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REVIEW

SUBJECT COLLECTION: MECHANOBIOLOGY

Mechanobiology of the cell wall – insights from tip-growing plant and fungal cells

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ABSTRACT

The cell wall (CW) is a thin and rigid layer encasing the membrane of all plant and fungal cells. It ensures mechanical integrity by bearing mechanical stresses derived from large cytoplasmic turgor pressure, contacts with growing neighbors or growth within restricted spaces. The CW is made of polysaccharides and proteins, but is dynamic in nature, changing composition and geometry during growth, reproduction or infection. Such continuous and often rapid remodeling entails risks of enhanced stress and consequent damages or fractures, raising the question of how the CW detects and measures surface mechanical stress and how it strengthens to ensure surface integrity? Although early studies in model fungal and plant cells have identified homeostatic pathways required for CW integrity, recent methodologies are now allowing the measurement of pressure and local mechanical properties of CWs in live cells, as well as addressing how forces and stresses can be detected at the CW surface, fostering the emergence of the field of CW mechanobiology. Here, using tip-growing cells of plants and fungi as case study models, we review recent progress on CW mechanosensation and mechanical regulation, and their implications for the control of cell growth, morphogenesis and survival.

KEY WORDS: Cell wall, Growth, Cell mechanics, Morphogenesis, Plants, Fungi, Yeast

Introduction

Mechanosensation in animal cells influences processes ranging from cell migration and differentiation to organ development and function (DuFort et al., 2011). Surface molecules, such as Piezo channels, cadherins and integrins, allow animal cells and tissues to detect stimuli as diverse as shear forces, touch, stretch or compression, and transduce them into adaptive responses (Ingber, 2003). For walled cells, such as those of plants and fungi, the functions and mechanisms of surface mechanosensation remain poorly understood (Bacete and Hamann, 2020; Mishra et al., 2022; Wolf et al., 2012). However, walled cells are continuously challenged with surface forces that are orders of magnitude larger than those in animal cells, deriving from their turgid cytoplasm and contacts with neighboring cells or obstacles (Boudaoud, 2010; Hamant and Traas, 2010; Mishra et al., 2022). These entail risks of CW breakage and cell lysis, raising the question of how forces on the CW might be detected in space and time and transduced to ensure surface integrity and survival.

Walled cells of plants and fungi are generally non-motile and exploit diverse modes of growth to colonize space, reproduce or infect. One wide-spread mode is tip growth, in which cells elongate in a polar manner while maintaining tube-like shapes (Fischer et al., 2008; Hepler et al., 2001). Tip-growing cells include multiple yeast species, filamentous fungi and stramenopiles (oomycetes, brown algae; also called heterokonts), as well as specialized plant cells, such as pollen tubes, rhizoids and root hairs. Tip-growth speeds can vary by two to three orders of magnitude between species, from yeast cells that elongate at ∼1 µm/h up to fungi, such as *Neurospora crassa*, or plant pollen tubes that elongate as fast as ∼500 µm/h (López-Franco et al., 1994; Qin and Yang, 2011; Taheraly et al., 2020). Tube diameter also varies widely, from a fraction of a micron in infecting hyphae of the pathogen *Fusarium oxyparum* (Ruiz-Roldán et al., 2010), to ∼10–20 µm in the fungus *Sclerotinia sclerotiorum* (Fischer-Parton et al., 2000) or in the pollen tubes of *Lilium longiflorum* (Campàs et al., 2012) (Table 1). In spite of this diversity, tip-growing cells share one common feature, their growth is defined by the assembly and irreversible expansion of the CW.

CWs are built from cross-linked polysaccharides, and also contain specific proteins. They are often multilayered with thicknesses ranging from ∼50 to 500 nm, and compositions that vary among species or across life cycles. In fungi, α- and β-glucans, chitin and galactomannans are the most abundant sugar chains (Bowman and Free, 2006). In plant pollen tubes, rhizoids and root hairs, CWs are mostly composed of hemicellulose, cellulose, pectins and callose (Chebli et al., 2012; Schoenaers et al., 2017). Polysaccharides elongate in the Golgi and/or at the plasma membrane; this is mediated by the catalytic activity of transmembrane enzymes, such as glucan or callose synthases, which are under the control of Rho-GTPases (Rho in fungi and ROP in plants) (Anderson and Kieber, 2020; Bowman and Free, 2006). CW remodeling, digestion or crosslinking involves other sets of enzymes, such as transferases, hydrolases and lyases, which often are directly secreted into the CW matrix (Bowman and Free, 2006; Chebli and Geitmann, 2017; Hoffmann et al., 2021) (Fig. 1A). During tip growth, CW assembly and remodeling are restricted to cell tips, and to sites of cell division in septate species. This is achieved through the polarized activity of the cytoskeleton and secretion machineries (Hepler et al., 2001; Riquelme, 2013). In many plant and fungal cells, this polar activity might also be influenced by a tip-focused Ca^{2+} gradient, which affects actin assembly, secretion or CW biochemistry (Jackson and Heath, 1993; Pierson et al., 1994). Growth is powered by a large osmotically generated turgor pressure, which pushes newly synthesized wall portions at cell tips forward (Hepler et al., 2013; Lew, 2011). An important consequence is that growing tips are often the most fragile parts of cells, as exemplified by fungal and plant cells with

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Table 1. Geometrical and mechanical parameters of some model tip-growing cells

		Tip size and growth		Mechanical parameters			
Model		Diameter	Growth speed	CW thickness	CW elastic modulus	Turgor pressure	References
Pollen tube	*A. thaliana*	5 µm	0.5 µm/min	200 nm	35–75 MPa	0.2 MPa	Chebli et al., 2012; Chen et al., 2015; Shamsudhin et al., 2016; Vaz Dias et al., 2019
	L. longiflorum	10–20 µm	12 µm/min	200–700 nm	20–90 MPa	0.1–0.4 MPa	Benkert et al., 1997; Shamsudhin et al., 2016; Vogler et al., 2013
Root hair	*A. thaliana*	10 µm	> 1 µm/min	100–150 nm	1–7 MPa	0.7 MPa	Galway, 2000; Grierson et al., 2014; Lew, 1996; Shibata et al., 2022
Fungi	*S. pombe*	4 µm	0.02–0.04 µm/min	130–170 nm	30–70 MPa	1–1.5 MPa	Abenza et al., 2015; Atilgan et al., 2015; Davi et al., 2019; Minc et al., 2009; Taheraly et al., 2020
Fungi	*A. nidulans*	2.5 µm	0.2–0.8 µm/min	60–90 nm	50–150 MPa	0.3–1.4 MPa	Chevalier et al., 2022; Gervais et al., 1999; Horio and Oakley, 2005; Zhao et al., 2005
Fungi	*C. albicans*	2 µm	0.3 µm/min	100–200 nm	3–7 MPa	1–3 MPa	Ene et al., 2015; Puerner et al., 2020; Thomson et al., 2015

mutations in factors that regulate the CW lysing there (Banavar et al., 2018; Hill et al., 2012; Miyazaki et al., 2009). Thus, tip growth might be viewed as a life-threatening process in which CW deformation must be acutely monitored to adapt wall reinforcement and ensure its integrity, highlighting the importance of mechanical feedback. Here, by focusing on work in model plant and fungal tip-growing cells, we will first review recent models for tip-growth and experimental assays developed to measure CW stiffness, thickness and turgor, and then describe molecular CW mechanosensors and their function as core components of mechanochemical feedback that supports CW integrity.

Mechanics of tip-growing cells

Sustaining turgor pressure

CW failure

The CW can be viewed as a thin elastic shell, which deforms when a force is applied to it and returns to its original shape when the force is released. In walled cells, the main surface forces derive from turgor pressure, P. Turgor puts the CW under a tension proportional to Pr, with r being the cell radius. The typical values of CW tension, ∼1–10 N/m, are two to three orders of magnitude higher than tensions required to rupture the plasma membrane, highlighting the vital role of the CW (Tan et al., 2011). This tension deforms the elastic CW, with a strain proportional to $\sim Pr/Eh$, where E is the elastic modulus of the CW and h its thickness. Typical elastic strains measured in fungi and plant cells are in the range of ∼10–30% (Davi et al., 2019; Vogler et al., 2013), smaller yet close to estimated critical failure strains of ∼45% that rupture the CW in yeast (Stenson et al., 2011). Thus, an increase in turgor, or a reduction in CW elastic modulus or thickness, might bring the wall closer to a rupture point. Indeed, CW rupture and lysis phenotypes in both plants and fungi have been reported in mutants or conditions that affect the CW, and are most often alleviated by reducing turgor with osmoprotectants (Cruz et al., 2013; Miyazaki et al., 2009; Munoz et al., 2013; Neeli-Venkata et al., 2021). Similarly, exposure to hypoosmotic conditions that increase turgor can cause CW rupture (Bartnicki-Garcia and Lippman, 1972; Hill et al., 2012; Nakayama et al., 2012). Interestingly, in tip-growing cells, CW rupture is most often observed at cell tips or at ingressing division septa, suggesting that remodeling CWs are more fragile than other CW portions (Bartnicki-Garcia and Lippman, 1972; Hill et al., 2012; Munoz et al., 2013). These considerations highlight the importance of measuring turgor and CW mechanical properties around cells to understand surface integrity.

Assessing turgor pressure

Several methods had been developed to measure turgor by as early as the 1960s (Bastmeyer et al., 2002; Beauzamy et al., 2014; Lew et al., 2004) (Table 1). The pressure probe is the most direct method, though intrusive. Here, an oil-filled micropipette impales the cell, and a transducer measures the pressure needed to maintain the cell cytoplasm or vacuole in place. Other methods include osmometry of cell extracts, plasmolysis (by determining the dose of external osmolytes needed to detach the membrane from the CW), strain assays that identify external osmolarity needed to deflate cells as much as when piercing the CW, or micro-indentation with force probes (Fig. 2A). In pollen tubes, for instance, turgor was found to be ∼0.3 MPa, based on micro-indentation and mechanical modelling (Vogler et al., 2013), consistent with pressure probe measurements in the range 0.1 to 0.4 MPa (Benkert et al., 1997). These values differ from estimates of 0.8 MPa obtained with plasmolysis (Benkert et al., 1997), possibly owing to osmoregulation. Similar values, ranging from ∼0.5 MPa to ∼1.5 MPa were reported in different fungi (Atilgan et al., 2015; Chevalier et al., 2022 preprint; Gervais et al., 1999; Lew et al., 2008) (Table 1). These large pressures are comparable to that in a bottle of champagne, and 100–1000 fold higher than within animal cells (Stewart et al., 2011).

Measuring CW elastic moduli

The mechanical properties of CWs can be measured with micro-indentation by applying small forces (nanonewtons to micronewtons range) with atomic force microscope (AFM) or larger forces (micronewtons to millinewtons) with a micro-indenter – a tip indents the CW, and its force–displacement curve is measured (Fig. 2A). For displacements smaller than the CW thickness, the curve is mostly sensitive to CW mechanics (Milani et al., 2013). For larger displacements, the curve often appears linear. Its slope is known as ‘apparent stiffness’ and depends on CW mechanics, thickness, turgor and cell shape, as well as indentation tip geometry, and was measured in pollen tubes and multiple fungal species (Bolduc et al., 2006; Geitmann and Parre, 2004; Gibbs et al., 2021; Smith et al., 2000; Vogler et al., 2013; Zhao et al., 2005). Mechanical properties of whole pollen tubes or fungal hyphae have

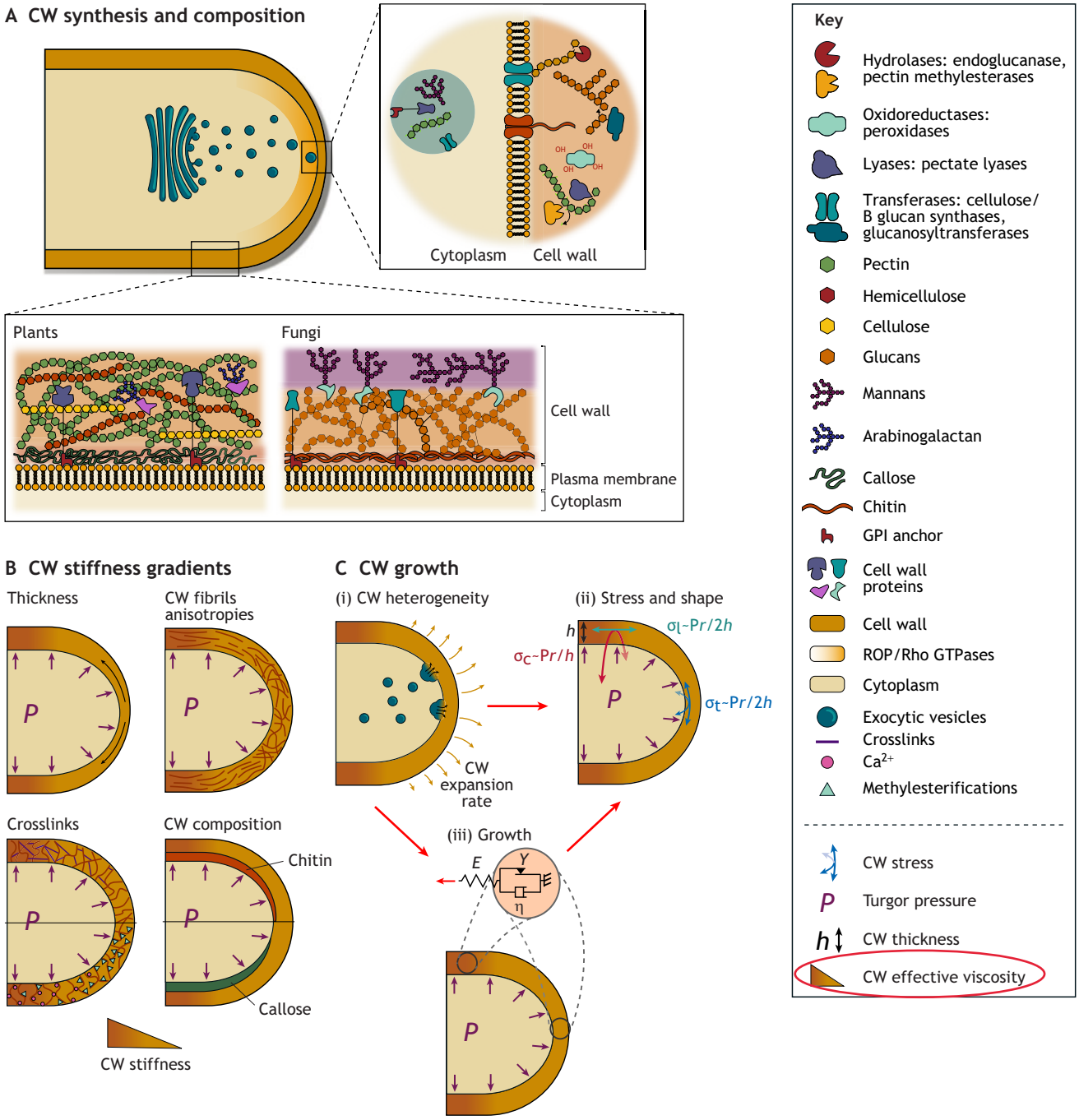

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Fig. 1. Cell wall assembly, composition and mechanics in tip-growing fungal and plant cells. (A) Schematic illustration of a tip-growing cell with secretory vesicles secreting CW synthesis enzymes to the membrane and other remodeling enzymes into the CW. A more-detailed diagram of a typical CW composition with the different types of polysaccharides for fungal and plant CWs is shown below. (B) Possible mechanisms to generate gradients of CW stiffness, with tips being softer than flanks. These include gradients in CW thickness, anisotropies in CW polysaccharides arrangements, graded modulations of polysaccharide crosslinks, or differences in CW composition. (C) Mechanisms that might account for polarized cell growth. (i) CW synthesis and remodeling create tips that might be effectively softer and less viscous, expanding faster that other parts of the cell. Expansion of CW can be properly mapped using surface tracers, and is found to be much higher at cell tips. (ii) Local CW curvatures allow the computation of tensile stresses, denoted with σ, imparted by turgor on the CW from Laplace's law. σ_t, CW stress at cell tips; σ_l, longitudinal stress on flanks; σ_c, circumferential stress on flanks. Local stresses combined with expansion maps allow to estimate patterns of effective viscosities, η. (iii) In many visco-plastic models for tip growth, growth speed is proportional to the effective viscosity, η, at cell tips and to the tensile stress at cell tips, above a plastic yield stress, Y.

also been assessed by bending cells in microfluidic flow devices (Couttenier et al., 2022; Nezhad et al., 2013), or by reducing turgor and measuring CW deflation (Abenza et al., 2015; Atilgan et al., 2015; Hu et al., 2017; Nezhad et al., 2013) (Fig. 2A). Recently, such a deflation assay was combined with sub-resolution imaging of CW thickness, enabling measurements of CW mechanics at the subcellular scale and with higher throughput than indentation-based methods (Chevalier et al., 2022 preprint; Davi et al., 2019) (Fig. 2B). Although the obtained values vary between these reports, possibly because methods such as AFM are more sensitive to matrix

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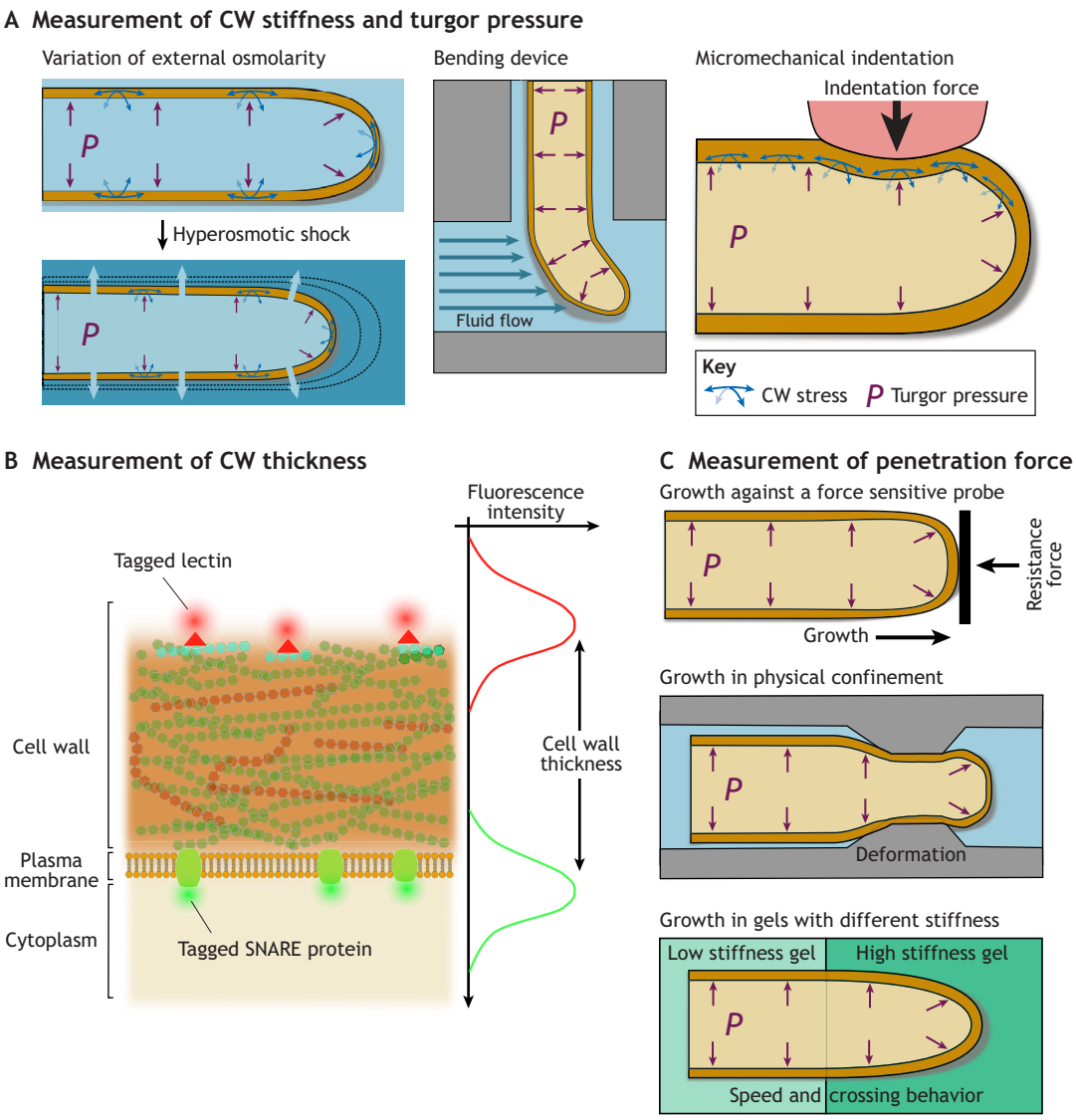

Fig. 2. Methods to measure cell wall mechanics and turgor in tip-growing cells. (A) Different methods used to measure global or local CW stiffness. Left, turgor reduction after a hyperosmotic shock causes the CW to shrink. Quantification of strain changes for the computation of CW stiffness and estimation of turgor from the osmolarity needed to completely relax the CW. Middle, cell bending with a microfluidic flow device. Fluid forces are used to compute CW stiffness from the amount of bending they cause. Right, indentation of the CW with a force probe. (B) Subresolution imaging to measure CW thickness in live cells based on the local measurement of the distance between fluorophores at the inner or outer CW surfaces. (C) Approaches to measure penetration forces for tip-growing cells and assay cell responses to external forces. Top, growth against a force sensitive probe. Middle, growth in a narrow deformable channel. Bottom, growth in gels with different stiffness.

polysaccharides (Milani et al., 2013), they nevertheless suggest apparent stiffnesses of a similar magnitude to pressure-derived tensions of ∼0.5–5 N/m, and bulk elastic moduli of 10–100 MPa, akin to a material such as rubber (Table 1).

Mechanical anisotropy of the CW

In a cylindrical cell, circumferential CW tension is twice that of longitudinal tension. In some bacterial cells and epidermal plant cells, circumferential tension can be resisted by the organization of CW strands in circumferential arrays (Baskin, 2005; Carballido-López, 2006). In contrast, ultrastructural data in tip-growing cells, including root hairs and fission yeast indicate that CW fibrils are organized in layers parallel to the cell surface but with no intrinsic polarity within each layer (Galway et al., 1997; Newcomb and Bonnett, 1965; Takagi et al., 2003). In the flanks of pollen tubes, cellulose fibrils are nearly longitudinal (Chebli et al., 2012). Cell deflation experiments are also consistent with there being a low mechanical anisotropy of the CW in pollen tubes but also in multiple fungi (Abenza et al., 2015; Atilgan et al., 2015; Chevalier et al., 2022 preprint; Vogler et al., 2013). All these observations suggest that there is no need for circumferential reinforcements of the flanks of a tip-growing cell.

Gradients of CW mechanical properties

Interestingly, multiple measurements in plant and fungal cells indicate marked gradients in CW stiffness with tips being ∼1.5 to 5 times softer than the cell sides (Bolduc et al., 2006; Chevalier et al., 2022 preprint; Davì et al., 2018; Zhao et al., 2005). Such gradients could emerge from spatial variations of CW thickness, as observed in fission yeast (Davì et al., 2018) and in a brown alga (Rabillé et al., 2019), or of its biochemical properties (Fig. 1B). This second possibility has been extensively assessed in pollen tubes, where CW

composition exhibits a longitudinal gradient (Chebli et al., 2012). Notably, pectins are highly esterified at the apex, whereas they are instead de-esterified at the flanks. De-esterification elicits Ca^{2+} binding to negative charges on pectins, enabling pectin cross-linking to stiffen the CW at cell flanks (Chebli et al., 2012; Parre and Geitmann, 2005a; Röckel et al., 2008). Callose deposition in the flanks might also increase stiffness there (Chebli et al., 2012; Leszczuk et al., 2019; Parre and Geitmann, 2005b).

In conclusion, turgor deforms the CW close to its failure point, which entails risks of CW failure and cell death. These risks might be enhanced at cell tips where freshly assembled walls are apparently softer, possibly due to polarized CW assembly and remodeling.

Setting the pace of tip growth

An increase in CW expansion rate could lead to CW over-thinning and rupture. To understand surface integrity, it is therefore important to investigate how turgor and CW mechanics control CW expansion and tip growth. Although the elastic modulus that links the wall tension to its instantaneous deformation, as discussed above, can 'easily' be assessed experimentally, its correlation to cell growth is more indirect. Indeed, growth requires an irreversible plastic and/or viscous expansion of the CW. Accordingly, the influential mathematical model for CW expansion introduced by Lockhart (Lockhart, 1965) is based on a visco-plastic description of the CW, with growth occurring above a threshold plastic strain, and in proportion to the tensile stress created by turgor and to an effective CW viscosity (Fig. 1C).

Role of turgor

The assumed role of turgor in Lockhart's model is supported by a large body of data in pollen tubes and fungal hyphae, which show that reducing turgor by increasing medium osmolarity can decrease the average tip growth rate, often in a dose-dependent manner (Gervais et al., 1999; Haupt et al., 2018; Lew, 2011; Minc et al., 2009; Zonia et al., 2006). Interestingly, however, the natural tip growth rates of fungi and pollen tubes are not generally correlated with turgor values (Benkert et al., 1997; Chevalier et al., 2022 preprint; Minc et al., 2009), and in the oomycetes *Achyla bisexualis* and *Saprolegna ferax*, an abolishment of turgor does not completely halt tip growth (Money and Harold, 1993). One plausible explanation is that growth could be limited by the conductivity of the plasma membrane to water (Dumais, 2021). An alternative is that CW expansion is primarily set by dynamic changes in its mechanical properties.

Patterns of surface expansion

The applicability of Lockhart's general framework to tip-growing cells requires mechanisms to polarize CW expansion at the tip. CW expansion can be mapped by following the movement of static tracers deposited on the CW surface (Dumais et al., 2004; Hejnowicz et al., 1977) such as fluorescent microspheres (Shaw et al., 2000). Using this approach, steep longitudinal gradients in CW expansion were measured in root hairs of *Medicago truncatula* (Shaw et al., 2000; Dumais et al., 2004), with highest expansion rates at the apex (Fig. 1C). Similar results were also obtained in yeast and fungal hyphae (Abenza et al., 2015; Bartnicki-Garcia et al., 2000), suggesting that the patterns of CW expansion in tip-growing cells might be based on conserved mechanisms.

Patterns of effective viscosity

Lockhart introduced an effective viscosity (also referred to as the inverse of CW extensibility), which does not simply reflect the fluid-like properties of the CW material, but rather the coupling between CW mechanics and remodeling. This effective viscosity is defined as the ratio between tensile stress in the CW and expansion rate of the CW. It can thus be determined by combining maps of CW expansion with CW geometry. Indeed, Laplace's law relates surface tension, pressure and surface curvature from mechanical balance, and allows to compute patterns of CW tensile stresses from local CW curvature (Abenza et al., 2015; Dumais et al., 2004; Hejnowicz et al., 1977) (Fig. 1C). Such analysis has been performed in root hairs, pollen tubes and multiple fungi, and suggests that CW expansion and tensile stress are respectively maximal and minimal at cell tips, so that the effective CW viscosity is minimal there (Dumais et al., 2004; Shaw et al., 2000). Which biochemical mechanism patterns this viscosity remains an important open question, but it has been suggested to derive from the polar distribution of secretory vesicles that control CW remodeling and turnover (Abenza et al., 2015; Chevalier et al., 2022 preprint; Emons and Ketelaar, 2009; Geitmann and Emons, 2000; Ketelaar et al., 2008).

Mechanical models

As turgor pressure is uniform, expansion at cell tips requires the CW to be either heterogeneous (consistent with most measurements described above) or anisotropic (which seems unlikely based on the above). Accordingly, models of tip growth all rely on the existence of patterns of CW mechanical properties. One type of model proposes a polar distribution of effective viscosity (following observed patterns of extensibility) and yields elongated cells with a stationary shape (Dumais et al., 2006; Campàs et al., 2012; Campàs and Mahadevan, 2009; Rabillé et al., 2019). Another type of model assumes a polar distribution of CW stiffness (following experimental measurements), along a thin shell inflated by turgor and takes the new shape as a reference shape, with subsequent iterations of the process (Abenza et al., 2015; Drake and Vavylonis, 2013; Fayant et al., 2010; Goriely and Tabor, 2008; 2003a,b). These two types of model yield similar outputs, likely because elastic increments between successive reference shapes are equivalent to viscous relaxation.

Models coupling polarity and mechanics

Early models for tip-growing cells were mostly based on geometric rules (Koch, 1982; Ricci and Kendrick, 1972; Trinci and Saunders, 1977). For instance, the hyphal geometry was considered to be driven by a so-called vesicle supply center, from which vesicles are emitted, and it was modeled how patterns of CW secretion could govern cell morphology through CW expansion (Bartnicki-Garcia et al., 1989; Gierz and Bartnicki-Garcia, 2001). Later, such a vesicle supply center was combined with CW mechanics, which predicted elongated cells (Eggen et al., 2011; Tindemans et al., 2006). A similar idea was applied to the germination of fission yeast spores (Bonazzi et al., 2014) to predict the transition from spherical spores to elongated tip-growing cells.

Overall, inspection of the literature indicates that tip growth speeds might be primarily determined by CW remodeling rates at cell tips, with turgor-derived tension being required for CW expansion but not dictating tip growth speeds per se. However, CW expansion poses another fundamental issue for surface integrity; it must be appropriately balanced with synthesis to ensure that CWs remain intact as they expand. Evidence for feedback systems coordinating these processes, and underlying mechanisms are discussed in the next sections.

Mechanical feedback and mechanosensing during tip growth

Although most of the above studies point to important links between CW composition and steady spatial gradients in CW mechanics, only a few address the dynamic interplay between CW synthesis, growth and mechanical integrity. However, if CW expansion occurs much faster than CW synthesis, the CW will thin over time, bearing larger and larger stresses, eventually yielding to rupture. To prevent failure, cells would need to sense and respond to mechanical stress associated with CW thinning.

Mathematical models with feedback

Several models have been developed to understand the stability of CWs and how cells prevent bursting. The mechanical feedback considered in theoretical models mainly concerns wall synthesis or remodeling. For example, in a model for pollen tube elongation, cell elongation was assumed to downregulate pectin deposition in the CW (Rojas et al., 2011), whereas for fission yeast, it was proposed to upregulate wall synthesis (Davì et al., 2018). Without such assumptions, steady growth would be unstable; the models would predict wall thickness to vanish or growth to stop following perturbations of the steady state. These assumptions might account for proteins that sense the mechanical state of the CW (Banavar et al., 2018; Davì et al., 2018). Alternatively, feedback could rely on stretch-activated channels and ion dynamics, as modeled in several studies (Kroeger et al., 2011; 2008; Liu and Hussey, 2014). For example, one proposed model is based on a sensor that detects differences in water potential between the extracellular medium and the cytoplasm, which can modulate the deposition rate of CW material at the tip (Hill et al., 2012). Another study modeled ion dynamics and found it to be sufficient to account for a feedback between cell growth (through ion dilution) and CW synthesis, suggesting that mechanosensing is not entirely necessary (Liu et al., 2010).

Experimental signatures of mechanical feedback

Mechanical feedback systems for CW dynamics imply that specific surface sensors probe CW tensional stress or strain rates to trigger adaptive responses that adjust CW synthesis (see below), ensuring that CW thickness, strain or stress remain close to the steady values that are compatible with both surface growth and integrity (Fig. 3A).

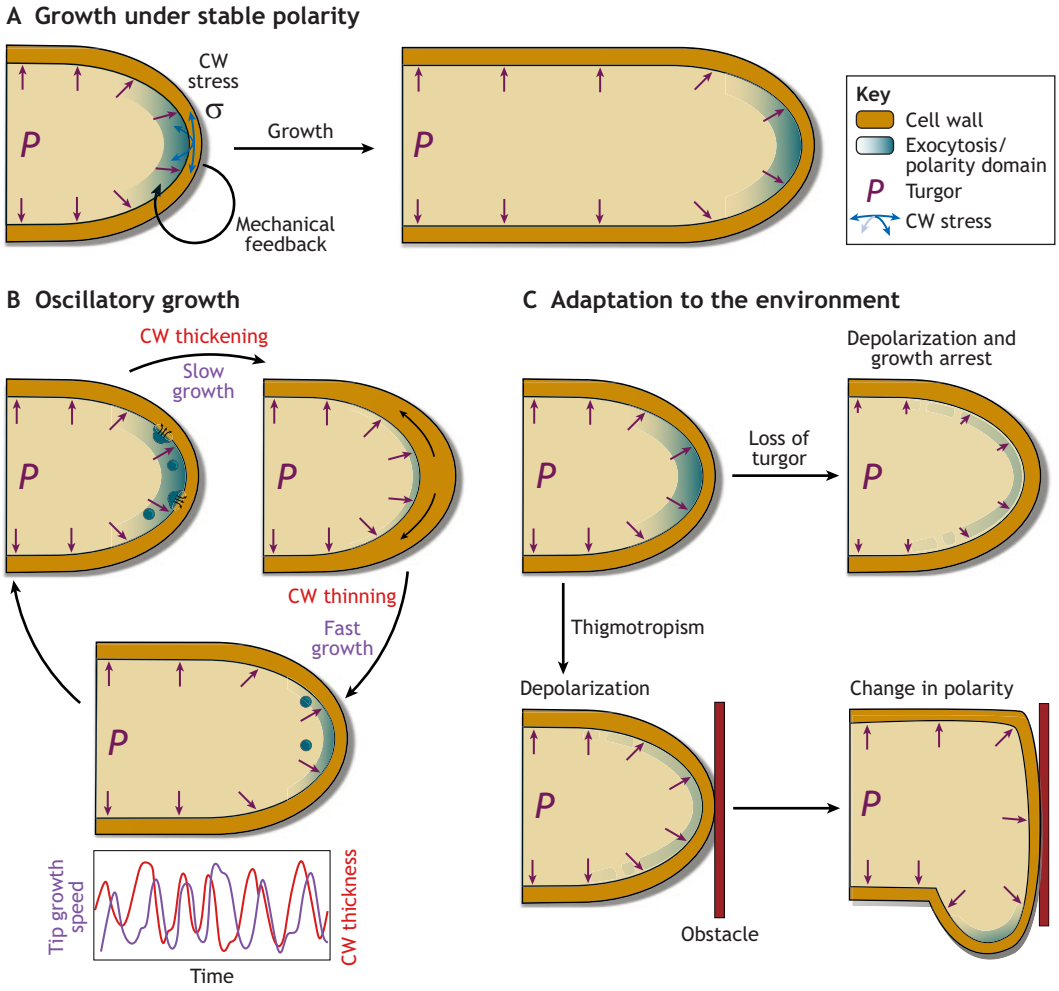

Fig. 3. Signatures of mechanical feedback systems in tip-growing cells. (A) Stable tip growth with a near constant CW thickness, secretion and mechanics requires the presence of feedback mechanisms between wall mechanics or its deformation and polarized secretion for the modulation of CW synthesis and remodeling. (B) Oscillatory growth is typical for many tip-growing cells, such as pollen tubes or filamentous fungi, and has been suggested to rely on a delayed mechanical feedback, which creates an out-of-phase increase in CW thickness and variations in elongation speed. (C) Loss of turgor in most fungi and plant cells results in halted growth and the detachment of polarity and secretion domains from cell tips. Similarly, halted growth upon encountering an obstacle creates a transient depolarization that is followed by the stabilization of a new polarity domain away from the obstacle, thereby allowing cells to resume tip growth in a different direction.

The mere existence of mutants in surface sensors, downstream kinases or transcription factors linked to CW synthesis, which exhibit tip bursting in plant and fungal cells, is a strong indication that such feedback exists and is relevant to tip growth (Banavar et al., 2018; Davì et al., 2018; Li et al., 2015; Zhou et al., 2021). These feedback systems could be particularly important during growth transitions, when the CW must rapidly change geometry or mechanics, such as during yeast mating (Banavar et al., 2018), fungal host invasion (Puerner et al., 2020; Ryder et al., 2019) or pollen tube navigation in the confined spaces of the pistils (Zhou et al., 2021).

Another signature of mechanical feedback is the existence of oscillations in growth and CW mechanics. Oscillatory growth has been documented for decades in filamentous fungi, pollen tubes and root hairs (Cardenas et al., 2008; López-Franco et al., 1994; Monshausen et al., 2007; Qin and Yang, 2011). It provides a natural situation to study how modulations in elongation rates might feedback on CW synthesis and mechanics. It has been, for instance, suggested to result from feedback that couples CW deformation and synthesis (Rojas et al., 2011), giving rise to delayed out-of-phase oscillations between growth, CW secretion, CW thickness and apparent stiffness (McKenna et al., 2009; Zerzour et al., 2009) (Fig. 3B). CW thickness dynamics in fission yeast also exhibits fluctuating behavior with delayed feedback (Davì et al., 2018).

Adaptation of CW synthesis or mechanics to abrupt changes in growth speeds is another signature of mechanical feedback. Changes in tip growth rates might be caused by natural barriers, such as the rigid wall encasing fungal spores, or by alterations of the environment, for instance when pollen tubes enter specific plant compartments. However, it can also be triggered by growing cells against microfabricated obstacles, in narrow gaps, or by affecting turgor (Bonazzi et al., 2014; Burri et al., 2018; Haupt et al., 2018; Reimann et al., 2020; Sanati Nezhad et al., 2013; Thomson et al., 2015; Zhou et al., 2021). One study analyzed the behavior of pollen tubes passing through gaps of different sizes and observed increased diameters after cells pass through gaps, suggesting that tip CWs become softer when facing increased mechanical resistance (Sanati Nezhad et al., 2013). Other evidence of mechanical feedback comes from growing pollen tubes in matrices with different stiffnesses. By studying different species, a ‘durotropic’ behavior was observed for pollen tubes from species where transmitting tracts are solid – tubes growth rates increase in stiff matrix – and the opposite for tubes from species with hollow tracts (Reimann et al., 2020). Mechanistically, pollen tube growth in a stiffer medium could decrease callose and pectin synthesis, making the CW more deformable (Parre and Geitmann, 2005a,b).

Growth arrest that occurs upon the presence of physical obstacles might also alter the location of CW assembly, by causing cortical polar domains of active Rho-GTPases to detach from cell tips, and to reform along a mechanically favorable direction that drives polar CW synthesis and growth away from the obstacle (Brand et al., 2007; Burri et al., 2018; Haupt et al., 2018; Thomson et al., 2015) (Fig. 3C). This process, often called ‘thigmotropism’, supports the existence of positive feedback between growth and polarity stability, and might allow pathogenic fungi to sense substrate topology and mechanics to optimize navigation in host tissues (Almeida and Brand, 2017).

Overall, tip-growing cells are equipped with homeostatic feedback mechanisms that allow them to modulate CW mechanics and/or reorient sites of synthesis when facing mechanical resistance. How growth modulations, contact with a physical barrier, or more generally mechanical cues on the cell surface, may be sensed by cells, to feedback onto CW synthase, Rho-GTPase activity, vesicle trafficking or Ca^{2+} signaling, is therefore an important open question, which we discuss in the next section.

Molecular mechanisms for CW mechanosensation

CW mechanosensors

Perturbations in the CW might be directly sensed by proteins embedded in the CW. In fungi, a conserved class of sensors are those that activate the CW integrity signaling pathway (CWI), which promotes CW synthesis in response to damages, such as those caused by CW-perturbing chemicals (Cansado et al., 2021; Dichtl et al., 2016). These sensors belong to the ‘cell wall integrity and stress response component’ (WSC) or ‘mating-induced death’ (MID) families. They can signal to downstream effectors of the CWI, including guanine nucleotide exchange factors (RhoGEFs) that activate Rho for CW synthesis, and protein kinase C, which is upstream of a MAPK cascade that controls CW regulatory genes (Fig. 4B). Typically, fungal mutants lacking these sensors exhibit reduced colony growth, frequent tip bulging and bursting that can be suppressed by an osmostabilizer, indicative of soft and fragile CWs (Cruz et al., 2013; Dichtl et al., 2012; Maddi et al., 2012; Ohsawa et al., 2017; Rodicio et al., 2008; Tong et al., 2016). Both sensor types share a similar structure of a signal peptide, a head group, an extracellular serine/threonine-rich (STR) domain, embedded in the CW, followed by a transmembrane domain and a cytoplasmic tail (Elhasi and Blomberg, 2019; Rodicio and Heinisch, 2010) (Fig. 4A). The head group differs between families; MID-type sensors have a N-glycosylated asparagine, whereas the WSC-type have a polysaccharide-binding WSC domain (Heinisch et al., 2010; Wawra et al., 2019). The STR domain is highly glycosylated and AFM experiments suggest it behaves like a ‘nano-spring’ ∼30–50 nm in length, that could potentially compress when forces are applied to the CW (Dupres et al., 2009). Accordingly, both MID-type and WSC-type sensors have been suggested to be involved in the survival of cells grown under mechanical compression (Delarue et al., 2017; Mishra et al., 2017; Neeli-Venkata et al., 2021). In addition, a recent study showed that fission yeast Wsc1 can form large clusters in subcellular regions where the CW is subjected to enhanced mechanical stress, allowing the formulation of hypotheses for how cells might detect local forces on their CW (Neeli-Venkata et al., 2021) (Fig. 4B).

Other fungal CW sensors might help cells cope with mechanical stresses by regulating turgor. In fungi, the high-osmolarity glycerol (HOG) pathway is essential for the adaptation of turgor to hyperosmotic conditions, with the mucin proteins Hkr1 and Msb2 serving as putative surface sensors (Saito and Posas, 2012). These are transmembrane proteins with a large glycosylated STR domain followed by a Hrk1-Msb2 homology (HMH) domain, which both are embedded in the CW, a transmembrane domain and a cytoplasmic tail (Fig. 4A). Both form clusters at the cell surface when subjected to hyperosmotic stresses, and have been proposed to detect CW tension through a conformational change that exposes the HMH domain and activates the HOG pathway (Tatebayashi et al., 2007; Yang et al., 2009). Msb2, but not Hrk1, is also involved in the adaptation of cell growth under mechanical compression (Delarue et al., 2017). MsbA, the Msb2 ortholog in the fungus *Aspergillus fumigatus*, is a CWI sensor that influences CW composition, thickness and cell growth (Gurgel et al., 2019) (Fig. 4B).

Several CW-binding mechanosensors have also been identified in plants and described in excellent recent reviews (Anderson and Kieber, 2020; Bacete and Hamann, 2020; Monshausen and

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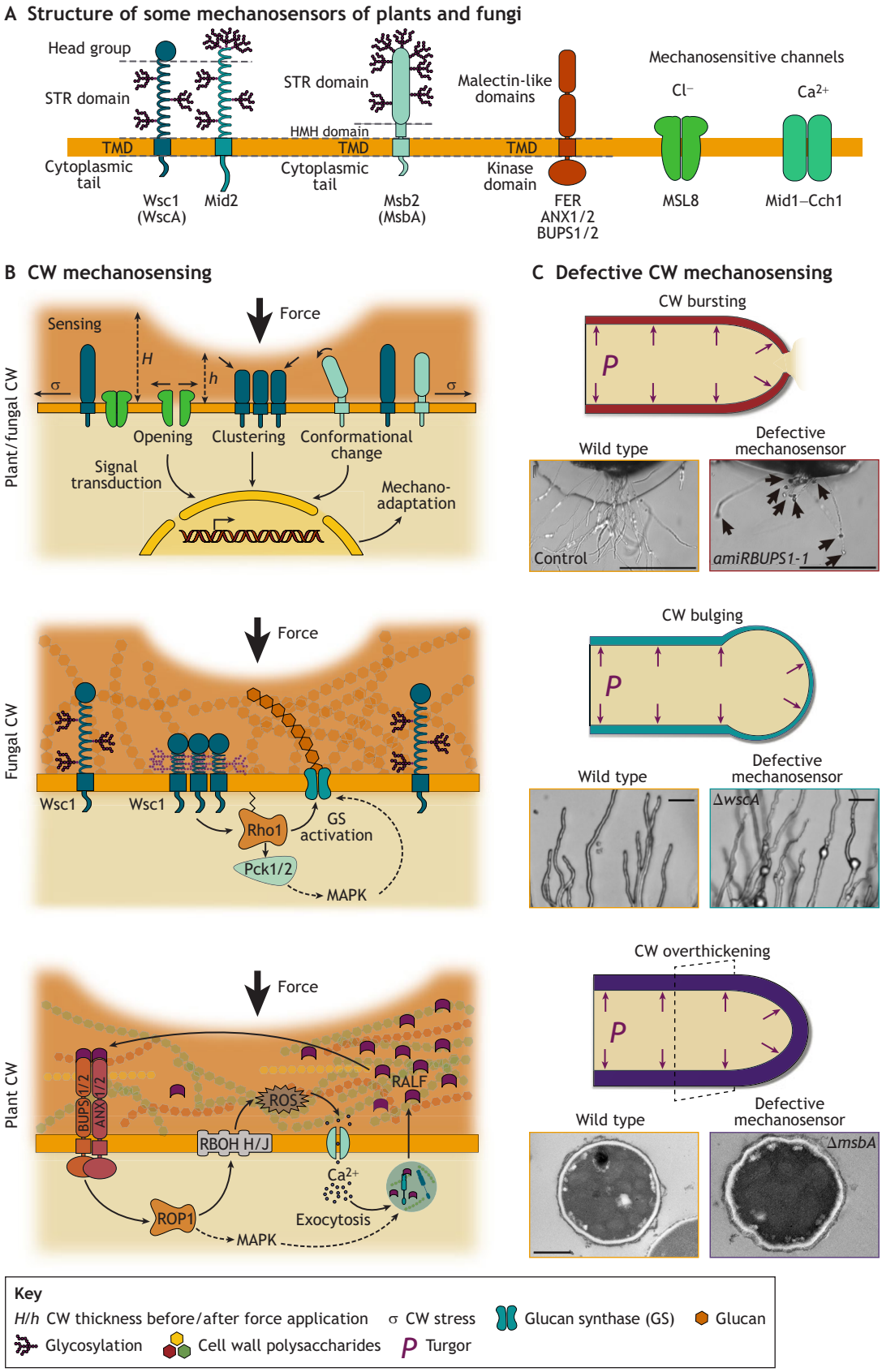

Fig. 4. See next page for legend.

Fig. 4. Molecular mechanisms for mechanosensation in the cell wall. (A) Schematic illustration of the structure of some plant and fungi mechanosensors – the CWI sensors from *Schizosaccharomyces pombe*, Wsc1 and Mid2, the HOG sensor Msb2 from *Saccharomyces cerevisiae*, the plant CrLKs, FER, ANX1 and ANX2 (ANX1/2), BUPS1 and BUPS2 (BUPS1/2), the mechanosensitive MSL8 channels from *A. thaliana* and Mid1–Cch1 from *Saccharomyces cerevisiae*. STR, serine/threonine-rich; TMD, transmembrane domain; HMH, Hrk1-Msb2 homology. (B) Top, overview of some characterized surface sensors in plant and fungal tip-growing cells. In response to CW stress (denoted with σ) or modulation of its mechanical properties, these might alter their conformation, that is, STR-domain-containing sensors might compress, bend and/or cluster, and membrane ion channels could open. These changes then lead to the downstream activation of repair pathways that adapt the properties of CW or turgor (mechanoadaptation). Middle, illustration of a proposed mechanism for mechanosensing in the fungal CW by Wsc1 in the fission yeast *Schizosaccharomyces pombe*. The WSC domain could mediate clustering of the sensor to optimize mechanosensing, whereas a glycosylated STR domain might compress to activate CW synthesis through Rho1 and Pck1 and Pck2 (Pck1/2), which initiate a MAPK cascade. Bottom, in pollen tubes following mechanical stress, RALF4 and/or RALF19 signal peptides interact with BUPS1/2–ANX1/2 to activate a signaling cascade involving ROP1 and a NADPH oxidase (RBOH H/J) that leads to tip-localized ROS production. ROS also mediate activation of Ca^{2+} channels and subsequent exocytosis of CW materials, as well as of RALF4, to amplify the signal. (C) Examples of phenotypes associated with mutants in different mechanosensors. Top, tip bursting in pollen tubes of knockdown mutant *amiRBUPS1* (arrows). Adapted from Zhou et al. (2021) with permission from Elsevier. Middle, *ΔwscA* mutant of the fungus *A. nidulans*, which forms large bulges indicative of weakened CWs (WscA is a Wsc1 homolog in *A. nidulans*). Adapted from Futagami et al. (2011) with permission from the American Society of Microbiology. Bottom, *ΔmsbA* mutant of the fungus *A. fumigatus* exhibit a thicker CW indicative of defects in the homeostatic systems that control synthesis (MsbA is a Msb2 homolog in *A. fumigatus*). Adapted from Gurgel et al. (2019), where it was published under a CC-BY 4.0 license. Scale bars: 200 µm (top); 10 µm (middle); 0.5 µm (bottom).

Haswell, 2013; Rui and Dinneny, 2020). Here, we focus on those characterized in tip-growing cells. The transmembrane *Catharanthus roseus* receptor-like kinase (CrRLKs) subfamily is found throughout the plant kingdom, and many members have been implicated in tip growth (Boisson-Dernier et al., 2011; Franck et al., 2018; Nissen et al., 2016). Among them, FERONIA/SIRENE (FER/SIR) has attracted most attention. Loss-of-function *feronia* (*fer*) mutants are characterized by retarded growth with short, collapsed or bursting root hairs (Duan et al., 2010; Li et al., 2015), suggesting an impaired CW integrity and a loss of mechanical transduction. Indeed, *fer*-mutant roots exhibit diminished ability to penetrate hard agar as compared to wild-type roots, reflecting a defective adaptation of CW mechanical rigidity (Shih et al., 2014). In analogy with STR- and WSC-domain-containing sensors in fungi, FER has been proposed to interact with pectins to detect defects in the CW under stress and elicit Ca^{2+} signaling to reinforce pectins and preserve surface integrity (Feng et al., 2018). Finally, the cytoplasmic domain of FER also activates the GEF-plant Rho GTPase (ROP/ARAC), which subsequently phosphorylates RBOHD (Franck et al., 2018) to produce reactive oxygen species (ROS) that control root hair development (Duan et al., 2010).

CrRLKs involved in pollen tube growth have also been identified in *Arabidopsis thaliana*. In particular, BUDDHA'S PAPER SEAL 1 and 2 (BUPS1 and BUPS2) are required for normal tip growth of pollen tubes, and mutations in BUPS1 drastically reduce fertility (Ge et al., 2017; Zhou et al., 2021; Zhu et al., 2018). BUPS1 was recently shown to sense mechanical changes of the CW and promote CW strengthening when pollen tube tips emerge from compressing female tissues (Zhou et al., 2021). Indeed, mutants with pollen tube *BUPS1* knockdown (*amiRBUPS1-1*) grown in a microfluidic channel, to mimic the confined *in vivo* pistil growth path, exhibit a much higher rupture frequency than wild-type pollen tubes when they emerge from a narrow structure; this impaired CW integrity was associated with defects in the adjustment of CW rigidity (Zhou et al., 2021). BUPS1 and BUPS2 interact with other CrRLKs, such as ANXUR1 (ANX1) and ANX2, and both receptors bind to the RALF4 and RALF19 signal peptides to maintain pollen tube integrity (Ge et al., 2017; Mecchia et al., 2017; Zhou et al., 2021; Feng et al., 2018; Ge et al., 2017; Xiao et al., 2019). This binding activates a signaling cascade involving a RopGEF, ROP1 and a NADPH oxidase, which leads to ROS production to produce tip-localized H_2O_2. ROS also mediates activation of Ca^{2+} channels and subsequent exocytosis of CW materials, as well as RALF4, to amplify the signal (Zhou et al., 2021) (Fig. 4C).

Other putative mechanosensing systems

Other types of plant and fungal surface sensors might indirectly regulate CW integrity, or turgor, without interacting with CW polysaccharides. For instance, in *A. thaliana*, the plasma membrane MSL channels, which are homologs of the *Escherichia coli* mechanosensitive MscS channels, have been proposed to serve as tension-regulated osmotic safety valves. They enable cells to loose ions to decrease turgor in response to hypoosmotic shocks that tense the cell surface (Basu and Haswell, 2017). Notably, in pollen tubes of *A. thaliana*, MscS-LIKE IONS CHANNEL 8 (MSL8) is required for cellular integrity during germination and tube growth (Hamilton et al., 2015) (Fig. 4A). In fission yeast, the homologs of these channels, Msy1 and Msy2, localize to the endoplasmic reticulum and are essential for turgor adaption and survival under hypoosmotic conditions (Nakayama et al., 2012).

Mid1 and Cch1 are the subunits of a conserved stretch-activated Ca^{2+} channel that localizes in the plasma membrane (Kanzaki, 1999) (Fig. 4A). This channel has been suggested to promote CW integrity by sensing compressive stress in budding yeast (Mishra et al., 2017). In *Candida albicans*, Mid1 mediates the re-orientation of hyphal growth in response to changes in topography (Brand et al., 2007), and in *N. crassa*, *mid-1* mutants exhibit slow growth and lower turgor than seen in wild type (Lew et al., 2008). Furthermore, fission yeast mutants of Yam8, the Mid1 ortholog, are hypersensitive to CW-damaging agents (Carnero et al., 2000; Tasaka et al., 2000). MID1 COMPLEMENTING ACTIVITY 1 (MCA1) and MCA2 are two Ca^{2+}-permeable mechanosensitive channels that have been identified in *A. thaliana* based on partial complementation of Mid1-deficient budding yeast, and exhibit weak similarity to yeast Mid1 (Yoshimura et al., 2021). Although their role in tip growth is unknown, the inability of roots of *mca1*-null mutants or *mca1*- and *mca2*-null double mutants to penetrate a harder medium suggests that these proteins have a role in mediating mechanical feedback (Furuichi et al., 2012; Nakagawa et al., 2007; Yamanaka et al., 2010).

Pkd2 is a membrane channel of the transient receptor potential (TRP) family, which influences CW synthesis and Ca^{2+} homeostasis in fission yeast and is essential for cell viability (Aydar and Palmer, 2009; Ma et al., 2011). It has recently been described as a putative surface sensor that regulate turgor (Sinha et al., 2022). Finally, Sln1 is a transmembrane histidine kinase, that act as another upstream surface sensor of the HOG pathway (Reiser et al., 2003; Saito and Posas, 2012). It mediates the large upregulation of turgor during fungal appressorium formation needed for plant infection (Ryder et al., 2019). Interestingly, two Sln1 orthologs, the *Arabidopsis thaliana* histidine kinases AHK1 and CRE1, have also been proposed as turgor sensors based on their ability to complement budding yeast *sln1*Δ (Reiser et al., 2003; Urao et al., 1999).

Mathematical models for mechanosensing

Although quantitative data for how walled cell mechanosensors detect and transduce surface forces are still mostly lacking, mathematical models might help researchers to understand which signals and properties of the signals (e.g. their time-average, increments and/or pulses) are sensed, and guide future experiments (Fruleux et al., 2019). The stretch-activated mechanosensitive channels introduced above have received considerable attention (Basu and Haswell, 2017). Models have been established to reproduce the observed relationships between membrane tension (or osmotic pressure) and ionic current (Monshausen and Haswell, 2013) by considering the free energy landscape of the protein complex and its interaction with the plasma membrane (Wiggins and Phillips, 2004; 2005). The incorporation of membrane-mediated interactions between the channels in these models gives rise to cooperative gating (Haselwandter and Phillips, 2013), which could help buffer noise and avoid small-scale or transient mechanical fluctuations being transduced. Such buffering could also be mediated by sensor clustering and cooperative sensing, to form 'sensosomes' as well described in the case of animal integrins, which form clusters at focal adhesions. The state and dynamics of integrins can be modeled using reaction–diffusion equations (Ali et al., 2011; Welf et al., 2012). Here, the prediction of clustering relies on a reduction of integrin diffusion when a force is applied to their extracellular domain (Ali et al., 2011) or when they bind to the extracellular matrix (Welf et al., 2012). It remains to be tested whether similar models applied to CW mechanosensors could explain their clustering in response to force as observed in yeast (Neeli-Venkata et al., 2021).

Conclusions

As is the case for animal mechanobiology, the field of mechanobiology of cells with a CW is progressing thanks to the combination of mechanical measurements, mechanical manipulations, mathematical models and characterization of mechanotransduction pathways. Interestingly, akin to animal cell behavior, both fungal and plant cells can exploit mechanochemical feedback to actively sense the mechanics of their environment or contact with their neighbors, and rapidly adapt their CW and growth properties. The existence of surface sensors that directly interact with CW polysaccharides, and form clusters as putative 'sensosomes' to mediate mechanosensing is also reminiscent of how animal sensors, such as integrins, interact with the extracellular matrix to sense tensile forces (Elhasi and Blomberg, 2019; Ingber, 2003). However, the existence of a CW leads to additional challenges – measuring large forces associated with turgor pressure, characterizing the dynamics of CW composition, as it is difficult to visualize specific polysaccharides *in vivo*, and properly dissecting the function of CW mechanosensing pathways, given the dramatic effects a defective CW has on plant or fungal development. Consequently, many aspects of CW mechanobiology remain unclear. Notably, how the composition and structure of the CW determine its expansion, how surface forces are detected, and how they feedback on the CW remain outstanding open questions. We envisage future progress in the field to come from studying a broader range of species, the generation of new fluorescent CW tags, or from reconstituting synthetic CWs with known composition and structure to better understand mechanosensing (Calcutt et al., 2021; Luo et al., 2015; Shi et al., 2019).

Finally, although the functions, geometries and compositions of CWs vary greatly among plant and fungal cells, our comparative survey in tip-growing cells suggest common shared general principles. These include similar orders of magnitude of turgor and CW elastic moduli and the presence of mechanical gradients (Table 1), as well as the dynamic regulation of CW mechanics or turgor by similar mechanochemical pathways, often implicating the same types of proteins. We speculate that these common principles have been selected in evolution as they serve as minimal ingredients to support integrity and fast expansion in tip-growing cells.

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Competing interests

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Summary: A Review of how cells with a cell wall, especially fungi and plants, sense and transduce surface forces to regulate growth and morphogenesis.

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