THE COMPONENTS OF LEAF WATER POTENTIAL

II.* PRESSURE POTENTIAL AND WATER POTENTIAL

By J. Warren Wilson†

Summary

The relation between the relative water content (R) and the pressure potential can be expressed through the coefficient of enlargement (e). The assumption that e does not vary with R is for many leaves a useful first approximation even when R is so low that pressure potential is negative. e is estimated at between 7 and 84 bars for various leaf types.

Expressions are derived for calculating the water potential and its components for any R, given three constants: the sum of osmotic and matric potentials at full turgor ($\pi_t + \tau_t$), the proportion of water bound by matric forces, and e. These constants characterize the tissue as regards internal water relations, and from them an improved Höfler-type diagram can be drawn. Their values vary with species and environmental history; with drier growing conditions ($\pi_t + \tau_t$) falls and e rises, but the ratio $e/[-(\pi_t + \tau_t)]$ usually lies in the range 2–3.

I. Introduction

The first paper in this series (Warren Wilson 1967a) considered how osmotic potential (π) and matric potential (τ) vary with relative water content (R). This paper proceeds to consider variation in pressure potential (P) with R, and so to discuss how the water potential (ψ) is determined through its components:

$$\psi = \pi + \tau + P .$$

As discussed in Part I, the components of ψ vary spatially in magnitude among cell types and among parts of a single cell: for example the value of the pressure potential is usually very different for the vacuolar water and the wall water. In the absence of methods for measuring potentials on a micro scale, average values for the cell or tissue as a whole have to be accepted.

Since the term "pressure potential" includes no reference to turgor, it should be noted that it is taken to include only those hydrostatic pressures that originate in turgor, and not hydrostatic pressures originating in capillary forces, which are assigned to matric potential.

Pressure potential is commonly estimated as the difference between the water potential of living tissue and the water potential of the same tissue after killing. From the above equation this gives P, if it is assumed that killing (1) brings P to zero, (2) does not alter $(\pi+\tau)$. How far these assumptions are true is uncertain.

II. Theoretical Treatment

(a) Relation between Pressure Potential and Relative Water Content

Theoretical treatments of internal water relations usually assume that when water is taken up P rises linearly with increase in the volume of the vacuole, cell, or tissue. In fact it is likely that the relationship takes various non-linear forms according to the type of tissue, but data are meagre and subject to the errors mentioned above, and we here accept as a first approximation the assumption that, when water is gained or lost by living tissue, P is linearly related to R.

For the fully turgid state (shown by subscript "t") at which $R_t = 1$, we take $\psi_t = 0$ and $P_t = -(\pi_t+\tau_t)$. As R decreases through loss of water P falls, and at zero turgor (shown by subscript "0") $P_0 = 0$ and $\psi_0 = \pi_0+\tau_0$. If the linear relation of P to R is assumed to continue as still more water is lost, P becomes increasingly negative as R falls below R_0.

Some authors have questioned whether the negative pressure potentials obtained as differences between water potentials for living and killed tissue really represent negative turgor pressures (Slatyer 1960; Begg et al. 1964; Gardner and Ehlig 1965). It has been suggested that the negative values of P are due to matric forces. This is possible if the methods include certain matric forces in estimates of water potential for living tissue but exclude them for killed tissue. There is no reason to expect this, though the magnitude of τ may be altered to an unknown extent by killing or by sap expression. Present methods are admittedly unsatisfactory; however, most of the leaf types examined in this paper showed negative P, and there is evidence of negative hydrostatic pressure in some species (e.g. Huber 1956; Scholander et al. 1965). In what follows, therefore, negative values of P are taken to represent negative pressures, this being a simple assumption and not inconsistent with present evidence.

We thus assume that over the whole range of R for living tissue P_2-P_1 is proportional to R_2-R_1 where the subscripts "2" and "1" indicate any two water statuses at which P and R are measured. It is customary to express the change in R (or volume) in relation to its value at the reference state of zero strain. Thus

$$P_2-P_1 = e(R_2-R_1)/R_0 , \qquad (19)*$$

where e is a constant. e has been termed a modulus of elasticity, or Young's modulus, but it is doubtful whether this is legitimate (Haines 1950; Preston 1952); the term "coefficient of enlargement" proposed by Broyer (1952) seems preferable. Equation (19) can be written

$$e = R_0 \tan \alpha , \qquad (20)$$

where $\tan \alpha$ is the slope of the relation between P and R.

* Equation numbers are consecutive with those in Part I. It would simplify this equation to replace the reference value R_0 by $R_t = 1$, giving $e = \tan \alpha$. Here R_0 is retained to conform with Frey-Wyssling (1950), Broyer (1952), and Philip (1958).

(b) Estimation of the Coefficient of Enlargement

Methods described in Part I estimate $(\pi_t+\tau_t)$ but not R_0. It is therefore convenient to express e in terms of $(\pi_t+\tau_t)$ and α rather than R_0 and α. When the water statuses "2" and "1" are full and zero turgor,

$$\tan \alpha = (P_t-P_0)/(R_t-R_0) = -(\pi_t+\tau_t)/(1-R_0) \ ,$$

whence

$$R_0 = [(\pi_t+\tau_t)/\tan \alpha]+1 \ .$$

Substituting this expression for R_0 in equation (20) gives

$$e = (\pi_t+\tau_t)+\tan \alpha \ . \tag{21}$$

If $(\pi_t+\tau_t)$ is known, e can now be estimated from data on P and R, since

$$\tan \alpha = (P_t-P)/(R_t-R) = [-(\pi_t+\tau_t)-P]/(1-R) \ ,$$

whence, for $R_{\text{lethal}} < R < R_t$,

$$e = (\pi_t+\tau_t)-[(\pi_t+\tau_t)+P]/(1-R) \ . \tag{22}$$

If experimental errors are independent of water status, this estimate of e is more accurate the greater the departure of P and R from $-(\pi_t+\tau_t)$ and 1; so that where data on P and R are available for more than one water status it seems preferable to give greater weight to values from leaves of lower water status. Accordingly the estimates of e below were calculated from

$$e = (\pi_t+\tau_t)- \left\{ \sum_1^n [(\pi_t+\tau_t)+P_n] \middle/ \sum_1^n (1-R_n)\right\},$$

where R_n is the value of R when $P = P_n$.

If $(\pi_t+\tau_t)$ and e are known, P can be calculated for any R from equation (22) reset as

$$P = R[e-(\pi_t+\tau_t)]-e \ . \tag{23}$$

(c) Water Potential determined by the Sum of its Components

Equations (14), (15), and (23) yield π, τ, and P for any value of R, provided $(\pi_t+\tau_t)$, B, and e are known. Assuming that equations (14) and (15) apply irrespective of P, i.e. for living as well as killed tissue, the water potential is thus obtained as the sum of these three components:

$$\psi = (\pi_t+\tau_t)\frac{(1-B)}{R}+(\pi_t+\tau_t)\frac{B(1-B)}{R(R-B)}+R[e-(\pi_t+\tau_t)]-e \ . \tag{24}$$

Combining π and τ, this simplifies to

$$\psi = (\pi_t+\tau_t)\frac{(1-B)}{(R-B)}+R[e-(\pi_t+\tau_t)]-e \ . \tag{25}$$

For tissue with negligible matric potential

$$\psi = (\pi_t/R)+R(e-\pi_t)-e \ . \tag{26}$$

This equation can be compared with two previous treatments of ψ. Expressed in the symbols used here, Philip (1958) gives

$$\psi = (\pi_0 R_0/R) + e(R - R_0)/R_0 ,$$

and Gardner and Ehlig (1965) give

$$\psi = (\pi_t/R) + e(R - R_0)/R_0 .$$

The treatment developed here has two advantages. Firstly, it recognizes that for real tissues the so-called "osmotic potential" often deviates from the reciprocal relation to R, because it includes matric as well as osmotic forces, and the treatment allows for these deviations by an expression for τ. Secondly, for tissues where τ is negligible it expresses ψ in terms of R and two constants [e and $(\pi_t + \tau_t)$] instead of three constants (e, R_0, and π_0 or π_t).

TABLE 1

ESTIMATES OF $(\pi_t + \tau_t)$, B, AND e FOR VARIOUS LEAF TYPES

| Source of Data | Methods* | | Species | $\pi_t + \tau_t$ (bars) | B | e (bars) |
	ψ	$(\pi + \tau)$				
Warren Wilson (1967a)	g	g	*Helianthus annuus*	$-3 \cdot 1$	$0 \cdot 27$	$7 \cdot 3$
			Brassica napus	$-3 \cdot 5$	$0 \cdot 43$	$9 \cdot 5$
			Zea mays	$-4 \cdot 9$	$0 \cdot 22$	$15 \cdot 8$
Gardner and Ehlig (1965)	p	p	*Helianthus annuus*	$-10 \cdot 0$	$0 \cdot 26$	$27 \cdot 7$
			Gossypium hirsutum	$-11 \cdot 5$	$0 \cdot 00$	$28 \cdot 6$
Slatyer (1957)	g	c	*Lycopersicon esculentum*	$-11 \cdot 0$	$0 \cdot 11$	$21 \cdot 5$
			Gossypium barbadense	$-16 \cdot 9$	$0 \cdot 22$	$29 \cdot 6$
			Ligustrum lucidum	$-21 \cdot 3$	$0 \cdot 02$	$26 \cdot 6$
Begg et al. (1964)	g,p	g,p	*Pennisetum typhoides*	$-15 \cdot 9$	$0 \cdot 00$	$33 \cdot 4$
Slatyer (1960)	g	c	*Acacia aneura*	$-22 \cdot 1$	$0 \cdot 00$	$84 \cdot 3$

* g, gravimetric vapour exchange; p, psychrometric; c, cryoscopic.

The constants $(\pi_t + \tau_t)$, B, and e are characteristics of a tissue: they indicate, for that tissue, how ψ, π, τ, and P vary with R. These relations, when expressed graphically as in Figures 1–3, correspond to the classical Höfler diagram except that:

(1) R replaces volume on the horizontal axis; this avoids discrepancies caused by the assumption that solute, matric, and airspace volumes are negligible.

(2) τ is shown separately from π, instead of being ignored or included in osmotic pressure.

(3) Since ψ, π, and τ are negative (whereas diffusion pressure deficit and osmotic pressure are positive) their curves lie below the horizontal axis instead of above; ψ is given by $(\pi + \tau) + P$, whereas diffusion pressure deficit is given by osmotic pressure — turgor pressure.

III. Analysis of Data

(a) Application of Theory to Observations

The values of the constants $(\pi_t+\tau_t)$, B, and e are likely to vary with the species and environmental history of the leaf. In order to examine this variation, Table 1 records values not only for the three leaf types studied in Part I but also for leaves
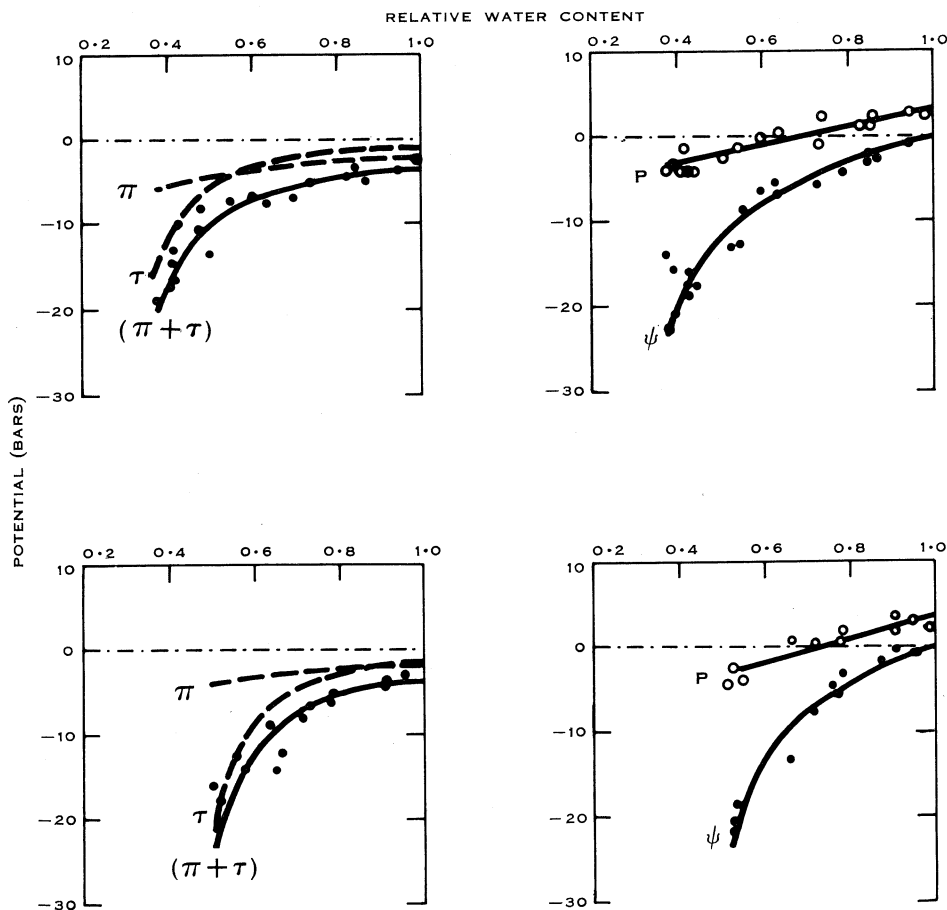

Fig. 1.—Relations between relative water content and osmotic potential (π), matric potential (τ), pressure potential (P), and water potential (ψ) for leaves of (above) sunflower and (below) rape. To avoid confusion between potentials two graphs are given for each species, with π, τ, and $(\pi+\tau)$ on the left and P and ψ on the right.

from those published investigations which provide suitable data. The results are tabulated in order of increasing soil water stress during growth; they include plants grown in nutrient culture (Warren Wilson 1967a); in soil in pots watered frequently (Gardner and Ehlig 1965); in pots watered only when lower leaves were wilted at sunrise (Slatyer 1957); in the field with little rain in the 3 weeks prior to study (Begg *et al.* 1964); and in the field in arid conditions (Slatyer 1960). The values of

$(\pi_t + \tau_t)$ and B used are means of estimates from two regressions computed as in Part I.

Figures 1–3 show for four selected leaf types the original data together with curves obtained by inserting in equations (14), (15), (23), and (24) the constants from Table 1.
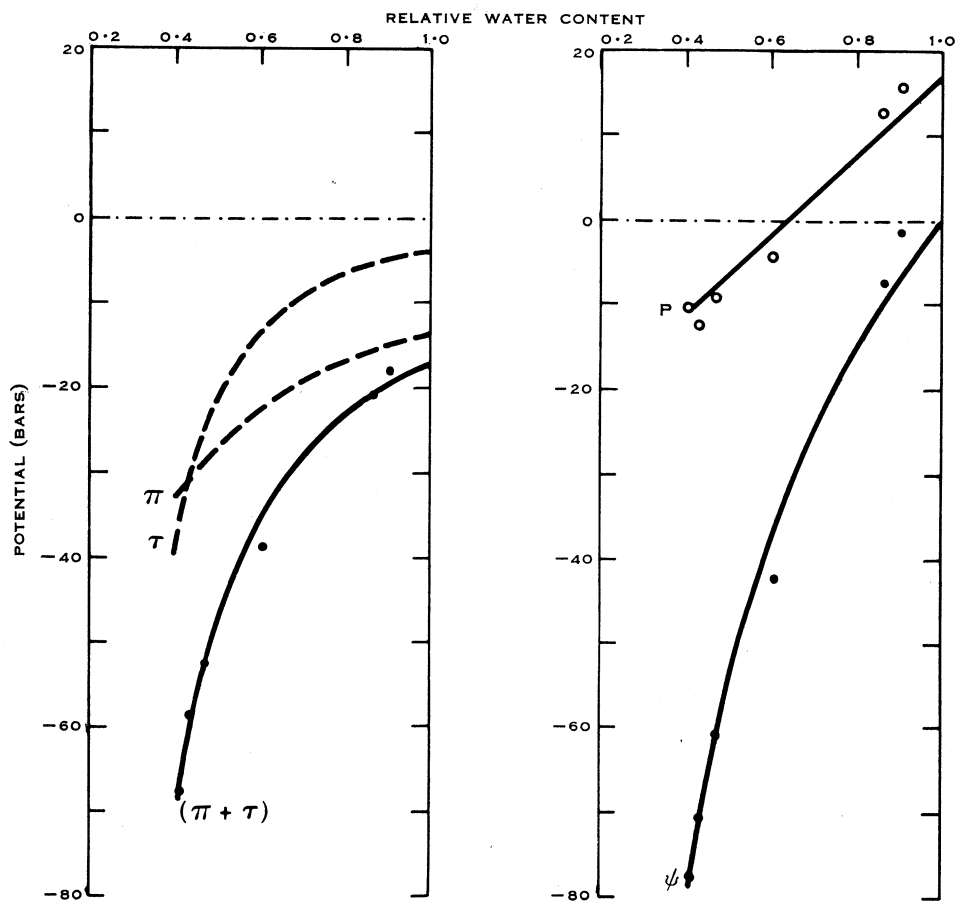

Fig. 2.—As for Figure 1, but for cotton (data of Slatyer 1957).

The largest discrepancy between fitted curves and original data is in *Pennisetum* (Fig. 3) where the assumption that P is linearly related to R is unsatisfactory; e, instead of being constant, varies from a high value at P_t to near zero at P_0 and rises again as P becomes more negative. Gardner and Ehlig (1965) similarly find e highest near full turgor and falling to low values near zero turgor: they give separate estimates of e for different ranges of R, and some such procedure is clearly required where e varies so much that a mean value is misleading. In two of their four leaf types the data on P suggest that variation in e is not large, and these two are included in Table 1. This non-linearity is not apparent in the data of Slatyer (1957), nor in our own, perhaps because changes in P are small. Other curves in Figures 1–3 fit the data tolerably well.

(b) Values of the Constants $(\pi_t + \tau_t)$, B, and e for Various Leaf Types

Although the values in Table 1 do not adequately separate the effects of species and of growing conditions, they suggest that both affect the values of the constants. The effect of growing conditions is especially marked: it was noted above that the observations cover a wide range of soil water stress.
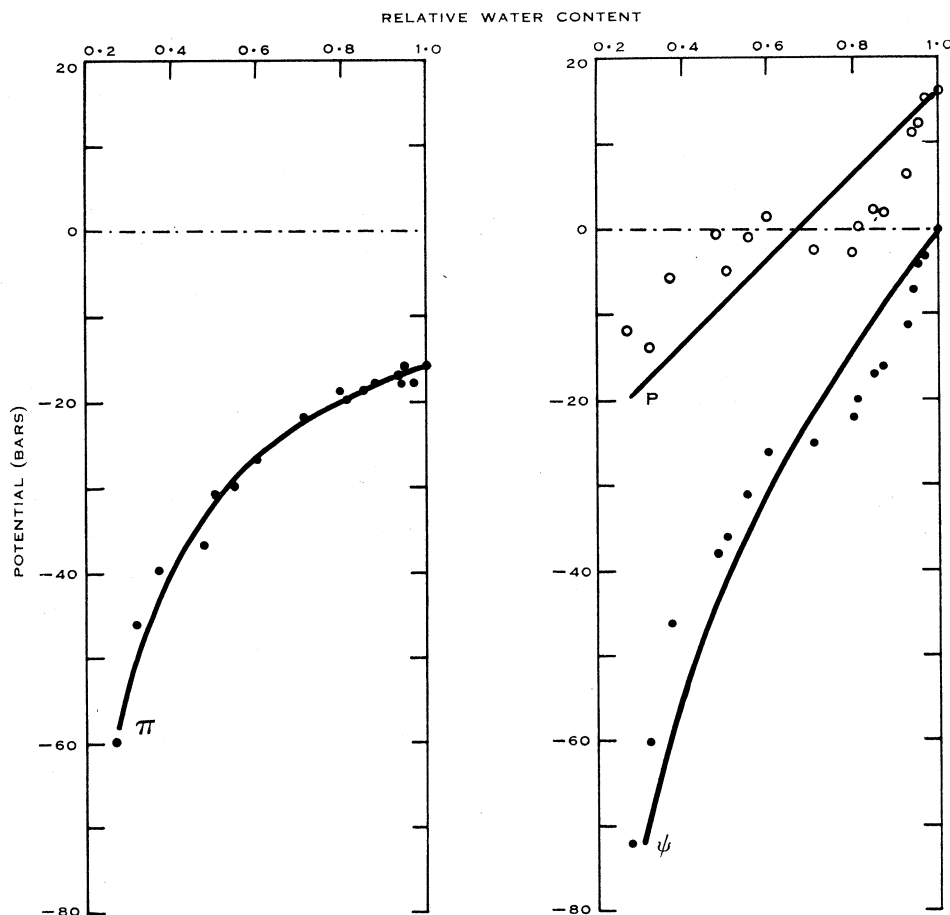

Fig. 3.—As for Figure 1, but for bulrush millet (data of Begg *et al.* 1964). The data give no evidence of matric potential.

Values of $(\pi_t + \tau_t)$ are lower for plants raised in drier root environments. Previous investigations have shown a similar trend in "osmotic potential"; however, the latter was measured at field water status, so that the lower water status in drier environments directly reduced $(\pi + \tau)$. It is therefore of interest to find the trend confirmed for leaves at the standard status of full turgor. These estimates of $(\pi_t + \tau_t)$ are rather higher than the usual estimates of "osmotic potential", perhaps again because of the difference in water status. The values in nutrient culture are especially high; however, values of "osmotic potential" above -3 bars have been recorded by Harris (1934) and Walter (1951), notably in marsh plants.

Values of B in Table 1 tend to fall with drier growing conditions. However, the trend is not clear: the zero value for *Acacia* is uncertain, for although it fits the three available estimates they are restricted to $R > 0 \cdot 7$. Previous work has shown that when bound water is expressed as a proportion of field water content it tends to be greater in drier habitats, but when expressed as a proportion of turgid water content (as here) or of dry matter it may vary little with habitat conditions (Kramer 1955). Further study is needed to clarify the variation in B with species characteristics, growing conditions, and water status.

Values of e vary from 7 to 33 bars, and for *Acacia* there is a value of 84 bars but this depends on an uncertain estimate of $B = 0$. The only published estimates of e for leaf material seem to be those of Gardner and Ehlig (1965). These are expressed on the reference water content R_t; when converted to reference value R_0 to be comparable with those in Table 1 they fall in the ranges 28–42 bars, when $P > 2$ bars, and 2–11 bars, when $P < 2$ bars. The estimates in Table 1 are thus of the same order. They show further that e tends to increase with drier growing conditions; it is perhaps not unexpected that leaves of drier environments should have firmer cell walls. It is noticeable that the increase in e is roughly parallel to change in $(\pi_t + \tau_t)$; the ratio $e/[-(\pi_t + \tau_t)]$ is usually in the range 2–3. It will be shown in Part III (Warren Wilson 1967b) that this ensures that R_0 stays within certain limits.

IV. REFERENCES

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