General and Analytic Solutions of the Ortega Equation

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Ortega (1985) proposed a simple first-order differential equation to describe plant cell extension and, unlike the Lockhart equation (Lockhart, 1965), it takes into account elastic deformation of the cell wall. Cosgrove (1985) and Ortega (1985) solved the equation for the particular case of a previously growing plant cell that is deprived of its water source; thus, GR = 0. The results (confirmed by experiments) show that P(t) decreases exponentially to the turgor threshold Y due to the cell wall-loosening process. In this article, their results are extended to the more general case, where water absorption is included; thus, GR ≠ 0. The problem of the growth rate change in the course of time is also considered here. For the large-scale period (days), growth is well described by the sigmoid curve and consists of three phases: acceleration, linear growth with maximal velocity, and cessation of cell elongation (Fogg, 1975; Schopfer and Mohr, 1995). Then, from the mathematical point of view, the growth rate is of the type of \( \sim t^2 \exp(-t^2) \) (a time derivative of the sigmoid curve). This function, however, leads to nonanalytical solutions with no clear interpretations. In this study, the time-dependent growth rate GR(t) is modeled with a mathematical function that approximates the exact function very accurately. Importantly, the new approximate function leads to analytical solutions with new predictions for the behavior of P(t) and valuable interpretations of the parameters within the solutions.

THEORY

The proposed procedure of solving the Ortega equation for a general case is as follows. (1) Water uptake is taken into account (i.e. \( 1/V \ dV/dt \neq 0 \)). (2) Growth rate is given from the experiment. (3) The elastic modulus \( \varepsilon \), as well as the cell wall yielding \( \Phi \), may generally depend on time, thus:

\[
\varepsilon = \varepsilon(t) \text{ and } \Phi = \Phi(t).
\]

For further consideration, we rearrange the original Ortega equation

\[
1 \frac{dV}{V \ dt} = \Phi(P - Y) + \frac{1}{\varepsilon} \frac{dP}{dt}
\]

into the following useful form

\[
\frac{d(P - Y)}{dt} = \varepsilon \cdot GR - \Phi \varepsilon \cdot (P - Y),
\]

where pressure \( P = P(t) \), turgor threshold \( Y \) is constant, and the initial condition of pressure \( P = P_0 \) for \( t_0 = 0 \). (Because the focus of this article is theoretical analysis [through the Ortega equation] of the relationships between growth rate and change in turgor pressure during all three phases of elongation growth, the initial condition stands for the pressure in the beginning of the first phase [where the elongation process starts]. In experiments, the studied seedlings are growing initially in the same experimental conditions. Then, at \( t = t_0 \), segments are cut from the elongation zone of the seedlings and constitute a sample isolated from the water supply, while the remaining seedlings continue growing in the aerated water solution. Of course, one may more generally take \( t_0 > 0 \), i.e. in any elongation phase; still, because we are interested in pressure alteration during the whole elongation process, \( t_0 = 0 \) can be accepted, without loss of generality.)

First, we solve the homogeneous equation (GR = 0, no water uptake)

\[
\frac{d(P - Y)}{dt} = -\Phi \varepsilon \cdot (P - Y)
\]

\[
\downarrow
\]

\[
P - Y = (P_0 - Y) \cdot e^{-\int \Phi \varepsilon \ dt}.
\]

Assuming \( \Phi \) and \( \varepsilon \) are constant, the above formula transforms into the solution originally obtained by Ortega (1985) and Cosgrove (1985):

\[
P = Y + (P_0 - Y) \cdot \exp(-\int \Phi \varepsilon \ dt).
\]

Now, the way of solving the inhomogeneous Equation 2 is standard and based on the constant variation method. This article presents only the final result:

\[
P(t) = Y + (P_0 - Y) \cdot e^{-\int \Phi \varepsilon \ dt} + e^{-\int \Phi \varepsilon \ dt} \int GR(t) \cdot e^\int \Phi \varepsilon \ dt \ dt.
\]

The above general solution of the Ortega equation consists of two terms; the first term describes the exponential decrease of the turgor pressure when the cell is deprived of its water supply, and the second term expresses the additional pressure resulting from the...
presence of the water source. Thus, the left side of Equation 5 represents the pressure of a turgid plant cell.

The general expression, Equation 5, depends on the evolution of the growth rate in time. One may distinguish two time scales of growth (Cosgrove, 2000). The large-scale period covers the whole life cycle of the plant cell: meristematic growth, vacuolization, and, finally, maturation and cessation of growth. Elongation is then well described by the sigmoid curve and fulfills the law of great growth. Here, for data adapted from Kutschera (1985), in this article the growth rate in the function of time. In

\[ P(t) = Y + (P_0 - Y)e^{-\Phi e t} + \frac{ea}{r} e^{\Phi e t} W(t) - \frac{24}{r} e^{-\Phi e t} \]  \hspace{1em} (6)

For \( r = 0 \), in turn, integration is easy: \( I = \int GR(t)e^{\Phi e t}dt = \int at^b dt = a/5 t^5 \) (the integration constant is equal to zero because of the initial condition). Therefore, the final equation follows:

\[ P(t) = Y + (P_0 - Y)e^{-\Phi e t} + \frac{ea}{5} t^5. \]  \hspace{1em} (7)

Now, the comparison of these expressions (Eqs. 6 and 7) gives some general correctness or, in other words, classes of the solutions and yields some interpretation of the parameter \( r \). One may check that the sign of \( r \), together with the magnitude of \( a \), divides the set of solutions of the Ortega equation into two classes. It is obvious that, from the general formula 5, the evolution of the turgor pressure in time \( P(t) \) depends on the growth rate. Accepting the growth rate in the form of \( GR(t) = at^b \exp(-bt) \), which is described by two independent parameters, \( a \) and \( b \), one may conclude that the solutions should also be classified by these parameters. In fact, the calculations prove that there are two classes described by \( a \) and \( r = \Phi e - b \). (To perform them, it is sufficient to calculate and compare time derivatives of the third terms [the additional pressures] in Eqs. 6 and 7.)

Let \( P_1(t) \), \( P_2(t) \), and \( P_3(t) \) be the solutions of the Ortega equation for which \( r_1 < 0 \), \( r_2 = 0 \), and \( r_3 > 0 \), respectively; above is equivalent to \( b_1 > \Phi e \), \( b_2 = \Phi e \), and \( b_3 < \Phi e \). Undoubtedly, \( b_1 > b_2 > b_3 \). (We assume \( \Phi e \) have the same values for all functions, \( P_1, P_2, \) and \( P_3 \).) If \( a_1 < a_2 = a_3 \), then \( GR_1/GR_2 = a_1/a_2 \exp[(b_1 - b_3)t] \) is decreasing and \( GR_2/GR_3 = a_2/a_3 \exp[(b_2 - b_3)t] \) is increasing for every \( t > 0 \) (thus, \( GR_1 < GR_2 < GR_3 \); see Fig. 2A). Moreover, the final volume (i.e. the volume after completing the elongation process, mathematically defined as a limiting value of the volume when \( t \) tends to infinity), will also satisfy the relations \( V_1^t < V_2^t < V_3^t \), where \( V_1 \) is the initial volume and \( V^t \) is the final volume. Such character of variability of the growth rate affects, through Equations 6 and 7, the form of the pressure \( P(t) \). One can check that the pressures \( P_1, P_2, \) and \( P_3 \) fulfill the relations \( P_1(t) < P_2(t) < P_3(t) \) at every instant \( t > 0 \). What follows from the above calculations is that the negative \( r \) results in the turgor pressure lower than the pressure for \( r = 0 \), which, in turn, is lower than the pressure for the positive \( r \). The functions \( P_1, P_2 \), and \( P_3 \) for which \( r_1 < 0 \), \( r_2 = 0 \), and \( r_3 > 0 \), and \( a_1 < a_2 < a_3 \), represent one class of the solutions of the Ortega equation and are shown in Figure 2B.
the plant cell volume for which the growth rates $GR_1$, $GR_2$, and $GR_3$ satisfy the conditions $a_1 \leq a_2 \leq a_3$ (A) and $a_1 > a_2 > a_3$ (C). Plots on the right side (B and D) represent the theoretically predicted changes in pressure over time, $P(t) = P_{GR_1} + P_{GR_2} + P_{GR_3}$, corresponding to these functions (according to Eq. 5, solutions of the Ortega equation depend on $GR(t)$). Thus, B corresponds to A and D corresponds to C. In all plots, solid lines represent the volume or pressure for which $r = 0$, dashed lines $r < 0$, and dotted lines $r > 0$. Thin solid lines in B and D visualize the exponential decrease of pressure when $GR = 0$.

For the case of a large-scale growth period, the growth rate versus time may be approximated by the function $a t^4 \exp(-bt)$ with two parameters strictly related to the quantities measured in experiments: the maximal growth rate $GR_m$ and the time $t_m$ at which the maximal growth rate takes place: $b = 4/t_m$ and $a=GR_m e^{4/3t_m}$, where $e$ is the Euler number, $e \approx 2.78$. In fact, from the experimental viewpoint, the function $a t^4 \exp(-bt)$ could also be rewritten in the form including both the empirical quantities:

$$GR(t) = GR_m \left( e^{4/t_m} \right) \exp \left( -\frac{4t}{t_m} \right). \tag{8}$$

The proposed function fits well to the experimental data (see Fig. 1) and leads to analytical solutions as well. Then, Equation 5 transforms to Equation 6 or 7. This approach also provides the new parameter $r$, which reflects the relationship between growth and irreversible/reversible properties of the cell wall via the simple mathematical expression $r = \Phi e - b$. The irreversible/reversible properties of the cell wall are represented by the cell wall yielding coefficient $\Phi$ (plastic deformation) and Young’s elastic modulus $c$, respectively. The parameter $b$, in turn, is related to the quantities $GR_m$ and $t_m$, thereby to the width and the height of the considered curve. Because both quantities $GR_m$ and $t_m$ depend on $b$, one may conclude that this parameter determines the strength of growth. Interpretation of $r$ is therefore as follows: its value (equal, less than, or greater than zero) reflects the coupling between the growth process and mechanical properties of the cell wall; for $r \neq 0$ ($b < \Phi e$ or $b > \Phi e$), which can be expressed in the form $b = \Phi e \pm [c]$, there exists an additional set of parameters $[c]$ coupled to biological processes affecting growth. Such parameters would reflect enhancement or dissipation of the growth rate and consequently, via Equations 6 and 7, increase or loss of pressure in the plant cell. Worth emphasizing is the fact that the validity of this theoretically based conclusion is strengthened by some predominantly experimental studies (i.e. Proseus et al., 1999, 2000; Ortega, 2004).

One may suppose that the parameter $r$ may also depend on various, both internal and external, factors affecting growth. Let us notice that Figure 2A resembles (at least qualitatively) some experimental results, well known in the literature, where the influence of phytohormones (abscisic acid [ABA]; Montague, 1997; indole-3-acetic acid [IAA]; Ross et al., 2002), or abiotic factors (Cd, Pb; Obroucheva et al., 1998) on growth was studied. Among other researchers, Montague, in particular, studied the effect of jasmonic acid and ABA on elongation of Avena internodal tissue (figures 2 and 5 in Montague, 1997). Ross and others (figure 3 in Ross et al., 2002), in turn, investigated auxin-GA interactions and their influence on plant growth, while Obroucheva and her coworkers studied the root growth responses to Pb in primary roots of maize (Zea mays; figure 2 in Obroucheva et al., 1998). These figures, in addition to

**DISCUSSION**

The article presents a theoretical approach that consists in accepting the growth rate functional dependence on time as given from the experiment. Then the general solution takes on the form given in Equation 5.
Solutions of the Ortega Equation

Figure 2A presented in this article, reflect the fact that, when applying growth stimulators (e.g. IAA), a plant organ elongates faster \((r > 0)\) than the same organ with no added growth factors \((r \approx 0)\). Applying inhibitors (e.g. ABA, Cd, Pb) slows the growth down \((r < 0)\) until it finally ceases. Similarly, the final volume (precisely length of coleoptile or internode cell or primary root as in most cases of these experiments) is greatest in the case of the stimulator and least in the case of the inhibitor.

The second class of solutions of the Ortega equation (Fig. 2, C and D) would represent growth (Fig. 2C) and pressure (Fig. 2D) change over time for different plant species or tissues. Also, it is likely to represent the character of GR(t) and \(P(t)\) changes in various environmental conditions (e.g. temperature, pH, water and soil factors, light, etc.).

These hypotheses must, however, be put forward in a way that leaves no doubts as to their appropriateness. This is due to the fact that when applying the mentioned growth regulators as well as for different species, tissues, or organs, not only do parameters \(a\) and \(b\) differ, but the cell wall yielding coefficient \(\Phi\) and the elastic modulus \(\varepsilon\) do as well. This fact may slightly change both classes of solutions. The validity of the hypotheses should also be proved empirically.

While studying the elongation of, for instance, maize coleoptiles, roots, or internode cells of Chara and Nitella, we are interested in whether any qualitative and quantitative agreement between the experimentally measured pressure and Equations 6 and 7, theoretically determined, exists. If parameters \(a\) and \(b\) describing the growth rate satisfy the inequalities considered in the last two paragraphs of the previous section, the pressure should behave as it has been derived there. Actually, experiments should verify which classes of solutions—Equations 6 and 7, Figure 2, A to D—are physiologically realized in nature and under what conditions. Experimental study leading to calculation of the parameter \(r\) would also be an interesting task in this research area. Nonetheless, it is worth stressing that the time dependence of plant cell turgor pressure obtained here (presented in Fig. 2, B and D, dashed lines) stays in agreement with some data obtained from experiments (e.g. see Kutschera and Koehler, 1993, 1994; Kutschera, 2000).

Unfortunately, another problem also arises. Are the data obtained from the study of the Ortega equation sufficient to get reliable results? Certainly, they are not complete because the coupling (and possible dependence) between cell wall yielding and pressure has not been considered. In fact, the relation \(\Phi = \Phi(P)\) must take place as both the physical quantities (simultaneously and opposite) influence growth. They stay in delicate balance during plant growth so alteration of the pressure induces change of cell wall yielding. This statement is also experimentally supported by Proseus et al. (1999, 2000). Therefore, the expression \(\Phi = \Phi(t)\), accepted in order to find analytic integrals in Equation 5, was a simplifying assumption that has largely limited our consideration. The next step is to include the dependence \(\Phi = \Phi[P(t), t]\).

Likewise, although the possible time dependence of the elastic modulus \(\varepsilon\) has been taken into account in the general procedure of solving the Ortega equation, it has been accepted as constant in time for the case of analytic solutions. In fact, cell wall features evolve during plant development. The elastic properties of the cell wall are not the same for a juvenile plant cell or the cell in the elongation stadium (when the cell wall is thin and very elastic) or, at least, for the mature cell (when the cell wall is thick and rigid; e.g. see Proseus et al., 1999; Cosgrove, 2000; Ortega, 2004). These properties affect the elastic modulus \(\varepsilon\). Further study should include the dependence of Young’s modulus in function of time, \(\varepsilon(t)\), which naturally can be obtained from experiments; however, the challenge would be to determine it theoretically.

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LITERATURE CITED


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