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An Analysis of Irreversible Plant Cell Elongation

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A model for plant cell elongation has been developed from rate equations for osmotic uptake of water and irreversible expansion of the cell wall. Assuming elastic equilibrium and a linear viscoelastic wall, cell elongation rate is derived as a function of osmotic pressure, "extensibility" of the wall, water permeability and cell size. The derived formulations predict growth curves comparable to those observed experimentally. Certain consequences of the derived formulations are discussed. It is shown that the turgor pressure of a growing cell will always be less than the water potential of the cell. This difference may be infinitesimal or finite, depending on the values of the physical parameters of the cell. It is also shown that at positive turgor pressures water must always move from a mature cell to a growing cell.

In the past few years a number of analytical studies have been made of plant cellular water relations (e.g. Broyer, 1952; Philip, 1958; Ray, 1960). These studies have all been based on the cell model developed by Ursprung & Blum (1924). They have served to clarify some of the quantitative relationships existing in elastic cell expansion. However, these discussions have been confined to the equilibration of the cell with water (and solutes). Irreversible increases in cell volume, the process responsible for plant cell growth, have been excluded from their studies. In spite of a number of discussions and analyses following the definitive work by Heyn (1931, 1940), the interpretation of cell elongation in relation to cell wall extensibility and osmotic pressure is less clear (Burström, 1948, 1961; Haines, 1952; Levitt, 1951; Meyer, 1956). The present paper develops an expression for rate of cell elongation as a function of the physical parameters which may be expected to influence cell expansion.

For the present discussion the cell will be assumed to be a cylinder with a constant radius. This is realistic for cells of many plant organs. Isothermal conditions are assumed at all times.

Some of the principal terms to be used here are defined as follows:

M (atm). The difference in the water potential (partial molar free energy of water) of the cell contents and pure water at atmospheric pressure. The negative of this value is often referred to in the plant physiological literature as the "diffusion pressure deficit" (DPD) or "suction force". We shall use Dainty's definitions and terminology (1963), where $M = \Delta\mu_w/\bar{V}_w$, the water potential of the cell, assumed to be equal to the difference between the osmotic pressure and the hydrostatic pressure of the cell contents, $(P-\Pi)$.

Π (atm). The concentration of osmotically active solutes within the cell, taken to be equal to the hydrostatic pressure which must be exerted on an osmometer containing the same solution to maintain flux equilibrium with pure water at atmospheric pressure (Moore, 1955).

Π_e (atm). The osmotic pressure of the solution in which a cell is immersed, equal to 0 for pure water at atmospheric pressure.

$\Delta\Pi$ (atm). $\Pi-\Pi_e$.

P (atm). The hydrostatic pressure of the cell contents in excess of atmospheric pressure, the turgor pressure.

K_w (cm.atm^{-1}.hr^{-1}). The water permeability of the cell membrane per unit surface area.

Φ (cm.cm^{-1}.atm^{-1}.hr^{-1}). A property of the cell wall expressing its rate of irreversible flow under stress as change in length per unit length, referred to here as extensibility.

ϕ (cm.cm^{-2}.atm^{-1}.hr^{-1}). $\phi = \Phi/2\delta$, where δ is the cell wall thickness. This is a different form of extensibility which will be used to simplify later equations. This quantity depends on wall thickness as well as the physical properties of the wall.

F (atm.cm^2). The force on the end walls of the cell, assumed to be the force responsible for tensile stress, equal to the turgor pressure times the cross-sectional area of the cell.

Elastic and Irreversible Cell Expansion

In general, elongation of a cylindrical plant cell or tissue can be expressed as the sum of the change in length due to irreversible extension and the change in length due to elastic stretching. If l is the observed length and s is the length under 0-force, e.g. at incipient plasmolysis, then

$$\mathrm{d}l = \mathrm{d}s + \mathrm{d}(l-s). \tag{1}$$

From Hooke's law

$$\frac{l-s}{s} = \frac{F/\alpha}{E} \tag{2}$$

where E is Hooke's modulus, α is the cross-sectional area of the cell wall, and F is the applied tensile force.

Differentiation of this expression gives:

$$\mathrm{d}(l-s) = \frac{I}{E}\left[(F/\alpha)\,\mathrm{d}s + s\mathrm{d}(F/\alpha)\right]. \tag{3}$$

Substituting into the first equation and differentiating with respect to time, at a constant force, gives:

$$\frac{\mathrm{d}l}{\mathrm{d}t} = \left[\frac{F/\alpha}{E} + I\right]\frac{\mathrm{d}s}{\mathrm{d}t} = \frac{l}{s}\frac{\mathrm{d}s}{\mathrm{d}t}. \tag{4}$$

Evidently when $\mathrm{d}F = 0$, (e.g. at elastic equilibrium), $(I/l)\,\mathrm{d}l/\mathrm{d}t = (I/s)\,\mathrm{d}s/\mathrm{d}t$. Furthermore, $\mathrm{d}F = 0$ whenever $\mathrm{d}(M) = 0$; thus all that is required for this relationship to hold is a constant elongation rate. The relationship $(I/l)\,\mathrm{d}l/\mathrm{d}t = (I/s)\,\mathrm{d}s/\mathrm{d}t$ will be assumed to hold throughout the present discussion. Further justification for this assumption is given below. Since for real plant cells elastic equilibrium occurs on a time scale of minutes while the time scale of irreversible extension is of the order of hours, even substantial deviations from elastic equilibrium will be transient and have little effect on irreversible elongation over moderately long time periods.

Irreversible Cell Elongation

For simplicity, the cell will be assumed to be a cylinder of such dimensions that the area of the end wall is insignificant compared to the area of the side walls. It will further be assumed that we are dealing with a cylindrical cell growing only in length (r is constant). Thus, increase in length is related to increase in volume by $\mathrm{d}V/\mathrm{d}t = \pi r^2.\mathrm{d}l/\mathrm{d}t$. For cell elongation to occur, water must enter the cell. The expression for increase in length in terms of rate of water entry for a simple osmometer is given by

$$\frac{\mathrm{d}l}{\mathrm{d}t} = \frac{K_w A}{\pi r^2}(\Delta\Pi - P) \quad \text{or} \quad \frac{I}{l}\frac{\mathrm{d}l}{\mathrm{d}t} = \frac{2K_w}{r}(\Delta\Pi - P) \tag{5}$$

where the area (A) is taken to be the area of the side walls, i.e. $2\pi rl$.

Irreversible elongation of a plant cell also requires an increase in the length of the cell wall. It is now generally believed that irreversible elongation of the cell wall is the result of the turgor pressure exerted on the wall (Burström, 1961). In order to develop a simple model it will be assumed that rate of irreversible strain is a linear function of turgor pressure, i.e. that the cell wall behaves as a linear viscoelastic element. On this assumption, the rate of irreversible cell wall extension will be given by

$$\frac{I}{s}\frac{\mathrm{d}s}{\mathrm{d}t} = \frac{F}{\alpha}\Phi \tag{6}$$

where Φ is the extensibility of the cell wall as defined earlier. It will be assumed that cell wall thickness remains constant throughout growth. This assumption generally has been experimentally verified (Burström, 1961).

The total tensile force exerted on the cell wall in the direction of the long axis of the cylinder is given by pressure times area, where the pressure is the turgor pressure of the cell and area is the area of the end wall of the cell. This may be expressed as

$$\frac{I}{s}\frac{\mathrm{d}s}{\mathrm{d}t} = \frac{\pi r^2}{2\delta\pi r} P\Phi = \frac{r}{2\delta} P\Phi. \tag{7}$$

The turgor pressure, then, can be expressed as a function of irreversible elongation rate and the extensibility of the wall, giving

$$P = \frac{I}{l}\frac{\mathrm{d}l}{\mathrm{d}t} \cdot \frac{2\delta}{r\Phi}. \tag{8}$$

Substituting this value into equation (5) and solving for elongation rate gives

$$\frac{I}{l}\frac{\mathrm{d}l}{\mathrm{d}t} = \frac{2rK_w\Delta\Pi\Phi}{4\delta K_w + r^2\Phi}. \tag{9}$$

To simplify subsequent equations, extensibility can be written in the form $\Phi/2\delta = \phi$. The basic formulation for cell elongation, then, will be given by

$$\frac{I}{l}\frac{\mathrm{d}l}{\mathrm{d}t} = \frac{2K_w r\Delta\Pi\phi}{2K_w + r^2\phi}. \tag{10}$$

A physical picture of the irreversible elongation of this model is straightforward. Following the rapid uptake of water to attain elastic equilibrium, the turgor pressure approaches the value of $\Delta\Pi$. This high turgor pressure results in stress on the cell wall which will yield as a result of this stress. This will tend to reduce the turgor pressure, resulting in a decrease in the water potential of the cell. Water will move into the cell in response to this potential gradient, and the wall again yields. Since the two processes occur simultaneously there will be no finite change, of course. When water permeability is high and the yield function has a moderate value, the turgor pressure and water potential gradient will differ only infinitesimally from equality. In terms of the equations above, turgor pressure (P) is a dependent variable, a function of osmotic pressure ($\Delta\Pi$), water permeability (K_w), and extensibility (ϕ).

Water potential. The water potential of a cell is given by $M = P - \Delta\Pi$. An expression for P as a function of the physical parameters can be obtained from equations (5) and (7). This gives

$$P = \frac{2K_w\Delta\Pi}{2K_w + r^2\phi}. \tag{11}$$

Water potential, then, is given by

$$M = -\Delta\Pi\left(\frac{r^2\phi}{2K_w+r^2\phi}\right). \tag{12}$$

Thus, the net water potential of an irreversibly expanding cell is a linear function of $\Delta\Pi$ and is a function of ϕ and K_w as well. The dimensionless quantity $r^2\phi/(2K_w+r^2\phi)$ can be denoted as γ where $0 \leq \gamma \leq I$, giving $M = -\Delta\Pi\gamma$. Evidently, M can take on values between $-\Delta\Pi$ and 0, depending on the relative values of ϕ and K_w. If γ is substituted into equation (10), elongation rate (equivalent to the water flux) will be given by $(I/l)\,\mathrm{d}l/\mathrm{d}t = (2K_w/r)\Delta\Pi\gamma$. The water flux is the product of the water conductivity of the cell membrane $(2K_w/r)$ and the water potential difference $(\Delta\Pi\gamma)$, i.e. force/resistance, the normal phenomenological relationship.

So long as water permeability is reasonably large, M will be small relative to $\Delta\Pi$ and P; but M is zero only when $\Delta\Pi$ or γ are equal to zero, i.e. when no irreversible elongation occurs. Apparently for a rapidly growing tissue, a measurable water potential may exist. Burström (1942) reported a decrease in turgor pressure during rapid growth. However, if growth is slow the gradient will almost certainly be infinitesimal. Bennett-Clark (1956) and Ray & Ruesink (1963) have reported measurable water potential gradients but these were measured during equilibration to a changed osmotic medium.

Yield stress. It may be that irreversible extension is not a linear function of turgor pressure. Specifically, turgor pressure may have to exceed a certain minimum value (the yield stress) before irreversible expansion occurs (i.e. the cell wall may behave as a Bingham solid). If wall extension is given by $(I/s)\,\mathrm{d}s/\mathrm{d}t = r\Phi(P-P_E)$, where P_E is yield stress, it can be shown that growth rate is given by

$$\frac{I}{l}\frac{\mathrm{d}l}{\mathrm{d}t} = \frac{2K_w r\phi(\Delta\Pi-P_E)}{2K_w+r^2\phi}. \tag{13}$$

Thus, if a yield stress does exist, no great complexity is added to the formulations. This still assumes that extension is a linear function of force at forces exceeding the yield stress. This assumption is considered further in the Discussion.

Growth at high water permeability. In spite of the fact that the exact function of extensibility with respect to force is not known, the growth formulations above define the relationships of specific physical parameters on cell growth. Evidently elongation rate is a hyperbolic function of both water permeability and extensibility. If water permeability is very large compared to the other parameters, as it may be for individual plant cells, growth rate will be determined approximately by

$$\lim_{K_w\to\infty}\frac{I}{l}\frac{\mathrm{d}l}{\mathrm{d}t} = r\Delta\Pi\phi \tag{14}$$

for limited ranges of $\Delta\Pi$ and ϕ. This is the basic relationship which might exist for elongation of a single cell immersed in an aqueous solution, and it may serve as an approximation for growth of stem sections as a function of osmotic pressure and extensibility.

Integration of the Growth Formulation

It has been assumed above that both $\Delta\Pi$ and ϕ are independent of time. However, growth would continue indefinitely if these parameters were independent of time for real cells. The original rate equation indicates that growth will cease when $K_w r\Delta\Pi\phi = 0$. It is evident that under normal physiological conditions either $\Delta\Pi$ or ϕ will go to zero at cell maturation.

When $\Delta\Pi$ or ϕ are functions of time equation (4) is no longer exactly true. The general solution of equation (3) can be given by:

$$\frac{I}{l}\frac{\mathrm{d}l}{\mathrm{d}t} = \frac{I}{s}\frac{\mathrm{d}s}{\mathrm{d}t} + \frac{s}{l}\frac{r}{2\delta E}\frac{\mathrm{d}P}{\mathrm{d}t} = \frac{I}{s}\frac{\mathrm{d}s}{\mathrm{d}t} + \varepsilon. \tag{15}$$

An approximate solution for ε, based on the assumption that P is given by equation (11), may be written as:

$$\varepsilon = \frac{s}{l}\frac{2K_w r}{E(4\delta K_w + r^2\Phi)}\left[\frac{\mathrm{d}(\Delta\Pi)}{\mathrm{d}t} - \frac{r^2\Delta\Pi}{4\delta K_w + r^2\Phi}\frac{\mathrm{d}\Phi}{\mathrm{d}t}\right]. \tag{16}$$

In order to determine whether ε attains significant values during normal cell elongation, the values of ε may be calculated using typical values for the various parameters taken from the literature. The values chosen are as follows. K_w will be assumed to be 2×10^{-4} cm.hr^{-1}.atm^{-1} (Davson & Danielli, 1952). Cell radius will be assumed to be 10 microns and cell wall thickness, 1 mμ. The initial osmotic pressure will be assumed to be 10 atm. In one case the cell will be assumed to increase in length threefold in 20 hours, and in the other case it will be assumed to increase 20-fold in 50 hours (Burström, 1961; Erickson & Sax, 1956). In addition, the elastic modulus will be assumed to be 5 atm^{-1}.hr^{-1} (i.e. an elongation rate of 10%/hr). Using these values the numerical solution of ε can be given by:

$$\varepsilon = I\times10^{-3}\left[\frac{\mathrm{d}(\Delta\Pi)}{\mathrm{d}t} - 2\frac{\mathrm{d}\Phi}{\mathrm{d}t}\right].$$

Under the conditions specified above the values of both $\mathrm{d}(\Delta\Pi)/\mathrm{d}t$ and $\mathrm{d}\Phi/\mathrm{d}t$ will be less than unity. Since expected values of $(I/s)\,\mathrm{d}s/\mathrm{d}t$ will be of the order of 0·1 hr^{-1}, the value of ε will be insignificant under these conditions. (Iteration, using the calculated value for ε to find a more accurate value for P, is evidently unnecessary for this case.) Thus, the assumption that $(I/l)\,\mathrm{d}l/\mathrm{d}t = (I/s)\,\mathrm{d}s/\mathrm{d}t$ is sufficiently accurate so that the solutions

developed here are fully valid for $\Phi(t)$ and $\Delta\Pi(l)$ for elongating cells and tissues bathed in aqueous solutions.

Case I. $\Delta\Pi$ *and* ϕ *independent of time.* In spite of the fact that the value of extensibility as a function of force is not yet known, it is of interest to investigate in what manner growth is described by the simple formulations developed above. The integral of equation (10), assuming ϕ and $\Delta\Pi$ are constant, is

$$\frac{l}{l_0} = \exp\left[\frac{2K_w r\phi\Delta\Pi}{2K_w + r^2\phi}\right] \tag{17}$$

where l_0 is length at time zero. Thus, for the case where ϕ and $\Delta\Pi$ are constant with time, length increases exponentially with time, i.e. growth rate is proportional to cell length.

Case II, where $\Delta\Pi$ *is a function of cell volume.* Osmotic pressure is probably constant throughout growth in an intact plant (Burström, 1961). Osmotic pressure also may be expected to remain approximately constant when stem sections are cultured in solutions containing sucrose or other sugars (or ions) available to the cell. However, when stem sections are cultured without an external source of osmotically active solutes, the solutes present in the cell generally will be diluted out by the increase in cell volume. In this case $\Pi l = \Pi_0 l_0$ (assuming $\Pi \equiv \Delta\Pi$) and the rate equation, from equation (10) is

$$\frac{\mathrm{d}l}{\mathrm{d}t} = \frac{2K_w r\phi\Pi_0 l_0}{2K_w + r^2\phi}. \tag{18}$$

In this expression all terms are constant with time, giving a growth rate constant with time. While the turgor pressure on the cell wall is constantly decreasing, the yield rate of the wall per unit force applied is increasing with length. This is an interesting example of linear growth in the absence of steady state conditions.

Case III, where ϕ *is a function of time.* In the intact plant and usually in excised sections as well, undoubtedly growth ceases because $\phi(t)$ approaches zero. The simplest expression of $\phi(t)$ as a decreasing function of time, is $\phi(t) = \phi_0 - ct$. (This is clearly an oversimplification, as shown by the data of Erickson & Sax (1956).) Substituting this function of $\phi(t)$ into equation (11) gives

$$\frac{1}{l}\frac{\mathrm{d}l}{\mathrm{d}t} = \frac{2K_w}{r}\Delta\Pi\left[\frac{\phi_0 - ct}{\phi_0 - ct + K}\right] \tag{19}$$

where $K = 2K_w/r^2$. Integration of this expression gives

$$\log\frac{l}{l_0} = \frac{2K_w}{r}\Delta\Pi\left[t + \frac{K}{c}\log\left(\frac{\phi_0 - ct + K}{\phi_0 + K}\right)\right]. \tag{20}$$

Case IV, where $\Delta\Pi$ *is a function of cell length and* ϕ *is a function of time.* An additional case, where osmotic solutes are dilute out with growth and

extensibility decreases with time, can also be evaluated. Growth rate can be shown to equal:

$$\frac{dl}{dt} = \frac{2K_w}{r} \Pi_0 l_0 \left[\frac{\phi_0 - ct}{\phi_0 - ct + K}\right]. \tag{21}$$

Integration gives:

$$\frac{l}{l_0} = \frac{2K_w}{r} \Pi_0 \left[t + \frac{K}{c} \log\left(\frac{\phi_0 - ct + K}{\phi_0 + K}\right)\right]. \tag{22}$$

Predicted growth curves. Assuming that $\phi(t)$ is a linearly decreasing function of time, it is possible to select reasonable values for the various parameters. The shape of the growth curve predicted by these simplified formulations can be determined and compared to available experimental results.

All parameters can be assigned relatively well established experimental values except $\phi(t)$ and the constant c. It is only necessary to assign typical values for final cell length and duration of growth to assign reasonable values to these parameters as well.

Two cases will be solved, one assuming the osmotic pressure remains constant and the other assuming it is diluted out. In each case the final length and the time to reach maturity (i.e. time for $\phi(t)$ to reach zero) are taken from reasonable values for single cells and the shape of the growth curve is determined.

A graph of equation (20) (where $\Delta\Pi$ is constant) is shown in Fig. 1. In

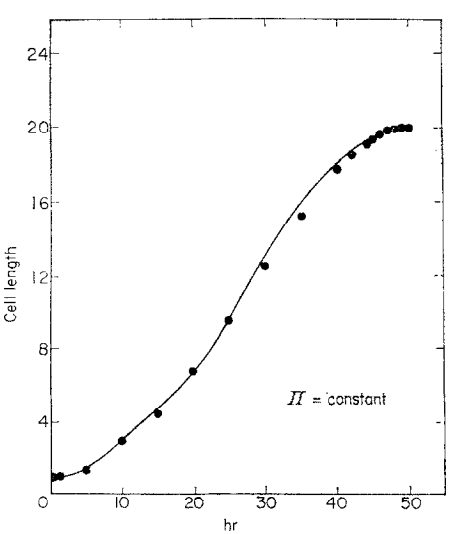

FIG. 1. Predicted growth curve where extensibility decreases lineally with time and osmotic pressure is maintained constant throughout elongation.

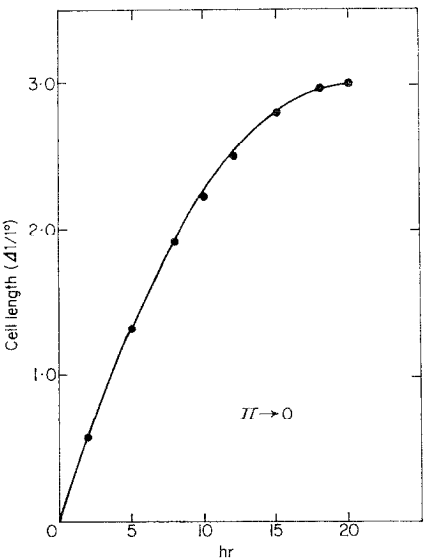

FIG. 2. Predicted growth curve where extensibility decreases lineally with time and osmotic solutes are diluted out with elongation.

this case the values given above were used and growth was assumed to cease after 50 hours with a final length 20 times greater than the original length. Equation (22), using the above values and assuming a threefold increase in length in 20 hours, is plotted in Fig. 2. The general resemblance of these growth curves to normal cell growth is clear. Thus, the model predicts curves which resemble those actually observed.

Discussion

The model described here is based on the following two assumptions: (1) the cell behaves as a simple osmometer; (2) the cell wall behaves as a linear viscoelastic polymer, whose thickness is maintained constant by the continuous deposition of new materials. Ursprung & Blum (1924) demonstrated that a plant cell responds in a manner comparable to a simple osmometer. It is not yet fully established that elongation of the cell wall is a direct function of the applied turgor pressure, as assumed here. Based on a wide range of experimental findings, it has been concluded that it is (Burström, 1961; Ray & Ruesink, 1963); but Preston (1961) has questioned this conclusion. Preston based his opinion to a great extent on the observation that during rapid growth turgor pressure decreases rather than increases. It has been shown here that this result will be a natural consequence of the

proposed physical system and thus represents evidence in support of rather than against the generally accepted mechanism.

Water movement. The formulations which have been developed here will be valid as long as turgor pressure does not change rapidly with time. When the physical parameters of the cell are constant with time and the bathing solution is not modified, this is straightforward.

To integrate growth as a function of time it was assumed that either ϕ or $\Delta\Pi$, or both, may vary with time. This results in a change in turgor pressure with time. The result of calculations using typical experimental cellular values indicate that changes in turgor pressure as a result of maturation of the cell wall or dilution of the osmotic solutes with growth are so slow that they can be completely ignored in most experimental situations. When a gross change is imposed on one of the physical parameters, a period of transition occurs but this may be expected to last only a matter of minutes for tissues such as excised Avena coleoptile sections (Ray & Ruesink, 1963). They also showed that the principal barrier to water movement into Avena coleoptile sections is the epidermis. Thus, the responses of this tissue should be described reasonably well by these formulations.

In an intact plant the water flux through the roots and stem will undoubtedly influence cell elongation. In this case the resistance of the plant to the flow of water from the source of water to the growing tissue will, in general, exert a marked influence on cell elongation. An analysis to include water transport terms is beyond the scope of the present paper.

Nature of irreversible extensibility. In most of the formulations developed here it has been assumed that the cell wall, when part of a growing cell, responds as a linear viscoelastic material. This is a reasonable initial assumption since it has been found by various workers that the irreversible extension rate of plant cell walls is constant with time under constant stress (Heyn, 1940; Tagawa & Bonner, 1957).

It appears unlikely that cell wall extensibility is actually a linear function of force. A yield stress has been demonstrated for isolated cell walls by Probine & Preston (1962), and is suggested for living cells by the work of Cleland (1959). He found that when growth of Avena coleoptile sections was measured against different external osmotic pressures (Π_e), elongation was a linear function of Π_e at low osmotic values for sections not treated with auxin. When auxin was added to the incubation solution, the shape of the growth *versus* Π_e curve changed. This result suggests that auxin may change elongation from a linear function of force to some non-linear function. Further studies of extensibility as a function of force are in progress.

On the basis of elegant temperature coefficient and time-course studies, Ray & Ruesink (1962) have shown that cell wall extensibility probably

cannot be considered to be a simple physical viscous flow process. They conclude that cell wall extensibility corresponds more nearly to "chemical stress relaxation" (Tobolsky, 1960). They discuss the mechanisms which may be involved in such a process. Should this general mechanism be verified, more accurate parameters could be added to the formulations developed here.

An interesting consequence of the formulations developed here is the demonstration that, at elastic equilibrium, the rate of irreversible expansion of plant cells is a direct function of the osmotic pressure of the cell. Thus, cell expansion ceases only when $\Delta\Pi = 0$ if the other parameters have values greater than zero. This conclusion will be true unless there is a yield stress, in which case elongation will cease when $\Delta\Pi = P_E$. Since growing cells have a positive water potential at all times, proportional to the $\Delta\Pi$ of the cell, this might account in part for the general observation that young, growing tissues are particularly resistant to wilting during periods of water stress. Water equilibrium between growing and mature cells (with the same osmotic pressure) should occur only at incipient plasmolysis, as shown above. At any lesser water stress, water will continually move from the mature cells to the growing cells.

One of the major purposes of this paper is to point up our lack of specific knowledge, particularly about the physical nature and characteristics of cell wall extensibility. As the phenomenological relations of cell wall extensibility are understood more completely, functions can be introduced into these formulations to describe cell elongation more precisely.

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