BIOLOGIA PLANTARUM (PRAHA)

13 (4) : 247–256, 1971

Which Water Potential? Differences Between Isopiestic Thermocouple Psychrometer Measurements of Intact and Excised Plant Materials

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Received September 4, 1970

Abstract. Water potentials of leaves from well-watered plants were measured. There were species-specific differences in both the total and the osmotic potentials of pea (*Pisum sativum*), tradescantia (*Tradescantia versicolor*), rose (*Rosa hybrida*), bitter lemon (*Citrus aurantium*) and olive (*Olea europaea*). With tradescantia the potential measured after the destruction of turgor by freezing was less negative than before, a result which suggests that the value obtained is not identical with the real osmotic potential of the leaf. Detached leaves of all species showed less negative water potential readings, and those of pea even a less negative osmotic potential, when cut into five pieces than when measured intact. Application of vaseline to the cut surface of the leaves reduced this effect with rose and olive, though not with tradescantia and pea. Measurements were also made of the water potentials of comparable leaves of tradescantia and bitter lemon, attached to and detached from their plants; when bitter lemon leaves were detached and watered through their petioles which protruded outside the thermocouple chamber, their potential became considerably less negative than when the same leaves had been attached to well watered plants. However, similar leaves whose cut petioles were introduced into the thermocouple chamber registered an even less negative potential.

The results are consistent with the hypothesis that when a leaf is cut off a plant, and even more so when it is cut into sections, the water previously held by matrix forces becomes available to dilute the "spilled" cell sap and to be absorbed by adjacent cells and thereby to increase their turgor and render the net water potential of the leaf less negative. Similarly, the apparent negative turgor of the succulent tradescantia leaves is likely to be due to dilution of the osmotic component by cell wall water. The discrepancies between the readings of attached and detached leaves indicate a considerable whole-plant matrix component, and the results as a whole suggest that thermocouple psychrometer readings carried out on detached and even more on cut-up leaves may be artifacts and that it is desirable to determine water potentials on leaves attached to their plants.

The work was supported by a Government of Israel Fellowship and was conducted at the Department of Pomology and Viticulture, Faculty of Agriculture of the Hebrew University of Jerusalem, Rehovot, Israel.

The thermocouple psychrometer is reputed to measure accurately the water potential of plant leaves as long as they are not under extreme water stress (BOYER and KNIPLING 1965, BARRS 1968, BOYER 1969). But it is

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considered necessary for measurements with the conventional apparatus that a leaf should be cut out of its lamina and immediately placed in the thermocouple chamber for vapour equilibration and subsequent measurements. BOYER (1968) found that water potentials of detached leaves of *Helianthus annuus* L. which were left intact were not significantly different from those of cut-up leaves, but MANOHAR (1966) had shown that the leaves of both *Pisum sativum* L. and *Tradescantia versicolor* L., when measured by a psychrometer based on the Peltier effect (SPANNER 1951) consistently indicated a less negative potential when cut up than when left intact, and BARRS (1968) refers to other similar reports. The leaf water potential of a number of morphologically different species was therefore examined in more detail (Part A). An extension of the work became desirable in which the effect of retaining the leaf on the plant during measurement was compared with the effect of severing it from the plant (Part B).

Terminology

The term "excision" may be applied both to detaching leaves from plants and to cutting them into pieces. In order to avoid confusion, I therefore will refer to "detached" and "cut-up" leaves respectively.

Leaf water potential (ψ) depends on three components: the osmotic potential (π) which may be considered the prime mover, the matrix potential (ψ_m), about which little is known (WIEBE 1966) and the turgor potential (P). π and ψ_m are invariably negative, whilst P, representing the pressure of the cell contents against the cell wall, is usually positive. The resultant value, the net ψ, is always less than zero (SLATYER and TAYLOR 1960). It follows that a greater force is required to move water of lower potential (a potential further removed from zero) but this has proved an unwieldly concept, and I will refer to low potentials as "more negative" and to high potentials as "less negative".

By "greater succulence" I mean a higher fresh to dry weight ratio.

Materials and Methods

In the present work, the isopiestic technique (BOYER and KNIPLING 1965) was used in order to eliminate any error due to lag in water vapour transfer. The design of the apparatus was similar for the experiments in parts A and B but in part B it was modified so that the leaves could remain attached to their plants during measurement. In this case measurements were made by attaching specially designed thermocouple chambers to the upper and lower side of a leaf. The two chambers were made of PVC and were insulated by a double-wall vacuumed glass casing. Instead of immersing the thermocouple assembly in a constant temperature water bath, the water of the bath was circulated under the vacuumed glass casing, in order to achieve the desired temperature control (to be published elsewhere).

The thermocouple psychrometer assembly employed for recording ψ or π of detached leaf samples was almost identical to the one used by BOYER and KNIPLING (1965) and is shown in Fig. 1. The thermocouples were made by soldering 0·1 mm thick constantan and chromel-P wires to a 0·5 mm thick silver ring of 2 mm inner diameter and 1 mm height. The junction was mounted on a brass plunger which was sealed into the aluminium chamber by a soft rubber washer, permitting it to be removed and resealed rapidly.

For making an isopiestic determination, the leaf sample was introduced (its abaxial surface upwards) in the thermocouple chamber whose inner walls had been coated with silicon grease in order to reduce adsorption of water vapour (Boyer 1967). A 0·01 ml droplet of water or solution was introduced on the silver ring with the help of a micro-syringe, and the plunger was then sealed into the chamber carrying the leaf sample. The entire thermocouple assembly (Fig. 1) was then immersed in the water bath maintained at 30° C. No fluctuations in the bath temperature could be detected with a 5° C Beckmann thermometer.

For deriving values through the isopiestic techniques, three observations were recorded with the same assembly, each after attaining a steady state of vapour transfer between the thermocouple junction and the chamber carrying the leaf: first carrying pure water, the second with the dry thermocouple, and the third with the junction carrying a NaCl solution with a water potential close to that of the leaf. The first and third readings were corrected for the heat of respiration measured by the second reading *i.e.* the dry bulb deflection (Barrs 1965) and the ψ values derived. A small trial was conducted to study the effects on the ψ value of opening the thermocouple chamber for introducing the "water potential solution" on the junction and the effect was found to be negligible, as also reported by Boyer (1968).

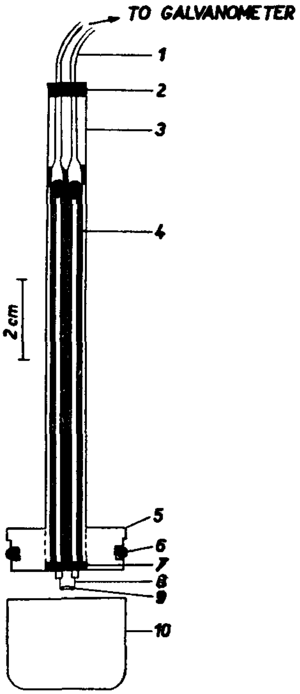

Fig. 1. Thermocouple psychrometer assembly for making isopiestic determinations on detached and cut-up leaves. 1. PVC-covered lighting flex, 2. Araldite seal, 3. Brass tube, 4. PVC-covered copper wire, 5. Brass plunger heat sink, 6. O-ring seal for chamber, 7. Araldite seal, 8. Chromel-P/constantan junction, 9. Silver loop, 10. Thermocouple chamber.

The thermocouple psychrometer apparatus was kept in a growth room maintained at 25 ± 0·5° C. Leaf samples of pea, tradescantia, rose, bitter orange and olive were used. Excepting rose and olive, the plants were raised in 15 cm pots in the same growth room under fluorescent light (14 h photoperiod). The rose leaves were obtained from uniform well-grown plants raised from cuttings growing in a glasshouse, and the olive leaves from a tree growing on a lawn of the Faculty of Agriculture. Entire leaves of olive and of trandescantia, a leaf without wings of bitter orange and a leaflet each of rose and pea formed the leaf samples. The sample leaf was washed with distilled water, 24 h prior to sampling, to counteract the possibility of error due to salt secretion (Klepper and Barrs 1968) and the mother plants were grown in soil maintained close to field capacity. Olive leaf samples were obtained a day after rain. The following trials were conducted using three replicate leaf samples, in each case employing the above method and materials.

Measurements of ψ and its Components

Water potential determinations were made on the leaf samples of the above five species. The individual thermocouple chamber carrying a leaf sample was then wrapped in aluminium foil and submerged in liquid air for 10 minutes to ensure complete destruction of turgor. After thawing, the chambers were taken out of their aluminium foil wrapping, the respective thermocouples again sealed onto them and the π determined. The P of each leaf was derived by subtracting the π from the ψ values.

Measurements of ψ on Whole and Cut-up Leaf Samples

ψ determinations were made on further leaf samples, each of which was then cut into 5 pieces by making four equally spaced cuts across each sample with a razor blade. The cut pieces were rearranged in their respective chamber to maintain the same geometry as previously and ψ measurements were again made.

Measurement of π on Whole and Cut-up Leaf Samples

π determinations of entire leaf samples were first made after destroying the P with liquid air. The leaf samples were then cut into 5 pieces as mentioned above whereupon the determinations were repeated.

Measurements of ψ on Entire Leaf Samples and After Cutting them up and Vaselining the Cut-up Surfaces

After determining the ψ of whole leaf samples, these were cut into 5 pieces as described before, but their cut surfaces were then coated with vaseline before determinations were repeated.

Measurements of ψ on Attached and Detached Leaves

The specially designed assembly was fitted to both surfaces of an attached leaf and ψ measurements made over both surfaces at the same time. The petiole was then cut at its proximal end with a razor blade and the cut end immersed immediately in de-gassed water and ψ of both surfaces of the now detached whole leaf was recorded. Soon after detaching the leaf from its parent plant both its surfaces started recording an increase in ψ and it was about 90 min. before the least negative ψ values got stabilized.

Simultaneously, leaf samples were also obtained from an adjacent leaf and their ψ recorded with the help of a conventional thermocouple assembly *i.e.* by placing the leaf sample inside the thermocouple chamber.

Results

Part A

Detached Leaves

Differences Within and Between Species

With the species grown under constant conditions in growth room there was good agreement between net ψ measurements made on three separate occasions (Tables 1, 2, 4). With those species grown out of doors or in the glasshouse, successive measurements of the net ψ differed, although the plants were freely watered. The successive measurements of the π however agreed well within all five species (Tables 1 and 3). Some of the differences between species in both net ψ and π were large (Table 1), even when they were grown under comparable conditions.

TABLE 1

MEASUREMENT OF THE WATER POTENTIAL and its components of detached but otherwise intact leaves with the isopiestic technique (means of 3 replications).

Species	Water potential (ψ) [J kg^{-1}]	Osmotic potential (π) [J kg^{-1}]	Turgor pressure (P) [J kg^{-1}]
Pea	− 843	−1 023	+ 180
Tradescantia	− 800	− 615	− 185
Rose	−1 223	−1 606	+ 383
Bitter orange	−1 218	−2 406	+1 188
Olive	−1 493	−2 646	+1 153

Turgor Pressure

The calculated P, derived from net ψ minus π ($P = \psi - \pi$), which, be it noted, takes no account of any ψ_m of the less succulent leaves of bitter orange and olive was appreciably more positive than that of the more succulent leaves of rose, pea and tradescantia (Table 1). With tradescantia, the most succulent leaf, the calculated P turned out negative, a result open

TABLE 2

EFFECT OF CUTTING-UP LEAVES on their water potentials as measured with the isopiestic technique (means of 3 replications).

Species	Water potential (ψ) measurements [J kg^{-1}]		% increase due to cutting-up leaves
	Whole leaf	Same leaf cut into 5 pieces	
Pea	− 716	− 633	11.59
Tradescantia	− 811	− 318	60·79
Rose	−1 707	−1 205	29·41
Bitter orange	−1 300	−1 206	7·23
Olive	−2 172	−1 903	16·99
Mean (E)	−1 341	−1 033	
Analysis of variance	*SEm* for E ± 24·55; *C.D.* at 5% = 72·56		

to grave doubt, since the plants were watered freely and the leaves showed no visible signs of water stress. This phenomenon will be discussed later.

Effects of Cutting the Leaves

With all five species on all occasions the ψ measured was less negative when the leaves were cut into five pieces than when they were left uncut. When expressed in terms of percentage change from the ψ measured on uncut leaves, this was particularly pronounced with tradescantia and rose,

TABLE 3

EFFECT OF CUTTING LEAVES on their osmotic potential as measured with the isopiestic technique (means of 3 replications).

Species	Osmotic potential (π) measurements [J kg^{-1}]	
	Whole leaf	Same leaf cut into 5 pieces
Pea	−1 165	− 978
Tradescantia	− 598	− 517
Rose	−1 623	−1 565
Bitter orange	−2 522	−2 523
Olive	−2 597	−2 613
Mean (*E*)	−1 701	−1 639
Analysis of variance *SEm* for *E* ± 21·26; *C.D.* at 5% = 62·84		

TABLE 4

EFFECT OF VASELINING THE CUT SURFACES on the water potential of cut-up leaves as measured with the isopiestic technique (means of 3 replications).

Species	Water potential (ψ) measurements [J kg^{-1}]	
	Whole leaf	Same leaf cut into 5 pieces and cut ends vaselined
Pea	− 925	− 831
Tradescantia	−1 039	− 711
Rose	−1 421	−1 434
Olive	−1 493	−1 493
Mean (*E*)	−1 219	−1 117
Analysis of variance *SEm* for *E* ± 16·64; *C.D.* at 5% = 49·18		

but the effect, though less striking, was still evident with the other species (Table 2). Surprisingly, cutting-up also resulted in a significantly less negative reading for leaves whose turgor had been destroyed by freezing and thawing *i.e.*, in a significantly less negative π, at least with pea and, to a lesser extent, tradescantia (Table 3).

By contrast, the application of vaseline to the cut edges of leaves prevented the measured net ψ from becoming less negative with rose and olive, though not with the more succulent leaves of tradescantia and pea (Table 4).

Part B

The Water Potential of Attached, Compared with Detached Leaves

A comparison was made (Table 5) between the net ψ of leaves of citrus attached to their plants and of the same leaves after they had been detached and the cut ends of their petioles placed in a vessel containing de-gassed water. It was intended to cut the petioles under water and retain them under water throughout but it cannot be considered certain that no air entered through the cut. The potentials both of the attached and of the "watered" leaves were measured with the modified apparatus where the petiole, intact or cut, remained outside the thermocouple chamber.

TABLE 5

THE WATER POTENTIAL OF ATTACHED, compared with detached leaves.

Species	Water potential (ψ) measurements [J kg^{-1}]		
	on attached leaf	on same leaf severed and imbibing water (cut petiole outside chamber)	on adjacent leaf detached and placed inside chamber
Citrus	Upper leaf surface −3 240 lower leaf surface −3 010	−2 905 −2 675	−1 457
Tradescantia	upper leaf surface −2 830 lower leaf surface −2 490		− 565

A further set of comparisons was made between the ψ of attached leaves of citrus (the same leaves as above) and also of attached leaves of tradescantia, using the modified apparatus and the potential of the respective adjacent leaves which had been detached and placed in the conventional thermocouple psychrometer chamber used in Part A.

The ψ measurements of the attached leaves were consistently the most negative. When the petioles of the citrus leaves, previously measured when attached to their plants, were severed and placed in de-gassed water, the readings began to rise within fifteen minutes and reached a steady, distinctly less negative value after ninety minutes. This value was however still much more negative than that of comparable leaves in part A. By contrast, the leaves adjacent to the attached ones, when placed in the conventional apparatus used in Part A, showed a considerably less negative ψ even than the leaves imbibing through their petioles while being measured, and the values of these adjacent leaves were similar to those in part A (Tables 1, 2, 4).

Discussion

Explanations are required for the discrepancies between the measurements of intact and of cut-up leaves, between leaves supplied with water through the roots and those imbibing water through the cut petiole, and between those whose cut petioles remained outside the thermocouple chamber.

Since the recordings within each group were consistent, the results must mean either that all the measurements, except possibly one set, were technical artefacts introduced by a deficiency in the measuring apparatus, or that the water potential of the tissue was changed during the preparations for measuring and all conditions measured, except possibly one, were physiological artefacts.

Let us postulate that there is, in addition to the osmotic and turgor components of the ψ, a significant matrix component. This is likely to consist of two parts: the whole-plant ψ_m and the leaf ψ_m. Of these, the whole plant ψ_m, depending on resistance to water flow within the plant (whatever it may be), is ideally represented by the difference between the readings of attached leaves and leaves cut off and watered direct through the petiole (Table 5), although the difference may be an underestimate of the real value if air entered the system when the leaf was cut off. The leaf ψ_m is likely to be determined by the cohesion of the vascular and the cell wall water. This leads to the consideration of the recorded differences in ψ between whole and cut-up leaves.

Several workers, concerned with a wide range of species, have found that the ψ as measured with the thermocouple psychrometer becomes less negative when a leaf is cut into pieces (BARRS 1968, MANOHAR 1966). No plausible explanation was advanced until BARRS and KRAMER (1969) after the present series of experiments had been completed, put forward evidence to support the ingenious hypothesis that the solutes from cells injured during cutting-up are actively re-absorbed by adjacent intact cells, whose π therefore becomes more negative, whereupon they are entered by the now more dilute external solution; this in turn causes a very considerable increase in turgor, with the result that the net potential of the leaf tissues as a whole becomes measurably less negative. Most of our results in part A are in fact consistent with this hypothesis. But I wish to suggest a modification which takes into account the ψ_m of the tissues and which does not necessitate the invocation of active absorption of electrolytes by intact cells. Our evidence fits the hypothesis that cutting a leaf off a plant severs it from a system whose inherent resistances result in a considerable (negative) ψ_m. The almost pure water in the vascular system and in the cell walls of the leaf is therefore now under less stress and is available to "flow out" of any cut in response to any solute gradient in water potential that may arise. Following the destruction of turgor when cells are injured by cutting, the solute potential of electrolytes and other soluble constituents lost from the cut cells is sufficiently negative to cause a flow of the vascular and possibly cell wall water out of the leaf through the cuts, to dilute the "spilled" contents. Since the potential of this "matrix water" is appreciably less negative than that of the "spilled" cell contents this may well result in a sufficient dilution of the latter, to result in turn in the increase in turgor postulated by BARRS and KRAMER (1969) which I agree may be responsible for the ultimately less negative net ψ of cut-up leaves.

Admittedly, for this hypothesis to be tenable it would be necessary not only that the spilled cell contents should at first have a potential more negative than that of the intact cells (which it clearly has) but also that it should be diluted by the vascular and cell wall water beyond equilibration with the potential of the intact cells. It is likely that the protoplasmic membranes offer sufficient resistance to the influx of water to cause this imbalance for a short but critical period. The hypothesis offered appears equally consistent with the evidence available as BARRS and KRAMER's. More work is required to show whether either is correct.

The other results are also not inconsistent with the general hypothesis that a matrix water factor has to be taken into consideration. For instance, that the reading of the π should be less negative after the frozen and thawed leaf has been cut up is surprising but indicates the existence of a residual matrix component which tends to be eliminated by cutting the leaf.

Similarly, the apparently negative turgor of the tradescantia leaves, an obviously suspect value, is likely to have arisen as follows: The tradescantia leaf is distinctly succulent, which is likely to mean (though this needs confirmation) that it carries a large proportion of cell wall water. This "matrix water", released on freezing and thawing, mixes with the cell sap and dilutes it to such an extent that the resultant reading is much less negative than the original π; which causes the calculated turgor to appear much less positive than it really is, and in this extreme case even negative.

There remains the discrepancy between the recorded (less negative) potentials of whole leaves placed entirely in a conventional psychrometer chamber and the potentials of similar leaves which are more negative although the cut ends of their petioles, kept outside the chamber, are supplied with water from a beaker. In this case the difference in the placing of the cut petioles suggests itself as the only probable cause of the difference: the increase in turgor postulated by BARRS and KRAMER, with or without our modification due to vascular and cell wall water, would operate within the chamber, provided it included the cut end of the petiole; when the cut end is kept outside the chamber the more negative potential, *i.e.*, the ultimate cause for an increase in turgor of cut leaves placed in the conventional apparatus, does not occur within the chamber; on the other hand, why the turgor will not increase despite a virtually unlimited water supply when the petiole dips into water requires clarification.

It is hence concluded: Many values of ψ measured by thermocouple psychrometers are likely to be accurate though different according to the treatment of the leaf. Cutting the leaf off its plant renders the ψ value obtained less negative, and cutting the leaf into pieces renders it still less negative. Our tentative hypothesis is that because any cutting treatment is liable to modify the ψ_m of the vascular and cell wall system the measurement of the potential of an attached leaf is likely to be the only accurate one.

Acknowledgement

It is a pleasure to thank Professor R. M. Samish and Dr. Ben Ami Bravdo of the Department of Pomology and Viticulture, Faculty of Agriculture, the Hebrew University of Jerusalem, Rehovot, Israel for encouragement and for help in assembling the thermocouple psychrometer apparatus respectively. I am indeed also grateful to Dr. W. Heydecker, School of Agriculture, University of Nottingham, Sutton Bonington, England, for his valuable help in bringing this manuscript in this form.

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MAN SINGH MANOHAR, Universita Udaipur, Rajasthan, Indie: **Jaký vodní potenciál? Rozdíly ve výsledcích měření nepoškozeného a vyříznutého rostlinného materiálu isopiestickým termočlánkovým psychrometrem.** — Biol. Plant. 13 : 247—256, 1971.

Byl měřen potenciál listů rostlin dobře zásobených vodou. Jak v celkovém, tak i v osmotickém potenciálu hrachu (*Pisum sativum*), podeňky (*Tradescantia versicolor*), růže (*Rosa hybrida*), citroníku (*Citrus aurantium*) a olivy (*Olea europaea*) byly druhové rozdíly. U podeňky byl potenciál měřený po zrušení turgoru zmrazením méně negativní než předtím; to naznačuje, že zjištěná hodnota není totožná se skutečným osmotickým potenciálem listu. Odříznuté listy všech druhů měly méně negativní vodní potenciál, a u hrachu také méně negativní osmotický potenciál, jestliže byly rozřezány na pět částí, než byly-li ponechány vcelku. Potření řezných ploch listů vaselinou snížilo tento efekt u růže a olivy, ne však u podeňky a hrachu. Byl také měřen vodní potenciál srovnatelných listů podeňky a citroníku na rostlině a odříznutých, byly-li odříznuté listy citroníku zásobovány vodou řapíky vyčnívajícími z měrné komůrky termočlánku, jejich potenciál byl podstatně méně negativní než u týchž listů na rostlinách dobře zásobených vodou. Avšak podobné listy, jejichž uříznuté řapíky byly umístěny do komůrky termočlánku měly ještě méně negativní potenciál.

Výsledky odpovídají hypotéze, že v listu odříznutém od rostliny nebo dokonce rozřezaném na části se uvolňuje voda, dříve vázaná matričními silami, ředí „rozlitou“ buněčnou šťávu, je nasáta sousedními buňkami, zvyšuje jejich turgor a tím upravuje vodní potenciál listu na méně negativní hodnotu. Podobně zjevný negativní turgor šťavnatých listů podeňky je pravděpodobně působen zředěním osmotické složky vodou buněčných stěn. Rozdíly ve výsledcích u listů na rostlině a odříznutých svědčí pro značnou složku celorostlinné matrice, a výsledky vcelku naznačují, že měření termočlánkovým psychrometrem na odříznutých a tím spíše na rozřezaných listech jsou pravděpodobně artefakty a že je vhodnější určovat vodní potenciál neodříznutých listů přímo na rostlinách.