Loss of stability—a new model for stress relaxation in plant cell walls

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Abstract

This study addresses the mechanism of wall stress relaxation in growing plant cells. The current viscoelastic model of cell wall relaxation, which dates from the work of Preston, Cleland, Lockhart, and others in the 1960s, has serious shortcomings. It has been shown however that the theory of loss of stability (LOS) can be applied to materials in tension, leading to the conclusion that the relaxation of stresses in the walls of any pressure vessel is rigorously modeled using LOS. We propose that LOS also provides a more appropriate and versatile model of stress relaxation in growing plant cells. We argue that when treated as a manifestation of LOS, the regulation of cell turgor has a rigorous and demonstrable basis in the geometrical and physical properties of the cell wall and the cell's ability to import water. Thus plant cell growth can be regarded as an inherently self-limiting process, tunable by biochemical or structural means. Lastly, despite the current limitations of our model, we apply direct measurement of elastic modulus, wall thickness and cell radius obtained from cylindrical Chara corallina cells to generate an initial calculation of critical pressures in a hypothetical spherical cell with the same material properties.

Keywords: Plant cell; Growth; Turgor; Stress relaxation; Viscoelasticity

1. Introduction

In multicellular plants the individual cells are trapped within an extended system of common cellulosic walls. The biophysical behavior of this universal structural support system constitutes the most fundamental level of control over all plant growth and development. On the one hand, the rigidity of the wall must be sufficient to allow turgor pressure to build up, preventing wilting; while on the other, the rigid wall must be loosened in some way to permit cell enlargement during growth. Typical plant cell turgor pressures range from 0.3 to 1.0 MPa resulting in 10–100 MPa of tensile stress in the wall. The physical manifestation of wall loosening is termed stress relaxation. Stress relaxation reflects the fact that growth is accompanied by a lowering of the tension in the walls.

Our understanding of biochemical cell wall loosening has advanced considerably in the past 30 years (Cosgrove, 2001). Nevertheless, as far as the physics of stress relaxation goes, our understanding of the process has not changed significantly since the terminologies of creep, viscoelasticity, and yield threshold were introduced (Provine and Preston, 1962; Lockhart, 1965a, b; Cleland, 1967, 1971; Preston, 1974; Taiz, 1984). Creep was initially considered to be the best candidate for describing the instantaneous elastic or plastic extension behavior of growing walls, but it was found that creep rates in isolated wall material do not always coincide with the growth rates of the cells. Attention then turned to another stress relaxation mechanism, termed viscoelasticity, which was defined by Weber's studies on silk threads (see Dorrington, 1980). Using Weber's method of imposing a sudden change in strain on the specimen, stress relaxation experiments were done on Nitella, Penicillia and Acetabularia cell wall materials (Haugton et al., 1968; Haughton and Sellen, 1969). Experiments of this kind led to the proposal that cell wall growth was a biochemically controlled viscoelastic extension. Contemporaneous with Preston, Cleland, and Lockhart's work however, physiologists were revealing that Euler's well-known analysis of loss of stability (LOS) in columns under compression could equally well
be extended to materials in tension, and also to closed pressure vessels (Rzhansityn, 1955; Panovko and Gubanova, 1965). This work, which was appreciated in the world of physical mechanics, never entered the biological literature.

The mechanistic distinctions between viscoelasticity and LOS become apparent when we consider the defining condition for viscoelasticity illustrated by Weber's experiment in which the imposed strains or stresses were increased **suddenly**, a condition which clearly does not apply to growing plant cells. The conditions which support LOS however, are fulfilled when internal pressures and the resulting wall stresses in closed vessels increase **gradually**, leading to loss of stability when the pressure reaches the critical value determined by material properties and wall geometry (Panovko and Gubanova, 1965). We propose that the walls of a growing plant cell behave similarly; with turgor pressure rising **smoothly** to a critical point determined by wall properties and cell geometry, followed by a loss of stability that manifests itself as wall extension and growth. Wall stress relaxation can then be interpreted to result from the gradual escalation of normal stress conditions until they meet criteria predictably determined by the material and geometric characteristics of the pressurized cell.

2. Loss of stability (LOS)

The foundations of the theory were laid by the Swiss mathematician Leonhard Euler (1707–1783), one of the most prolific mathematicians in history. According to his analysis, the fact that two distinct equilibrium states can exist under constant loading conditions is itself an indication of instability, implying that the initial metastable equilibrium will give way to a second more stable state. Euler introduced the concept of LOS with the so-called “Euler column”, the well-known example addressing the problem of stability in a column under compression. Suppose a pair of balancing forces, each of magnitude $\lambda$, act at the ends of uniform column of unit length. To study the possible deflection (i.e. the stability) of the compressed column, Euler assigned $s$, ranging from 0 to 1, to be the arc length along the column, and $\theta(s)$ to be the angle of deflection at $s$. The governing equation then

$$EI\theta'' + \lambda \sin \theta = 0, \quad \theta(0) = \theta(1) = 0,$$

(1)

where $EI$ is a constant representing the elastic and geometric properties of the column. The eigenvalues of the problem about the trivial solution $\theta = 0$ turn out to be

$$\frac{\lambda}{EI} = k^2 \pi^2, \quad (k = 1, 2, 3, \ldots).$$

(2)

This means that when the gradually increasing load reaches a critical value $\lambda_{CR} = EI\pi^2$ (i.e. $k = 1$), the column will lose its straight configuration and bend abruptly (see Prescott, 1946).

In terms of our later interpretation of this result we emphasize two important features of LOS. First of all, LOS behavior will be apparent only if the load is increased gradually until it reaches the critical value. Secondly, the critical value is determined by the geometric and elastic properties of the system.

Because of high turgor pressure, plant cell walls are normally under tensile load. From the above example, however, the concept of LOS would seem to apply only to objects in compression. In other words, it would appear to be true that under tensile loading conditions one cannot speak of LOS at all. Rzhansityn, Panovko and others extended Euler's LOS theory to include both compressive and tensile conditions (Nadai, 1954; Rzhansityn, 1955; Panovko and Gubanova, 1965). They used the example of a cylindrical rod loaded in tension, and showed that if the tensile force $F$ is increased slowly, the relationship between rod elongation, $\nu$, and $F$ must follow the curve shown in Fig. 1A. The mathematical feature of this result is analogous to that of LOS under compression, i.e., there is a transition from stable to unstable states, represented in Fig. 1A as the peak of the curve.

The critical value of the force, $F_{CR}$, can be found by solving $dF/d\nu = 0$. The result is $F_{CR} = ES_0/\nu$, where $E$ is the elastic modulus of the rod material, $S_0$ is the initial cross-sectional area of the rod, $\nu$ is the base of natural logarithm. As in Euler's column, this critical value $F_{CR}$ also depends on the geometric and elastic properties of the rod.

3. LOS in a spherical shell

The analysis of LOS in a rod under tension suggests that an enclosed shell can also lose stability under high internal pressure, because as the internal pressure increases tension builds up in the shell wall. The relevant differential equations can be derived from the geometry and physical properties of the shell, enabling us to predict, in principle, the pressure at which LOS will occur. In reality however, analytical solutions for calculating the critical values are obtainable only for the simplest geometries because of the complexity of the 3D problem. Panovko used an isotropic, thin walled spherical shell to illustrate the problem of pressure-driven LOS (Panovko and Gubanova, 1965). As shown in Fig. 2A, a thin walled spherical shell with radius $R$ and wall thickness $t$ is subjected to an internal pressure $P$. The tensile stress in the wall is

$$\sigma = \frac{8P}{2t}.$$

(3)
The strain $\varepsilon$ should be calculated in accordance with logarithmic deformation, here the logarithmic deformation of a meridian line on the shell is

$$\varepsilon = \int_{R_0}^{R} \frac{d(2\pi R)}{2\pi R} = \int_{R_0}^{R} \frac{dR}{R} = \ln \frac{R}{R_0}. \quad (4)$$

The relationship between wall thickness and shell radius during the loading can be derived using the stress-strain relationship of a wall element (Fig. 2B). Assuming Poisson’s ratio $\mu = 0.5$, Panovko found

$$t = t_0 \left( \frac{R_0}{R} \right)^2, \quad (5)$$

where $R_0$ and $t_0$ are the original values of radius and wall thickness, respectively. Indeed, this relationship is equivalent to $4\pi R^2 t = 4\pi R_0^2 t_0$, asserting that the total volume of the wall material remains unchanged.

Substituting Eqs. (3)-(5) into the general stress-strain equation

$$\varepsilon = \frac{(1-\mu)}{E} \sigma. \quad (6)$$

Panovko obtained the relationship between the internal pressure and the shell parameters (radius, wall thickness, and wall elastic modulus). For convenience he expressed this relationship as the curve of $P$ vs. $(R - R_0)$, i.e. internal pressure vs. shell enlargement (Fig. 1B).

The curve shows that after a monotonic increase in pressure, LOS occurs when the pressure reaches a critical value $P_{CR}$. As in Fig. 2A, all points on the rising curve (solid line) are stable states, whereas points on the falling curve (dashed line) are unstable states. The onset of LOS corresponds to $dP/dR = 0$, which gives

$$P_{CR} = \frac{4E_0}{3\varepsilon R_0}. \quad (7)$$

Again, this equation shows that the critical pressure of an internally pressurized shell depends on the geometry of the shell and the elastic properties of the wall material.
In the case of a non-homogeneous shell, Panovko emphasized that LOS will be restricted to the site where $P_{CR}$ holds the lowest value. For instance, LOS will occur at the thinnest site on the wall if the modulus and radius are held constant, and vice versa (Panovko and Gubanova, 1965).

The essence of LOS theory is the existence of a transit from a stable state to an unstable state, represented by a peak on the stress-strain curve where the slope changes from positive to negative. The dashed line in Fig. 1B is a mathematical completion of the curve, but it has no physical meaning in that it does not represent any definable stress-strain relationship. In some cases, the system may even jump from one stable state (solid line) to another stable state (another solid line), skipping the unstable states (dashed line) in the between. Details of this discussion can be found in the Introduction to Stability and Oscillations of Elastic Systems (Panovko and Gubanova, 1965).

Panovko's work definitively documented the occurrence of LOS under tensile conditions, and particularly in pressure vessels. Since then it has been recognized that if the pressure in the shell increases gradually, LOS is the mechanism describing the stress relaxation in the wall when the pressure reaches its maximum value. It is, in fact, an inevitable result which can be predicted from first principles.

4. LOS—stress relaxation in the walls of growing cells

It is generally accepted that the fundamental behavior underlying plant cell growth is an irreversible stretching of primary cell walls due to the mechanical loads imposed by cell turgor pressure. The dependency of growth rate on wall properties and turgor pressure is represented by the empirically derived equation

$$
\frac{dV}{dr} = m(P - Y),
$$

where $V$ is cell volume, $m$ is wall extensibility, $P$ is cell turgor pressure, and $Y$ is the pressure (yield) threshold. This equation has been well documented, particularly in studies on the giant celled Characean alga *Nitella* in which turgor pressure has been measured directly during growth (Green, 1968; Green et al., 1971). These studies showed that growth can occur only when $P > Y$. Additionally, we observe that in a rapidly growing cell, a reduction in turgor of only 0.02 MPa has been shown to immediately stop growth (see also Taiz et al., 1981; Taiz, 1984).

Linking the pressure threshold for growth to a viscoelastic/creep-based yield threshold $Y$ presents difficulties which have been explained in a variety of ways by different researchers. Cleland suggested that the immediate cessation of growth mentioned above might represent a retarded elastic contraction (creep recovery) (Cleland, 1971). However, it was found that the creep recovery phase in mercury inflated *Nitella* walls was essentially completed in 5 min (Richmond et al., 1980; Kamiya et al., 1963), which was in total contradiction with the observed growth cessation phase which persisted for an hour or more (Green, 1968).

Preston also pointed out that viscoelasticity, creep, or other yield related concepts could not provide a reasonable cell turgor value. He noted that these concepts predicted cell turgor pressure of only 0.2 MPa, too low to explain normal working turgor values which are closer to 0.6 MPa (Preston, 1974). The theory of LOS resolves these problems because it makes it clear that the pressure value at which wall stress begins to relax coincides with the highest attainable pressure value in the stress-strain curve of pressure vessels.

Questions may arise as to whether LOS and viscoelasticity or creep may refer to the same physical phenomenon. In other words, is the $P_{CR}$ derived in Eq. (7) synonymous with the yield stress of viscoelasticity and creep? As has been detailed by Dorrington, the concepts of viscoelasticity and creep in biomaterials are based on Weber's experiments in which testing was initiated by sudden displacements (Dorrington, 1980). These experiments have one significant feature in common—which is that the materials always exhibit some degree of elasticity, even though they do not obey Hooke's law perfectly. This clearly illustrates the difference between viscoelasticity and LOS. Any material that exhibits some elasticity will have a stress-strain curve whose slope is continuously positive under increasing load (i.e., $dP/dt > 0$). Viscoelastic materials will thus also have positive slope at different strain rates. In contrast, LOS occurs only at the peak of the stress-strain curves, where $dP/dt = 0$. It is this relationship that enables LOS to encompass tensile loading situations, where it indicates the onset of stress relaxation in a pressure vessel.

The mathematical basis for viscoelasticity and creep (which was founded by Boltzmann after numerous materials had been tested on the Weber experimental setup, see Dorrington, 1980), also differentiates LOS from viscoelasticity and creep. Boltzmann stated that within the concepts of viscoelasticity and creep, the stress relation of a certain material (say, a cell wall strip) could start with many stress values depending on the sudden displacement imposed. Hence we can see that both viscoelasticity and creep can occur at various stress values. In contrast, stress relaxation due to LOS can only occur when the stress equals a particular value. LOS cannot occur if the pressure is below the critical value. This unique feature of LOS may resolve the puzzling observation that a reduction in the turgor pressure in growing plant cells of only 0.02 MPa can result in the immediate cessation of growth.
5. LOS cannot explain metabolically induced changes in $P_{CR}$

The predictive value of LOS theory is limited to conditions where the mechanical and geometric features of the cell are known. However, it is likely that $P_{CR}$ values for growing primary cell walls are continuously modifiable by metabolic or biochemical means. It has been reported, for instance, that the yield, $Y$, of Eq. (8) can change within minutes if the water status or auxin level changes (Green et al., 1971; Nakahori et al., 1991; Frensch and Hsiao, 1995; Okamoto-Nakazato et al., 2000). If the changes in water status or auxin level can be translated into quantifiable values for $E$, then LOS can predict the resulting changes in $P_{CR}$. The governing equations of LOS are essentially the stress-strain relationships of the system. For this reason our argument is confined to the regulation of stress and strain and does not extend to the underlying physiological and biochemical processes.

Practically, our lack of understanding of the detailed mechanics of real cell walls precludes a detailed mathematical treatment of LOS in a growing plant cell. For instance, the Poisson’s ratio predicted from different models of microfibril orientation can vary widely, and may even differ in the radial and tangential directions. Indeed, Eq. (7) was derived by assuming Poisson’s ratio = 0.5, an assumption that might be valid for an incompressible material such as rubber, but which probably does not apply to cell wall material. Nevertheless, the validity of the concept of LOS does not depend on a particular value for Poisson’s ratio, and therefore the concept of stress relaxation by LOS applies equally well to complex, composite materials. As Panovko pointed out, “The same qualitative phenomenon may be observed in the more complex case where the physical deformation law is given by nonlinear function as well as for Poisson’s ratio ≠ 0.5” (Panovko and Gubanova, 1965).

6. Localized LOS in growing plant cells

From Panovko’s analysis it appears that the only condition that is both sufficient and necessary for stress relaxation to occur in a pressure vessel is that the pressure increases to the level of $P_{CR}$. Panovko’s observation that variations in either wall thickness or modulus can result in the localization of LOS to thinner or lower $E$ regions of the wall can help explain the cell’s ability to control both the directionality and localization of cell wall deformation during cell growth. Furthermore, if, because of the composite nature of the wall, the local values of $P_{CR}$ show directional anisotropy, stress relaxation will occur only in the direction which has the lowest $P_{CR}$.

Panovko’s treatment of wall thickness in a mechanical pressure vessel assumed that total wall volume remained constant and that thin areas would remain thin. But in plant cells this is not always the case as additional material may be laid down on the wall inner surface at any time. Therefore LOS will not necessarily result in the thinnest regions of the wall become thinner and thinner. This leads directly to the conclusion that by means of local wall synthesis, or any method which raises the local $P_{CR}$, the cell may force the shifting of LOS to another part of the cell wall, enabling it to switch growth off completely at any given location on the cell wall. Similarly, elastic modulus $E$ is accessible to biochemical manipulation by the cell. In this sense we believe that with LOS, plant cell growth can be regarded as an inherently self-limiting process, tunable by biochemical or structural means. Furthermore, we must bear in mind that real plant cell walls are highly anisotropic, being composite materials composed of tensile fibers in a complex matrix. This adds a level of complexity to any interpretation of cell wall behavior according to LOS, but in no way obviates the fact that LOS will still occur at a $P_{CR}$ defined by local, interfibrillar matrix characteristics.

7. The regulation of turgor pressure

In order to establish whether or not plant cells exhibit this kind of LOS during growth we need to examine several aspects of their behavior under growth conditions. First of all, we note that the only way to increase the pressure $P$ in Fig. 2A is to force more and more liquid into the interior space. For a growing cell, the water potential gradient across the cell membrane, which is largely due to an osmotic potential gradient, provides the driving force for water movement. As water enters a cell, turgor pressure increases; once turgor pressure reaches its critical value, the wall loses stability, with wall stress relaxation and cell enlargement resulting. Meanwhile the water uptake mechanism keeps transporting water in, preventing a precipitous drop in turgor pressure.

Eq. (7) says that for a given cell size, the predicted critical pressure value derives strictly from the wall parameters (i.e. wall elastic modulus and thickness), and has nothing to do with the cell’s ability to transport water inwards. The real turgor pressure for any given cell, however, is determined not only by wall properties, but also by the cell’s ability to exploit the water potential difference between the inside and the outside of the cell. From this, it is clear that two different mechanisms are involved in the regulation of turgor pressure in living plant cells. One, based entirely on wall mechanics, regulates maximum attainable pressure through wall instability, the other, coming into play especially in
mature, non-growing cells, regulates cell turgor by manipulating the driving force for water movement. Whichever of these two factors has the lower threshold will effectively determine the turgor pressure.

In actively growing cells, even though the $P_{CR}$ values may rise due to increases in wall thickness or elastic modulus (or both), they may still be within reach of physiological turgor pressures thereby permitting LOS to accomplish stress relaxation. For this reason the turgor pressure of actively growing cells should be constantly hovering near the critical value ($P_{CR}$). In maturing cells however, the continued addition of secondary wall material and the lignification of the walls would raise the critical value $P_{CR}$ to a point unattainable by turgor, which would terminate growth.

In order to provide an initial test of the above argument, we performed a simple experiment on a giant-celled alga. We measured the width of flattened Chara corallina cell segments (wall tubes), divided by $\pi$ and assumed the result to be the radius $r_0$ of the spherical cell model. This assumption is based on the consideration that in a real cell the length is much greater than the width and therefore any possible boundary effect to the problem would mainly come from the cell width (Wei et al., 2001). We realize that this assumption will only allow us to arrive at an idealized calculation of $P_{CR}$, since an analytical solution for calculating the $P_{CR}$ of cylindrical pressure vessels is not yet available.

Wall thickness $t_0$ was measured by means of interference microscopy according to Mach-Zender (Aus Jena, Peraival, see Preston, 1974). For the calculation of the optical path difference we assumed the refractive index of the wall materials to be 1.55 (Preston, 1974). To estimate the elastic modulus of cell wall material, we used a computerized feedback-control device to measure the strain of the cell wall under a known load (Fig. 3). The Vitrodyne V-2000 (LiveCo Inc., Burlington VT) consists of a microprocessor controlled forcing frame supporting a pair of flexible, instrumented shims that hold the cell wall material, and a linear voltage displacement transducer (LVDT) to measure the deformation. Details of this device have been described elsewhere (Wei et al., 2001). We glued the ends of the freshly excised wall tube to the shims, and either maintained it at 100% relative humidity or submerged it in water (We found no significant differences between the results of these two treatments). Care was taken to ensure that the distance between the shims was 6 mm and that the wall material was not yet under tension. We measured the strain by increasing the tensile force to about 4 gramsforce (gf), and then reducing it to the initial zero value in about 0.3 gf increments. The entire loading and unloading cycle was repeated two or three times to ensure that the system remained in the elastic range.

![Fig. 3. Schematic of the device for tensile loading and unloading experiment on a excised C. corallina cell.](attachment:image)

Typical loading and unloading paths of the stretching experiment conducted on C. corallina wall material are shown in Fig. 4. The first loading path was not used in the analysis because it differed significantly from subsequent loading and unloading cycles, possibly because of wrinkling of the wall segment or labile encrustations on the surface (Wei et al., 2001). The $\varepsilon$ of data points in the remaining loading and unloading cycles consistently ranged from 0.90 to 0.94, which convincingly shows the elasticity of the cell wall material. The strain can be calculated by $\varepsilon = \Delta L/L$, knowing the original length (6 mm) of the excised C. corallina wall tube. The slope in Fig. 4, b(1), represents the elongation of the wall material per 1 gf change in load, which allows us to calculate the elastic modulus (Results are shown in Table 1).

In Table 2 we summarize calculations which apply measurements obtained from fresh Chara cell wall preparations to a hypothetical spherical cell model. Each of the three data fields for either growing or mature C. corallina cells represents six separate measurements recorded as a range of values. The maximum and/or minimum values for each data field are then used independently to calculate maximum and minimum estimates of $P_{CR}$ for the hypothetical spherical cell. Thus we are using measurements taken from a cylindrical and
highly anisotropic cell wall system to derive estimates of critical pressure in an imaginary spherical, isotropic wall system. Nevertheless, our estimates of critical pressure appear to be surprisingly close to recorded turgor values for immature, growing *Chara* cells, with $P_{CR}$ having a predicted minimum of 0.49 MPa, and a predicted maximum of 0.80 MPa. For mature cells our estimates of 1.41 MPa (minimum $P_{CR}$) and 2.37 MPa (maximum $P_{CR}$) would appear to put LOS driven growth beyond the range of reasonably attainable turgor values. For growing cylindrical *Chara* cells the real turgor limit set by $P_{CR}$ may be somewhat lower than the above estimates because of the lower rigidity of any cylindrical shape when compared to a sphere of the same diameter and construction.

8. Conclusion

While LOS theory does not directly address questions of molecular rearrangement during tensile deformation, or the biochemical mechanisms altering wall properties, it does provide insight into the physical behavior of growing cells. The essential characteristic of LOS embodied in the expression $\dot{c}_V/c_V = 0$ describes the nature of stress relaxation in the walls of pressure vessels. LOS combines both the elastic properties and geometric features of the walls in a single mathematical expression (Eq. (7)). It predicts that the critical stress value will vary with wall thickness as well as with wall modulus, which points to a mean by which wall extension may be controlled locally. It also predicts that in growing cells turgor values will be lower for the critical pressure for that portion of the wall which has the lowest $P_{CR}$.

One can imagine a cell where wall patterning arises by virtue of local variations in critical stress value, traceable to subtle local changes in wall biochemistry and/or thickness, or even to transient mechanical couplings to underlying cytoskeletal elements which could reinforce the wall and raise the critical pressure for LOS locally. This would have the effect of shifting LOS behavior to other regions of the wall characterized by slightly lower $P_{CR}$ values. In maturing cells the continued addition of secondary wall material would raise the critical value to a point unattainable by turgor, which would terminate growth.

Panovko makes a compelling argument for the application of Euler's work on critical instability to tensile pressure vessels, making it possible to extend LOS theory into the domain of living plant cells where it clarifies the intimate relationship between working turgor pressure and cell wall stress relaxation during growth. Lastly, LOS presents the intriguing prospect of understanding cell growth as an inherently self-limiting process, where a clearly defined critical pressure
introduces a negative feedback element into the relationship between increasing cell turgor and increasing cell volume. Any sudden volume increase will be accompanied by a drop in turgor pressure below Pcr and an immediate cessation of growth.

Clearly, the application of LOS theory to the problem of cell wall extension growth does not imply a final understanding of the process. The work done in recent years in the lab of J. P. Verbeelen at the University of Antwerp shows how the orientation of cellulose fibrils in the composite wall affects the wall’s mechanical properties, implying that the way microfibrils interact with one another is not constant across the thickness of the wall (Kerstens et al., 2001). The complex structure of all plant cell walls, and the possibility that LOS events may not only be asymmetrically distributed through the wall thickness, but also discontinuously distributed through the load-bearing region of the matrix at the sub-microscopic level, places any truly representative model of cell wall behavior beyond our reach at present.

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References


