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Cracking the green wall code: insights into cell wall integrity across organisms

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Cell walls are not just passive barriers; they are dynamic and adaptable structures that are actively remodeled in response to both internal and external cues. They are crucial in defining cellular identity, ensuring structural integrity, and mediating interactions with the environment. The concept of cell wall integrity (CWI) encompasses the mechanisms by which cells monitor and maintain their walls, ensuring proper function and response to challenges. While significant knowledge has been accumulated on CWI in certain model organisms, there remains a vast landscape of uncharted territory in others. In this review, we aim to bridge this gap, offering a comparative perspective on CWI across different evolutionary lineages, from the well-studied yeasts to the diverse world of plants. We focus especially on the green lineage –the group of green algae and land plants, hence the *green wall*–, but also consider some insights from organisms with radically different lifestyles and cell wall arrangements, which serves as a base to some intriguing questions about the role of CWI across evolution and environmental adaptation.

KEYWORDS

mechanosensing, cell wall plasticity, cell wall dynamics, cell wall physicochemical properties, Streptophyta, Zygnematophyceae, Bacillariophyceae, Charophyceae

1 Introduction

Across diverse organisms, from yeasts to algae and terrestrial plants, the presence of robust extracellular matrixes, known as cell walls, is a defining feature. Beyond providing mechanical support, these walls act as dynamic interfaces, mediating interactions with the environment and playing instrumental roles in growth and development (Levin, 2005; Anderson and Kieber, 2020; Zhang et al., 2021). Their adaptability is underscored by their compositional plasticity, which allows for modifications in tune with developmental transitions, environmental shifts, and stressors.

The concept of cell wall integrity (CWI) refers to the sophisticated mechanisms that enable cells to perceive and adapt to changes in this structure, ensuring their walls remain resilient and functional (Levin, 2005; Bacete and Hamann, 2020). This adaptability is not

just a passive trait; it is an active response, an essential function reflecting the cell wall's role in safeguarding cellular identity and mediating environmental interactions. While substantial knowledge has been generated in the last years regarding CWI in specific model organisms, a vast expanse remains unexplored in others. In this mini-review, we made a concerted effort to synthesize existing knowledge on CWI, drawing parallels and distinctions across different organisms. By putting together, the well-characterized mechanisms in yeasts with the emerging insights from the plant kingdom and the intriguing recent findings in some algae, this review seeks to offer a cohesive understanding of CWI with a focus on the green lineage i.e., the *green wall*.

2 Defining cell wall integrity

The very notion of an “integral” cell wall is a subject of ongoing debate. What does integrity mean in the context of cell wall integrity? Is it purely structural, or does it encompass functional and dynamic aspects of the wall?

While foundational principles of CWI have been elucidated in certain organisms, such as *Saccharomyces cerevisiae* (Levin, 2011), the vast diversity of cell walls across different organisms introduces layers of complexity. For instance, the multicellular nature of plants brings forth challenges stemming from intercellular dynamics, where cells can exert force on their neighbors, leading to intricate mechanical interactions within tissues (Coen and Cosgrove, 2023). Similarly, unicellular organisms like algae, with their unique evolutionary histories and environmental interactions, offer distinct perspectives on CWI, further broadening the scope of our understanding (Peaucelle et al., 2012; Galindo-Trigo et al., 2016).

As we explore the complex world of CWI, it becomes clear that a comprehensive view is crucial. Analyzing each organism's unique cell wall composition is only the beginning. We must also consider how CWI mechanisms interact with and adapt to the organism's environment and lifestyle. This interconnectedness provides a more nuanced understanding of “integrity” in the context of cell walls and sets the stage for exploring its implications across diverse biological systems.

3 Yeast: a model system for CWI studies

S. cerevisiae has for a long time been at the forefront of CWI studies. Its cell wall is primarily composed of glucans (glucose polymers), mannans (mannose-containing polysaccharides), and proteins. CWI is maintained through three mechanisms. First, the Cch1 and Mid1 proteins form a Ca^{2+} channel that detects membrane stretching, possibly from a weakened cell wall and high turgor pressure, leading to calcium ion influx and downstream signaling via calmodulin (Levin, 2005). Second, the cell-surface sensor kinase, Sln1, monitors turgor pressure. Under hyperosmotic stress, Sln1 activates the MAPK Hog1, enabling yeast cells to sense and adjust to turgor changes (Levin, 2005). Lastly,

CWI sensors containing cell wall integrity and stress response component (Wsc) domains such as Wsc1 and Wsc2 detect cell wall mechanical changes. These sensors interact with the G protein Rho1 upon deformation, triggering responses essential for cell wall biosynthesis and cytoskeletal organization (Levin, 2005; Dupres et al., 2009). Central to CWI is transcriptional regulation, where activated transcription factors, especially Skn7, modulate target gene expression, guiding cellular responses to environmental or developmental cues (Kono et al., 2016). CWI pathways of other fungi share significant similarities with that of *S. cerevisiae*, suggesting a conserved mechanism of cell wall stress response among yeasts (Dichtl et al., 2016).

4 Land plants: blooming of CWI monitoring systems

Land plants, spanning from simple to complex forms, provide a rich diversity of evolutionary adaptations. The cell wall, a key element in the transition from aquatic to land environments, is no exception, with compositions and structures that vary among plant species, developmental stages, tissues, and even across a single cell wall (Knox, 2008; Somssich et al., 2016; Gigli-Bisceglia et al., 2020). The primary cell walls of land plants, predominantly composed of cellulose, hemicellulose, and pectin recently reviewed by Cosgrove (2022), have evolved to offer flexibility during cell growth. In contrast, the secondary cell walls –recently reviewed by Zhong et al., 2019, found in specialized cells like tracheids, vessel elements, and fibers, are more rigid and provide structural support. These secondary walls are rich in cellulose, hemicellulose, and notably, lignin, which makes them rigid and resistant.

The diversity of plant cell walls is mirrored by their CWI systems, which are much more intricate than those of their unicellular counterparts (Table 1). *Arabidopsis thaliana*, the renowned eudicot model, has been instrumental in elucidating CWI mechanisms. The CWI in *Arabidopsis* is closely associated with receptor-like kinases (RLKs) and receptor-like proteins (RLPs) that perceive changes in the cell wall's integrity by putatively binding to glycan ligands. Once bound, these RLKs initiate intricate signalling cascades that modulate a range of cellular responses, ensuring the cell wall remains robust and functional (Bacete et al., 2018). The *Catharanthus roseus* receptor-like kinase1-like (*CrRLK1L*) family –comprising 17 members in *Arabidopsis*– is a prominent example of RLKs involved in CWI sensing, with THESEUS1 (THE1) and FERONIA (FER) being prominent examples (Decreux and Messiaen, 2005; Kohorn, 2016; Feng et al., 2018; Gonneau et al., 2018; Bacete et al., 2022; Ortiz-Morea et al., 2022; Zhong et al., 2022). Wall-Associated Kinases (WAK) and LysM RLKs such as chitin elicitor receptor kinase 1 (CERK1) are also key elements of the receptor-mediated CWI perception (Kohorn, 2016; Bacete et al., 2018; Mérida et al., 2018; Rebaque et al., 2021; Martín-Dacal et al., 2023). Beyond the molecular interactions, the physical aspect of cell wall perception cannot be overlooked. Mechanoperception, the ability of cells to sense and respond to mechanical stimuli, is integral to CWI. The displacement between the cell wall and plasma membrane caused

TABLE 1 Comparative analysis of cell wall integrity mechanisms in different organisms.

Organism	Signal Detected	Relevant Proteins	References
<i>Saccharomyces cerevisiae</i>	Membrane stretching	Cch1, Mid1	Levin, 2005
	Turgor pressure	Sln1, Hog1	Levin, 2005
	Cell wall mechanical changes	Wsc1, Wsc2, Rho1	Levin, 2005
<i>Arabidopsis thaliana</i>	Cell wall fragments	WAK1, CERK1	Kohorn, 2016; Bacete et al., 2018; Mérida et al., 2018; Martin-Dacal et al., 2023; Rebaque et al., 2021
	Cell wall mechanical changes	THE1	Bacete et al., 2022
	Membrane stretching	MCA1, MCA2, OSCA1.1, OSCA1.2, MSL2, MSL3, MSL8, MSL10	Basu and Haswell 2020; Hamilton et al., 2015; Hou et al., 2014; Maksaev and Haswell, 2012; Nakagawa et al., 2007; Yamanaka et al., 2010; Yuan et al., 2014
	Displacement of plasma membrane	AHK1, AHK4/CRE1	Tran et al., 2007; Urao et al., 1999; Wohlbach et al., 2008
<i>Marchantia polymorpha</i>	Cellular expansion and CWI	FER homologue	Westermann et al., 2019; Mecchia et al., 2022
<i>Poplar</i>	Secondary CWI in developing wood	Not specified	Coleman et al., 2008; Gorzsás et al., 2011; Ratke et al., 2018
Chlorophyta Green Algae	Osmosensing, cell wall-anchored surface receptors	SRCR-domain proteins (putative)	Cronmiller et al., 2019
Streptophyte Algae	Mechanical changes in cell wall	Microtubules, Unknown receptors	Hamant et al., 2019; Ochs et al., 2014; Mecchia et al., 2022; Morris et al., 2003
Diatoms	Cell wall plasticity, environmental cues	Unknown, Wsc domains in <i>T. pseudonana</i>	Pančić et al., 2019; Pondaven et al., 2007; McNair et al., 2018; Claquin et al., 2002; Hildebrand et al., 2018

by mechanical forces can activate membrane-bound receptors and ion channels (Basu and Haswell, 2020; Yoshimura et al., 2021; Codjoe et al., 2022). This mechanosensory capability ensures that plants can swiftly and effectively respond to physical challenges, from turgor pressure changes to external mechanical stresses (Bacete and Hamann, 2020).

The bryophyte *Marchantia polymorpha* offers insights into the evolutionary transition of plants from aquatic to terrestrial habitats,

with its CWI system hinting at evolutionary links with certain Arabidopsis receptors, including a FER homologue that regulates cellular expansion and cell wall integrity (Westermann et al., 2019; Mecchia et al., 2022). CrRLKs are present as well in other bryophytes such as *Physcomitrium patens* (Lehti-Shiu et al., 2009) although their implication in CWI sensing remains unclear. These observations give relevance to the importance of RLK-based mechanisms for plant CWI. However, no homologues for CrRLKs, WAKs, or any other relevant plant CWI RLK have been identified in fungi or algae. Conversely, the absence of Wsc sensors in plants, prevalent in other organisms, accentuates this evolutionary divergence, suggesting that plants might have evolved distinct mechanisms for CWI perception.

Poplar stands out as a model organism for studying CWI in woody plants, pivotal in understanding the intricacies of lignification and the development of secondary cell walls (Coleman et al., 2008; Gorzsás et al., 2011). However, the existence of a secondary cell wall CWI monitoring system has been questioned. Downregulation of xylan synthesis genes leads to changes in xylan content, improved lignocellulose saccharification efficiency, and stimulated growth. Shifts in cellulose orientation and cell wall thinning suggest the presence of a cell wall integrity monitoring mechanism that senses and responds to reduced xylan elongation in developing wood (Ratke et al., 2018). However, the analysis of the stem transcriptome in Arabidopsis xylan mutants revealed minimal changes, suggesting a lack of a robust secondary CWI response (Faria-Blanc et al., 2018). Grasses, like *Brachypodium distachyon*, with their differential cell wall attributes (Coomey et al., 2020), can further enrich our understanding of secondary CWI and reveal both conserved and unique mechanisms distinguishing monocots from eudicots.

5 Green algae: unicellular proxies to plant-esque cell wall integrity

The green lineage is split into two significant subgroups: Chlorophyta, containing most green algae species (Cronmiller et al., 2019); and Streptophyta, consisting of the land plants (Embryophyta) and streptophyte algae. Plant terrestrialization required numerous cellular adaptations, which allowed land plant ancestors to withstand novel stress conditions, such as high UV radiation and desiccation (de Vries and Archibald, 2018). These included changes in the cell wall composition and organization, and probably novel mechanisms to monitor and modify cell wall structure accordingly.

Chlorophyta green algae have very diverse cell wall compositions, from cellulose-pectin complexes to hydroxyproline-rich glycoproteins (Domozych et al., 2012). *Chlamydomonas reinhardtii* has emerged as a model system for this subgroup. Its cell wall, primarily composed of hydroxyproline-rich glycoproteins, is crucial for environmental protection. In an interesting work by Cronmiller et al. (2019), *C. reinhardtii* was shown to respond to gametolysis by rapidly activating over 100 cell wall-related genes. This activation is partly driven by osmosensing channels and cell

wall-anchored surface receptors, whereas no homologues for CrRLK1Ls, WAKs, or BR-signaling components for cell wall integrity were identified. Instead, the authors suggest that *C. reinhardtii* employs scavenger-receptor cysteine-rich (SRCR)-domain proteins as surface receptors. These SRCR proteins, including five TRP-type channels, are implicated in calcium-mediated signaling (Cronmiller et al., 2019). Intriguingly, Wsc domains, essential for CWI in yeast, can be found in the sequenced genomes of some other unicellular–*Dunaliella tertiolecta* and *Tetrademus obliquus*– and colonial –*Gonium pectorale*– Chlorophyta green algae (Hanschen et al., 2016; Carreres et al., 2017; Malerba et al., 2020).

Streptophyte algae, also known as charophytes, are the closest relatives to land plants. They can be split into the basal-branching Klebsormidiophyceae, Chlorokybophyceae, and Mesostigmatophyceae (KCM) and the higher-branching Zygnematophyceae, Coleochaetophyceae, and Charophyceae (ZCC) group (de Vries et al., 2016). ZCC group are the closest land plant relatives with cell walls comprised of polysaccharides present in land plants, unlike the KCM group (Sørensen et al., 2011). Similarities in cell wall composition between land plants and charophytes are additionally reflected by the presence of canonical cell wall biosynthetic enzymes and structural proteins in the genomes of these algae (Feng et al., 2023). Therefore, exploring CWI mechanisms in members of ZCC group holds great promise for understanding the evolution CWI processes in land plants. Surprisingly, no FERONIA homologs were found in the genomes of charophytes (Mecchia et al., 2022), indicating that these organisms utilize alternative CWI systems. Proliferation of CrRLK1L family of receptors in land plants is more likely to be an adaptation to complex multicellular body plans (Morris et al., 2003), in which cell-to-cell communication is essential for coordinated tissue growth and development. It is plausible that in the unicellular and simple multicellular Zygnematophyceae, mechanical changes in the cell wall can be registered by alternative pathways, such as sensing by microtubules, which were proposed to act as tension sensors in plant cells (Hamant et al., 2019). Indeed, depolymerization of microtubules by oryzalin in unicellular *Penium margaritaceum* leads to cell swelling and abnormal cell shape (Ochs et al., 2014). It remains unclear what type of receptors, if any, are involved in CWI mechanisms in complex multicellular forms from Coleochaetophyceae and Charophyceae classes. Future research and understanding of land plant evolution is currently hampered by the lack of molecular biology tools and reliable transformation protocols for charophyte algae. With new algal genomes being published at an accelerated pace, the time has come to answer previous calls (Rensing, 2017) and establish charophytes as molecular biology model systems.

6 Diatoms: the implications of a rigid cell wall

Diatoms, which are of high ecological and biotechnological relevance, arose from several secondary endocytosis events, with their plastid derived from a eukaryotic red algae (Nelson et al., 1995;

Yool and Tyrrell, 2003; Armbrust, 2009). There are estimated to be well over 100,000 diatom species, making it one of the most species-rich group of eukaryotic microorganisms (Mann and Droop, 1996). Interestingly, unlike most other photosynthetic organisms, their cell walls are not mainly composed of polysaccharides, but instead made up by two porous silica shells, called frustules, which fit together like a petri-dish (Hildebrand, 2008). This rigid cell wall is coated by an organic matrix composed of proteins, long-chain polyamines and polysaccharides, whose exact composition still remains to be studied more extensively apart from a few select examples mainly derived from the main model system for studying diatom cell wall biogenesis, *Thalassiosira pseudonana* (Sumper et al., 2005; Brunner et al., 2009; Richthammer et al., 2011; Kotsch et al., 2016). Beyond the already discussed cell wall roles of providing protection and supporting the large vacuole of the cell, recent studies suggest that the frustules act as a photonic crystal, improving conditions for photosynthesis inside while providing protection from UV light (De Tommasi et al., 2018; Goessling et al., 2018). While the process of cell wall formation has been studied extensively [for a review on the topic see (Hildebrand et al., 2018)], very little is known about the plasticity of their silicified cell wall. Silica content per cell varies widely among species, but has been shown to be correlated with cell size (Conley et al., 1989). Growth-limiting conditions generally result in increased silicification rates, thus resulting in an inverse correlation between silicification and growth rates (McNair et al., 2018). Limitation of silica content, however, results in a decrease of silicification without differences in growth speed (Claquin et al., 2002). However, there are select examples for adaptation of cell wall thickness in response to grazing: The diatom *Thalassiosira weissflogii* has been shown to increase silicification upon incubation with grazers without changes in growth rates (Pančić et al., 2019). Similarly, *Skeletonema marinoi*, a chain-forming diatom, strongly reduces chain lengths upon incubation with copepods, successfully reducing grazing rates (Pondaven et al., 2007). Thus, there are examples of cell wall plasticity in diatoms, suggesting a CWI perception system, but very little is known about how these environmental cues get translated into modifications of the silica cell wall and/or its organic matrix. And it is intriguing to think on a CWI system that perceives the physicochemical integrity of a rigid wall. Like in other unicellular algae, Wsc domains have been identified in sequenced genomes such as that of *T. pseudonana*, but their function is unknown.

7 Beyond the wall: perception of extracellular matrix in other eukaryotes

The perception and composition of extracellular structures in eukaryotes is not restricted to cell walls and CWI. Extracellular matrixes (ECMs) are diverse and serve various functions, from structural support to cellular communication, similar to cell walls.

So far, we have discussed eukaryotes from Plantae –plants and green algae–, Chromalveolates –diatoms and Phaeophytes (brown algae) and Unikonts (yeast) (Figure 1). Plantae have cell walls rich

in carbohydrates like cellulose, whereas certain Chromalveolates possess cell walls composed of materials like silica, and fungi in the Unikonts group have chitin-based cell walls. In contrast, animals, also part of the Unikonts, do not have cell walls but possess an ECM mainly composed of proteins like collagen (Frantz et al., 2010). This ECM serves multiple functions, including providing structural support and mediating cellular interactions through various types of receptors (Hynes, 2009). The perception of the ECM is often mediated by integrin receptors, which bind to specific ligands in the ECM and initiate cellular signalling pathways (Friedland et al., 2009). Interestingly, animals share with fungi and plants the presence of carbohydrate-binding proteins collectively known as lectins. This heterogeneous group of proteins plays crucial roles in important processes, from immune responses to cell adhesion (De Coninck and Van Damme, 2021; Radhakrishnan et al., 2023). Rhizaria and Excavates, two other eukaryotic groups, generally lack traditional cell walls but may possess unique extracellular structures. For instance, some Rhizaria have elaborate shells made of organic material or silica (Nakamura et al., 2018), while certain Excavates have a pellicle, a tough but flexible outer covering that provides shape and protection (Cavalier-Smith, 2010). The vital role of these extracellular structures for survival likely means these organisms have ways to sense and adapt to changes in their outer layers. However, the specific mechanisms remain a mystery.

8 Discussion

As we explore the complexities of CWI, the importance of investigating less-studied organisms and systems becomes increasingly clear. These could offer fresh perspectives and expand our understanding of CWI across a range of walled Eukaryote (Figure 1). One captivating aspect of CWI is the variety of cues that activate its monitoring systems. While we have made significant progress in understanding chemical cues, such as interactions between ligands and receptors, the role of physical cues like mechanical stress remains relatively uncharted territory. In animals, integrins serve as vital sensory molecules, converting chemical and physical cues from ECM into signals that guide cell behavior. They achieve this by responding to the ligand (proteins and glycoproteins) density and chemical affinity between receptors and ligands in the ECM, initiating processes like integrin clustering which in turn translate these cues into biochemical signals (Paszek et al., 2009). To date, no similar system has been identified in plants, where chemical and mechanical CWI cues have traditionally been studied separately (Bacete and Hamann, 2020).

How have different organisms tailored their CWI mechanisms to meet their unique environmental challenges and life cycles? The lack of certain CWI receptors in fungi and algae, compared to plants, suggests an evolutionary divergence that deserves further

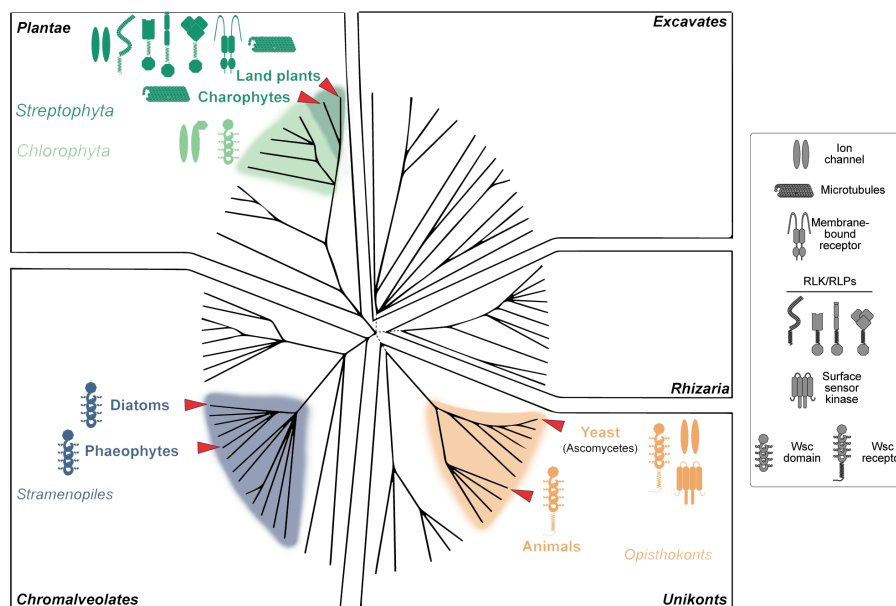


FIGURE 1

Distribution of cell wall integrity (CWI) sensors across the tree of life. Organisms with cell walls are distributed among various of the biological groups within the domain of Eukaryota. Plantae have cell walls rich in carbohydrates like cellulose, whereas certain Chromalveolates possess cell walls composed of materials like silica, and fungi in the Unikonts group have chitin-based cell walls. In contrast, animals, also part of the Unikonts, do not have cell walls but possess an extracellular matrix composed mainly of proteins like collagen, which serves to provide structural support and mediate cellular interactions. Rhizaria and Excavates generally lack traditional cell walls but may have other forms of extracellular structures for protection and support. Land plants, with complex cell walls and immobile cells bound together throughout the apoplast, have the most complex CWI system, comprised of different specialized receptors including receptor-like kinases (RLKs) and receptor-like proteins (RLPs), ion channels, and membrane-bound mechanoreceptors. In contrast, yeast have simpler systems, in a higher extend based on cell wall integrity and stress response component (Wsc) domain-containing receptors. Intriguingly, Wsc domains are widespread among Eukaryota, including animals, diatoms and brown algae (Phaeophytes). Based on the Eukaryotic tree of life created by Keeling et al. (2005).

study. Understanding these evolutionary intricacies could provide insights into why some CWI mechanisms are conserved across species while others are not. The unique challenges and life cycles of plants—composed of immobile cells connected to each other through their cell walls, in a dry environment and under the pressure of gravity—raise compelling questions about how they perceive and respond to mechanical stimuli affecting their cell walls. All in all, the plant cell walls of different cells are bound together forming the apoplast, and thus CWI alterations could be an efficient mechanism to transfer signals across the plant, but this would require specific systems different from those in motile cells. Given that plants can respond to CWI challenges with both death and growth, could the complexity of CWI mechanisms be linked to the complexity of the organism itself? In contrast, for unicellular organisms like yeasts, CWI is often a life-or-death issue, either due to severe damage or the death of a similar organism nearby. Charophytes live in water, which involves a very different context for mechanoperception and self-perception. This could be a reason for the lack of plant-like CWI receptors in these organisms. Interestingly, carbohydrate-binding Wsc domains are widespread in numerous unicellular organisms from yeast to green algae, although with unknown functions and in many cases lacking a transmembrane domain which would be essential for intracellular signal transduction. These domains are present even in mammals, where they are in some cases linked to diseases associated with a misperception of the extracellular matrix such as polycystic kidney disease (Weston et al., 2003). However, to date, there have not been identified in any member of the Streptophyta subgroup. Brown algae such as *Ectocarpus siliculosus* with more than 100 Wsc-containing proteins seem the only example of multicellular photosynthetic organisms with the possibility of a putative Wsc-based CWI monitoring system (Cock et al., 2010). The question of when and why this system was replaced by other CWI monitoring systems can shed light on the origins of multicellularity, the transition to land and the loss of cell motility.

Emerging technologies offer promising directions for CWI research. Non-invasive live-imaging methods are crucial for capturing real-time data on plant cell wall dynamics. Synthetic biology enables engineering cells with customized cell walls. Computational models are needed to integrate data across different organisms and cell types. These models could simulate how various factors affect CWI. Machine learning algorithms could predict how changes in one factor affect overall CWI. Nanotechnology can provide real-time insights into CWI through nano-sensors, providing immediate data crucial in such a dynamic process.

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Author contributions

NV: Writing – original draft, Writing – review & editing. MS: Writing – original draft, Writing – review & editing. LB: Conceptualization, Writing – original draft, Writing – review & editing, Visualization.

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Conflict of interest

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