OSMOTIC QUANTITIES OF PLANT CELLS IN GIVEN PHASES[1]

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(WITH TWO FIGURES)

I. Osmotic quantities to be distinguished

Some authors use seven or eight terms, others content themselves with two or even a single one. The points of view are much divided. In order to reach an objective judgment, let us consider a cell from the pith of *Impatiens noli-tangere,* a cell which has been accurately measured by Ursprung and Blum (**48**), Molz (**28**), Ursprung and Beck (**44**), and Ursprung (**46**). Cf. also Beck (**1**). Let V represent the volume of the given cell, and the indices n, g, and s, represent the normal phase, incipient plasmolytic phase (grenzplasmolytischen), and saturation phase respectively. We distinguish (fig. 1, schematic sketch of cell) the normal volume ($V_n = 14,122$ units) of the unchanged cell, the volume at incipient plasmolysis ($V_g = 13,209$ units), and the volume at complete saturation ($V_s = 14,779$ units). V_n had at the time of observation the value just given, which, however, changed as the water balance within the cell changed.

If we desire to measure the osmotic potential of the cell sap of the individual cell, we must begin with the phase of incipient plasmolysis. By means of the plasmolytic method we find first that the incipient plasmolysis value (*i.e.,* the osmotic value at incipient plasmolysis) is $O_g = 0.38$ mol cane sugar. This concentration of the cane sugar solution will cause the protoplasm of our cell to recede from the cell wall ever so little. In the absence of complicating factors, so that the volume changes of the cell have no other effects than corresponding changes in the concentration of the cell sap, one can calculate the osmotic value of the normal sap, O_n, from $O_g = 0.38$ by the equation: $O_n = O_g \dfrac{V_g}{V_n} = 0.355$ mol cane sugar. If we place the cell sap or an isosmotic cane sugar solution in an osmometer with a semipermeable membrane, the cell sap at incipient plasmolysis would develop an osmotic pressure (physicist's terminology) or a suction force (suction tension, suction[2]) (our terminology[3]) of 10.5 atm. In the condition of equilibrium the protoplasm must have the same suction force. Hence we may write: *The suction force (suction tension, suction) of the contents of the cell in the phase of incipient plasmolysis* is $S_{1g} = 10.5$ atm. Similarly the suction force (suction tension, suction) of the contents of

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[1] Translated by William A. Beck.

[2] Original: Saugkraft (Saugspannung, Saugung).

[3] The pros and cons of the matter of terminology will be discussed later.

the cell in the normal phase, S_{i_n}, or since for the sake of simplicity the modification referring to the phase is omitted, the *suction force (suction tension, suction) of the contents of the cell,* $S_{i_n} = 9.7$ atm. In a similar manner it is deduced that $S_{i_s} = 9.3$ atm.

The wall pressure (W), *i.e.,* the pressure which the stretched wall exerts upon the contents of the cell has the following values: At incipient plasmolysis naturally $W_g = 0.0$ atm.; in the saturation phase, $W_s = 9.3$ atm.; with the assumption that change in wall pressure is proportional to the change in volume the wall pressure in the normal phase may be calculated and shown to be $W_n = 5.4$ atm.

The turgor pressure (T), *i.e.,* the pressure which the contents of the cell exert upon the wall, is, at equilibrium, numerically equal to the wall pressure, since action and reaction are equal, but it acts in the opposite direction.

The *suction force (suction tension, suction) of the cell* (S_z) is the force per unit area with which the whole cell, consisting of the cell wall and the contents of the cell, tends to absorb water. If external forces that tend to produce tension or pressure are absent, it is composed of two forces (tensions) which operate in opposite directions: the suction force of the contents of the cell, and the wall pressure, which tends to force water from the cell. The relations may be expressed by the equation:

$$S_z = S_i - W$$

It follows that the *suction force of the cell,* in the phase of incipient plasmolysis, in the normal phase, and in the phase of saturation, has the following values respectively:

$$S_{g_z} = S_{i_g} - W_g = 10.5 - 0.0 = 10.5 \text{ atm.}$$

$$S_{z_n} = S_{i_n} - W_n = 9.7 - 5.4 = 4.3 \text{ atm.}$$

$$S_{z_s} = S_{i_s} - W_s = 9.3 - 9.3 = 0.0 \text{ atm.}$$

Our suction force equation contains three osmotic quantities which differ in their concepts and usually also in their numerical expression. It appears from the numerical expression given above, and even more clearly from the graphic representation in figure 1, that these three quantities behave in an altogether different manner as the cell changes from the phase of incipient plasmolysis to the phase of saturation. S_i varies but little; W increases very rapidly; and S_z decreases even more rapidly. Let particular emphasis be placed on the fact that the same cell may simultaneously possess an inner pressure of several atmospheres ($T_n = 5.4$ atm.), and nevertheless be able to take in water ($S_{z_n} = 4.3$ atm.).

Previously it was assumed that no foreign mechanical stress or strain was placed upon the cell; in this case $T = W$ numerically. If an external pressure $(+ A)$ or tension $(- A)$ is present, then $T = W \pm A$, and the equation expressing the suction force takes the form: $S_z = S_1 - (W \pm A)$.

SIGNIFICANCE OF THE OSMOTIC QUANTITIES

The significance of the osmotic quantities follows consequently from what has already been said.

The *suction force (suction tension, suction)* of the cell, $S_{z_n} = 4.3$ atm., is the quantity that is the dimensional standard for the intake, the extrusion, and the conduction of water. It is indispensable, for example, in the study of water economy.

The *suction force (suction tension, suction) of the contents of the cell,* $S_{1_n} = 9.7$ atm., must not be confounded with S_{z_n}. Thus it does not deter-

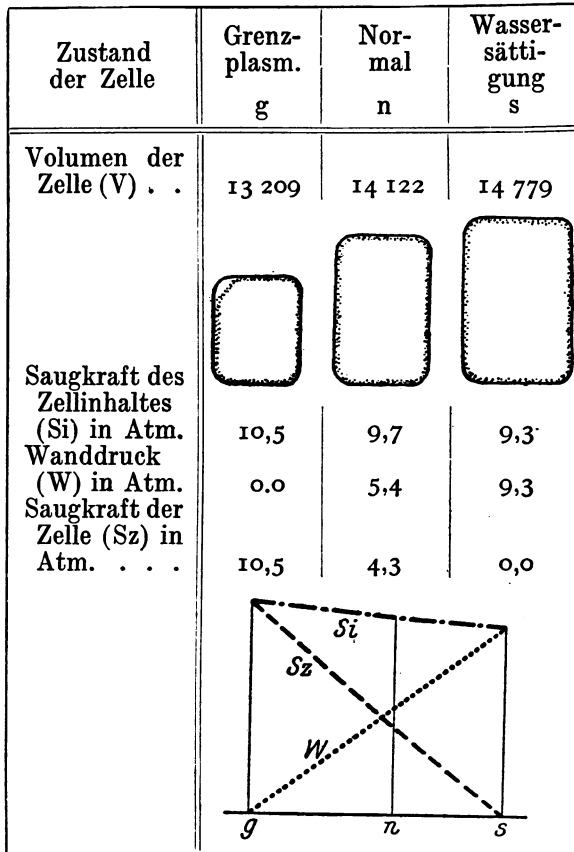| Zustand der Zelle	Grenz-plasm. g	Nor-mal n	Wasser-sätti-gung s
Volumen der Zelle (V) . .	13 209	14 122	14 779
Saugkraft des Zellinhaltes (Si) in Atm.	10,5	9,7	9,3ˑ
Wanddruck (W) in Atm.	0.0	5,4	9,3
Saugkraft der Zelle (Sz) in Atm. . . .	10,5	4,3	0,0

FIG. 1. Graphic representation of the osmotic quantities of a cell taken from the pith of *Impatiens*. (According to URSPRUNG 46.)

mine the amount of water absorption, but it is an important component of S_{zn}, as is shown by the equation $S_{zn} = S_{i_n} - W_n$. S_{i_n} is equal to the suction force of the protoplasm. It is furthermore a measure for the change in the water balance of the cell, provided the osmotic solute remains constant.

The *wall pressure*, $W_n = 5.4$ atm., naturally plays an important rôle in turgor movements. The measurement of this quantity has furthermore contributed in establishing the relations that exist between turgor pressure and growth. The rigidity of the soft-walled cell is the result of the combined action of the wall pressure and the turgor pressure. In the state of equilibrium $T = W$; when, however, asci burst open in plasmoptyse $T > W$.
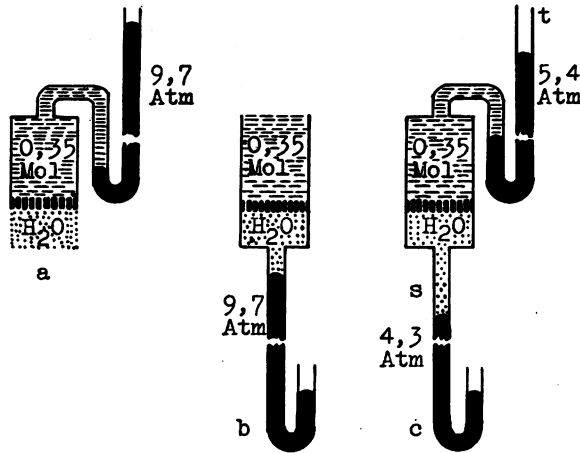

FIG. 2. Diagram of the suction force of an osmometer. (According to URSPRUNG 46.)

Turgor distention. For every change in volume, $V_s - V_g$, there is a corresponding equivalent change in turgor pressure, $T_s - T_g$, which will vary in different cells, the magnitude of which depends upon the distention. The turgor distention is the dimensional standard for the cell, in its rôle as a water reservoir, as also for turgor movements.

The *suction force (suction tension, suction) at incipient plasmolysis*, $S_{i_g} = S_{z_g} = 10.5$ atm., serves in the study of the regulation of osmotic relations (Studium der Osmoregulationen).

The *osmotic values*, O_g and O_n, are usually auxiliary quantities that are necessary in the determination of S_{i_g} and S_{i_n} of the individual cells.

II. Methods of measuring

Nothing more can be done here than to indicate the principle involved in each of the different methods and thus bring into greater relief the names employed to designate the various quantities.

1. The osmotic value at incipient plasmolysis, $O_g = 0.38$ mol cane sugar, is measured by the oldest method of measuring in this domain. It determines that concentration of a harmless non-permeable plasmolyte which at osmotic equilibrium causes the protoplasm to recede ever so little from the cell wall.

2. The *suction force (suction tension, suction) of the cell or of the cell contents at incipient plasmolysis,* $S_{z_g} = S_{1_g} = 10.5$ atm., is obtained by translating the value 0.38 mol cane sugar, obtained in method 1, into equivalent atmospheres. O_g and S_{1_g} refer, it is true, to an abnormal condition of the cell, but they nevertheless yield important results especially concerning the regulation of the osmotic relations in the normal cells.

3. The *suction force (suction tension, suction) of the contents of the cell in the normal phase,* $S_{1_n} = 9.7$ atm., may for example be determined by cryoscopy of the expressed juice. It must be remembered, however, that all methods employing press-juice yield only average values for the larger tissues or entire organs. The measurement of S_{1_n} for *individual cells* demands a knowledge of the value of O_n.

4. The *osmotic value of the contents of the cell in the normal phase,* $O_n = 0.355$ mol cane sugar, is deduced from O_g by means of the equation $O_n = O_g \dfrac{V_g}{V_n}$. The equivalent value in atmospheres is the value of S_{1_n}. The value of S_{1_n} cannot be determined directly from S_{1_g} by using the quotient of the volumes as a factor, because the suction force (osmotic pressure) of a solution increases at a greater rate than does the concentration.

5. The *suction force (suction tension, suction) of the cell* in the normal phase, $S_{z_n} = 4.3$ atm., is measured by determining the concentration of a harmless non-permeable plasmolyte (Osmotikum) in which the original cell volume remains constant. It is necessary that the cell wall is sufficiently distensible that the cell may show an appreciable change in volume with change of the external concentration.

6. The *wall pressure,* $W_n = 5.4$ atm., can be calculated for individual cells, in the absence of external pressure, from the equation $W_n = S_{1_n} - S_{z_n}$. The suction force of the cell, S_{z_n}, remains unintelligible so long as the wall pressure is not taken into consideration.

7. The *turgor pressure,* $T_n = 5.4$ atm., is numerically equal to the wall pressure in the absence of external forces, but it acts in the opposite direction. When external forces enter into consideration, then $T_n = W_n + A_n = S_{1_n} - S_{z_n}$.

III. Review and critique of the various terminological proposals

A. The older terminology

Before the newer methods were developed, it was customary to use either the method of incipient plasmolysis or the cryoscopic method. Sup-

pose we begin with the method of incipient plasmolysis, again taking our numerical examples from the data obtained with cells of *Impatiens*. The suction force at incipient plasmolysis was *measured*, $S_{z_g} = S_{l_g} = 10.5$ atm. The values obtained were frequently labeled as follows:

Osmotic pressure; this, however is actually only 9.7 atm.; error $= 0.8$ atm.

Turgor pressure; actual value is 5.4 atm.; error $= 5.1$ atm.

Suction force; actual value is 4.3 atm.; error $= 6.2$ atm.

The confusion is even greater in the following example: the author is studying water intake; he *requires to know* the suction force of the cell (4.3 atm.), but he *speaks* of turgor pressure (5.4 atm.) and he *measures* the suction force at incipient plasmolysis (10.5 atm.).

The difficulties of the cryoscopic method are similar. When this method is used to investigate water economy, *e.g.*, DIXON (**6**), HARRIS and his associates (**14–19**), KORSTIAN (**24**), the quantity determined is not the correct one. For there is no doubt that, in connection with water intake, the suction force of the cell contents does not come into consideration at all, but rather the suction force of the cell (4.3 atm.). The error of all investigations of water economy that depend on the cryoscopic method lies in neglecting to take the wall pressure into consideration.

The misunderstandings that have arisen as the result of the confusion of the osmotic quantities have been discussed elsewhere (URSPRUNG and BLUM **48**); further examples may readily be found by any one in the language with which he is familiar. The task of the new terminology must be to provide a nomenclature such that misconceptions will be avoided.

B. THE RECENT TERMINOLOGY

The quantities which are to be distinguished have been indicated in sections I and II. The individual terms will now be discussed.

INDIVIDUAL TERMS: (1) THE SUCTION FORCE OF THE CELL, $S_{z_n} = 4.3$ ATM.— As previously mentioned, the normal phase is indicated by the omission of the modification referring to the phase; consequently "suction force of the cell" is used instead of "suction force of the cell in normal phase." Of all the terms the expression "suction force" has been most objected to. Some authors criticize only the element "force" (Kraft); others reject the term "suction" as well.

(a) *Pros and cons of "suction."*—SHULL (**36**), to my knowledge the only author who has expressed himself as opposed to the term "suction" (Saugung), says: "If a careful analysis of water movement is made it will always be found that water is the active compound. The cell contents merely provide a medium of lower free water content into which water from regions of greater free water content moves. The pressure in any cell is caused by the free water entering from outside the cell. If the pressure in

a street car, when overcrowded with people who try to enter after the car is full, can be called a suction pressure, then the pressure in a cell can be called suction pressure, and the force of entry called suction tension."[4]   In answer to these statements the following remarks may be permitted. So far as I know, the actual cause of the osmotic phenomenon is unknown even today (cf., for example, FINDLAY 9) ; consequently there is no necessity for the physiologist to restrict the terminology to any particular theory.

The ordinary mode of expression *favors* the term "suction"; then there is in use a very old expression which we find for example in suction pump, suction root, suction hair. The justification of the term suction appears most clearly if the cell is replaced by a semipermeable osmometer to which in an appropriate manner a manometer has been attached. The osmometer contains a 0.355 mol cane sugar solution (fig. 2, c), which has an osmotic pressure of 9.7 atm. The wall pressure, numerically equal to the turgor pressure, is compensated by the mercury pressure of 5.4 atm. in the manometer t. Of special interest to us is the osmotic quantity, which amounts to 4.3 atm. (9.7–5.4 atm.) ; manometer s (fig. 2) registers it, and clearly as a suction which the osmometer exerts upon the water outside. According to the data indicated on the manometer s, which are objective and independent of any particular concept of the mechanism of osmosis, we have the right to speak of a "suction" force of the cell $S_{zn} = 4.3$ atm.

(b) *Pros and cons of "force."*—SHULL (37) says of suction force: "No unsuitable term should be considered immune from change, especially one not over 15 years old, just because it has been commonly employed in Europe." This assertion concerning the age of the contested term does not by any means agree with the facts. Incidentally PFEFFER (32, p. 77) speaks of "suction force," but particularly DEVRIES (51, p. 561) ; since that time the term is found in the literature of plant physiology in ever so many languages [e.g., NOLL (42) in STRASBURGER's Lehrbuch, p. 161; HABERLANDT (13, p. 351) ; FITTING (10, p. 209) ; VINES (50, p. 429) ; EWART (8, p. 77).] Consequently the term "suction force" is about as old as the history of osmotic relations in cells. Since it did not seem to me absolutely necessary to coin a new term, while developing mensural methods in 1916, I employed the term already in use. That the term is not strictly correct in the physical sense, I have already in 1916 emphatically pointed out (URSPRUNG and BLUM 47, p. 529) as follows: "With reference to the terminology, the term "force" should be retained, even though it is a matter of $\dfrac{\text{force}}{\text{area}}$, therefore a quantity not mensurable in kilograms, but in atmospheres."

[4] SHULL (38) also says in a later paper: "If the expansive force exerted in the interior of an automobile tire when we force air into it can legitimately be called a 'suction force,' then also we can call the expansive force of a cell when water is forcing its way into the cell a 'suction force.'"

(c) *Suggested substitutes for "force."*—Suction "pressure"—as suggested by STILES (**40, 41**), and BRIEGER (**4**), a student with RENNER—has the correct dimensions but is a physical impossibility, since a manometer can register either suction or pressure, but not both at the same time (URSPRUNG **45**, p. 196). The expression appears to have been abandoned, at least in German-speaking countries (RENNER **35**, p. 749; GRADMANN **12**, p. 635).

Suction "value" (GRADMANN **11, 12**, p. 636), suction "ability" (PRINGSHEIM **33**, p. 749), suction "potential" (OPPENHEIMER **30**, p. 131; **31**, p. 526) are terms that indicate sufficiently that there is a question of *capacity* which does not by any means always lead to water intake. This I had already said in 1916 (URSPRUNG and BLUM **47**, p. 530) and still more clearly in 1920 (URSPRUNG and BLUM **48**, p. 202) with the definition: Suction force of the cell = the force with which the cell *strives* to take in water. Of course it is evident that the cell cannot take in water if it does not suck more forcibly than the surrounding medium. I did not deem it necessary to emphasize that fact by applying a special term. One does not speak of "Pferdepotential" but of "Pfedekraft" even though the horse will pull the wagon only if the load is not too heavy.

Suction "tension" (SHULL **36**, p. 214; BECK **1**, p. 425) has the correct dimensions, and is physically more nearly correct than suction "force" (*cf.* also URSPRUNG **45**). If a new term had to be chosen, one would choose tension (Spannung); but since the term suction "force" is already a half century old and has given rise to no misconceptions, it may as well, as I see it, be retained in the future. Even the physicists tolerate a similar liberty in the use of terms, *e.g.*, using "Dampfspannung" instead of "Spannkraft" of steam (CHWOLSON **5**, p. 709); but if Spann"kraft" is permitted in physics, why should the term Saug"kraft" be forbidden in physiology? Furthermore, so long as we retain such terms as cryptogams, tracheae, and leucoplasts one has no right to forbid suction force. It is after all simply a matter of taste whether one, with deference to the historical development, continues to use an old term which has given rise to no misconceptions, or whether one prefers a faultlessly correct expression.

(d) *Counter suggestions for "suction force."*—"Suction" (SIERP in STRASSBURGER's Lehrbuch, 18th ed., p. 76) is a short and clear term but appears to have greater difficulty in becoming established than does suction force or suction tension.

"Water absorbing power" (THODAY **43**, p. 110) does not have the correct dimensions, and is rather lengthy.

"Pouvoir osmotique" (LECLERC DU SABLON **25**, p. 24) reminds one of PFEFFER's "osmotische Triebkraft" (**32**, pp. 76, 84) but it does not indicate whether it signifies suction or pressure.

Concerning the terms "Hydratur" and "Wasserzustand" the reader is referred to section (2) later.

"Turgor deficit" employed by CURTIS (private communication from BECK), it seems to me, can mean only one thing, *i.e.,* a difference between the maximum turgor pressure which is possible and the pressure which actually exists. As is shown in figure 1, the turgor deficit of our *Impatiens* cell is $9.3 - 5.4 = 3.9$ atm., while the suction force of the cell is $S_{z_n} = 4.3$ atm. Turgor deficit and suction force of the cell are not equal numerically, nor are the terms conceptually alike; they cannot therefore be used synonymously.

SHULL (37) "sees no good reason for using any other term than osmotic pressure in connection with the turgidity of plant cells." But how, then, shall our osmotic quantity 4.3 atmospheres be designated? The "osmotic pressure" is really 9.7 atm., the "turgor pressure" 5.4 atm.; accordingly the difference, if we are to preserve both these terms, must be designated as "the difference between the osmotic pressure and the turgorpressure," a term surely too detailed to find any support.[5]

"Traction" was suggested (LIVINGSTON, private communication to BECK, 1927) presumably to replace tension, but I have no further information concerning it.[6]

(e) *Other suggestions.*—Distinctions have been made between static and kinetic, between potential and actual (OPPENHEIMER **30, 31**; RENNER **35**), between absolute and relative suction force (HUBER **22**; BENEKE-JOST **3**, vol. I, p. 57), and between osmotic and swelling (imbibitional) suction force.

In water intake by the cell osmotic and swelling forces may be associated; the former are usually determinative. Both components in a state of equilibrium must of course be equal to one another: a change in one necessarily causes a corresponding change in the other.

The *Impatiens* cell (fig. 1) with its suction force, $S_{z_n} = 4.3$ atm., can take in water, exude water, or be in equilibrium with the environment. Which case actually obtains depends upon the value and the direction of the suction force gradient (Saugkraftgefälle) of the environment of the cell, as well as upon the resistance to transfusion (Filtrationswiderstand). Just as one in physics speaks of kinetic and static, of actual and potential energy, according to whether or not it results in motion, so one may of course do the same thing in physiology.

[5] SHULL has suggested "net osmotic pressure" for this quantity.

[6] Translator's note: The author refers to a letter from LIVINGSTON to the translator January 3, 1927, in which LIVINGSTON suggested in an informal way a number of terms which were submitted by the translator, of his own accord, to URSPRUNG. The discussion is too lengthy to be given here.

The only question is whether, to avoid misunderstanding, it is necessary to speak of a static suction force when the osmotic energy remains potential, and of a kinetic suction force when the osmotic energy becomes actual and sets the water in motion. An example from mechanics may serve to elucidate this. Suppose that two similar, one-horsepower tractors are attached to the same vehicle; in one case the tractors pull in the same direction and in the other they pull in opposite directions. It is quite unnecessary to refer in the first case to kinetic or actual horsepower and in the second to static or potential horsepower; similarly it is altogether superfluous to make a like distinction in physiology.

Moreover, the expressions *absolute* and *relative* suction force which are employed to signify that the cell with a suction force of 4.3 atm. is in the first case sucking against pure water, and in the second case against an osmotically active environment, are to say the least superfluous. As has already been shown (URSPRUNG and BLUM **49**, p. 2), the suction force is the same in both cases; the *suction force gradient,* however, is different in the environment of the cell. This fact is simply and unequivocally expressed by the use of this old term (suction force).

New and unnecessary terms should, in my opinion, be avoided, as they mean a useless complication of nomenclature which unnecessarily makes understanding difficult for the beginner and layman.

To summarize, then, for the quantity $S_{zn} = 4.3$ atm. the following terms are recommended: suction force of the cell, suction tension of the cell, or suction of the cell; in addition one may use the expressions suction force gradient, suction tension gradient, or suction gradient.

(2) SUCTION FORCE OF THE CELL CONTENTS, $S_{1n} = 9.7$ ATM.—What has just been said regarding suction force of the cell applies as well to the discussion of the cell contents. We may therefore give our attention immediately to the counter suggestions.

(a) *Counter suggestions.*—Osmotic pressure is an excellent term in the field of physics, which, however, has not proved adequate in plant physiology. Before 1916 all of the osmotic quantities measured or used were simply referred to as osmotic pressure, even when they differed in numerical value as well as in their concepts. For example, previous to that time osmotic pressure was sometimes understood to mean $S_{zn} = 4.3$ atm., sometimes it meant $S_{1n} = 9.7$ atm., sometimes $T_n = 5.4$ atm., sometimes $S_{zg} = 10.5$ atm. That such a state of affairs must lead to serious confusion is self-evident.

If the physiologist wishes to employ the term "osmotic pressure" he must use it in the sense of the physicist, *i.e.,* the maximum pressure which the cell sap can sustain in an osmometer which is provided with a semi-

permeable membrane. Accordingly it is correct to say that the "osmotic pressure" of the cell sap is 9.7 atm. Let us now examine this term and see whether it serves the physiologist's purpose.

Referring to figure 2, *b,* note that the 0.355 mol cane sugar solution exercises a *suction* upon the water which lies on the opposite side of the membrane and above the mercury, which amounts to 9.7 atm. In figure 2, *a,* the manometer shows a *pressure* of 9.7 atm. The 9.7 atm. may be regarded as a tension as well as a pressure. The cell which we have been considering possesses a turgor pressure of 5.4 atm. as well as an osmotic pressure of 9.7 atm.; since both pressures are the immediate result of the osmotic phenomenon, they may, though distinct, readily be confounded. Let a recent case serve as illustration. (For less recent cases *cf.* URSPRUNG and BLUM **48.**) WENT (**55**) says: "The osmotic pressure of the contents of the cell is received by the stretched cell wall." "Osmotic pressure" is spoken of, which in the case of our illustrative cell is 9.7 atm., while the author has in mind turgor pressure which is really 5.4 atm.

Since the 9.7 atm. (refer to equation $S_{zn} = S_{i_n} - W_n$) tend *to carry the water into the cell* and the 5.4 atm. tend *to force water from the cell,* it does not seem desirable to apply the same term "pressure" indiscriminately in both cases. Since there is no opposition to the term "turgor pressure" as here used, there remains nothing else but to drop the expression "osmotic pressure" if we are to avoid being misunderstood.

"Osmotic value" was suggested as a substitute for "suction force of the contents of the cell" by HÖFLER (**21**) and WALTER (**53**). The latter desires that the osmotic value should be expressed only in atmospheres, while I express it in molal units.

Under the caption "value" anything may be understood *a priori.* If, however, we are to give unequivocal expression to what we mean, we should agree upon one mode of expression of the quantity (*cf.* also sec. 4). WALTER's suggestion, to express the value only in atmospheres, is not practicable; first because we frequently need the molal expression (*e.g.,* in the equation $O_n = O_g \dfrac{V_g}{V_n}$, which is necessary for the determination of S_{i_n} of the individual cell), and then because it is not always possible to translate the molal value into atmospheres partly because the concentration data are insufficient. As we already have the expression "suction force (suction tension, suction) of the contents of the cell," the simplest course would be to continue to express the "osmotic value" in molal units.

"Osmotic concentration" has been used for a long time by HARRIS and his associates (**14–19**). Recently PRINGSHEIM (**33**) also has suggested the term as a substitute for "osmotic pressure." DIXON and ATKINS (**7**) as also KORSTIAN (**24**) speak of "sap concentration." These designations

are not to be recommended as substitutes for the quantity S_i, which is here in question, for it must be measured in atmospheres (as follows consequentially from the equation $S_z = S_i - W$). Logically a concentration should not be expressed in atmospheres.

"*Density of cell sap*" is used by KORSTIAN (**24**) as synonymous with "osmotic pressure." This expression also is unsuitable since density cannot be measured in atmospheres.

"*Water relations*," "*water conditions*," and "Hydratur" are expressions that WALTER (**52–54**) suggests as substitutes for "suction force (suction tension, suction) of the contents of the cell" and he expresses the quantity in atmospheres. He uses three methods for the measurement of "Hydratur" which yield results that are numerically different and are altogether different in concept: (1) Cryoscopy of the expressed sap which gives an average value of $S_{i_n} = 9.7$ atm.; (2) Determination of the vapor pressure of intact cells which gives values of $S_{z_n} = 4.3$ atm. and not values for S_{i_n}; (3) The method of incipient plasmolysis by which $S_{i_g} = S_{z_g} = 10.5$ atm. is determined. Not only do these methods yield quantities that are altogether different in themselves but they are rechristened and defined in a manner that introduces confusion. While WALTER thinks he is measuring the "water condition" or "Hydratur," usually by determining the quantity $S_{i_n} = 9.7$ atm., RENNER (**35**) explains that the "water condition" or "Hydratur" can agree in value only with the suction force of the cell $S_{z_n} = 4.3$ atm. This confusion follows from the fact that both authors are measuring different quantities and apply common names indiscriminately. WALTER studies the situation from the point of view of the suction force of the protoplasm, while RENNER regards it from the point of view of the suction force of the cell. These recent examples show how futile it is to form a new, indefinite and unnecessary terminology; it makes things very difficult for those who are not very familiar with the subject, while nothing of value is gained. I retained, whenever it was at all possible, the already-existing terms, precisely for the purpose of not overburdening the nomenclature.

(3) THE SUCTION FORCE AT INCIPIENT PLASMOLYSIS, $S_{i_g} = S_{z_g} = 10.5$ ATM.—Here again that which was already mentioned about "suction force" holds, *i.e.*, that "suction tension" or "suction" should be considered synonymous with it. The modifications "of the cell" and "of the contents of the cell" become superfluous, since $S_{i_g} = S_{z_g} = 10.5$ atm. At this time it is probably self-evident that only the suction force at incipient plasmolysis can be measured and not all other kinds of quantities. It follows that previous misunderstandings in so far as they arose from confusion of terms should henceforth be eliminated. The determination of $S_{i_g} = 10.5$ atm. by the plasmolytic method has rendered physiology great service (one has only to

recall the work of DE VRIES), and will continue to do so in the future (*e.g.,* in the study of osmotic regulation) if one only uses a proper plasmolytic agent, and if care is taken to interpret the results correctly.

(4) THE OSMOTIC VALUE, $O_n = 0.355$ MOL CANE SUGAR.—

(5) THE OSMOTIC VALUE AT INCIPIENT PLASMOLYSIS OR INCIPIENT PLASMOLYSIS VALUE, $O_g = 0.38$ MOL CANE SUGAR.—

The term "osmotic value" (when the attribute is lacking, "in the normal phase" is understood) signifies the molal expression of the concentration of the plasmolyte which is isotonic with the cell sap, when the cell has the normal volume (URSPRUNG and BLUM **48**; BECK **2**). The osmotic value at incipient plasmolysis, $O_n = 0.38$ mol cane sugar, must first be determined before the quantity $O_n = 0.35$ can be deduced from it. The deduction is made by means of the equation, $O_n = O_n \dfrac{V_g}{V_n} = 0.355$ mol cane sugar, in which V_g is the volume of the cell at incipient plasmolysis, and V_n the volume in the normal phase.

(a) *Other suggestions.*—HÖFLER (**21**) made the suggestion which was seconded by HUBER (**23**) that the osmotic value should be expressed in atmospheres as well as in molal units. According to this suggestion we should write: $O_n = 0.355$ mol cane sugar $= 9.7$ atm.

As previously mentioned, the term value may, *a priori,* be variously employed, but in the interest of a simple nomenclature, which admits of but one interpretation, we should agree upon some simple but adequate term. Furthermore, a 0.355 molal cane sugar solution can only be equivalent to but not identical with a pressure of 9.7 atm. Different quantities measured in different systems of units may not be given a common name just because they have equivalent values. Now if the quantity measured in atmospheres be designated as the suction force (suction tension, suction) of the contents of the cell, there is nothing to prevent us from calling the quantity with its equivalent values, expressed in molal concentration units, the osmotic value.

Osmotic concentration.—PRINGSHEIM (**33**) suggests that the term "osmotic value" be rejected as not sufficiently definite, while WALTER (**53**, p. 83) wishes to have the quantity introduced even into the suction-force equation. Let it be recalled that just as in the case of the term suction force, we are dealing with a *time-honored* term that for long has been employed in plant physiology. It harmonizes very well, too, with the ordinary modes of speech; for just as we speak of the monetary value of various things we may discuss the osmotic value of different cell saps. Accordingly it is certainly permissible to speak of the "osmotic value" as being 1 mol cane sugar solution. The substitute which PRINGSHEIM (**33**) proposes, "osmotic concentration" of 1 mol cane sugar solution, is decidedly not an improvement. In the first place the new term may give the impression that

the cell sap contains a 1 mol cane sugar solution; then again the concentration is measured in mols but not necessarily with cane sugar; finally the concentration is not the only factor to be considered in the osmotic phenomena for the chemical constitution of the sap is a factor too.

(6) THE WALL PRESSURE $W_n = 5.4$ atm.—

(7.) THE TURGOR PRESSURE $T_n = 5.4$ atm.—

From the nature of things it follows that the wall pressure is the pressure that is exerted by the wall upon the contents of the cell. Turgor pressure is generally admitted to be the pressure exerted by the contents of the cell upon the wall. In a condition of equilibrium $T = W$, when no foreign forces enter the consideration. If foreign forces are to be considered, $T = W \pm A$. I am not aware of any terms that may have been suggested as substitutes for these.

(b) *The suction-force (suction tension) equation.*—My equation reads: The suction force of the cell = the suction force of the contents of the cell – the wall pressure; $S_z = S_1 - W$; of course suction force may be replaced by suction tension or by suction. If foreign forces enter into consideration the equation becomes: $S_z = S_1 - W \pm A$. T is given by $W \pm A$.

Suggested substitutes.—RENNER (**34**) : Saugkraft der Zelle = osmotische Druck – Turgordruck.

$$S = P - T.$$

This equation was published before mine; both were established independently.

THODAY (**43**) : Water absorbing power = osmotic pressure – turgor pressure.

$$p = P - T.$$

HÖFLER (**21**) : Saugkraft der Zelle = osmotischer Wert (in Atm.) – Turgordruck.

$$S = O - T.$$

LECLERC DU SABLON (**25**) pouvoir osmotique du liquide exterieur = pouvoir osmotique du suc cellulaire – turgescence.

STILES (**40, 41**) : suction pressure = osmotic pressure – wall pressure.

$$S = P - T.$$

WALTER (**53**) : Saugkraft = osmotischer Wert (in Atm.) – Wanddruck.

SIERP (**39**) : Saugung der Zelle = Saugung des Zellinhaltes – Wanddruck.

Several of the suggested substitutes place turgor pressure in the place of wall pressure in my equation; I do not recommend this form of writing the equation as it does not indicate the actual condition. The quantity which acts counter to the intake of the water is not the turgor pressure but the wall pressure (ev. $W \pm A$).

Other variations often consist in replacing S_1 by the osmotic pressure. As was shown previously (2) this is not to be recommended; first because it leads to confusion with the turgor pressure, and then again because it is to no good purpose to use the common term "pressure" for a quantity which tends to press water from the cell and another which tends to draw water into the cell.

The why and the wherefore of expressing the osmotic value in molal units rather than in atmospheres has been discussed (cf. sections 2, 4, 5).

If suction tension or suction is to be preferred to suction force it is a matter of taste so far as I am concerned.

(c) *Suggestions on the reduction of the number of terms.*—As was mentioned above, SHULL (36–38) prefers to use no term other than "osmotic pressure" in connection with the turgidity of plant cells. Similarly LUBI-MENKO (27) speaks only of "pression osmotique" and "pression de turgescence."

HÖBER (20) speaks of "osmotischen Druck" and "Turgor." OLT-MANNS (29) even tries to get along with the term "turgor" alone.

In itself, of course, the notion of reducing the number of terms is very welcome; but for all that, the basic purpose, *i.e.*, the possibility of clear expression of ideas and the elimination of misunderstandings, must not be sacrificed. That two terms will not suffice to express unequivocally seven quantities will probably not be questioned in view of the illustrations which were drawn from various authors, and further demonstration will hardly be necessary. Referring again to SHULL's reviews, he wrote (36) in reference to BLUM's measurements of suction force in alpine plants: "These suction force studies show in a different way by plasmolytic means, just what HARRIS's studies of freezing point depressions have shown, a general correspondence of plant cells to the conditions of the habitat." If he intends to convey the notion that the same quantity was measured in two different ways, he is in error.[7] HARRIS—referring once again to the illustrative cell of *Impatiens*—measured $S_{1n} = 9.7$ atm.; BLUM measured $S_{zn} = 4.3$ atm. The fact is that the two quantities usually do vary in the same sense. Thus while passing from the phase of incipient plasmolysis to the saturation phase (*cf.* fig. 1), both experience a decrement, but it is slight in S_1, *i.e.*, from 10.5 to 9.3 atm., and considerable in S_z, *i.e.*, from 10.5 to 0.0 atm. If the quantity S_{1n} is determined in the study of the water economy, faulty individual values are obtained, because the real indicator of the conditions is S_{zn}.

Whoever attempts to carry on with only one or two terms is bound to fall into the same errors that were committed in the past, *i.e.*, labeling indiscriminately $S_{zn} = 4.3$ atm., $T_n = 5.4$ atm., $S_z = 10.5$ atm., whichever quantity is desired, as "osmotic pressure."

[7] He had no such intention.

Summary

The earlier studies of osmosis in plants led to confusion because a common name was applied to different quantities and because of attempts to measure these quantities by a common method. The creation of methods which permit the determination of the different quantities numerically as well as in concept, constitutes the essential difference between the more recent studies and the older ones. In order to avoid misunderstandings a new terminology became necessary. It embraces the expressions: Suction force (suction tension, suction) of the cell, S_{z_n}; suction force (suction tension, suction) gradient; suction force (suction tension, suction) of the contents of the cell, S_{i_n}; suction force (suction tension, suction) at incipient plasmolysis $S_{z_g} = S_{i_g}$; osmotic value, O_n; osmotic value at incipient plasmolysis = incipient plasmolysis value, O_g; wall pressure, W_n; turgor pressure, T_n; and the turgor distention produced by the turgor pressure. The terms are, as they should be, unequivocal, simple, and easy to understand. In so far as it was possible, they were linked to the old terminology. The terms suction and pressure were chosen in accord with the indications on the manometer. Wherever the manometer permits both designations, the form that seems best adapted to avoid misunderstandings has been chosen. The prime purpose of terminology is simplicity and the elimination of error. When these ends can be obtained in different ways a certain flexibility in the mode of expression should be tolerated. With me it is a matter of taste whether suction tension or suction be considered synonymous with suction force. Even though it is desirable to use but a single term for a given quantity, it is not absolutely necessary, so long as the essential purpose of terminology is not defeated. For decades the significance of terminology was underestimated, but we need not for all that go to the other extreme.

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