SOME GROSS CORRELATIONS BETWEEN GROWTH ENLARGEMENT AND THE SOLUTE AND WATER RELATIONS OF PLANTS, WITH SPECIAL EMPHASIS ON THE RELATION OF TURGOR PRESSURE TO DISTENTION OF CELLS

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(WITH FOUR FIGURES)

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Introduction

In discussions of the dynamics of the growth process, three main views regarding the mechanism of cell enlargement are held. One suggests “that the cell wall must first be subjected to elastic (reversible) or plastic (irreversible) stretching as a result of a turgor pressure developed by the cell sap” (16). It is assumed that this is then followed by addition of material substance to the wall through intussusception or apposition, or if unaccompanied by the incorporation of new material, by attenuation of the wall accompanying increase in area. A second idea suggests “that active growth of the cell wall,” as a result of “the intercalation of additional molecules between those already present, . . . is the primary step in cell enlargement. Entrance of water into the cell is considered to be a result of the increase in the volume of the cell rather than its cause” (18). A third concept, related in part to each of the former, suggests that the initial step is an increased plasticity of the cell wall, followed by a lowering of the turgor pressure and influx of water, tending to approach a new osmotic equilibrium (compare (12)). These views, and experimental results in support of each, are presented at length in a recent monograph (7). Certain limited experimental data, published earlier (16) for other purposes, would appear to afford evidence greatly favoring the first hypothesis. It is desired to represent these data, with further information, and attempt to show that, under the conditions studied, the distention of roots is primarily the result of turgor pressure developed in the internal phases of cells.

Theoretical aspects of turgor in roots

The system to be discussed, involves the root systems of plants in relation to the soil solution under natural conditions. The discussion is based on the simplified, integrated plant osmometer system as treated earlier, elsewhere (1). The terminology used, however, is in general that most common in the literature (7).
The osmotic equation may be expressed as follows:
\[ \text{DPDD} \ (\text{NDPD}) = (\text{OP}_1 + \text{MP} + \text{nMP}_e) - (\text{OP}_e + \text{HP}'_1 + \text{HP}''_1 + \text{nMP}_1). \]  
(1)

Assuming rapid flux of water across the protoplasmic membrane interposed between the external and internal solution phases, i.e., assuming approach toward osmotic equilibrium, then \( \text{DPDD} = 0. \)

Under the conditions of the present experimentation any \( \text{nMP}_e \) is unknown \textit{per se}, but is included, at least in part, in \( \Delta \ T_f \) of soil as measured.²

Further, \( \text{nMP}_1 \) probably is insignificant in value in the internal phase, since as is assumed here, the internal lumina are probably relatively free of colloidal inclusions. In any event, its value is included, at least in part, in \( \Delta \ T_f \) of sap as measured. Again, since an extrinsic hydrostatic pressure, related to intercellular pressure or tension, or transpiration, is ineffective in the integrated osmotic system here (see footnote 1), then \( \text{HP}'_1 = \text{TP}_1. \)

Finally, the curves of Figure 1, especially assuming linearity at their upper \( \text{OP}_e \) limits, do not suggest the participation of a metabolic pressure in the water relations of this system. Therefore, \( \text{MP} \) is zero or insignificant. We have for the present discussion then, that

\[ \text{TP}_1 = (\text{OP}_1 - \text{OP}_e). \]  
(2)

The total work expended by the system with time, in the process of expansion is given by the expression

\[ W = \int_{V_a}^{V_b} P \, dV, \]  
(3)
in which \( W \) is the work expended with change in volume \( dV \) in going from Volume \( V_a \) to volume \( V_b \), and \( P \) is the internal pressure (here the turgor

² Symbols and their designation for osmotic quantities of the simplified, integrated osmotic system:

\( \text{DPDD} \) or \( \text{NDPD} \) = the diffusion pressure deficit difference or net diffusion pressure deficit.
\( \text{OP}_e \) = the osmotic pressure of the external bathing medium.
\( \text{OP}_1 \) = the osmotic pressure of the internal medium.
\( \text{MP} \) = a possible metabolic pressure.
\( \text{nMP}_e \) = a nonmetabolic pressure in the external phase, for example an imbibitional tension (negative then, in value). See (1).
\( \text{nMP}_1 \) = a non-metabolic pressure in the internal phase, for example an imbibitional tension (negative then, in value). See (1).
\( \text{TP}_1 \) = the turgor pressure within the internal system of any osmotic system, equal to a resultant internal hydrostatic pressure (\( \text{HP}_1 \)), where \( \text{TP}_1 = \text{HP}_1 = \text{HP}'_1 + \text{HP}''_1 \) (1).

TP₁, here, is used in the usual sense (3).

\( \text{HP}'_1 \) = the intrinsic hydrostatic pressure in the internal phase (1).
\( \text{HP}''_1 \) = an extrinsic hydrostatic pressure in the internal phase, related, for example, to an intercellular pressure of tension, or tension or pressure arising through transpiration, etc. (1).

² Limited information is available (9, pp. 191-192) concerning the influence in solutions of the presence of inert materials possessing large specific surface, on freezing point depressions and concentrations of solute computed therefrom.

* See errata.

\( \text{P}, \ \text{V} \).
or hydrostatic pressure). At any time $t$, the work of expansion is given by

$$W = P \Delta V,$$

and will depend in part on the immediate plasticity or elasticity of the limiting surface.

In the above analysis, it was assumed for simplicity of discussion, that approach toward water equilibrium throughout the system was readily attainable. It should be recognized however, that often in nature this is not the case. On the contrary, frequently the rate of water flux is limited by the differential permeability of the protoplasmic membrane (11) or other causes. Then, of course, equation 2 is incomplete. The current discussion is based upon the proposition that this equation approximately holds.

**Experimental technique and observations**

Early methods for measuring the "concentration" of the cell sap of plants included the plasmolytic and the cryoscopic methods. It has been shown (8) that certain errors, inherent in the plasmolytic method may lead to aberrant results in osmotic pressure measurements. Under some circumstances, data obtained through the freezing point procedure may also lead to false inferences. In the latter case, the error appears to lie in the pretreatment of the material (5). If the plant tissue is pretreated by freezing at low temperatures followed by expression of the composite sap, comparable data at least, may be consistently obtained.

It has been pointed out earlier (15) that the osmotic pressure of plant tissue fluids, both from shoots and roots, varies markedly with the time of harvest during the day. This is primarily related to the differential production of organic products of photosynthesis and is modified between tissues by translocation. Another factor which is involved is related to the differential rate of transpiration from the shoots.

The data to be discussed herein were, as far as possible, without objection from the variables referred to. Corn plants were allowed to grow in a silty loam soil in 3-gallon jars. The total soil moisture was maintained throughout the experiment. The concentration of the soil solution was varied by the addition of soluble salts. The same amount of water was added to each jar, and maintained by means of an inverted funnel that extended to six inches from the bottom of the container and a glass tube that penetrated a wax seal at the soil surface. The soil solution was augmented by the addition of different amounts of a solution consisting of a Shive 3-salt mixture viz., calcium nitrate, magnesium sulphate and potassium phosphate. The plants were placed into a dark chamber for one day preceding experimental study. This treatment minimized the effect of organic solutes in the tissues as well as the transpiration factor. The roots were carefully separated from the soil mass and washed with distilled water. This treatment, though brief in order not to modify
significantly the osmotic pressure value of the roots, tended to further minimize the transpirational factor therein. These conditions, therefore, yielded root material with which equation 2 would probably hold fairly closely. The roots were frozen in closed containers, followed by thawing and expression of composite sap at a pressure of 300 kg. per square centimeter. Freezing point depression measurements were made on this expressed sap as well as on the relatively undisturbed soil mass. The data obtained are shown in table I. From the observed data, osmotic pressures have been calculated and other values computed as indicated elsewhere.

![Graph](#)  
**Fig. 1.** Relationships between the osmotic pressures of internal and external media of roots.
The osmotic pressure relations between root sap and soil solution are shown in figure 1. Several conditions may be observed. Curve I represents the relative osmotic pressures of the internal and external media of the root osmometer system. It may be seen, that over a wide range of external osmotic pressure values the internal osmotic pressure exceeds that of the bathing medium. A high external osmotic pressure value is reached at which it approaches in magnitude the osmotic pressure of the expressed sap. Curve II represents, in a general way, the varying accumulation of solute in the sap relative to the external medium. It may be seen that the osmotic pressure ratio decreases with increase of the external osmotic pressure, from a very high value, and approaches unity as a lower limit. The partial molal free energy expenditure for accumulation is approximately proportional to the logarithm of this ratio (see later discussion relative to data of figure 2). Curve III represents the varying difference in osmotic pressure between the two media of the root osmometer system with changes in the external osmotic pressure. It may be seen that a complicated curvilinear relationship is obtained. Three portions of this curve may be distinguished. Where the external osmotic pressure is moderate, the osmotic pressure difference between the two media reaches a maximum which may extend over some range, relative to the bathing solution. Where the external osmotic pressure is low, the osmotic pressure difference decreases with decreasing osmotic pressure of the external medium. Where the external osmotic pressure is relatively high, the osmotic pressure difference again decreases, but with a corresponding increase in the osmotic pressure of the external medium. This latter portion of the curve appears to be nearly linear in shape. (Compare discussion of Curve I.) The curve approaches the x axis at an external osmotic pressure value corresponding to where the internal osmotic pressure equals that externally (Curve I) and where the osmotic pressure ratio approaches unity (Curve II).

In the foregoing presentation of experimental data, the relationship between the relative osmotic pressures corresponding to the internal and external media has been stressed. Another phase of plant activity must be discussed which primarily bears on the internal osmotic pressure level attainable under any particular set of circumstances. Assuming that the solutes primarily concerned within the root for osmotic purposes are of inorganic nature, obviously the overall concentrations of these are important. Under the conditions discussed, internal concentrations are higher than external concentrations, throughout. From earlier work (2) it is clear that diffusion of solutes is not primarily concerned in the net accumulation of inorganic solute required. Although various modes of influx are involved, the primary means of influx is related to the net inward movement associated with metabolic energy expenditures. From the internal and external osmotic pressure values, an approximation of the
corresponding salt concentrations can be calculated and from these, the energy expenditure, per mole of salt accumulated, on the part of the plant roots.

Computation of the energy requirement per mole of inorganic solute accumulated, at any particular set of relative values of the internal and external media, has been made in the following manner (2). The concentrations of the two solution phases have been calculated from

$$ \text{OP} = i \text{ CRT}, \quad (5) $$

in which $i$ is the van't Hoff coefficient, $C$ is the solute concentration in moles per liter (which may be corrected to molalities from density infor-
mation), $R$ is the appropriate gas law constant, and $T$ is the absolute temperature (here, $25^\circ C$ is used as the reference temperature). From these concentrations (or better, activities—obtained by correction), the partial molal free energy requirements can be calculated from

$$\Delta f = RT \ln \frac{a_i}{a_e} \quad (6)$$

in which, $\Delta f$ is the partial molal free energy required, $a_i$ and $a_e$ are the activities of the solute species in the internal and external phases respectively, and other factors as before. Obviously these computations are approximations, but serve a real purpose in linking the factors involved. The computed values are recorded in table I.

**TABLE I**

<table>
<thead>
<tr>
<th>RELATIONS OF THE OSMOTIC QUANTITIES OF A ROOT OSMOMETER SYSTEM AND THE ENERGIES REQUIRED FOR ELECTROLYTE ACCUMULATIONS</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>SOIL</strong></td>
</tr>
<tr>
<td>$\Delta T_s$</td>
</tr>
<tr>
<td>--------------</td>
</tr>
<tr>
<td>0.10</td>
</tr>
<tr>
<td>0.25</td>
</tr>
<tr>
<td>0.50</td>
</tr>
<tr>
<td>1.00</td>
</tr>
</tbody>
</table>

(Computed) *

| 0.101†       | 0.381†     | 1.21         | 4.59| 3.8    | 3.38 | 0.025  | 0.094| 3.90 | 0.591 | 807  |
| 0.165        | 0.455      | 1.99         | 2.48| 2.75   | 3.49 | 0.047  | 0.112| 27.6 | 0.439 | 559  |
| 0.281        | 0.549      | 3.38         | 6.61| 1.96   | 3.23 | 0.069  | 0.135| 1.96 | 0.291 | 397  |
| 0.412        | 0.624      | 4.96         | 7.31| 1.51   | 2.55 | 0.102  | 0.153| 1.50 | 0.176 | 240  |
| 0.600        | 0.860      | 7.22         | 8.19| 1.13   | 0.97 | 0.147  | 0.167| 1.14 | 0.054 | 74   |

(Computed) *

| 8.60         | 8.80       | 1.0          | 0.00| 0.175  | 0.175| 1.00   | 0.000| 0 |

* Values computed from extrapolations of curve I, figure 1.
† Data of McCool and Millar (15).

The partial molal energy expenditure requirements are plotted in figure 2. The energy quantities are related here to both the varying external osmotic pressure as well as the concentration for reference in discussion. It may be observed, that at low values of external osmotic pressure or concentration a very high energy per mole of salt influx is required, decreasing rapidly with increase of the external values of concentration. At high external osmotic pressures or concentrations, little energy expenditure is required per mole of salt accumulated, approaching zero where the relative concentrations of the solutions in the two phases approach each other. Energy here may be expended through a salt respiration, but thermodynamically little to no energy is required except possibly in main-
tenance of the relative solute levels in the dynamic efflux and reinflux of salt at an established steady state for specific ion species characteristic-
ally associated with the plant type.

The effectiveness of root respiration for solute accumulation has been pointed out elsewhere (17). In figure 3, the approximate relationship between the rates of accumulation of salt and respiration in cells are plotted against the varying concentration of the external medium. Curve I shows that the solute accumulation rate increases with increase of the concentration of the external medium approaching a limiting maximum rate at from 20-40 millimoles per liter of external salt, for storage tissues of carrot. The maximum was attained with barley roots at somewhat lower levels (10). Curve II, where the solute accumulation per unit respiration increase is plotted against the concentration of the external medium, shows a trend similar in form to that of curve I and nearly congruent. The important suggestion which emerges is that the efficiency of the respiratory energy supply for accumulation, approaches a maximum level at about 20-40 millimoles per liter of external salt supply. This is more
evident when plotted as a percentage efficiency (see curve II when expressed in terms of per cent. efficiency on the right hand ordinate based on the thesis of electron transfer in accumulation of solute through an associated oxidation-reduction process (17)). It should be particularly observed, that the accumulation efficiency of salt respiration decreases rapidly from this maximum as the concentration of the external solution decreases.

One further line of experimental evidence may be referred to at this point. From the nature of the turgor pressure curve (curve III, fig. 1), a relationship would be expected especially between variation in root yield and variation in osmotic pressure of the external solution. It has been shown earlier, in studies of plant yield under saline conditions, that over a fairly wide range of external solute concentrations, there is a linear negative correlation between the relative growth of the plant and the salt level bathing the roots. This is exemplified by figure 4. Like observations have been obtained for diverse types of crops (13, 14), other conditions being similar. The only variation from that shown in this graph is that "Salt-tolerant crops have a slightly sloping regression line, whereas salt-sensitive crops have a steeply sloping one" (13). The similarity of this line (fig. 4) with that of the osmotic pressure difference between the in-
ternal and external media in figure 1, particularly where higher external solution concentrations are concerned, should be noted. Compare beet yields in figure 2 (14) and discussion thereof on page 155, therein.

Discussion

The various lines of experimental data would appear to point toward certain gross correlations between growth and the solute and water relations of plants. An important sequence of processes seems to be involved at any particular time, especially during the grand period of growth. The first step seems to be concerned with the presence of an increased respiration (oxidative metabolism) of roots where bathed by salt media. Inorganic solute is accumulated in accord with regulatory influences associated with the process of salt influx for the particular plant species (4). The rate of influx is determined by the differential permeability of the protoplasm to the solute as accumulated, the concentration of the solution (modified in part by the quality of the ionic supply) bathing the roots, the efficiency of the energy supply, and the energy requirement at any particular ratio of inorganic solute concentration (or better activity) between the internal and external phases. Governed by the particular inorganic solute difference between the two media at any time t, water moves into (or out of) the system by osmosis. The rate and extent are primarily concerned with this difference. Where and when extrinsic factors (transpiration, imbibition by soil, etc.) are not dominant in their influence, this solute concentration difference in large measure determines the turgor pressure in the internal phase. Turgor distention of cells on water entry leads to over-all enlargement of the organ with further surface exposure to the bathing medium. Attended by favorable cell division and differentiation, the growth of roots, and possibly less directly of shoots, is thus determined.

"In other words, enlargement of plant tissues—growth—is a direct function of turgescence which in turn is partially conditioned upon the force with which water is withheld from the plant. It has been observed . . . that there is a fairly close relationship between vegetative growth and the average moisture stress, if other factors affecting growth are not limiting and are kept as uniform as possible" (18).

Although several factors enter into the sequence of growth, it would appear that turgor pressure holds a key position therein. (Compare especially curve III, figure 1 with figures 2, 3 and 4). Thus, where turgor pressure (see equation 2) approaches zero, distention of roots should not continue. At low turgor pressures, growth is restricted. Thus, on the one hand the distention may be limited at too low an external solute concentration where permeability and effective energy supply are adverse. Again, the enlargement may be restricted at too high an external solute concentration due to a limited attainable osmotic pressure difference, even though the efficiency of the energy supply for solute accumulation may be
more favorable. There appears to be an optimum, intermediate range of external solute concentrations where all factors operate in mutual accord toward a maximal turgor pressure within cells, and maximal growth.

One of the most intensive and extensive studies on growth has been carried forward with sugar cane in Hawaii. Here, plant enlargement has been particularly related to the water regime applied to the crop (6). It would seem that here as well, the prime factor concerned is the turgor pressure maintenance during development.

Although the discussion herein has revolved around the root and its environment, this relationship of turgor to growth enlargement is probably extendable to include the shoot and fruiting bodies (compare earlier quotations from (18)). Here however, other factors may be of more importance relative to turgor pressure, or circumstances may be such that less favorable correlations may be observed with other organs. However, the growth data obtained under various conditions of salinity around roots suggest that the enlargement of the plant as a whole is related to turgor pressure in a large degree.

It should be recognized, that there may be times in the production of crops when maximum enlargement growth is not desirable for one reason or another (cf. (6)). This for example might be the case during the late fall with winter cereals or in later stages of the development of crops where maturation of the fruiting bodies or storage organs requires relatively less enlargement in favor of the storing up of compounds of commercial and/or nutritional value.

One should not infer that other factors than turgor pressure do not directly or indirectly come into play to modify growth enlargement. Limitation in the supply of any growth factor will certainly, and often critically, restrict the development of plants in accordance with Mitscherlich's law. Certain compounds supplied from without or produced within plants may prove noxious to growth. On the other hand, growth hormone studies indicate that compounds may be formed within plants which at favorable concentrations may allow more optimal growth enlargement. Also, it has been shown that water deficits may modify other process rates, e.g., photosynthesis and respiration (11).

The main thesis of this discussion is clear: "It would appear that the furnish an ample supply (rather, should afford conditions for maximum relative accumulation) of nutrients, yet have such a low osmotic value that water absorption is not markedly reduced." (other conditions being favorable). The particular values in any of the curves, their shapes etc., are probably subject to variation depending upon the species of plant and environmental conditions. Experimentation now in progress should yield important information on variations from the general trends herein.

3 Parentheses here are author's inserts in quotation from (14) page 163.

See errata, p. vi.
described. It may be suggested, that it can be envisioned that as physiologists now diagnose deficiency incipience for inorganic elements by foliar analysis, so a progressive analysis of the freezing point depressions of soils and the root saps of crops could yield information in large scale plantings which could afford important information on the future regime of watersolute supply for optimal crop production.4

Conclusions
An analysis of the sequence of factors concerned in the growth enlargement of cells is presented. It is inferred from the data presented, that turgor pressure or attendant conditions within cells is the primary factor concerned with their distention or growth enlargement in association with the laying down of new cells through division and differentiation. Even the latter may be modified by the former. In that a maximal turgor pressure is desirable under most circumstances, the inorganic solute ratios and total concentrations in the external medium relative to that in the plant are an immediate concern of the physiologist. It is suggested that progressive information on the turgor pressure within roots as a crop is developing, may be of diagnostic value to the agriculturalist in order to obtain maximum yield of crops.

LITERATURE CITED

4 Similar information may be possible by measurements with soil tensiometers after correlation of tensiometric data with information of the present sort.


