

Modelling of carrot tissue as a fluid-filled foam

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Experimental values of the stiffness of carrot tissue were compared with the predictions from models of fluid-filled closed cell foams. Compared to an experimental value of 7 MPa for fresh carrot, predictions gave moduli in the range 2 to 33 MPa based on a compressible fluid, an isotonic state turgor pressure of 0.8 MPa, a cell wall modulus of 100 MPa and cell lengths from 54 to 3 times the wall thickness. The modulus was predicted to increase linearly with turgor pressure in agreement with experiment for turgor pressures up to about 1 MPa, whereafter the experimental modulus increased more sharply, reaching a value of 14 MPa at a turgor pressure of 2.1 MPa, closer to the predicted rate of increase in an earlier shell model. Predictions based on an incompressible fluid gave initial and equilibrium moduli of 14 and 2 MPa, respectively, in agreement with the experimental values at high and low levels of turgor, again assuming a cell wall modulus of 100 MPa but requiring small cells of length ratio less than three times their wall thickness.

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1. Introduction

Studies of plant food texture are dependent on defining structure and mechanical properties at a number of length scales [1, 2]. Relating the mechanics to the structure of plant material is therefore necessary but has rarely been achieved in the literature. For instance, Nilsson *et al.* [3] found good agreement between the calculated modulus and their experimental results when studying the stiffness of potato as a function of turgor. Pitt [4] subsequently modelled cells as thin-walled fluid-filled vessels and established a relationship between stiffness and turgor. It is evident that turgor plays a major role and other parameters need to be taken into consideration such as the mechanical properties of the cell wall itself. In general, it is well accepted that the structure of plant tissue material resembles that of a closed cell foam filled with an incompressible liquid [5, 6]. Comparing biological material to a foam structure and modelling its mechanical properties has been used by Rajan [7] on bone, Hayter and Smith [8] on cereal extrudates, Attenburrow *et al.* [9] on food sponge and Maiti *et al.* [10] on wood where a scaling law between relative mechanical property and relative density operates [6]:

$$\frac{E_c}{E_m} = k \left(\frac{\rho_c}{\rho_m} \right)^n \quad (1)$$

where the E_c is the modulus of the cellular structure, E_m is the modulus of the cell wall, ρ_c is the density of the cellular structure and ρ_m is the density of the cell wall and k is a constant.

This approach has generally been applied to air-filled foams although some studies have used this type of relationship for plant tissues. Gibson *et al.* [11] have

modelled the iris leaf using sandwich beam theory with fibre composite layers separated by a low density foam core, although they did not include any turgor variation. Niklas [12] used the Gibson and Ashby scaling law to describe the variously-dried flower stalks of *Allium sativum* and found a relationship for relative elastic modulus which obeyed a cube power of relative density. Vincent [13] found a power law relationship between shear stiffness and bulk density for parenchymatous tissue of different apple cultivars.

A later development of the theory allowed for multiple contributions to the mechanical properties of foams. Gibson and Ashby [6] gave the stiffness of a closed cell foam filled with a compressible fluid as follows:

$$\frac{E_c}{E_m} = C_1 \phi^2 \left(\frac{\rho_c}{\rho_m} \right)^2 + C_2 (1 - \phi) \frac{\rho_c}{\rho_m} + C_3 \frac{P}{E_m} \frac{(1 - 2\nu_c)}{(1 - \rho_c/\rho_m)} \quad (2)$$

This equation takes into account the solid fraction of the cell wall, ϕ , the internal pressure of the cell, P , and the Poisson ratio, ν_c . Gibson and Ashby [6] assumed that the constants $C_1 = C_2 = C_3 = 1$. This equation is composed of three contributions, the first one being related to the stiffness of the edges (bending), the second one describing the stiffness of the faces (stretching) and the third one being related to the contribution of the compression of the fluid in the cells.

However Equation 2 applies to gases as compressible fluids. Gibson and Ashby [6] indicate that the fluid term is normally small at low gas pressures near atmospheric, although they commented it would become significant at higher pressures. Since the plant cell is

not impermeable and the liquid will be driven through the membrane there may be some basis for a pressure term as conceived for a compressible fluid although the assumption of Boyle's law is broken. Notwithstanding, the Gibson and Ashby theory was applied to closed cell foams to assess the turgor contribution of the intracellular liquid and how the foam dimensions affect stiffness. Some confidence in an expression of this type is based on the Nilsson *et al.* [3] model of deforming potato tissue. They assumed the cell thickness was much less than the cell radius and derived an equation for the case of spherical cells:

$$E_c = 3.6P + 2.5 \quad (3)$$

This equation is of a similar form to Equation 2.

The results are also compared with the foam theory developed for liquid-filled foams by Warner and Edwards [14], which gives limits for modulus corresponding to initial application of stress and later equilibrium. The upper, E_{cu} , and lower, E_{cl} , limits are given by:

$$E_{cu} = E_m \left(\frac{t^2}{l^2} + \frac{t^4}{l^4} \right) \quad (4)$$

$$E_{cl} = E_m \left(\frac{t^4}{l^4} \right) \quad (5)$$

In the present study, the stiffness of carrot tissue was modelled as a fluid-filled foam using the approach for compressible gases proposed by Gibson and Ashby [6] (Equation 2) which takes into account the stiffness of the cell wall at the edges and the faces of the cells and the turgor pressure, and is based on several assumptions concerning the geometry of the cells in carrot tissue. The Warner and Edwards prediction (Equations 4 and 5) is also applied together with the Nilsson equation (Equation 3).

2. Methods

2.1. Preparation of carrot strips

Carrots were washed thoroughly and strips of tissue were removed from the phloem parenchyma using a slicer (Baker and Nixon, Norwich, UK). This enabled the production of specimens of homogenous composition. The width and the length were accurately measured using a strip cutter designed in our laboratory consisting of a supporting metal plate and a parallel sliding metal strip measuring with precision the width of the specimen. The dimensions were typically 20 mm length, 1–2 mm thick and 7 mm wide. Strip ends were glued using cyanoacrylate (Eurobond Adhesives Ltd., Sittingbourne, UK) to small stainless steel square shaped plates (8 × 8 mm).

2.2. Osmotic manipulation and volume measurement of carrot tissues

The cell turgor pressure was manipulated by soaking the carrot strips in different solutions of mannitol ($C_6H_{14}O_6$) (Sigma, Poole, UK). The concentrations of

the solutions used were 0, 0.1, 0.3, 0.8 and 1 M. The strips were soaked overnight at room temperature and then tested the following day.

Before mechanical testing, dimensions of strips were measured (3 replicates) carefully using vernier callipers before and after each osmotic treatment after lightly blotting with absorbing paper.

2.3. Modulus measurements

The Polymer Laboratories Dynamic Mechanical Thermal Analyser (DMTA) was used in the tensile mode at a frequency of 1 Hz and strain level setting of $1/\sqrt{2}$ (corresponding to a nominal peak to peak displacement of 11 μm). The heating rate was 2°C min^{-1} . This follows a similar approach for bean tissues reported earlier [15]. In this mode, the sample was mounted such that its length was parallel to the drive direction. The gap between the drive shaft and the frame was adjusted to 1.5 cm. Glueing tissues to the steel plates which were clamped to the drive-shaft and the frame of the tensile head prevented any slippage in the DMTA. Three samples were tested for each mannitol concentration.

3. Results and discussion

3.1. The turgor pressure of carrot tissue

It is assumed in these calculations that the solute content of the cell remains constant and the water potential is mainly caused by water. In that case, the osmotic pressure, π , is proportional to the changes in cell volume. Therefore, π is expressed as follows [16, 17]:

$$\pi = \pi^0 \left(\frac{V^0}{V} \right) \quad (6)$$

where π^0 is the osmotic pressure at incipient plasmolysis, V^0 is the cell volume at incipient plasmolysis and V is the cell volume in the given osmoticum solution [17]. It is also assumed that the volume change in carrot tissue is proportional to the changes in cell volume. The turgor pressure, P is determined by the difference of ψ and π , where ψ is the water potential [16], expressed by the Gas law: $\psi = -MRT$ where M is the molarity, T is the temperature (K) and R is the molar gas constant. The turgor pressure at incipient plasmolysis is assumed to be zero [17] and hence $\pi^0 = \psi = -M^0RT$, where M^0 is the molarity of the osmoticum at incipient plasmolysis.

Incipient plasmolysis is obtained from the osmoticum concentration corresponding to least change in volume [17]. A concentration of mannitol of 0.8 M was found from the relative change in volume, $(V - V_i)/V_i$ plotted against mannitol concentration in Fig. 1, where V_i and V are the initial volume and volume of carrot tissue after mannitol treatment, respectively. The volume at incipient plasmolysis, V^0 , was also determined to calculate π from Equation 6. Values of -1.9 MPa and -1.1 MPa were obtained for π and ψ , respectively, resulting in a value of 0.8 MPa for P , corresponding to tissue manipulated to the isotonic condition as indicated by $(V - V_i)/V_i = 0$ in Fig. 1. This corresponds to a mannitol concentration of 0.42 M.

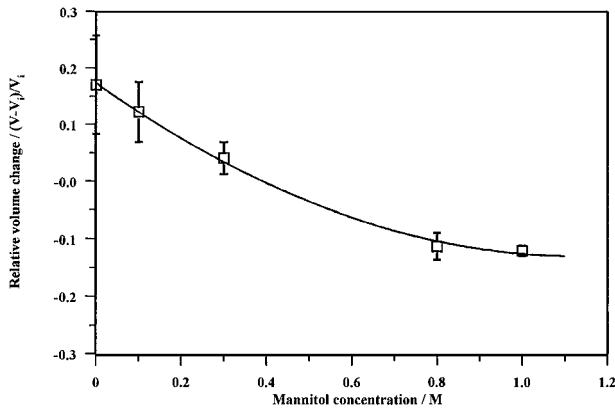


Figure 1 Relative volume change as a function of mannitol concentration (M). Means and standard deviations shown.

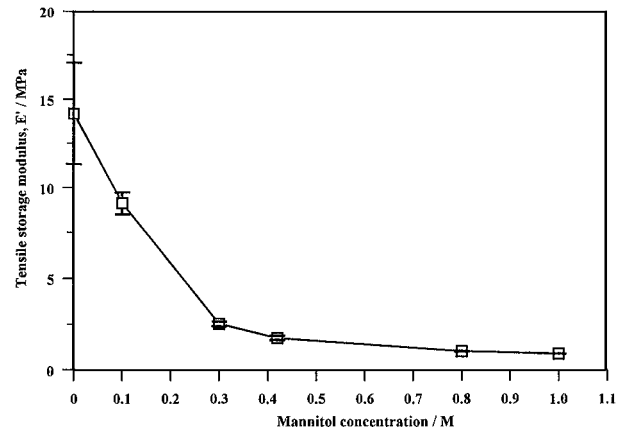


Figure 2 Tensile storage modulus, E' , at 20°C as a function of mannitol concentration (M). Means and standard deviations shown.

These results are comparable to data reported by McGarry [18] who found values of approximately -1.1 MPa and -0.8 MPa for π and ψ , respectively. McGarry [18] measured these pressures directly whereas the values obtained in the present work were calculated from Equation 6. He calculated the turgor pressure of phloem tissue in two varieties of carrot (Camden and Tamino) and found values varying between 0.38 and 0.46 MPa. He also reported that turgor pressure decreased from approximately 0.8 to 0.2 MPa for another variety (Narbonne). It is therefore evident that the turgor pressure of plant tissue would vary within a test piece and from one variety to another.

Manipulation of the turgor of carrot strips was carried out using mannitol as an osmoticum and the elastic modulus measured using DMTA. Fig. 2 shows that the tensile storage modulus (E') decreased with increasing mannitol concentration corresponding to a reduction in turgor. An increase in stiffness with increasing turgor was observed by Pitt and Chen [19] and Jackman *et al.* [20] who studied the rheology of apple and tomato tissue at various turgor pressures, respectively. Ramana and Taylor [21] investigated the complex shear modulus (G^*) of carrot cells as a function of turgidity. Their values, of the order 1 to 6 kPa, are lower than that obtained in the present study (Table I), although they used cells rather than tissues.

Rojas *et al.* [22] found a maximum in the firmness of melon at 0.4 M mannitol from a study in the range of 0 to 0.8 M mannitol. Nilsson *et al.* [3] expressed the Young's modulus as a linear function of turgor pressure in potato and showed that experimental results agreed with the mathematical model for very thin specimens. The authors only mentioned the cross section of specimens to be 10 mm^2 , comparable to the dimensions of the carrot strips that is 7 to 14 mm^2 cross section. Their prediction of the modulus was based on the assumption that plant cells follow Hooke's law which is the case for small deformation. Furthermore, Jackman *et al.* [20] observed a linear relationship between stiffness and turgor pressure and found a quadratic equation relating the turgor pressure to the osmoticum concentration. When combining these two relationships linking stiffness to turgor pressure and turgor pressure to osmoticum concentration, it is evident that the stiffness follows a non-linear relationship with the osmoticum concentration as demonstrated by the measurements of Ramana and Taylor [21] and the results of the present study (Fig. 2).

Tissue manipulated under an isotonic condition is indicated by $(V - V_i)/V_i = 0$ in Fig. 1 which corresponds to a mannitol concentration of 0.42 M. Fig. 2 shows that the tissue modulus at this molarity was lower

TABLE I Estimated Young's modulus of fresh carrot tissue according to Gibson and Ashby (Equations 2) and Warner and Edwards (Equations 4 and 5) models

		E_c prediction				E' experimental		
		$E_m = 10$ (MPa) (55% ww)		$E_m = 100$ (MPa) (40% ww)		$E_m = 2000$ (MPa) (0% ww)		7 ± 1 (MPa)
		Gibson-Ashby model ^a (Equation 2)	Warner-Edwards model (Equations 4 and 5)	Gibson-Ashby model ^a (Equation 2)	Warner-Edwards model (Equations 4 and 5)	Gibson-Ashby model ^a (Equation 2)	Warner-Edwards model (Equations 4 and 5)	
$l = 4.5 \mu\text{m}$	3.3		L: 0.2	32.8	L: 1.6	654.8	L: 32	
$t = 1.6 \mu\text{m}$			U: 1.4		U: 14.2		U: 285	
$l = 87 \mu\text{m}$	0.2		L: 10^{-6}	2.4	L: 10^{-5}	42.0	L: 10^{-4}	
$t = 1.6 \mu\text{m}$			U: 0.003		U: 0.03		U: 0.67	

E_m , the modulus of cell wall material at various water contents, ww (wet weight basis) [30].

l , the cell wall length; t the cell wall thickness.

L, lower limit, E_{cl} ; U, upper limit, E_{cu} .

^aAssumes a turgor pressure of 0.8 MPa calculated from the isotonic state.

than that of the fresh specimens (Table I). This kind of discrepancy was previously observed by Ramana and Taylor [21] and was evident in comparison of fresh with isotonically equilibrated melon [22].

3.2. Predictions

The Gibson and Ashby [6] equation (Equation 2) takes into account the solid fraction of the cell wall, ϕ , the density of the cell wall, ρ_m , the density of the foam itself or bulk density, ρ_c , the turgor pressure of the cell, P , the Poisson ratio, ν_c and the modulus of the cell wall, E_m . When applying this equation to the determination of the stiffness of vegetable tissue, several terms require specification.

3.2.1. Cell geometry: a tetrakaidecahedron

When observing the geometry of cells of plant tissue, several shapes can be distinguished and in this regard, considering the latter as a polyhedral cell, more particularly, a tetrakaidecahedron has been suggested by several authors such as Kimmel [5] who reviewed the prediction of the modulus for pressure supported cellular systems and Nilsson *et al.* [3] who used the tetrakaidecahedron geometry to predict the modulus of potato tissue. Gao and Pitt [23] also used this cell shape and proved that this could model the plant cell realistically. As a consequence, this geometry is used for carrot tissue in this study.

3.2.2. Cell wall thickness, t

The cell wall thickness has not been measured directly. It was assumed that the thickness of the edge will be similar to that of the faces when considering the cell geometry. This approximation is not necessarily true as it is likely that the thickening of the cell wall, ϕ , would be greater at the edges of the cell than that at the faces. Fuchigami *et al.* [24] presented several scanning electron micrographs (SEMs) of fresh carrot parenchyma and an approximate value of $1.19 \mu\text{m}$ has been calculated. Another value of $2.02 \mu\text{m}$ has been determined based on SEMs of carrot tissue reported by McGarry [25], in relatively good agreement with the previous value. However, Carpita [26] gave a value of $0.1 \mu\text{m}$ for carrot cell suspensions. For the purpose of the calculation, a mean value of $1.6 \mu\text{m}$ was chosen, also in agreement with thickness of approximately, $1 \mu\text{m}$, calculated on micrographs published by Préstamo *et al.* [27] who studied the microstructure of carrot cells.

3.2.3. Length of the cell, l

The length of the polyhedron, l , has been measured on the SEMs presented by McGarry [25] who studied carrot tissue structure. The range of length was found to be between $4.5 \mu\text{m}$ and $87 \mu\text{m}$. These limits will be used for the following calculation. Light micrographs given by Fuchigami *et al.* [28] and Préstamo *et al.* [27] also show cells of diameter in this range. Environmental scanning electron microscopy, which has the advantage of allowing examination of samples without preparative

artefacts, has been used by Thiel and Donald [29] who give a range of $30\text{--}50 \mu\text{m}$ for carrot cell diameters.

3.2.4. The stiffness of cell wall

Previous experiments have shown that the storage modulus of pressed carrot cell wall material determined by DMTA decreased from 2000 MPa to 10 MPa with increasing water content from 10% to just over 50% (wet weight basis, w.w.b.), with a modulus value of 100 MPa for 35–40% (w.w.b.) [30]. A stiffness of 2000 MPa would agree with the values obtained by Hiller *et al.* [31] from modelling micro-penetration of potato tissue. In general, moduli $>1 \text{ GPa}$ are associated with glassy materials [30, 32]. For comparison, recent measurement of the tensile modulus of the cell wall of the giant alga *Chara corallina* was in the range 440–660 MPa [33].

3.2.5. The cell wall fraction in the edges, ϕ

It is possible to determine the cell wall fraction in the edges, ϕ , and consequently the cell wall fraction in the faces, $(1 - \phi)$ from the thickness of the cell wall, t , and the length, l . Gibson and Ashby [6] reported the equation linking ϕ to the thickness and the length, l , for a three dimensional tetrakaidecahedron:

$$\phi = \frac{t_e^2}{t_e^2 + \frac{Z_f}{\bar{n}} t_f l} \quad (7)$$

where t_e , is the thickness at the edges, t_f , is the thickness at the faces, Z_f , is the number of faces that meet at an edge, \bar{n} , is the average number of edges per face on a single cell and l is the length of the cell. The thickness of the edges was assumed to be equal to that of the faces, defined as t . In a tetrakaidecahedron, Z_f equals 3 and \bar{n} equals 5.14 [6]. Considering the thickness chosen to equal $1.6 \mu\text{m}$ and the length to range between 4.5 and $87 \mu\text{m}$, ϕ will lie between 0.38 and 0.03.

3.2.6. The Poisson ratio, ν_c

Ahmed *et al.* [34] used a value of 0.25 when calculating the modulus of deformability of raw and variously processed carrot discs. A value of $\nu_c = 1/3$ was suggested by Gibson and Ashby [6] for filled closed foams and Nilsson *et al.* [3] also used a value of $1/3$ when they modelled the rigidity of potato tissue. Mohsenin [35] reviewed the Poisson ratio for various plant materials and reported values of 0.21 to 0.49 for apple and potato, respectively. A value of $1/3$ was adopted for use in Equation 2.

3.2.7. The relative density, ρ_c/ρ_m

The relative density is calculated from the cell wall thickness and cell length [6], and for a tetrakaidecahedron is:

$$\frac{\rho_c}{\rho_m} = 1.18 \frac{t}{l} \quad (8)$$

where ρ_c is the bulk density and ρ_m is the density of the cell wall. With l , the length of the carrot cell, varying

between 4.5 and 87 μm and t , the thickness equalling 1.6 μm , the relative density, ρ_c/ρ_m , will vary from 0.42 to 0.02. As noted in Section 3.2.5, ϕ correspondingly varies from 0.38 to 0.03.

3.2.8. Calculation of Young's modulus of the tissue

Based on the assumptions made earlier and the values of the various parameters, the Young's modulus, E_c , has been calculated and the values are presented in Table I. It shows that the modulus varied from 0.2 to 655 MPa. When compared to the DMTA tensile storage modulus for fresh carrot specimens, of approximately 7 MPa, it is obvious that taking a value of 2000 MPa for the modulus of cell wall (E_m) overestimates the Young's modulus of fresh tissue. The experimental modulus of 7 MPa for carrot is comparable with reported values of 7–9 MPa using other methods [36, 37].

The relative density, ρ_c/ρ_m , varied from 0.02 to 0.42 and is defined geometrically (Section 3.2.7). This should not be confused with the relative density calculated from the masses of the tissue and cell wall. For example, Nielsen and Martens [37] reported a density of 1017 $\text{kg} \cdot \text{m}^{-3}$ for carrot tissue which includes the mass of the cellular fluid. Taking the density of the cell wall as 1500 $\text{kg} \cdot \text{m}^{-3}$ [10], the ratio ρ_c/ρ_m is 0.68. However a range of ρ_c/ρ_m from 0.10 to 0.16 was calculated by Niklas [12], again based on mass of the tissue, for progressively dried *Allium sativum* flower stalks.

The cell wall solid fraction at the edges, ϕ , could only be estimated and a more accurate determination would have required a thorough measurement of cell wall thickness at the edges and at the faces of the carrot cells, from SEMs for instance, which was not performed. Nevertheless, the approach proposed by Gibson and Ashby [6] for fluid-filled closed cell foams, appears to predict the stiffness of carrot tissue providing several physical parameters characterising the cell wall are known or can be accurately measured.

3.2.9. Calculation of effect of turgor pressure

Fig. 3 shows the experimental storage moduli, E' , from Fig. 2, now plotted as a function of initial turgor pressures calculated for different mannitol concentrations. Osmotic pressures were calculated from Equation 6 using the data of Fig. 1, which shows the relative volume change as a function of mannitol concentration. Equations 2 and 3 predict a linear dependence of stiffness on initial turgor pressure. Furthermore, Jackman *et al.* [20] observed a linear relationship between stiffness and turgor pressure of up to 0.45 MPa for tomato.

The contribution of the pressure term is small as Gibson and Ashby suggested for pressures near atmospheric. This is shown by the almost constant moduli in Fig. 3 for each of the conditions. The prediction underestimated the observed values at pressures above 1.1 MPa for high values of cell length (87 μm) at wall moduli of 10 or 100 MPa, although high moduli were predicted for the low values of cell length (4.5 μm) at $E_m = 100$ MPa (Fig. 3). A length of 10 μm resulted in

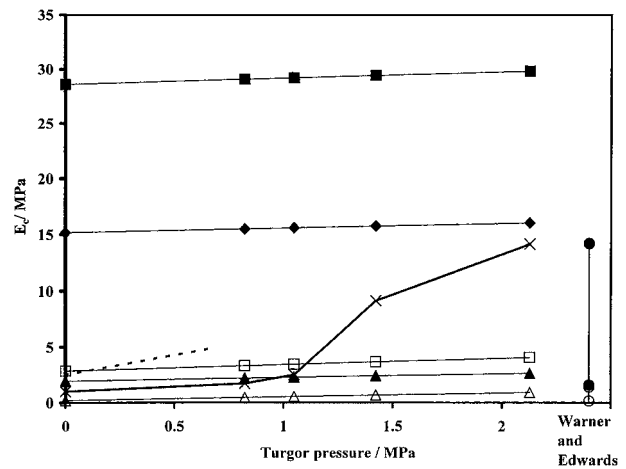


Figure 3 Prediction of cellular modulus, E_c , as a function of osmotic pressure, P , using Gibson and Ashby [6] (Equation 2) for: wall modulus, E_m , 100 MPa; cell length/cell wall thickness ratio of 2.8 (■), 6.3 (◆) and 54 (▲); wall modulus, E_m , 10 MPa; cell length/cell wall thickness of 2.8 (□) and 54 (△). Warner and Edwards [14] (Equations 4 and 5) limits, E_{cu} and E_{cl} , cell length/cell wall thickness ratio of 2.8 for: wall modulus, E_m , of 100 MPa (●); 10 MPa (○). Nilsson *et al.* [3] (Equation 3) (---). Experimental tensile storage moduli, E' , for carrot (—X—) (from Fig. 2).

a predicted modulus in agreement with the experiment at a turgor of 2 MPa. One possibility for the discrepancy between prediction and experiment is the assumed values of the constants in Equation 2 are not unity but depend on the turgor range. The fit is reasonable for turgor pressures up to 0.8 MPa (osmoticum range from 1 to 0.42 M mannitol) where tissues are plasmolysed, but the value of C_3 for pressures above 0.8 MPa where the tissues are turgid (mannitol concentration less than 0.42 M) could be significantly greater than C_2 and C_1 .

The modelling prediction of Nilsson *et al.* [3] for potato (Equation 3) is also shown in Fig. 3 within their pressure range up to 0.6 MPa. The predicted stiffness is higher than the experimental data for carrot. Lin and Pitt [17] reported that the stiffness of potato and apple increased with turgor pressure up to 0.4 MPa after which there was little increase. Their data are in better agreement with the magnitude of the Nilsson *et al.* [3] prediction than the carrot experimental results.

The Warner and Edwards approach [14] is more physically appropriate for modelling liquid-filled foams and predicts two levels of stiffness, with a predicted high initial value which falls to a lower value. These values are closest to the experimental values at 0 and 2 MPa turgor for a wall modulus of 100 MPa (Fig. 3), but only for the cell length of 4.5 μm (Table I).

4. Conclusion

The structure of raw carrot tissue has been compared to that of a closed cell foam filled with a “compressible” liquid or in reality an incompressible liquid that is forced through the permeable cell wall and membrane. Subject to this assumption, the results showed that the effect of turgor pressure on stiffness was through a linear term which was only adequate at pressures up to 1 MPa, just above the isotonic state pressure of 0.8 MPa. Prediction of the higher moduli could only be made with

a wall modulus of 100 MPa and cells of length over six times their wall thickness. The treatment of the tissue as a closed cell liquid-filled foam gives upper and lower limits which agreed with the experimental data best for a wall modulus of 100 MPa and smaller cells of length less than three times the wall thickness.

This analysis indicated that the foam stiffness depended on the stiffness of the cell wall which in turn depends to a great extent on the water content. Fruits and vegetables contain approximately 80 to 90% water and therefore it is likely that the *in vivo* cell wall will be in a hydrated state. Additionally, the thickness of the cell wall was assumed to be uniform which leads to the simplification in the calculation of the cell wall fraction in the edges and the faces of the cells. The turgor pressure has been estimated but the value could only represent an average of the turgor pressures existing in the cells, individually. The turgor for a particular vegetable will vary from one type of tissue to another making its determination difficult.

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References

1. R. L. JACKMAN and D. W. STANLEY, *Trends Food Sci. Tech.* **6** (1995) 187.
2. K. W. WALDRON, A. C. SMITH, A. J. PARR, A. NG and M. L. PARKER, *ibid.* **8** (1997) 213.
3. S. B. NILSSON, C. H. HERTZ and S. FALK, *Physiol. Plant.* **11** (1958) 818.
4. R. E. PITT, *Trans. Amer. Soc. Agric. Engrs.* **25** (1982) 1776.
5. E. KIMMEL, *Int. J. Mech. Sci.* **34** (1992) 809.
6. L. J. GIBSON and M. F. ASHBY, "Cellular Solids, Structure and Properties" (Cambridge University Press, Cambridge, UK, 1997).
7. K. RAJAN, *J. Mater. Sci. Lett.* **4** (1985) 609.
8. A.-L. HAYTER and A. C. SMITH, *J. Mater. Sci.* **23** (1988) 736.
9. G. E. ATTENBURROW, R. M. GOODBAND, L. J. TAYLOR and P. J. LILFORD, *J. Cereal Sci.* **9** (1989) 61.
10. S. K. MAITI, L. J. GIBSON and M. F. ASHBY, *Acta. Metall.* **32** (1984) 1963.
11. L. J. GIBSON, M. F. ASHBY and K. E. EASTERLING, *J. Mater. Sci.* **23** (1988) 3041.
12. K. J. NIKLAS, *Amer. J. Bot.* **76** (1989) 929.
13. J. F. V. VINCENT, *J. Sci. Food Agric.* **47** (1989) 443.
14. M. WARNER and S. F. EDWARDS, *Europhys. Lett.* **5** (1988) 623.
15. A. J. DOWNIE, D. M. R. GEORGET, A. C. SMITH and K. W. WALDRON, *Food Sci. Technol.* **30** (1997) 312.
16. P. J. KRAMER and J. S. BOYER, "Water Relations of Plants and Soils" (Academic Press, San Diego, USA, 1995).
17. T.-T. LIN and R. E. PITT, *J. Texture Stud.* **17** (1986) 291.
18. A. MCGARRY, *J. Hort. Sci.* **68** (1993) 431.
19. R. E. PITT and H. L. CHEN, *Trans. Amer. Soc. Agric. Engrs.* **26** (1983) 1275.
20. R. L. JACKMAN, A. G. MARANGONI and D. W. STANLEY, *J. Texture Stud.* **23** (1992) 491.
21. S. V. RAMANA and A. J. TAYLOR, *J. Sci. Food Agric.* **64** (1994) 519.
22. A. M. ROJAS, M. A. CASTRO, S. M. ALZAMORA and L. N. GERSCHENSON, *J. Food Sci.* **66** (2001) 111.
23. Q. GAO and R. E. PITT, *Trans. Amer. Soc. Agric. Engrs.* **34** (1991) 232.
24. M. FUCHIGAMI, N. HYAKUMOTO and K. MIYAZAKI, *J. Food Sci.* **60** (1995) 137.
25. A. MCGARRY, *Ann. Bot.* **75** (1995) 157.
26. N. C. CARPITA, *Plant Physiol.* **79** (1985) 485.
27. G. PRÉSTAMO, C. FUSTER and M. C. RISUEÑO, *J. Sci. Food Agric.* **77** (1998) 223.
28. M. FUCHIGAMI, K. MIYAZAKI and N. HYAKUMOTO, *J. Food Sci.* **60** (1995) 132.
29. B. L. THIEL and A. M. DONALD, *J. Text. Studies* **31** (2000) 437.
30. D. M. R. GEORGET, A. NG, A. C. SMITH and K. W. WALDRON, *J. Sci. Food Agric.* **78** (1998) 73.
31. S. HILLER, D. M. BRUCE and G. JERONIMIDIS, *J. Texture Stud.* **27** (1996) 559.
32. D. R. COFFIN, M. L. FISHMAN and T. V. LY, *J. Appl. Poly. Sci.* **61** (1996) 71.
33. G. A. TOOLE, P. A. GUNNING, M. L. PARKER, A. C. SMITH and K. W. WALDRON, *Planta* **212** (2001) 606.
34. E. M. AHMED, S. MIRZA and A. G. ARREOLA, *J. Food Qual.* **14** (1991) 321.
35. N. N. MOHSENIN, *J. Texture Stud.* **8** (1977) 169.
36. B. E. VERLINDEN, T. DE BARSY, J. DE BAERDEMAEKER and R. DELTOUR, *ibid.* **27** (1996) 15.
37. M. NIELSEN and H. J. MARTENS, *J. Food Sci.* **62** (1997) 1167.

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