and continue to grow, with *D′* and later *C′* declining in importance (Fig. 1). The variation of intensities with composition is similar to that seen in the tremolite-ferroactinolite series, and there is again no significant shift of individual peaks as the ratio of Fe to Mg varies.

The overtone band shows similar features (*1*). Single, sharp peaks occur at 7180 and 7068 cm^{-1} in tremolite and grunerite, respectively, with additional peaks in mixed Fe-Mg amphiboles (Table 1). In the actinolite with 15 percent Fe^{2+}, the intensity ratios for light vibrating along α, β, and γ are $A_\alpha = 22$; $A_\beta = 0$; $A_\gamma = 5$; and the extinction angle γ/z is 19° ± 2° in the obtuse angle beta. In both the fundamental and the overtone bands, the four peaks in the tremolite-ferroactino-