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Mathematical modelling of the cellular mechanics of plants

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The complex mechanical behaviour of plant tissues reflects the complexity of their structure and material properties. Modelling has been widely used in studies of how cell walls, single cells and tissue respond to loading, both externally applied loading and loads on the cell wall resulting from changes in the pressure within fluid-filled cells. This paper reviews what approaches have been taken to modelling and simulation of cell wall, cell and tissue mechanics, and to what extent models have been successful in predicting mechanical behaviour. Advances in understanding of cell wall ultrastructure and the control of cell growth present opportunities for modelling to clarify how growth-related mechanical properties arise from wall polymeric structure and biochemistry.

Keywords: modelling; mechanics; materials; cell wall; cell; plant

1. INTRODUCTION

From resisting wind and gravity to anchoring themselves in the soil, mature plants achieve mechanically demanding tasks. The structural mechanical properties of the plant result from its mature tissues, specifically from the thickened, lignified walls of cells in woody and sclerenchymatous tissues. However, as the plant develops, the mechanical properties of its primary tissues are the key to overcoming challenges posed by growth. Cells expand and divide in a coordinated manner to generate tissue and plant structure, while at all times supporting the intracellular pressure. The pressure, up to 10 atmospheres, allows the roots to grow through soil and the organs to withstand imposed loads. How the tissue properties arise from the wall and cellular structures is of interest from several viewpoints. As efficient structures using small quantities of material to achieve their structural goals, plants may be models or inspiration for engineered structures. The fact that the wall is 'on duty' during construction is notable. Both the construction and adaptation of the cell wall during growth, and the genetic control over these complex processes, are being elucidated by cell biology research. Mathematical modelling of cellular mechanics can contribute to the structure–function debate by exploring feasibility of wall structural models. In addition to these reasons for academic interest, the plant cell wall is of great practical significance; as a food for ruminant animals, as construction material, the basis of textiles and the potential source of novel biochemicals. For these varied reasons, research continues into the mechanical attributes of cell walls and how they arise from structure.

On a mechanical level, plants are hierarchical structures made of materials with subtle properties that can be changed by the plant. In understanding the mechanics of plants, quantitative descriptions or models have great value, because a model enables the ideas underlying it to be tested by experiment. Any model is an idealization of the real system, so its predictive abilities are constrained by the realism with which the structure and materials are abstracted. It may be adequate in the case of modelling the bending of a tree limb under its own weight to consider the limb as a tapering beam made of continuum solid material, perhaps with location-dependent properties. But this approach is less tenable when the mechanics of a leaf or shoot are under scrutiny because there may be only a few cells across the smallest dimension. At this scale, the continuum approach becomes unacceptable because the response to external loading or imposed deflection of the structure depends on the interplay between the walls and fluid contents of a few cells, so modelling of the cellular nature of the structure is called for. At the next higher magnification, the subtleties of the behaviour of cell walls make them a modelling challenge, in which the objective may be to quantify how the structural polymers give rise to wall mechanical properties. Linking across these hierarchies of structure to summarize some functionality derived from a lower level is a further modelling challenge.

This paper reviews the modelling of the mechanics of plant materials from the level of cell wall to tissue, and illustrates how modelling can contribute to the understanding of these materials. The mechanical properties of the material of plants originates in the cell wall. Unless the wall or the intercellular bond fails, the wall and its interaction with the cell contents determine the mechanical behaviour, so this review focuses to a large extent on modelling of wall properties. This is supplemented by less extensive sections on modelling the mechanics of cells and tissue.

2. STRUCTURE OF CELL WALL, CELL AND TISSUE

Wall structure and composition differ markedly between species and between tissues, specialized as they

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are, from the thin, hydrated walls of parenchyma cells (e.g. the flesh of a potato tuber) through thickened-wall, hydrated, collenchyma cells (e.g. celery stem fibre) to cells that have developed a massively thick wall of closely packed cellulose fibres; fibre cells of wood are bound and waterproofed with lignin, whereas sclerenchyma fibres found in flax and cotton have little lignin. The mechanical properties of these cell types are very different, but all arise from their composition and architecture. For a detailed explanation of wall biochemistry and physiology, and a useful summary of wall mechanical behaviour, the reader is referred to Brett & Waldron (1996).

The primary wall comprises a fibrous network of cellulose microfibrils and hemicellulose that is coextensive with a matrix of pectic polymers. The plasma membrane within the wall gives the structure low permeability to water so that the fluid take-up, driven by osmosis, can develop the wall stress needed to support stems and leaves against gravity. The high tensile strength of the cellulose fibrils enables the wall to withstand this stress. Structure and hence properties of the primary wall are influenced by the cell's bioprocesses, under genetic control. Structure and composition of primary cell walls are reviewed by Carpita & Gibeaut (1993) and McCann & Roberts (1994). Conceptual models have been hypothesized of primary wall structure at the molecular scale, e.g. by Carpita & Gibeaut (1993), but no conceptual model has yet, to my knowledge, been validated or used as the basis of a mathematical model.

Regarding the relation between growth and turgor, it is now known that growth is not initiated by an increase in turgor. The essence of cell growth is extension of the wall under the control of the cell (McQueen-Mason 1995). Relaxation of stress in the wall, achieved by rearrangement of wall polymers and mediated by enzyme and acidity in a complex manner, reduces turgor. This initiates the uptake of water and hence the expansion of the cell. Introgression of new polymers into the wall follows. Although wall behaviour is well described from experiments on excised, de-natured sections of, for example hypocotyls, a sound theoretical basis for modelling the mechanics of the wall has yet to be established. This is arguably the next major challenge for plant cell modelling. A good summary of recent experimental work on the regulation of physical and biochemical changes to cell walls in growing plants is given by Schopfer (2000).

In those cells that form a secondary wall, this occurs by thickening of the original primary wall by the addition of closely packed cellulose fibres. The fibre structure determines properties; for walls with a helicoidal structure, in which the fibre orientation alters between successive layers, the properties in the plane of the wall are isotropic, whereas with a helical fibre structure, in which orientation is consistent from layer to layer, the properties are highly anisotropic, being dependent on helix angle. In some tissues, for example wood and sclerenchyma, the pectin matrix is replaced by lignin, which bonds the fibres more strongly than the pectin it replaces. Lignification eliminates water from the wall to result in a structure that is hydrophobic and rigidified. Removal of water eliminates the viscosity of the wall and so results in a material that is able to resist compression, bending and shear; forces off-axis to the cellulose fibril direction are transmitted to the fibres through shear properties of the matrix. In other tissues, for example flax stem fibre, from which linen is manufactured, and cotton, the wall becomes thickened, but little lignin deposited. For more details of the biochemistry of secondary wall formation, the reader is referred to Brett & Waldron (1996).

In mechanical terms, a tissue is simply a conglomerate of a similar type of cells adhered together. The attachment between cells ranges from strong enough such that failure occurs by wall rupture, e.g. in potato tuber, to sufficiently weak that cells separate without rupturing, e.g. a 'mealy' textured apple. Hence tissue properties are very dependent on cell attachment, and a tissue model must, implicitly or explicitly, include this factor.

Readers interested in pursuing the subject of the mechanics up to the scale of organs and plants are directed to Niklas (1992).

3. MECHANICAL PROPERTIES AND MODELLING APPROACHES

The mechanical behaviour of materials may be divided into two categories, namely fundamental physical properties of a material, such as elastic modulus, and properties that depend on the particular test piece of material, such as strength. All the material in a simple test piece is involved in producing the extension in response to an applied force, whereas the strength is determined by the stresses in the vicinity of flaws in the particular test sample. For test samples it is not usually possible to know the number or size of flaws, and as a consequence strength can be predicted only if a statistical description of flaws is available. For these reasons, most modelling of cellular tissue in plants has focused on predictions related to the force–deflection behaviour or, put more generally, the state of stress and strain in the modelled entity. This is despite the fact that some applications for a good understanding of the mechanics of fresh plant tissue relate to aspects where tissue failure is crucial, e.g. cracking and bruising of fruit and vegetable tissue. However, because strength is a function of both stress and flaw dimension, the prediction of stress is certainly of value in strength calculations. Readers interested in fracture are directed to Jeronimidis (1980, 1991) and Vincent (1990).

When modelling cellular plant material, an important question is, at what level of hierarchy is a material considered as a continuum rather than a structure? For a model of a whole single cell or of tissue, a continuum material description of cell wall may be adequate, whereas at a higher scale, it may be satisfactory to treat tissue as a continuum material. Within the wall, the complex structure of polysaccharides can be modelled with theories derived for fibre–matrix composites or for entangled polymers. At this level there is the possibility of modelling some of the biological activity of the wall, for example, the loosening of the wall by enzymes to allow extension at a turgor that the wall would otherwise contain. A model may allow several levels of structural hierarchy to be connected; a description of cell wall behaviour based on its polymeric nature may be summarized into a constitutive relation for a continuum material appropriate for a mathematical model.

All mechanics of primary plant cells is essentially a problem of interplay between turgor and wall properties. One approach is to describe the mechanical properties of cell walls by using theory developed for continuum, isotropic materials. In a perfectly linear elastic material where engineering strain is proportional to true stress, the only parameter that determines the stiffness of the material is the modulus of elasticity, E. The Poisson's ratio of the material, ν, becomes involved if the sample is not free to expand or contract. Conventional elastic theory is restricted to strains typically less than a few per cent, but theory of membranes allows large deformations in thin samples to be modelled. The form of primary plant cell walls, which are thin relative to their area, suggests that the theory of membrane mechanics is an appropriate tool for modelling cell walls, and various analyses of biological materials have been conducted using membrane theory. The usual method is to assume, or determine, a strain energy function, explained in the following paragraph, and then to obtain the force–stretch relations by partial differentiation. A set of differential equations is thus obtained, the solution of which yields the membrane shape and stresses due to the deformation. Although the term 'linear' in describing a constitutive relation refers to the linearity of the stress–strain equation for the material, it may avoid confusion to note that classical theory of elastic–plastic deformations derives a linear stress–strain equation from a quadratic strain energy equation (Sokolnikoff 1956). When dealing with large deformations of membranes, it is convenient to describe deformation in terms of 'stretch ratios' than strains because a stretch ratio depends only on the state of strain and not on the choice of reference axis. The stretch ratio approach simplifies the analysis and allows three strain invariants, I, to be defined. The strain energy function for a Mooney–Rivlin type of material is defined in terms of the strain invariants and material constants that need to be determined by experiment.

There are two main approaches to model formation. The classical theory of Newtonian mechanics results in force and momentum balances. Identified forces perform work on the system and result in motion and deformation. In models of plant growth the driving force is presumed to arise from cell turgor, an increase in which also serves to balance external compressive forces in studies of deformation. This approach has two drawbacks. First, it presumes that all forces acting on the system are identified. Second, form of the constitutive relations usually has to be assumed. This limits the model's ability to test hypotheses about mechanical and biochemical processes occurring in plant tissue. The second main approach to modelling cell growth or response to deformation consists of combining an energy balance statement with a constitutive strain relation. This approach, which arises from theories of analytical mechanics, uses the change of thermodynamic potential energy as the process performing the work. Although these theories have no advantages in simple mechanical systems where the forces are easily identified, they are to be preferred where the forces driving motion in a complex system are not completely known. Compared with the force balance method, the energy balance approach can be applied more generally, in that the thermodynamic relations of both mechanical and biological processes are included in the analysis, and the form of the constitutive relation need not be defined.

Once the governing equations and boundary conditions that describe a particular problem have been formulated, numerical approaches to solution of the equations have advantages over analytical approaches in that problems can be easily defined and complex geometries and irregular material properties can be used.

Because of the practical difficulties of characterizing cell wall properties by manipulation of the wall in any plant material other than, for example, the large cells of the alga *Nitella*, the cell wall properties have been inferred by some authors from measurements on single cells or samples of tissue. Calculation of wall mechanics requires a model, formulated in terms of the constitutive relation of the cell wall material, of the deformation of the test sample. Where the sample is an isolated sphere compressed between two parallel plates, or in an osmotically manipulated environment, the model will express the balance between tension in a pressurized spherical membrane and pressure within the cell. Although this approach at first sight seems straightforward, it has limitations. First, the form of the constitutive relation may not be known, so the data need to be good enough to determine the form as well as the (several) parameters. Some parameters are required that cannot be easily determined for the test cell, for example wall thickness and initial radial stretch of the inflated cell, so values may have to be assumed. The determination of the material characteristics and properties of test samples is clearly vital for a mathematical model to be verified, and readers are referred to Smith *et al.* (1998) who review a range of biophysical approaches. Further consideration of the characterization of materials is beyond the scope of this review.

4. MODELLING CELL WALL AS A MATERIAL

First, models are considered in which the wall is treated as a continuum material, then as a material with properties that depend on its polymeric nature. For those interested in the current state of knowledge on cell wall architecture, Cosgrove (2000) reviewed current models (conceptual rather than mathematical) of the cell wall for their ability to account for the mechanism of cell wall enlargement.

The continuum approach was taken by Hettiaratchi & O'Callaghan (1974) who developed a model that describes cell extension, in which the walls of the cells were modelled as thin shells subjected to an internal inflationary pressure. The cell wall was represented by a rubber-like material with a linear elastic stress–strain characteristic, the molecular structure of which resembled that of the wall, given the extent to which wall structure was known at the time. The authors identified that finding a suitable expression for the strain energy function was the major difficulty with this approach. Having no evidence to support more than the simplest formulation of the strain energy function, they used a linear elastic material as did, for example, Pitt & Davis (1984). For tomato cell wall, Lardner & Pujara (1980) chose a constitutive model of the Mooney–Rivlin type, commonly used to describe rubber-like materials that are incompressible and can undergo large elastic deformations (Mooney 1940; Rivlin 1948).

Davies *et al.* (1998) developed a model of deflection of a membrane by a probe acting normally to the membrane at its centre, and solved it analytically. They worked with a Mooney–Rivlin constitutive model with two material constants, though for verification only one was estimated with experimental data, the other being zero because a linear elastic material was assumed. Having verified the technique on a rubber membrane, which was also tested in a uniaxial manner to check the calculated properties, the authors calculated the single parameter of the constitutive model for the walls of potato tuber parenchyma cells.

Cell walls would be expected to behave differently from rubber because they contain relatively inextensible microfibrils. To account for the presence of microfibrils, Hettiaratchi & O'Callaghan (1978) and Wu *et al.* (1988) developed models of fibre-reinforced rubbers by introducing stiffening factors. However, the assumptions that the microfibrils were inflexible and that they did not slip during cell expansion did not allow for realistic volume changes to occur. The modelled extension was only appropriate to an artificially induced increase in cell volume as a result of manipulating its osmotic environment.

Recognizing that cellulose fibrils are the major component of the cell wall with an identifiable structure, authors have attempted to explain the characteristics of cell wall as a two-component material of fibre and matrix. Wu *et al.* (1985) developed the work of Hettiaratchi & O'Callaghan (1978) to describe the pressure–volume relation for pressurized spherical and cylindrical cells. Their work was based upon the stress–strain relation for a polymeric material established by Wu & Sharpe (1979). They assumed two phases of cell expansion, the first occurring without the need for stressing the microfibrils and the second as a result of microfibril extension, the transition being at the point of incipient plasmolysis. Chaplain (1993) extended and simplified the theory of Wu *et al.* (1985, 1988) by characterizing the elastic properties of the ideal, isotropic cell wall in terms of a general strain energy function, so as to be able to describe better the nonlinear relation between pressure and volume in cell expansion. The advantage of this general function is that as the cell expands, the wall thins and the microfibrils introduce shear interactions. Chaplain (1993) also distinguished between the two components of the cell wall and defined a two-term strain energy function, one term each for the matrix and the microfibril phases, thus producing a model of the wall as a fibre composite material. The two most important variables in cell expansion were shown to be microfibril extensibility and matrix shear modulus. He also noted that the action of enzymes known to mediate cell wall extensibility (for one family of enzymes see McQueen-Mason (1995)) could be incorporated into the model by assuming shear modulus to be some function of enzyme concentration. Wall viscosity would appear to be a more appropriate characteristic to choose.

That plant cell walls are viscoelastic has been demonstrated experimentally by several authors (e.g. Preston 1974; Sellen 1980; Nolte & Schopfer 1998; Kohler & Spatz 2002), but modelling of cell or tissue mechanics in which the walls have a viscous component added to their to their solid properties has not yet been addressed. This is partly because the mathematical formulation and solution are challenging, and partly because the viscous term is difficult to determine with useful precision from experimental data, though Kohler & Spatz (2002) have made progress in this area. A method of calculating the viscous term from the structure and properties of the polymers in the walls is needed, but wall structure is not yet well enough defined to allow theories developed for structured and entangled polymers to be fully applied. However, Veytsman & Cosgrove (1998) have modelled plant cell wall extension by using concepts of thermodynamics of polymer mixtures. They formulated a simple model for a cylindrical plant cell where the free energy of the cell wall was the sum of the contribution of the free energy of the cellulose microfibrils and that of the hydrogen bonds, by which hemicellulose is attached to the surface of the cellulose. Their analysis accounted for aspects of polymer structure such as the number of rotatable link lengths. It was shown that macroscopic properties of cell walls are explicable in terms of the microscopic properties of interpenetrating networks of cellulose and hemicellulose. Such work makes incorporation of the action of wall-loosening enzymes in a model a more realistic possibility.

Wall loosening induced by topical application of enzymes has been observed to initiate production of leaf primordia in the tomato (Fleming *et al.* 1997) but the phenomenon has not yet been studied mathematically. Chaplain & Sleeman (1990) examined how the form of the strain energy function can allow bifurcation to occur, which may be sufficient to initiate a new growing tip in a unicellular marine alga.

Smith *et al.* (1998) progressed beyond an elastic description of walls in their model. They used a constitutive model that is linear elastic with an elastic limit, at which a transition to plastic behaviour takes place, and with a finite hydraulic conductivity. They examined how far it is possible to determine uniquely the form of the constitutive relation from experimental data on compression of isolated spherical yeast cells, and conclude that high-quality data on parameters of the cells being used, together with a comprehensive model including hydraulic conductivity of the wall, are needed to be able to calculate both the form and the constants of the constitutive relation. It would therefore be a significant advance if the form of a constitutive relation could be calculated from wall structure and polymer composition.

For modelling based on events at molecular scale, it is not feasible to specify the forces acting on the system so an energy-based approach is appropriate. McCoy (1989) presented a model based on energy balances in which a change in thermodynamic potential energy was the driver for cell wall extension. The model allows for water uptake and biosynthesis as well as mechanical deformation, and does not assume a form for the strain energy function. This work brings together the purely mechanical aspects of cell mechanics with important biological aspects, and points the way towards models that integrate the two.

Hepworth & Bruce (2000) avoided assuming the form of the constitutive relation *a priori*, but only by working within a deformation time-scale of 15 s to avoid any effects of cell wall viscosity and hydraulic conductivity. They ascribed the cell wall tensile properties to the fibre component of the wall and deduced the stress–strain curve of this fibre component by fitting to experimental data on

compression of potato tuber. A nonlinear relationship of stress–strain up to fibre failure emerged that agrees well with published data on native cellulose. In this model the orientation of the microfibril component of the cell wall was specified for each of four layers in the cell wall, the in-plane angular separation of which was specified as 45° to give the isotropic properties considered appropriate for modelling potato tuber parenchyma. However, in elongating cells, e.g. root epidermal cells of *Arabidopsis thaliana* there is a net orientation of cellulose microfibrils (Verbelen & Kerstens 2000) that gives rise to direction-dependent tissue mechanical properties (Kerstens *et al.* 2001). By selection of the angle between the microfibril layers, the model of Hepworth & Bruce (2000) could, in principle, be used to model the deformation of cells with anisotropic wall properties over a short time-scale but it would not be appropriate for modelling of elongation growth. The work of Kerstens *et al.* (2001) at cell scale adds to the analysis at tissue scale of Green *et al.* (1996) in emphasizing that biophysical properties play a significant role in determining phenotype. A sound mathematical analysis of the mechanics of cell wall anisotropy remains, however, to be established.

5. PRIMARY CELL AND TISSUE MODELLING

The behaviour of individual cells, in interaction with adjoining cells in simple two- or three-dimensional arrays, approximates to the behaviour of tissues. Such tissue models may be divided into 'dry' models, in which cell contents are compressible gas and strain is achieved by bending of the structural members, and 'wet' models, in which the cell contents are incompressible (or nearly so) liquid, forcing the strain to be achieved by stretching of the structural members. Pressure-driven fluid flow may be included. A further class of tissue model is the rheological model in which the behaviour of tissues is represented by the ideal, simple behaviour of devices such as springs and dashpots. Rheological models, of which there are many, are essentially descriptive of experimental data and will not be considered in this paper.

In this section, models of single cells and tissues with thin, primary walls are considered. Single cells have been modelled as spheres (Lardner & Pujara 1980), as cylinders (McLaughlin & Pitt 1984) and as polyhedra (Pitt & Davis 1984). Tissue has been modelled by using the 'dry' and 'wet' approaches just described, and with hybrid models and theories developed for foams.

Nilsson *et al.* (1958) provided the original direction for this work by deriving a linear relation between tissue stiffness and turgor pressure for externally applied infinitesimal deformations of a spherical or polyhedral cell. Displacements of points on the cell wall were assumed to be linearly dependent on their position, so-called 'affine' deformation. Most subsequent models computed the tissue properties as proportional to those of a single compressed cell, i.e. the implied structure of the tissue was one of independent columns of such cells all subject to the same stress. An example of such tissue would be the columnar structure in apple parenchyma along a radius from the core. Gates *et al.* (1986) developed such a model to calculate tissue response. They used the model presented by Lardner & Pujara (1980) of compression of a spherical cell filled with incompressible liquid, which itself was a development of the compressible sphere model of Feng & Yang (1973). Gates *et al.* (1986) explored four constitutive relations and selected a nonlinear one that gave good agreement for data from osmotically induced inflation of apple and pear parenchyma cells. Although cell behaviour had thus been forced to agree with the model, predicted tissue stiffness was much lower than from experiment. Subsequently Gao *et al.* (1990) modified the model so that the spherical cells were bonded in contact over a finite area before compression was initiated. Although the area of intercellular bonding had a strong effect on the macroscopic properties of the tissue, and the model predicted the tissue would have a higher stiffness as a result of the finite contact area, predicted tissue stiffness was still not as high as observed.

Pitt & Davis (1984) modelled a parenchyma cell as a thin-walled, fluid-filled sphere and as a cylinder, and used finite element analysis to determine the response of a cell compressed between adjacent cells of the same size and shape. The analysis required maintenance of a constant fluid volume within the cell and a changing contact area between adjacent cells, which was initially a point contact only. Despite the linear elastic constitutive relation, the calculated curves of stress versus applied strain were concave upwards, simply as a result of the geometry of the membrane in combination with the incompressible fluid. This is a general finding for such fluid-filled cellular tissue and shows why it is difficult to infer accurately any constitutive relation other than a linear one from tests on tissue.

Gao & Pitt (1991) considered a three-dimensional cell model based on a shape having eight hexagonal and six square faces. Each cell face bonds the cell to one of its 14 neighbours, allowing a realistic approximation to the close packing of cells found in potato tuber parenchyma tissue, in which intercellular voids account for less than 1% of tissue volume. The compression of a single cell of this type, between opposing hexagonal and between opposing square faces, was modelled by using a nonlinear elastic constitutive law. Viscous effects and outflow were ignored but the attachment between adjacent cells allowed shear to appear in the model. The predicted behaviour correlated well with experimental data on potato tissue stiffness and rise in 'turgor pressure' in response to compression. It appears that, to give realistic tissue stiffness of parenchyma tissue, a model must represent the close packed nature of the tissue and the stresses generated between cells. Cell orientation relative to the direction of loading had a substantial effect on the likelihood, location and direction of cell wall rupture, intercellular debonding and intercellular slippage. Cell orientation had little effect on the predicted rise in turgor during compression or on the macroscopic stress–strain relation for the tissue as a whole. The important mechanical features of parenchyma tissue were summarized as being the cell wall stress–strain relation, cell turgor pressure and intercellular bonding in multiple directions.

Modelling of single cells has been advanced by studies on single mammalian, bacterial and yeast cells, the mechanics of which are important in agitated fermentation vessels. Though mammalian cells are much weaker than plant cells because they are bounded by a membrane rather than a structural wall, the same analysis can be applied to both

cell types because it is the wall constitutive properties, not the basis of the deformation, that differs. For single mammalian cells, Zhang *et al.* (1992) modelled the quantitative relation between force and distance between the compression surfaces using membrane theory so that the bursting membrane tension, bursting pressure and the elastic area compressibility modulus of the compressed cells could be obtained. Linear elastic constitutive properties were assumed for the mouse hybridoma TB/C3 cells they used for validation of their model. The analysis predicts that the bursting membrane tension is independent of cell size and the bursting force in compression is linearly related to cell size. This has not yet been tested on plant cells. Liu *et al.* (1996) used the same theory to model the deformation and bursting strength of single, liquid-filled microcapsules, *ca*. 65 μm diameter and with a thin polymeric membrane wall with nonlinear, Mooney–Rivlin description of elastic properties. The model of Smith *et al.* (1998) of an inflated sphere compressed between two plates included a hydraulic conductivity term to allow for expulsion of fluid through the exposed area of cell wall in response to the calculated turgor pressure. The wall model allowed for in-plane tension and shear. For a fundamental approach to the mechanics of mammalian cells in terms of flexible polymers, networks and membranes, the reader is referred to Boal (2002).

Returning to plant cells, in which intracellular pressure is a dominant characteristic, various approaches have been taken to the representation of the effect on cell mechanics of the fluid within a cell loaded externally. Analytical models have represented the fluid as a load applied to the inside surface of the cell. The pressure is incremented as the cell is progressively compressed such that constant volume is maintained. The fluid is thereby defined to be incompressible, and the pressure required to maintain the constancy of volume is interpreted as the turgor pressure. However, other approaches are possible. Pitt & Davis (1984) modelled the fluid as a solid with a high volumetric modulus, i.e. nearly incompressible, and with low elastic modulus and zero initial compression, i.e. turgor pressure is initially zero. Burrows (1994) reinvestigated this problem and concluded that the difference between the two methods is significant, particularly if the objective of modelling is to calculate the change in internal pressure with strain.

Pitt (1982) represented cells as a 'dry' array of hexagonal prisms, the sides of which were springs. Though relatively simple, this model predicts several experimentally verified phenomena, such as that the strength of the cellular conglomerate decreases as turgor pressure increases.

An analysis leading to a hybrid 'wet and dry' model was presented by Jeronimidis & Liu (1994), who represented turgid tissue by liquid-filled cells in which the cell walls were represented not simply as thin membranes but as struts and plates. Thus the walls were capable of supporting bending and compression as well as resisting fluid pressure. The model predicted very well a limited set of observations of stress–strain behaviour for potato tuber parenchyma up to a large nominal strain, 0.4, but although the authors set out to predict cell wall fracture and tissue damage, no test results for this aspect were presented. This approach has potential for modelling tissue in which cells are not thin-walled, as are parenchyma cells, but have undergone some secondary thickening, e.g. collenchyma.

The model of Hepworth & Bruce (2000) for tissue compressive stiffness, referred to previously, links elements of structure from microfibrils and walls through to tissue. They represented the cell wall as a mesh of initially randomly oriented fibre that can reorientate when the wall is deformed. Cells were not explicitly represented, and the tissue was represented as a conglomerate of planar cell walls characterized by two angles of orientation. When the modelled tissue is compressed, under an assumption of constancy of volume justified by experiment, short-term changes in wall dimensions are calculated from affine deformation of the cell corners. Reorientation and length changes of microfibrils in each wall are calculated from these changes in wall dimensions. The model predicted force deflection for samples of swede root parenchyma tissue, though the material characteristic for the cell wall fibre, in the form of a stress–strain curve, was inferred by the same model from experiments on potato tuber tissue, rather than from an independent source. The calculated tensile modulus and strength of the fibre material do, however, agree well with those of cellulose, and the analysis thus indicates that the cellulose microfibrils control completely the short-term response of parenchyma tissue to compression.

Rather than build a tissue model from a model of a single cell, tissue mechanical properties may be modelled based on theories developed for foams, manufactured materials comprising gas-filled cells formed from polymers. The mechanics of both open-cell and closed-cell foams has been studied extensively and the reader is referred to the book by Gibson & Ashby (1997) for a comprehensive introduction, and to Gibson (1989) for a review of modelling of cellular materials. Theory of gas-filled foam has been used to understand by analogy types of plant tissue such as cork and seasoned wood. The mechanics of liquid-filled foams is not as well studied but is appropriate to fluid-filled plant tissue whether primary or secondary. Warner & Edwards (1988) presented a theory for liquid-filled cellular foam, and the subject is included in a review by Weire & Fortes (1994) and considered for food materials by Jeronimidis (1988).

6. SECONDARY CELL WALLS, CELLS AND TISSUE

Wood, or more precisely secondary xylem, has been studied in depth because of its commercial importance, and models have been developed that describe mechanics of entities from single cells (tracheids) to whole trees, as well as timber. The literature on the subject of wood mechanics is vast because of the economic importance of timber, paper and other wood products, and the interested reader is directed to Mark (1967) for an introduction to wood mechanics at a cellular scale.

A model of the tensile properties of a single cell, sometimes termed a fibre, of flax schlerenchyma has been presented by Davies & Bruce (1997). The theory they developed describes the relation between stress and strain in structures composed of thick-walled, concentric cylinders. Each cylindrical layer comprises an orthotropic material with a given filament winding angle that can be different in each layer. The analysis supports an arbitrary

number of layers, though for flax there are three secondary layers known as S1–S3. The model extends earlier work in that the effect of internal or external pressure and torsional loading can be included in addition to uniaxial loading. Given the material properties of the fibre and matrix component materials, the elastic properties of the cell wall are calculated for a given winding angle of fibre, from which the properties for any other angle can be calculated using tensor manipulation. Linear elasticity theory by Lekhnitski (1981) is used. A set of simultaneous equations is developed, and solved analytically by using matrix methods. Constants determined by the solution of these equations are then used to obtain explicit formulae for stress, strain and displacement at every location in each layer. Stress variations through the thickness of the wall were predicted to be significant, and the peak stress in the wall was predicted to be significantly greater than the mean stress. Yamamoto & Kojima (2002), who were primarily concerned with wood shrinkage, pursued a similar approach but their formulation accounted for not only structural factors, such as the microfibril angle and the thickness of each layer, but also environmental conditions, specifically the influence of moisture content on material properties of the cellulose framework and the lignin–hemicellulose matrix. The effects of the moisture content and the microfibril angle upon the longitudinal Young's modulus and the Poisson's ratio of the wood fibre were simulated. This work points the way to development of models of deformation that fully account for the effects of moisture, which has such a strong influence on mechanical properties of hygroscopic materials.

7. CONCLUSIONS

Mathematical models of cellular mechanics have developed in response to both the economic importance of cellular plant tissues and to the intellectual challenge of understanding how the subtleties of cell wall structure and composition determine mechanical function. Looking forward, the main challenge at cell-wall scale is to be able to predict deformation mechanics from fundamental considerations of the polymeric nature and architecture of the wall, enabling calculation of phenomena such as wall anisotropy and the effects of bond disruption by enzymes during growth. At the level of individual cells, mathematical challenges arise from the need to use material properties such as viscosity, plasticity and hygroscopicity, and to work with nonlinearity. To give improved predictions of tissue-scale mechanics, models will need to combine material properties that are soundly based at lower hierarchical levels with a sufficiently detailed, three-dimensional understanding of tissue structure. As better models emerge of stress and strain during deformation, improved prediction of failure events in cell wall and tissue will be enabled.

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