THE COMPONENTS OF LEAF WATER POTENTIAL

III.* EFFECTS OF TISSUE CHARACTERISTICS AND RELATIVE WATER CONTENT ON WATER POTENTIAL

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Summary

A theoretical treatment suggests that osmotic, matric, and pressure potentials $(\pi, \tau, \text{ and } P)$ and their sum the water potential (ψ) for any relative water content (R) can be calculated if three quantities that characterize the tissue are known: the sum of osmotic and matric potentials at full turgor $(\pi_t + \tau_t)$, bound water content as a proportion of total water content at full turgor (B), and coefficient of enlargement (e).

ψ falls with rise in e (acting through P) or fall in $(\pi_t + \tau_t)$ [acting through $(\pi + \tau)$ and P]. At high R, change in ψ with R depends more on P than on $(\pi + \tau)$ and the slope is near linear; at low R, $(\pi + \tau)$ becomes dominant and the slope increases. τ is high at high R, but as R falls to low values τ may fall steeply and accentuate the fall in ψ.

The curve relating ψ to R is sometimes used to describe tissue characteristics. However, similar curves can occur for tissues with different values of $(\pi_t + \tau_t)$ and e, and hence different physiological responses, because the components $(\pi + \tau)$ and P can compensate for one another in ψ.

To avoid wilting, leaf ψ at zero turgor (ψ_0) must be lower than soil ψ. ψ_0 is lowered by fall in e or $(\pi_t + \tau_t)$; but these falls reduce R_0. Lowering of ψ_0 without change in R_0 can be obtained by fall in $(\pi_t + \tau_t)$ coupled with a proportionate rise in e.

I. Introduction

Parts I and II in this series (Warren Wilson 1967a, 1967b) showed that, if certain assumptions are made, the values of the osmotic, matric, pressure, and water potentials can be calculated for any relative water content (R) provided the values of three characteristic constants are known for the tissue concerned. These three constants are:

$(\pi_t + \tau_t)$, the sum of osmotic and matric potentials at full turgor;

B, bound water content as a proportion of total water content at full turgor;

e, coefficient of enlargement.

The subscripts "t" and "0" signify full and zero turgor. Probably, values of B and e within a particular tissue vary with R, but present methods cannot accurately estimate this variation and it is therefore assumed as a first approximation that B and e are constant; errors thereby introduced are discussed in Parts I and II, where

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it is also pointed out that values of osmotic, matric, and pressure potentials are averages for quantities that vary spatially among and within the cells of any particular tissue.

The equations derived in Parts I and II are summarized below, both for tissue in which the proportion of water bound by matric forces is negligible ($B = 0$, $\tau = 0$; in this case the constants are reduced to two: π_t and e), and for tissue with appreciable bound water.

	$B = 0$	$B > 0$
Osmotic potential (π)	$\dfrac{\pi_t}{R}$	$(\pi_t + \tau_t)\dfrac{(1-B)}{R}$
Matric potential (τ)	0	$(\pi_t + \tau_t)\dfrac{B(1-B)}{R(R-B)}$
Osmotic + matric potential ($\pi + \tau$)	$\dfrac{\pi_t}{R}$	$(\pi_t + \tau_t)\dfrac{(1-B)}{(R-B)}$
Pressure potential (P)	$R(e - \pi_t) - e$	$R[e - (\pi_t + \tau_t)] - e$
Water potential ($\psi = \pi + \tau + P$)	$\dfrac{\pi_t}{R} + R(e - \pi_t) - e$	$(\pi_t + \tau_t)\dfrac{(1-B)}{(R-B)} + R[e - (\pi_t + \tau_t)] - e$

Values tabulated in Part II show that $(\pi_t + \tau_t)$ usually lies in the range -5 to -20 bars, B in the range $0 \cdot 0$ to $0 \cdot 4$, and e in the range 5–80 bars. This paper considers the significance of the actual values of these three constants in the internal water relations of tissue.

II. Effect of Relative Water Content on the Components of Water Potential for Tissues with Various Characteristics

For simplicity consider first the case where no water is bound ($B = 0$, $\tau = 0$). The roles of π_t and e in determining the responses of tissues to change in R can then be displayed as in Figure 1, which plots values of π, P, and ψ for nine tissues representing all combinations of $\pi_t = -5$, -10, and -20 bars, and $e = 5$, 20, and 80 bars. As R varies:

(1) Osmotic potential depends only on π_t; the lower is π_t the less is π for tissue at high R and the steeper is the fall in π as R decreases.

(2) Pressure potential has the value $-\pi_t$ at $R = 1 \cdot 0$. As R falls P decreases; the slope is given by $\tan \alpha = e - \pi_t$, from equation (21).* Thus P falls more steeply with higher e or lower π_t.

(3) Water potential, given by the sum of π and P since τ is taken zero, is at any particular level of R lower with rise in e (acting through P) or fall in π_t (acting through P and π). When R is high, change in ψ with R depends more on P than on π, but as R falls π becomes more important and at low R it is the dominant component. Because of this shift in the relative magnitudes of P and π the line relating ψ to R is near linear at high R but curved away from the R axis at low R; this reflects the form normally obtained by direct observation (e.g. Jarvis and Jarvis 1963).

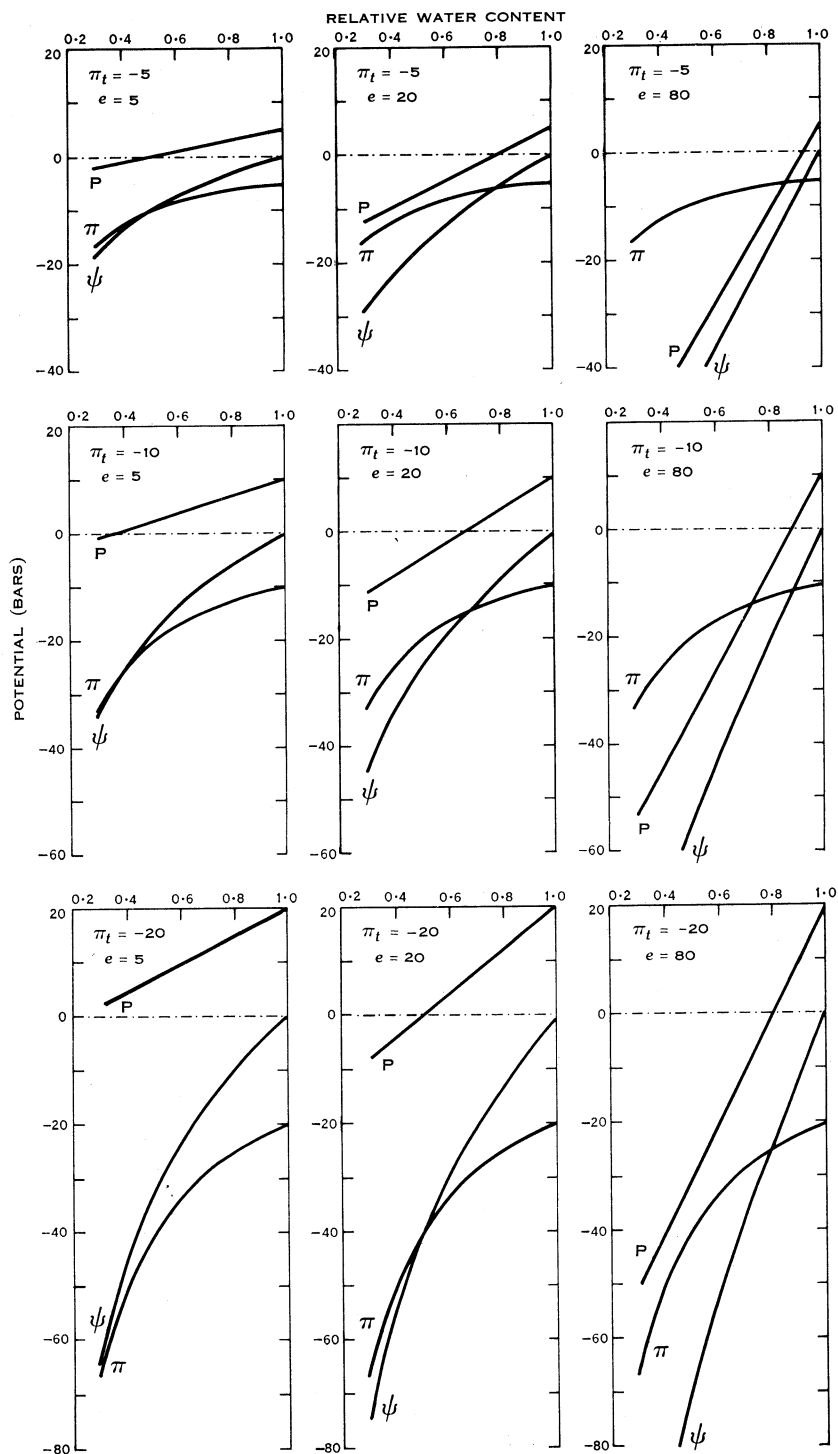* Equations are numbered consecutively in Parts I–III of the series.

Fig. 1.—Relation between relative water content and osmotic potential (π), pressure potential (P), and water potential (ψ) for nine tissues having values of π_t and e (bars) as shown.

If water bound by matric forces is present, the values of π and τ at full turgor tend to fall as $(\pi_t+\tau_t)$ falls; but the partitioning of the potential into π and τ depends on B, for $\pi_t/\tau_t = (1-B)/B$. Since B (here assumed not to vary with R) is commonly
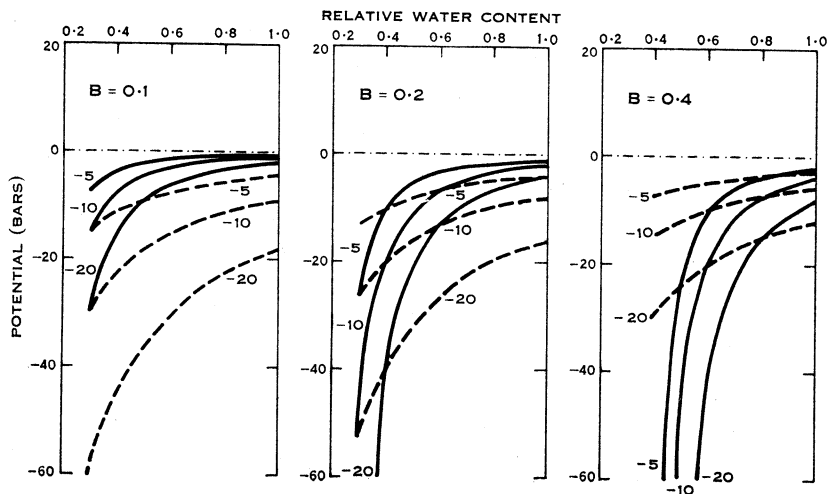

Fig. 2.—Relation between relative water content and matric potential (continuous lines) and osmotic potential (broken lines) for nine tissues having three levels of $(\pi_t+\tau_t)$, shown in bars, and three levels of B.
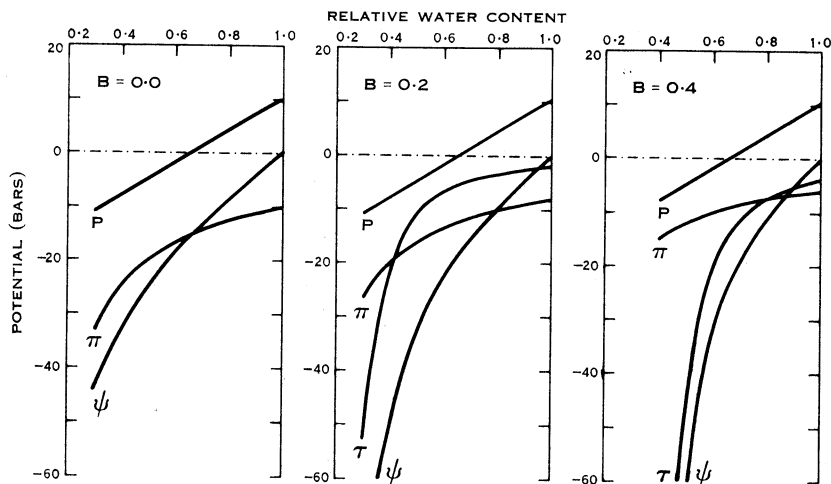

Fig. 3.—Relation between relative water content and osmotic potential (π), matric potential (τ), pressure potential (P), and water potential (ψ) for three tissues having $(\pi_t+\tau_t) = -10$ bars, $e = 20$ bars, and levels of B as shown.

less than $0\cdot 5$, π is usually lower than τ at full turgor, as in the examples for normal ranges of $(\pi_t+\tau_t)$ and B shown in Figure 2. As R falls, both π and τ fall; but at lower levels of R the fall is steeper for τ than for π, and τ becomes more important. When $R = 2B$, $\tau = \pi$; and at lower values of R, τ is lower than π.

The influence of the amount of bound water on the water potential is shown in Figure 3, for tissue with $(\pi_t + \tau_t) = -10$ bars and $e = 20$ bars. At high levels of R, B has comparatively little effect on ψ; but as R falls τ becomes increasingly important, and the fact that it falls faster than π can greatly steepen the curve for ψ at low R. These graphs suggest that the presence of water bound by matric forces can bring falls in ψ which usefully enhance the water-absorbing forces of plants with serious water deficits.
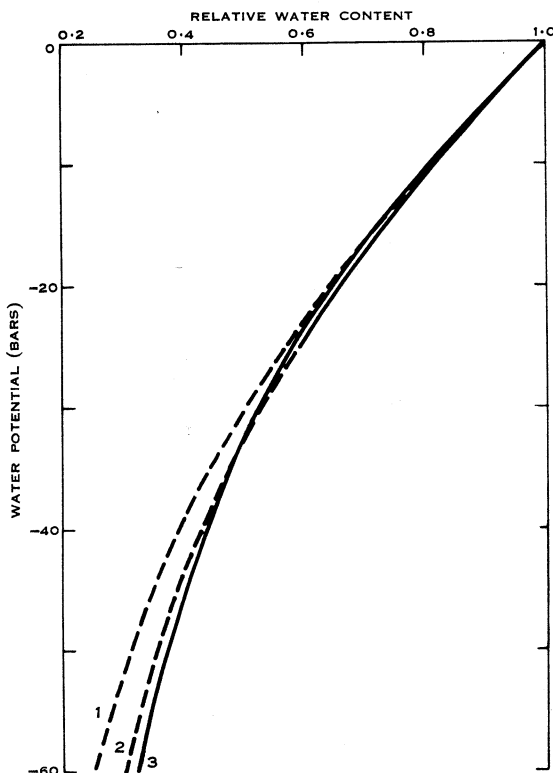

Fig. 4.—Relation between relative water content and water potential for three tissues having: (1) $\pi_t = -10$, $e = 30$; (2) $\pi_t = -15$, $e = 20$; (3) $\pi_t = -20$, $e = 5$ bars. Continuous and broken lines indicate positive and negative pressure potential respectively.

III. Effect of Tissue Characteristics on the Form of the Curve relating Water Potential to Relative Water Content

The curve relating ψ to R has been used to characterize the internal water relations of plant tissues (e.g. Weatherley and Slatyer 1957), just as the moisture characteristic curve for a soil is used to describe its water-holding properties. The form of the curve varies with species and growing conditions. Xerophytes and plants grown under water stress tend to have steep curves, i.e. a comparatively low ψ for a particular R. Jarvis and Jarvis (1963) discuss the ecological and physiological significance of the slope of these curves.

The preceding section showed that the curve steepens with rise in e or fall in $(\pi_t + \tau_t)$. In effect these two constants can largely replace one another: higher e compensates for higher $(\pi_t + \tau_t)$. This is illustrated in Figure 4 by three curves which nearly coincide at high and moderate values of R, though they are for different

combinations of e and π_t (taking B as zero). The values of π and P which together constitute ψ differ greatly between these three tissues. Thus at $R = 0 \cdot 6$, one of them ($\pi_t = -15$ bars; $e = 20$ bars) is near zero turgor, one is fairly turgid, and another is severely wilted. These differences between the tissues, though important physiologically, are not revealed by the curves relating ψ and R.

This limitation of this type of curve in characterizing tissue water relations is not as severe as at first appears because, as discussed below, the ratio $e/[-(\pi_t+\tau_t)]$ does not vary widely. Nevertheless it seems that a tissue is more thoroughly characterized by the constants $(\pi_t+\tau_t)$, B, and e than by the curve relating ψ to R.

IV. WATER POTENTIAL AND RELATIVE WATER CONTENT AT ZERO TURGOR

The value of ψ at zero turgor is significant as a guide to the magnitude of soil water potential that a plant can tolerate without its turgor falling below zero. Slatyer (1957) summarizes evidence that many physiological processes—elongation and photosynthesis for example—cease when turgor falls to about zero. Further, the wilting which occurs in many species at about zero turgor makes the plants vulnerable to mechanical damage. For successful growth, therefore, P must exceed zero.

Also, in order for absorption to occur, leaf ψ must be lower than soil ψ; if it is not, the plant water content will fall. The two requirements, that P must exceed 0 and that leaf ψ must be lower than soil ψ, cannot both be satisfied unless leaf ψ_0 is lower than soil ψ. This section discusses how ψ_0 and R_0 are affected by the values of $(\pi_t+\tau_t)$, B, and e.

From equation (23),

$$R = \frac{e+P}{e-(\pi_t+\tau_t)} \, .$$

At zero turgor, $P = 0$; hence

$$R_0 = e/[e-(\pi_t+\tau_t)]. \tag{27}$$

Equation (16) gives for zero turgor

$$\pi_0+\tau_0 = (\pi_t+\tau_t)\frac{(1-B)}{(R_0-B)} \, .$$

Substituting for R_0 according to equation (27), and recognizing that $\psi_0 = \pi_0+\tau_0$,

$$\psi_0 = (\pi_t+\tau_t)\frac{(1-B)[e-(\pi_t+\tau_t)]}{e-B[e-(\pi_t+\tau_t)]} \, . \tag{28}$$

When $B = 0$, this reduces to

$$\psi_0 = \pi_t(e-\pi_t)/e \, . \tag{29}$$

Figure 5, in which the lines pass through equal values and can be regarded as contours, shows that both ψ_0 and R_0 fall with decrease in e or π_t. These values are based on $B = 0$; where $B > 0$, R_0 is unaffected by it but ψ_0 falls with increase in B.

A fall in ψ_0, such as may enable a plant to maintain $P > 0$ in spite of falling soil ψ, can be attained by lowering of e or π_t. Either of these changes will also cause

R_0 to fall; that is, the increased ability to withdraw water from a drying soil is obtained at the expense of a lower R. Any considerable lowering of R causes damage to plant functions [Jarvis and Jarvis (1963) show that the damage seems to be associated with R rather than with ψ]; for many species, stomata close at about $R = 0\cdot8$, and with further lowering of R there is increasing metabolic disturbance until death occurs at about $R = 0\cdot3\text{--}0\cdot4$ (Pisek 1956; Jarvis and Jarvis 1963; Ehlig and Gardner 1964).
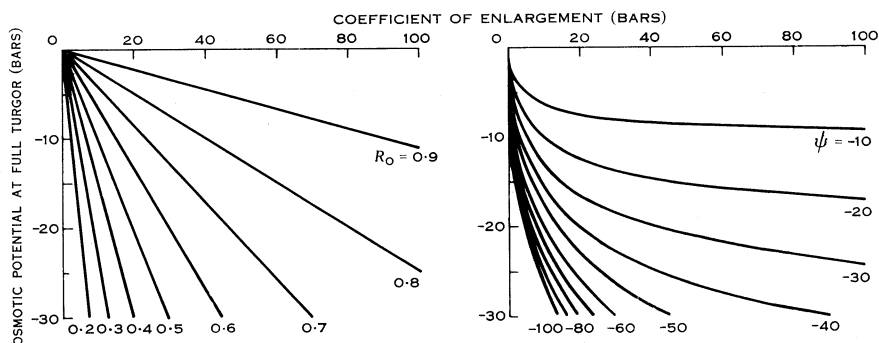

Fig. 5.—Variation in (left) relative water content at zero turgor (R_0), and (right) water potential at zero turgor (ψ_0), with π_t and e. Contours join equal levels of R_0 or ψ_0.

However, Figure 5 reveals that ψ_0 can be lowered without a fall in R_0, if lowering of π_t is coupled with an appropriate increase in e. For example, movement down the $R_0 = 0\cdot7$ contour of Figure 5 brings an associated shift in ψ_0 from higher than -10 bars at the top of the graph to lower than -40 bars at the bottom.
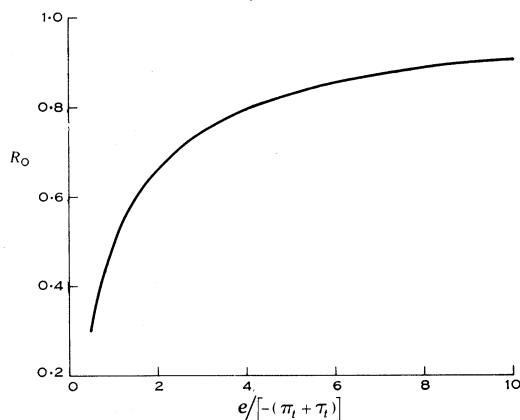

Fig. 6.—Relation between R_0 and $e/[-(\pi_t+\tau_t)]$.

From equation (27)

$$\frac{e}{-(\pi_t+\tau_t)} = \frac{R_0}{(1-R_0)} .$$

This indicates the ratio of e to $-(\pi_t+\tau_t)$ required to maintain a particular value of R_0 (Fig. 6); for example, $e/[-(\pi_t+\tau_t)] = 2\cdot33$ maintains R_0 at $0\cdot7$.

When values of ψ_0 and R_0 are calculated from equations (27) and (28) for the 10 leaf types for which $(\pi_t + \tau_t)$, B, and e are given in Part II, it is found that R_0 is relatively uniform, usually lying between $0 \cdot 6$ and $0 \cdot 8$, whereas ψ_0 varies sixfold (Table 1). This is now seen to correspond with the point mentioned at the end of Part II, that the ratio $e/[-(\pi_t + \tau_t)]$ was generally about 2–3. It seems that this rough proportionality allows the development of low ψ_0 in leaves grown in dry conditions without the lowering of R_0 and consequent damage that would occur if the fall in ψ_0 were achieved by fall in e or $(\pi_t + \tau_t)$ alone.

TABLE 1

ESTIMATES OF ψ_0 AND R_0 FOR VARIOUS LEAF TYPES

Original data from several sources listed in Table 1 of Part II (Warren Wilson 1967b)

Species	ψ_0 (bars)	R_0	Species	ψ_0 (bars)	R_0
Helianthus annuus	$-5 \cdot 3$	$0 \cdot 70$	Lycopersicon esculentum	$-17 \cdot 8$	$0 \cdot 66$
Brassica napus	$-6 \cdot 7$	$0 \cdot 73$	Gossypium barbadense	$-31 \cdot 4$	$0 \cdot 64$
Zea mays	$-7 \cdot 1$	$0 \cdot 76$	Ligustrum lucidum	$-38 \cdot 7$	$0 \cdot 56$
Helianthus annuus	$-15 \cdot 7$	$0 \cdot 73$	Pennisetum typhoides	$-23 \cdot 4$	$0 \cdot 68$
Gossypium hirsutum	$-16 \cdot 2$	$0 \cdot 71$	Acacia aneura	$-28 \cdot 0$	$0 \cdot 79$

V. MINIMUM REQUIREMENTS FOR ESTIMATING THE TISSUE CHARACTERISTICS

The constants $(\pi_t + \tau_t)$, B, and e can be estimated from as few as four measurements:

For tissue at full turgor:

(1) water potential of killed tissue, $(\pi_t + \tau_t)$;

For the same tissue at a low water content:

(2) water potential of living tissue, (ψ);

(3) water potential of killed tissue, $(\pi + \tau)$;

(4) relative water content, (R).

It can be shown from equation 16 that

$$B = \frac{R(\pi + \tau) - (\pi_t + \tau_t)}{(\pi + \tau) - (\pi_t + \tau_t)} \ , \tag{30}$$

and from equation (22) that

$$e = (\pi_t + \tau_t) + \frac{(\pi + \tau) - (\pi_t + \tau_t) - \psi}{(1 - R)} \ . \tag{31}$$

These values of B and e are averages for the range of water content between the two observed levels. Variation in B and e within this range is not revealed, but in any case it has been shown that current methods are hardly adequate for examining this.

Experimental errors are inevitable. For B and e these errors are magnified by equations (30) and (31) to a degree which depends on leaf characteristics but can be judged by inserting trial values in the equations. For a mesophytic leaf, a 1%

error in any of the measured quantities leads to errors in B and e of the order of 2%. Replicate measurements for leaves brought to similar water content by methods such as those described in Part I will yield replicate estimates of $(\pi_t + \tau_t)$, B, and e from which means and estimates of error can be obtained.

VI. REFERENCES

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