

Compression Induced Intercellular Shaping for Some Geometric Cellular Lattices

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ABSTRACT

The wall perimeter fraction, which contact neighboring cells, was named compression ratio (α). A zero compression ratio indicates maximum intercellular (air) volume (v_G , v/v) and neglectable contact among cells, while $\alpha=1$ indicates complete adherence between neighboring cells and no v_G in the lattice. The maximum intercellular air volume ($\mathbf{b} v/v$), when $\alpha=0$, was 0.593 for triangular, 0.2146 for square and 0.0931 for hexagonal lattices. The equation $\alpha=1 - (v_G/\mathbf{b})^{1/2}$ was derived to relate α , \mathbf{b} and v_G in the studied lattices. The relation ($P_S=p/\alpha$) between cell turgor (P_S) and the tissue aggregating pressure (p), defined as the compression to keep in place a layer of cells, was demonstrated using the compression ratio concept. Intercellular deformations of *Ipomea batatas* L. roots obtained with pressure chamber were used to test α , v_G , p and P_S as a function of compression. Volumetric and transversal elastic extensibilities and the lamella media tearing forces were obtained and α constancy was considered as a criteria of cellular shape stability.

Key words: Elastic modules, compression, external force, intercellular air volume, *Ipomea batatas*, pressure chamber

INTRODUCTION

Internal and external forces shape the cells inside multicellular organs. Internally the turgor P_S causes cell wall stretching (Lockhart, 1965) and the tearing forces between walls at the lamella media facing an intercellular air volume (Calbo *et al.*, 1995), while the apoplasmic tension (P_A) compresses the cell wall matrix (Calbo & Pessoa, 1994) and conceivably have some cellular aggregating force. The action of external forces as cellular shaping agents seems to be less relevant than P_S and P_A but they are important during the plant development and in the post harvest life (Calbo *et al.*, 1995) and were considered in studies about elastic extensibilities and hydraulic

conductivity (Ferrie & Dainty, 1976; Steudle *et al.*, 1981).

Hulbary (1944) in a biometrical study of three-dimensional shapes of cell considered that the formation of intercellular air volumes could be important to understand cellular shape determination. Most articles related to patterning and organ shaping, however, avoid the involvement of intercellular air volumes. Cummings (1996) to obtain a general geometric treatment of thick epithelial tissues discarded not only intercellular air volumes but also the cellular structure, which was loosely included in a mathematical framework.

In this work, intercellular air volume shaping of presumed identical flexible thin walled cells enclosed by hexagonal, square and triangular

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lattice, in which individual cells were subjected to compression, were studied. The developed equations were used to obtain information about compression ratios, maximum lattice intercellular volume, elastic modules and lamella media tearing forces from assays in which the intercellular air volume of sweet-potato root was reduced with use an external compression.

MATERIALS AND METHODS

Sweet-potato roots *cv.* Princesa and Coquinho produced at Embrapa-Hortaliças (Brasília, DF) were covered by a plastic sealant and externally compressed. In such pressure chamber assays intercellular air volume deformation was estimated according to the amounts of air evolved through an air outlet (Calbo *et al.*, 1995) or by a direct measurement of the organ deformation (Calbo & Nery, 1994).

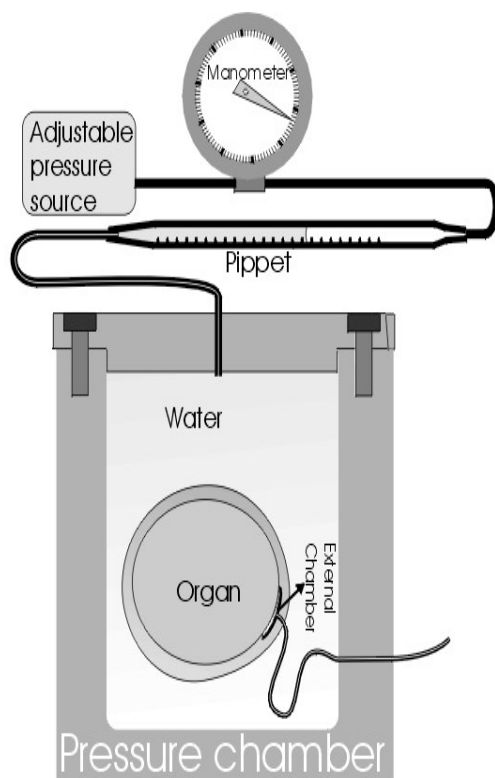


Figure 1 - Pressurized potometer to study intercellular air volume in compression assays.

The simplified pressurized potometer presented in (Fig. 1) allowed the direct measurement of the intercellular volume deformation caused by the external compression. In this potometer a low dead volume chamber (Nery & Calbo, 1994) was attached to the organ covered with plastic sealant

to allow the maintenance of barometric pressure inside the intercellular air volumes. Compression was applied to the water meniscus in the measuring pipette. Only pressures smaller than that required to remove the first droplet of apoplasmic sap in the capillary outlet (Fig. 1) were employed to respect the presumed V_G deformation conditions, as close as possible.

Measurement of V_G and V_C

The organ mass was measured and its empujo after immersion in water was recorded. From mass and empujo the organ volume was estimated according to the Archimedes principle. The total intercellular air volume V_G was measured according to the maximum deformation of the organ in the potometric measurement (Calbo & Nery, 1994) or according to the total amount of air removed from the compressed organ (Calbo & Nery, 1994; Calbo *et al.*, 1995). The volume of the cells V_C was obtained as the difference between the organ volume (V_o) and its intercellular air volume (V_G).

Physical approach

The following simplifying assumptions were considered in this study:

- 1- A constant number of identical cells;
- 2- Each cell can be enclosed by a prism;
- 3- Thin and flexible cell walls not subjected to growth;
- 4- Intercellular air intrusions formed by lamella media border separation under the action of turgor dependent forces;
- 5- External compression affects uniformly the turgor of all cells in the tissue and
- 6- Temperature is constant.

Some of the geometric relations involved in the intercellular air volume shaping of a few particular cellular lattices are:

- 1- Intercellular air volumes (V_G) at the corners of square prisms with side S (Fig. 2) can be approximated by :

$$V_G = (4\pi)Lr^2 \quad [1]$$

in which, r is the curvature radius of the cell wall facing V_G and L is the cell length.

- 2- For this square lattice one cell volume (V_C) can be computed directly considering s as the part of

the side S (Fig. 2), in which the considered cell touch its neighbor.

$$V_C = L (\pi r^2 + s^2 + 4sr) = L [S^2 - (4-\pi)r^2] \quad [2]$$

or as a difference between the prism volume (LS^2) and V_G (Eq. 1)

$$V_C = L [S^2 - (4-\pi)r^2] \quad [3]$$

3- The radius associated to V_G (Fig. 2) r in Eq. 1 can be replaced by $(S-s)/2$:

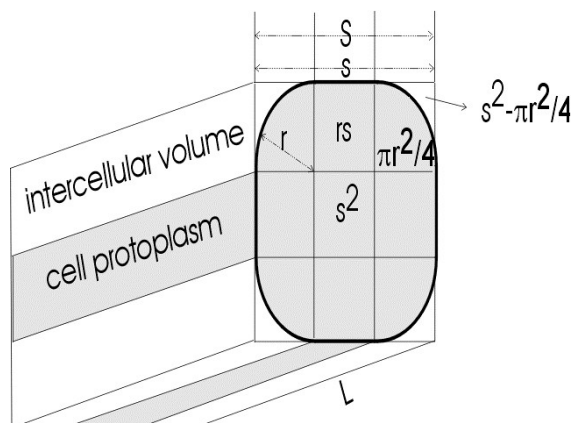


Figure 2 - Idealized cell, of length L , enclosed by a square prism of side S , facing identical cell neighbors, through plane s cross section. The cell wall curvature radius r faces an intercellular air volume. The areas expressed are a rectangle, a square, a quarter of a circle areas and a difference between a square of side r and a quarter of a circle of radius r .

$$V_G = L (S^2 - 2sS + s^2)(4-\pi)/4 \quad [4]$$

4- Defining compression ratio as $\alpha = s/S$ a relation between V_G and α can be obtained dividing Eq. 4 by the prism volume ($V_G + V_C = LS^2$):

$$v_G = (1 - 2\alpha + \alpha^2)(4-\pi)/4 \quad [5]$$

In Eq. 5 $v_G = V_G / (V_G + V_C)$.

5- The analogous expression for a triangular cellular lattice is:

$$v_G = \left(\frac{3}{2} - \frac{\mathbf{p}}{2\sqrt{3}}\right)(1 - 2\mathbf{a} + \mathbf{a}^2) \quad [6]$$

and for an hexagonal cellular lattices is:

$$v_G = \left(1 - \frac{\mathbf{p}}{2\sqrt{3}}\right)(1 - 2\mathbf{a} + \mathbf{a}^2) \quad [7]$$

6- In Eq. 5, 6 and 7 v_G is null when $\alpha=1$. The maximum v_G (v/v) intrusion allowable, for $\alpha=0$, in these square, triangular and hexagonal lattices is the factor that relates v_G with $(1-2\alpha+\alpha^2)$. As a consequence it seems relevant to suppose that the

gaseous volume intrusion of an irregular cellular lattice could be related α by:

$$\frac{v_G}{\mathbf{p}} = (1 - 2\mathbf{a} + \mathbf{a}^2) \quad [8]$$

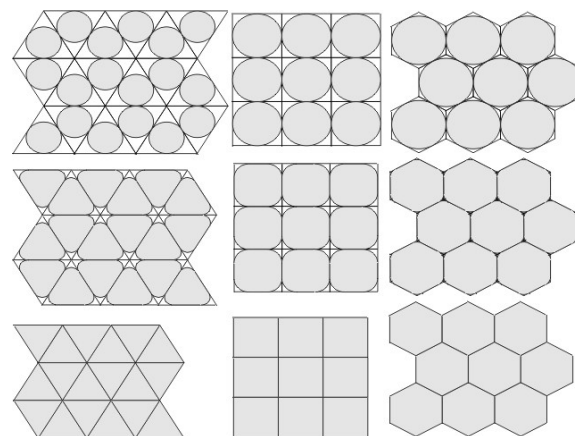


Figure 3 - Idealized behavior of cells arranged in cubic and hexagonal packing, without external compression with some compression and subjected to a compression larger than P_s .

in which β is the maximum allowable v_G (v/v) intrusion and one of the roots of this equation is:

$$\alpha = 1 - (v_G/\beta)^{1/2} \quad [9]$$

7- The crosssection perimeter b of these cells is:

$$b = 2\pi r + 4s \quad [10]$$

From Eq. 9 an expression for b as a function of v_G can be obtained, after making $r=(S-s)/2$ and $s=\alpha S$.

$$b = S[4 - 2\sqrt{(4 - \mathbf{p})v_G}] \quad [11]$$

8- The ratio $V_G/(V_G+V_C)$ represented by v_G depends only of the considered lattice (Fig. 3) and is independent of the cell size. From this fact, by induction, the following axiom was proposed: "Whole organs of any shape composed of prismatic cells arranged according to an uniform lattice can be treated as an unique cell having typical emptied V_G corners, enclosed by one similar larger prism with the total organ volume". This axiom should be valid for volume related properties

Compression and aggregating forces

A plane lamella between a pair of cells is an evidence that they have similar turgor and as a consequence a tissue composed of polyedric cells is an evidence of near turgor uniformity and of lamella media gluing forces. Without such gluing, the tissue should become a mass of ellipsoidal cells. The aggregating force F , which keeps in place a rectangular area sL of the cell wall herein considered (Fig. 2) can be related to the turgor P_s by:

$$F = P_s L S \quad [12]$$

F can also be calculated as the product between average pressure p times the prism face SL (Eq. 13). This average pressure p will be defined as the aggregating pressure.

$$F = p S L \quad [13]$$

A relation between turgor (P_s) and p is then obtained replacing s by $S\alpha$ in Eq. 12 and making it equal to 13:

$$P_s = p/\alpha \quad [14]$$

If p receive additions of an externally applied pressure (Δp) then Eq. 14 can be rewritten as:

$$P_s = P_{s0} + \Delta P_s = (\Delta p + p_0)/\alpha \quad [15]$$

In Eq. 15 p_0 is a parameter (P_{s0}/α) to be estimated from assays in which α (Eq. 9) is measured as a function of Δp .

Compression under nearly constant turgor

When a force increment dF is applied to a cell layer (Fig. 2) without causing turgor (P_s) and cell length (L) increase it, then, can be written as:

$$dF = d(SLp) = P_s ds \quad [16]$$

According to Eq. 12 and 13 the division of Eq. 17 by SLp yields:

$$\frac{d(Sp)}{Sp} = \frac{s}{s_0} \quad [17]$$

Integration from s_0 to s and from S_0p_0 to Sp generates:

$$\frac{Sp}{S_0p_0} = \frac{s}{s_0} \quad [18]$$

using α (s/S) an a_0 (s_0/S_0) Eq. 18 can be rewritten as:

$$p = p_0 \alpha/\alpha_0 \quad [19]$$

If $a_0=1$ the substitution of Eq. 9 into Eq. 19 allows the representation of v_G as a function of the external pressure Δp as:

$$V_G/\beta = [1 - (p_1 + \Delta p)/p_0] \quad [20]$$

In Eq. 20 p is the initial aggregating pressure, Δp is the external pressure and p_0 is the minimum compressive load required to keep in place the cells with zero intercellular volume.

Constant cell volume compression

For a cell with length L and perimeter b in a square lattice the transverse Hookean elastic modulus (ϵ) is:

$$\frac{db}{b} = \frac{d(F/L)}{\epsilon} \quad [21]$$

Considering that $F=pSL$ the integration of Eq. 21 yields:

$$\ln \frac{b}{b_0} = \frac{p_0 S_0 - pS}{\epsilon}$$

Replacing the v_G expression of b (Eq. 11) equation 22 generates:

$$\epsilon \ln \left\{ \frac{S[2 - \sqrt{(4 - p)v_G}]}{S_0[2 - \sqrt{(4 - p)v_{G0}}]} \right\} = pS - p_0 S_0 \quad [23]$$

If the ratio $a=L/S$ is constant, then it can be substituted in Eq. 23 as $S=a^{-1/3}(V_G+V_C)^{1/3}$. A numerical adjustment allows the fitting of p_0 and ϵ , according to changes of v_G caused by variations in the external pressure (Δp). In this procedure V_C remains constant by definition.

Elastic volumetric modulus and V_G

In a compression assay the organ volume (V_G+V_C) reduction is functionally associated to an elastic volumetric elastic modulus E by:

$$\frac{dV_G}{V_G + V_C} = -\frac{dp}{E} \quad [24]$$

The integration of Eq. 24 yields:

$$\ln \frac{V_G + V_C}{V_{G0} + V_C} = \Delta p/E \quad [25]$$

A different equation could be written, considering only the elastic modulus E_1 associated to the walls surrounding the intercellular air volume.

$$dV_G/V_G = dp/E_1 \quad [26]$$

Eq. 26 is integrated to:

$$\ln (V_G/V_{G0}) = \Delta p/E_1 \quad [27]$$

Plant size and turgor at constant α

For an uncompressed organ in which $a=L/S$ and $C=b/S$ are constants, α should not change as a function of turgor and the integration of Eq. 21, in this particular condition yields:

$$\varepsilon \ln S^2 / S_0^2 = a S^2 P_s - a S_0^2 P_{s0} \quad [28]$$

from which turgor can be separated as:

$$P_s = 2 \varepsilon / S^2 \ln S/S_0 - S_0^2 S^2 P_{s0} \quad [29]$$

RESULTS AND DISCUSSION

The curve of v_G reduction as a function of the applied external compression was smoother (Fig. 4) than the method of collecting the air removed in the outlet. Additionally, this method do not have the problems of gas solubilization previously acknowledged by Calbo *et al.* (1995). For this reason the results obtained with the potometric method using the equipment illustrated in Fig. 1 should be preferred.

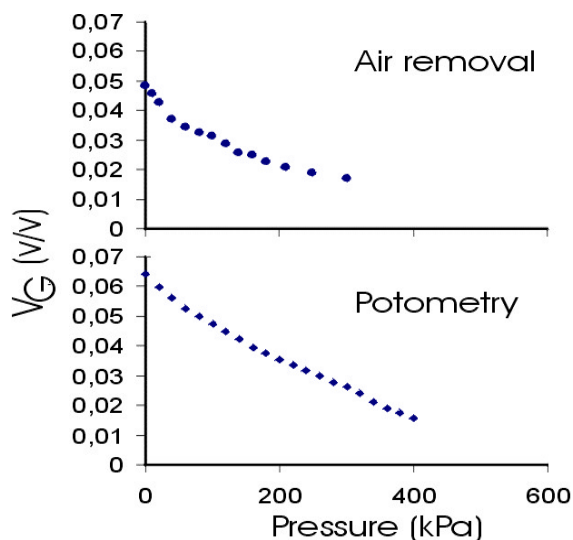


Figure 4 - Typical v_G (v/v) measurements of sweet-potato roots as a function of compression obtained by pressurized measurements of potometry and a air extracted volume from the same compression assay.

V_G compression under presumed constant turgor
The reduction of v_G with compression for the constant turgor model, yield good fitting (Table 1). Most of the experimental variation (>99%) was explained by this model, which conveys to the idea

that the equation is valuable despite of some significant unexplained residual components. To fit Eq. 20 β was set to $(4-\pi)/4$, because the additional fitting of β caused no goodness of fit improvement, and the estimated β values were close to this theoretical value.

This constant turgor model yield an aggregating pressure p_i of 700kPa and an estimated turgor p_0 of $\cong 1200$ kPa.

Elastic cell wall extension

Equation 23 was developed to represent V_G versus compression for a repeating cellular lattice in which the cell crosssection area remains constant while the walls are elongated by the stretching caused by turgor increase in the compressed tissue. The compression induced V_G reduction in this case is associated to the cell wall perimeter (b) increase, which causes the turgor increase.

The elastic modules ε , the tissue initial aggregating pressure at the beginning of the compression assay p_i and the turgor of the cells at the point where v_G is zeroed (p_0), were obtained during the computational fitting (Table 1). For studies of organs subjected to external compression (Eq. 23) and for pressure volume dendrometric studies (Eq. 29) the Hookean elastic modules (ε) seems to be of potential interest.

In these compression assays no water was lost but some water exchange between the symplasm and apoplasm may have occurred. The adjustment for v_G versus pressure under presumed constant cell volume (symplasm volume, Eq. 23) was better than for cells at presumed constant constant turgor (Table 1). The improvement, however, was minor and could be explained considering the transverse cell wall elastic modules.

The aggregating pressure ($p_i=584$ kPa) in this model was slightly smaller than the constant turgor model. The turgor estimated at $v_G=0$ ($p_0=1440$ kPa) was not significantly different from the one obtained using the constant turgor model. The linear elastic modules (3248 N/m) value was about ten times as large as the values reported for *Chara carollina* (Steudle *et al.*, 1991). No similar results were found for other storage roots.

Table 1- Average coefficients (n=5) and mean standard deviation for physical models adjusted to ten assays of V_G reduction versus compressive load (Δp), performed with sweet potato cv Princesa using a pressurized potometer and five with cv Coquinho using the amounts of air removed during compression assays.

Parameter	cv. Princesa		cv Coquinho	
	mean \pm se	R ² (average)	mean \pm se	R ² (average)
Volumetric elastic modulus E of the organ [$v_G = \exp(\Delta p/E) - v_C$]				
v_{Co} (v/v)	0.9433 \pm 0.0036	0.976	0.9593 \pm 0.0014	0.925
E_1 (kPa)	8302 \pm 353		9844 \pm 1369	
Volumetric elastic modulus E_1 from the walls surrounding V_G [$v_G = v_{Go} \exp(-\Delta p/E_1)$]				
v_{Go} (v/v)	0.0609 \pm 0.0030	0.993	0.0431 \pm 0.0015	0.973
E (kPa)	295.0 \pm 30.5		258 \pm 35	
V_G compression under constant cell turgor { $v_G = 0.2146[1 - (p_i + \Delta p)/p_o]^2$ }				
p_i (kPa)	678.5 \pm 32.7	0.9901	819.5 \pm 127.0	0.9538
p_o (kPa)	1430 \pm 89		1460 \pm 208	
V_G compression for cells with elastic walls in the absence of water exchange (Eq. 23)				
p_i (kPa)	584.4 \pm 26.0	0.9921		
p_o (kPa)	1440 \pm 86.0			
ε (N/m)	32486 \pm 3180			

The aggregating pressure estimates similarities between these models were encouraging considering the conceptual difficulties involved. The differences were of less than 10% for aggregating pressures and were within the experimental errors for turgor at $\alpha=1$.

Tissues with thin walled cells under stable V_G , presumed from compression ratio (α constancy in the absence of external compression turgor can be evaluated from ε . To use Eq. 29 the side S (or diameter) with an Alvim (1975) dendrometer, a LVDT (Klepper *et al.*, 1972) or volumetric measurements are needed. Conversely given estimates of turgor Eq. 29 allows the estimation of the linear elastic modulus of plant cells according to the restrictive assumptions used in this work.

Considerations about volumetric elastic modulus

The volumetric elastic modulus (E) for the whole organ under compression (Eq. 25) yielded the worst adjustment (Table 1). The volumetric elastic modulus E_1 associated to the cell wall facing V_G (Eq. 27) gave a better adjustment (Table 1), because the elasticity of the walls facing V_G is related to the external pressure response.

The values of the volumetric elastic modulus E, for organ compression, and the volumetric elastic modulus E_1 , for compression of the walls around V_G depend on the turgescence intercellular air volume and cell wall elasticity. Differently, intercellular air volume are excluded as a variable in the volumetric elastic modulus obtained by changing the cell water content and using a pressure-chamber (Murphy & Ortega, 1996) or using a pressure probe (Murphy & Ortega, 1995). Calbo *et al.* (1995) acknowledged that in external compression assays, similarly to pressurizing a fruit between two fingers, which causes cellular deformations not involved in other methods to evaluate organ elasticity.

V_G formation spontaneity

One procedure to consider V_G formation spontaneity is by evaluating free energy reduction. In the first ideal system from this article, turgor was considered to be constant and the free energy reduction (w) caused by formation of intercellular air volumes is:

$$w = P_s \Delta V_C \quad [30]$$

For the second model, the cell volume was considered to remain constant and V_G formation, as consequence, is related to the elastic work produced, free energy reduction, while the cell perimeter is reduced from b to b_0 according to Eq. 31.

$$w = \varepsilon(b^2 - b_0^2)/2 \quad [31]$$

Another valuable form to consider the V_G formation spontaneity is by estimating the tearing tension at the lamella media. In the absence of an external compression, the tearing tension per unit of cell length ($T_L = F/L$) acting at one of the two lamella media bordering points that determine the segment s in Fig. 2 is the force ($F = sLP_S$) divided by 2 times the cell length (L).

$$T_L = s P_S / 2 \quad [32]$$

Meristematic tissues are geometrically similar to soap bubbles (Sifton, 1945 and 1957) in which intercellular air volumes can not be observed at an optical microscope. The tissue pattern changes during differentiation, and intercellular air volumes are gradually developed among the plant cell walls. Possibly cell growth associated or not to a lamella media biochemical weakening, which increase its susceptibility to the turgor dependent tearing forces (Eq. 32) acting at the corners among three or more cells (Jeffree *et al.*, 1986), play an important whole in the development of intercellular air volume intrusions.

An inspection of Eq. 32 associated to other previously considered geometric considerations allows the following inferences about tearing forces at the lamella media and the development of intercellular air volume intrusions:

1- The smaller the cells, the smaller are the tearing forces at their corners;

2- The tearing forces reduce as v_G increases (Eq. 9 and 14);

3- Cell separation occurs as the tearing tension is being reduced to a threshold limit. This threshold should be under strict plant molecular control.

In sweet-potato roots, tearing force was estimated in 6 N/m at the lamella media V_G edge. A resistance to a tension of this magnitude or even larger is required to assure V_G stability. From a macroscopic perspective such V_G stability could be stated as "The intercellular volumes remains stable while the compression ratio α remains constant". This inference should be valid in

absence of applied external compression in non-growing tissues.

ACKNOWLEDGMENTS

This research was supported by research grants from the Brazilian Scientific and Technological Council (CNPq).

RESUMO

A fração do perímetro da parede celular em contato com células vizinha foi denominada razão de compressão (α). Razão de compressão zero indica volume intercelular (v_G , v/v) máximo e contato negligível entre as células, enquanto $\alpha=1$ ocorre quando há completa aderência com as células vizinhas ($v_G=0$). O volume (gasoso) intercelular máximo (β , v/v), quando $\alpha=0$, foi 0,593, 0,2146 e 0,0931 para latices triangulares, quadradas e hexagonais. A equação derivada para relacionar α , β and v_G nas latices estudadas foi $\alpha=1 - (v_G/\beta)^{1/2}$. A razão de compressão foi em seguida empregada para estabelecer a relação $P_S=p/\alpha$ entre a pressão de turgescência (P_S) e a pressão de agregação (p), definida com a compressão para manter uma camada de células no seu lugar. As deformações intercelulares de batata-doce obtidas com procedimentos de câmara-depressão foram empregados para obter informações sobre as variações de α , v_G , p e P_S em função da compressão empregando módulos de elasticidade transversal e volumétrico. A constância de α foi sugerida como critério de estabilidade de latices celulares.

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Received: August 17, 1999;

Revised: October 26, 1999;

Accepted: July 12, 2000.