



A model of crosslink kinetics in the expanding plant cell wall: Yield stress and enzyme action

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HIGHLIGHTS

- ▶ We present a model of crosslink dynamics in an expanding plant cell wall.
- ▶ Yield can be explained by the dependence of crosslink breakage rate on elongation.
- ▶ Enzymes that target crosslink binding can soften the wall in its pre-yield state.

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ABSTRACT

The plant primary cell wall is a composite material containing stiff cellulose microfibrils that are embedded within a pectin matrix and crosslinked through a network of hemicellulose polymers. This microstructure endows the wall with nonlinear anisotropic mechanical properties and allows enzymatic regulation of expansive cell growth. We present a mathematical model of hemicellulose crosslink dynamics in an expanding cell wall incorporating strain-enhanced breakage and enzyme-mediated crosslink kinetics. The model predicts the characteristic yielding behaviour in the relationship between stress and strain-rate seen experimentally, and suggests how the effective yield and extensibility of the wall depend on microstructural parameters and on the action of enzymes of the XTH and expansin families. The model suggests that the yielding behaviour encapsulated in the classical Lockhart equation can be explained by the strongly nonlinear dependence of crosslink breakage rate on crosslink elongation. The model also demonstrates how enzymes that target crosslink binding can be effective in softening the wall in its pre-yield state, whereas its post-yield extensibility is determined primarily by the pectin matrix.

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1. Introduction

Plant cells are surrounded by a tough primary cell wall which maintains a high internal turgor pressure while allowing significant anisotropic expansion. Such growth is driven by irreversible stretching of the cell wall under the action of the turgor pressure, with the growth rate being dependent on the mechanical properties of the cell wall. The plant primary cell wall is a composite material containing stiff cellulose microfibrils (CMF), embedded within a pectin matrix and linked through a network of

hemicellulose crosslinks (Carpita and Gibeaut, 1993; Cosgrove, 2005). This structure exhibits mechanical anisotropy because the CMF are typically orientated in a preferred direction, making the wall much less extensible in a direction parallel to the CMF than perpendicular to them (Baskin, 2005; Suslov and Verbelen, 2006; Van Sandt et al., 2007). Stresses acting perpendicular to the CMF (and in the plane of the wall) are shared between the hemicellulose network and the pectin matrix, with some authors suggesting the former are dominant in some circumstances (Van Sandt et al., 2007; Vissenberg et al., 2000). During growth, it is thought that new wall material is continually deposited on the inner face of the wall to maintain its integrity (Cosgrove, 2005; Vissenberg et al., 2000). To understand plant cell growth and its regulation, we must therefore determine how the properties of this evolving composite structure relate to the macroscale mechanical properties of the cell wall (see Burgert and Fratzl, 2007; Cosgrove, 2000; Geitmann, 2010; Geitmann and Ortega, 2009 for recent reviews).

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Many researchers have followed Lockhart (1965) in modelling the cell wall at the macroscopic level as an anisotropic Bingham material, displaying a yield stress Y below which no irreversible deformation occurs and an extensibility Φ which determines how the cell (or tissue) elongation rate relates to the driving stress, provided this stress exceeds Y . To illustrate, consider an isolated circular cylindrical cell of length $\ell(t^*)$ and radius R at time t^* having CMF oriented in a hoop-like manner orthogonal to the axis of the cell, preventing radial expansion. The turgor pressure P , acting on the flat end-plates of the cell, generates a force $\pi R^2 P$ that is balanced by the axial stress resultant (or tension) Σ^* in the curved cell wall (distributed around the cell perimeter $2\pi R$), so that $\Sigma^* = \frac{1}{2}RP$; the hoop stress resultant RP is borne by the CMF. The Lockhart (1965) equation describing the expansion of the cell may then be written as

$$\frac{1}{\ell} \frac{d\ell}{dt^*} = \begin{cases} 0 & (\Sigma^* < Y), \\ \Phi(\Sigma^* - Y) & (\Sigma^* > Y), \end{cases} \quad (1)$$

Experimental studies have found that the Lockhart equation (1) is a reasonably good description of plant cell-wall mechanics when water fluxes needed to maintain cell turgor are not rate-limiting (see for example, Green et al., 1971). Variants of (1) can be used to describe the elongation of sections of cell wall, whole cells or multicellular tissues, making it a natural building block in integrative multiscale models of plant growth and development (Chavarría-Krauser et al., 2005; Chickarmane et al., 2010; Mirabet et al., 2011). Note that instead of using Σ^* , (1) may be expressed in terms of turgor pressure P or the extensional stress Σ^*/h (where h is the cell wall thickness), with the definition of extensibility and yield being adapted accordingly by incorporating appropriate geometrical factors, indicating the importance of cell and tissue geometry in determining plant growth rate. The Lockhart equation (1) can be interpreted in two equivalent ways, making it a particularly powerful tool in describing plant growth: it may be read from left to right as growth rate being determined by the internal stresses within the plant tissue, modulated by cell and tissue properties; equivalently it can be read from right to left as a statement of the constitutive properties of cell wall or plant tissue, describing how material stress is related to strain rate.

A number of previous studies have addressed the relationship between the empirical parameters Φ and Y and the cell wall's microstructure, and the broader applicability of (1). For example, Ortega and co-workers showed how strain-hardening may arise via recruitment of hemicellulose crosslinks (as reviewed in Geitmann and Ortega, 2009). Dyson and Jensen (2010) derived a version of (1) from a continuum mechanics model of the wall of the elongating cell, treating the wall as a thin sheet of viscous fibre-reinforced fluid. Their model demonstrates explicitly how, when the CMF are orientated perpendicular to the axis of the cell, the extensibility is determined by a viscosity that characterises the pectin matrix (and the embedded CMF and hemicellulose crosslinks). Similar conclusions about the importance of the properties of the pectin–hemicellulose matrix have been reached in Carpita and Gibeau (1993) and Dumais et al. (2006). When the CMF are not oriented perpendicular to the cell axis, the fibres may reorient passively as the cell elongates (following the so-called 'multi-net model' Preston, 1982), in which case more complex expressions of the form:

$$\Sigma^* = f(\alpha^*, \ell), \quad \alpha^* \equiv \frac{1}{\ell} \frac{d\ell}{dt^*} \quad (2)$$

can arise; f is a nonlinear function of the cell length ℓ and the elongation rate α^* . (Here we adopt the convention common in the continuum mechanics literature and write stress as a function of strain or strain-rate.) Such a function was derived in Dyson and Jensen (2010) to show how growth may be suppressed by fibre

reorientation, and alternative functions may be used to mimic viscoelastic behaviour (Geitmann and Ortega, 2009), as is necessary to model the rapid response of a cell to a sudden change in its external loading. Note that in the case of the classical Lockhart equation (1), f is independent of ℓ and is linear in α^* when $\alpha^* > 0$, such that the 'effective extensibility' Φ_{eff}^* , defined here by

$$\Phi_{\text{eff}}^* \equiv \left(\frac{d\Sigma^*}{d\alpha^*} \right)^{-1} \quad (3)$$

takes the values $\Phi_{\text{eff}}^* = 0$ in the pre-yield state ($\Sigma^* < Y$) or $\Phi_{\text{eff}}^* = \Phi$ in the post-yield state ($\Sigma^* > Y$).

A few previous models address the mechanical properties of the interacting cellulose-hemicellulose network (Kha et al., 2010; Passioura and Fry, 1992; Veytsman and Cosgrove, 1998). Passioura and Fry (1992) consider a simple model in which it is assumed that crosslinks extend as they gradually detach from the CMF, become progressively load-bearing as the wall stretches (assuming the number of load-bearing tethers is proportional to the distance between CMF) and rupture according to a time-dependent law. Their model assumes uniform properties across the cell wall, while acknowledging Preston's (1982) observation that CMF are carried towards the outer surface of the elongating cell wall. They assume each bond behaves like a Bingham element (with a yield stress), and propose a relation between the macroscopic yield and the molecular yield parameter. The computational WallGen model (Kha et al., 2010) predicts anisotropic elastic properties from a virtual cell wall assembled from individual polymers, but this model does not allow for crosslink breakage, growth or irreversible viscous deformation of the cell wall. Veytsman and Cosgrove (1998), developing the concept of the 'sticky network' model (Cosgrove, 2000), use a thermodynamic formulation to relate the elastic stress in the composite cell wall to the properties of the CMF and hydrogen bonds between the CMF and glucan (hemicellulose) molecules, predicting the existence of an elastic yield stress above which the cell wall will exhibit creep. However their model captures neither the anisotropic stresses arising in ordered polymer networks (for which CMF have a predominant orientation, which may be orthogonal to the direction in which the wall elongates), nor the deposition of new material into the cell wall, nor viscous stresses associated with crosslink detachment and reformation.

These previous descriptions of cell-wall mechanics have typically not considered the role of enzymes. During growth, the cell wall's structure is thought to be modified by various remodelling enzymes, different families of which act on different components of the cell wall. Pectin methyl esterase (PME) affects the consistency of the pectin ground matrix, removing methyl groups by breaking ester bonds. This enables pectin to be crosslinked by calcium ions, stiffening the cell wall and reducing cell expansion (Boyer, 2009; Derbyshire et al., 2007; Proseus and Boyer, 2006); recent progress has been made in quantifying PME action in a chemorheological model of the pectin matrix (Rojas et al., 2011). Some members of the XTH enzyme family loosen the wall via XEH (xyloglucan endohydrolase) activity, which involves breaking a bond between two hemicellulose crosslinks, whereas other members of this family carry out XET (xyloglucan endotransglucosylase) action, whereby the crosslink is broken and then one free end is rejoined to another free crosslink end within the tissue (see Fig. 1) (Rose et al., 2002). In addition, expansins break the hydrogen bonds between the CMF and the hemicellulose strands (McQueen-Mason et al., 1992). The different remodelling enzymes are therefore likely to affect the macroscale cell-wall properties, and hence the cell's growth rate, in different ways. Hormonal regulation of plant growth is thought to be in part via regulation of these remodelling enzymes (Catala et al., 1997;

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