



**HAL**  
open science

## Gazing at cell wall expansion under golden light

Bénédicte Charrier, Hervé Rabillé, Bernard Billoud

► **To cite this version:**

Bénédicte Charrier, Hervé Rabillé, Bernard Billoud. Gazing at cell wall expansion under golden light. Trends in Plant Science, 2019, 24 (2), pp.130-141. 10.1016/j.tplants.2018.10.013 . hal-02183603

**HAL Id: hal-02183603**

**<https://hal.science/hal-02183603v1>**

Submitted on 15 Jul 2019

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

# 1 **Gazing at cell wall expansion under a golden light**

2

3

4 Bénédicte Charrier<sup>1,\*</sup>, Hervé Rabillé<sup>1</sup>, Bernard Billoud<sup>1</sup>5 <sup>1</sup>UMR8227, CNRS-Sorbonne Université. Station Biologique, Place Georges Teissier, 29680

6 Roscoff, France.

7 \*Correspondence: [benedicte.charrier@sb-roscoff.fr](mailto:benedicte.charrier@sb-roscoff.fr) (B. Charrier)8 <http://www.sb-roscoff.fr/en/team-morphogenesis-macroalgae-mma>

9

10

11 **Keywords:** Brown algae, Cell wall, Mechanics, Evolution, Polysaccharides, Remodelling

12

## 13 **Abstract**

14

15 In plants, cell growth is constrained by a stiff cell wall – at least this is the way textbooks usually  
16 present it. Accordingly, many studies have focused on the **elasticity and plasticity** of the cell wall  
17 as prerequisites for expansion during growth. With their specific evolutionary history, cell wall  
18 composition and environment, brown algae present a unique configuration offering a new  
19 perspective on the involvement of the cell wall – viewed as an inert material with yet intrinsic  
20 mechanical properties – in growth. In light of recent findings, we explore here how much of the  
21 functional relationship between cell wall chemistry and intrinsic mechanics on the one hand, and  
22 growth on the other hand, has been uncovered in brown algae.

23

## 24 **Cell wall expansion: does the known matter really matter?**

25 The most common paradigm of plant cell growth involves the generation of tensile stress, mainly  
26 due to cell turgor, causing the cell wall to yield. In response to this tensile stress, cell volume  
27 increases due to the influx of water and cell wall biosynthesis is activated, maintaining cell wall  
28 thickness and preventing disruption [1]. This increase in volume tends to attenuate turgor, but the  
29 ongoing re-establishment of the intracellular osmotic potential maintains the tensile stress. These  
30 dynamic processes lead to continuous growth – but only if the cell wall is able to yield. Many

31 studies in land plants, fungi, green and yellow-green algae have attempted to link the intrinsic  
32 chemical and mechanical (elasticity, plasticity, as assessed by short-term experiments) features of  
33 the cell wall to its potential for **growth** (a potentially long-term process). Seemingly intuitive, this  
34 relationship can be tested using current technologies that allow the acquisition of quantitative  
35 mechanical data. However, it remains plausible that cell wall growth does not necessarily involve  
36 cell wall resistance countering strong tensile stress, like two players pulling a rope in opposite  
37 directions, but instead may build on collaborative factors where tensile stress and **remodelling**  
38 factors work in concert to promote growth. In some cases, the regulation of the intrinsic  
39 mechanical properties of the cell wall may only be a potential third player, whose role depends on  
40 its relative influence in the physical scrimmage. Determining the extent to which cell wall growth  
41 directly depends on the intrinsic features of the cell wall – viewed as an inert material that  
42 nevertheless has dynamic intrinsic properties – will benefit from widening the range of walled-  
43 organisms studied.

44

#### 45 **Uncoupling cell wall growth from the intrinsic mechanical properties of the cell wall**

46 Growth implies an irreversible deformation of the cell wall, and thus implicitly involves the  
47 plasticity of the material that makes up the cell wall. By definition, irreversibility is detected after  
48 the growth event has taken place. Hence, growth can be a two-step process in which the cell wall  
49 yields according to the elastic nature of the material and this deformation is simultaneously made  
50 irreversible through consolidation of cell wall material [2]. Or, growth can be a one-step process  
51 based on the plastic nature of the cell wall material, for which deformation itself is irreversible  
52 and deformation takes place only when the applied stress exceeds a given threshold (the ‘yield  
53 threshold’). These two cases rely on the intrinsic mechanical properties of the cell wall taken as a  
54 physical material (Figure 1A) in which growth is made possible only when the mechanical  
55 properties of the cell wall are modified. A third mechanism is characterised by cell wall  
56 remodelling without modifying the intrinsic mechanical properties of the cell wall (Figure 1B). In  
57 this process, yielding is made possible – or is enhanced – due to modification in the organisation  
58 of the cell wall material, and not necessarily in its actual chemical composition. These two  
59 mechanical properties, *i.e.* (1) intrinsic mechanical properties (namely elasticity and/or plasticity)  
60 and (2) remodelling can theoretically be involved in cell wall growth in all organisms.

61

62 Experimentally, assessing the intrinsic mechanical properties of the cell wall is easier than  
63 deciphering the process by which the cell wall remodels. In particular, many available techniques  
64 can quantify cell wall elasticity, such as indentation using atomic force microscopy (AFM), or  
65 stretching [3,4] (Table 1). As a result, reports abound on the close relationship between growth  
66 and the intrinsic elasticity of the cell wall (e.g., recently in fungi [5]). Emergence and growth of  
67 buds in the *Arabidopsis* apical meristem have been correlated with an increase in elasticity [6], in  
68 a process similar to that occurring in the tip-growing pollen tube, in which elasticity continuously  
69 decreases from the tip to 20  $\mu\text{m}$  behind it [7]. Similar observations have been reported in fungal  
70 hyphae [8], but far away from the growth zone. However, the technical flaws pertaining to AFM  
71 techniques (Table 1) recently highlighted by D. Cosgrove [9] raises *de facto* some issues about the  
72 thus far demonstrated role of intrinsic elasticity in growth. At the cellular level, physical  
73 measurements of the cell wall ability to yield, which requires quite large cell wall surfaces (e.g.,  
74 *Chara* and *Vaucheria*, [10]), are rarely performed to confirm AFM data, especially in living cells.  
75 Nonetheless, in some cases, cellular expansion in response to hypo-osmotic treatments has  
76 confirmed the overlapping patterns of cell wall elasticity and cell growth [11].

77 When neither of the two intrinsic mechanical properties discussed above seem to be involved, and  
78 when growth is shown to require heat and/or living cells, then cell wall remodelling factors  
79 releasing the load-bearing bonds are introduced as necessary factors for the cell wall to yield  
80 (Figure 1B). The extent to which remodelling is separate from the intrinsic mechanical properties  
81 has been debated and most likely depends on the cell, species and growth mode (diffuse or  
82 localised, e.g., at the tip of an apical cell). Since the 1892 demonstration that ascomycete *Peziza*  
83 hyphae bursts at the base of the apex where growth is slower and not at the tip where growth is  
84 higher [12], it has been clear that the most deformable positions do not necessarily correlate with  
85 actively growing zones. Similarly, **stiffness** does not correlate with slow-growing cells either. The  
86 inner layer of the cell wall of *Aspergillus* spores is extremely stiff (elastic modulus  $E$  up to 30  
87 GPa; [13]); nevertheless, this is where bud emergence takes place to initiate hyphal growth.  
88 Bamboo culms grow very fast via cell elongation at the base of internodes (cumulative growth  
89 rate of  $\sim 30 \text{ mm.h}^{-1}$ ), where secondary cell wall biosynthesis and lignification, initiated before the  
90 cessation of cell elongation, lead to very stiff cell walls ( $E \sim 20 \text{ GPa}$ ; [14]). This cell wall is  
91 10,000 times stiffer than the cell wall of the pollen tube which has an elongation rate 100 times  
92 slower ( $\sim 300 \mu\text{m.h}^{-1}$ ). Beyond these simple observations, experimental data have since

93 demonstrated further this lack of correlation between the intrinsic mechanical properties and  
94 growth in land plant cell walls ([15], reviewed by [16]).

95 Brown algae are macroscopic, multicellular organisms displaying many differences with their  
96 land counterparts. Their ancestor likely diverged  $> 1.6$  Mya [17], a period during which three  
97 endosymbiotic events took place [18], leading to organisms with specific cellular and genomic  
98 features [19,20]. More importantly here, their environment features mechanical properties  
99 completely different to those experienced on land. When immersed, most of their growing cells  
100 are permanently exposed to seawater moving at a density more than 1000 times greater than the  
101 air, generating forces similar to hurricane-forces every few seconds [21]. Wave-swept animals  
102 develop very stiff bodies to resist these forces, but seaweeds opted for a different strategy: their  
103 stiffness is  $\sim 100$ -1000 times lower than land plants, and they have high extensibility. In addition,  
104 due to periodic tides in their natural environment, brown algae are usually exposed to a large  
105 range of osmotic variations due to dehydration at one extreme of the range and to flooding with  
106 rainwater at the other. When immersed in pure water or 2 M NaCl (corresponding to four times  
107 the seawater concentration), cells of the brown alga *Ectocarpus* respectively expand by up to 70%  
108 (in pure water) and shrink down to 35% of their volume (corresponding to 40% of their surface  
109 area; unpublished personal data). In comparison, cells of the tomato shoot apical meristem expand  
110 and shrink by about 9% in surface area [11].

111 Nevertheless, there is a disconnection between these intrinsic mechanical properties of the cell  
112 wall and growth potential (Figure 1C). For example, in the apical cell of the filamentous brown  
113 alga *Ectocarpus*, treatment with the actin-depolymerising drug latrunculin B promotes doubled  
114 growth in width, but fully blocks cell swelling in the same axis after immersion in half-  
115 concentrated seawater (unpublished personal data). This strongly suggests that in these conditions,  
116 the underlying mechanics required for growth is distinct from the elasticity/plasticity involved in  
117 rapid volume changes, regardless of the exact role of actin in this process. Similar cell wall  
118 stiffening has been observed in the pollen tube in response to cytochalasin D, another actin-  
119 destabilising drug [22], but the morphological effects are less pronounced and this result was  
120 attributed to micro-indentation artefacts due to the dome shape. This explanation is excluded  
121 when elasticity is measured from changes in cell volume and when deformability can be directly  
122 measured in the plane of the cell wall, as performed in the case of *Ectocarpus*.

123

124 **Cell wall growth: demystifying polysaccharide chemistry**

125 Cell walls are a mixture of compounds whose relative organisation is still obscure, especially in  
126 brown algae. At the chemical level, > 80% of brown algal cell wall is chemically different from  
127 land plant cell walls (Table 2). As in land plants, polysaccharides are the main components, but  
128 they are represented by large and rare cellulose microfibrils immersed in abundant alginates  
129 (~40%) and sulphated fucans (~40%)([23], Figure 2). That results in cell walls with a much lower  
130 degree of crystallinity compared to land plants, and altogether these major differences hinder any  
131 reliable transposition between the two groups of organisms.

132 In the context of growth, a link between cell wall chemical composition and its propensity to  
133 expand is intuitively natural. Fungal cell wall biosynthesis mutants are impaired in cell growth  
134 [24] and the level of pectin methylesterification in angiosperm pollen tubes is directly  
135 proportional to growth rate [25]. However, the role of alginates in growth, and especially of  
136 mannuronans which are described as ‘soft’ components in *in vitro* studies [26], has no support  
137 thus far. In the brown alga *Sargassum*, the position of new buds is not correlated with a specific  
138 spatial pattern of alginates [27], and no correlation has been found between the active growth site  
139 in the rhizoid of the embryo of the brown alga *Fucus* and the presence of soft or stiff alginates  
140 [28].

141 In brown algae, can the polysaccharide composition control the intrinsic mechanical properties of  
142 the cell wall, if not its expansion? ‘Soft’ mannuronan alginates have been shown to be  
143 preferentially extracted from organs with flexible properties, whereas stiff guluronan alginates  
144 [26], which form *in vitro* complexes with calcium as pectins do (Figure 2), have been extracted  
145 from load-bearing organs exposed to drag forces (e.g., kelp stipes in environments exposed to  
146 waves [29], and references therein). However, completely contrasting observations have also been  
147 reported. Miller et al. [30] found that the highest levels of the stiff guluronans were measured in  
148 the most mucilaginous and flexible seaweeds of their study, regardless of their age. This echoes  
149 similar observations made in the *Arabidopsis* shoot apical meristem, where an increase in pectin  
150 demethylesterification co-locates with an increase in elasticity [6], but stiffens the cell wall in the  
151 shanks of the pollen tube [25]. Therefore, these examples illustrate that, in brown algae as in land  
152 plants, the complexity of the mechanics of the cell wall, and moreover of growth cannot be  
153 reduced to the presence or absence of a single, or even a handful of polysaccharides. Knowledge  
154 of the complete interacting molecular network is the first step before translating chemical  
155 composition into mechanics [31]. Even in land plants where most of the cell wall chemical  
156 components have been identified and where there is a comprehensive set of positional patterns of

157 cell wall components (e.g., along the tip-growing pollen tube; [32]), the interactive network  
158 remains vague and incomplete [33], preventing any simple, straightforward conclusion as to the  
159 role of these compounds in growth. Other factors such as the degree of hydration, the ion  
160 concentration or the rate of degradation of polysaccharides are alternative driving forces in cell  
161 growth (as discussed in [34,35]).

162 As a result, attempts to piece together partial knowledge lead to complex scenarios, such as those  
163 featured for pollen tube growth, where differential and often counter-intuitive gradients of factors  
164 including calcium concentration and pectin-methylesterase enzyme (PME) activities, are squeezed  
165 into a possible mechanism of tip growth [36,37]. However, the different biological contexts call  
166 for putting all the cards back on the table. In brown algae, alginate stiffness is described as  
167 depending directly on the calcium concentration, but this relationship degenerates when calcium  
168 concentration is 10 times that of the seawater [38], a situation that can be reached locally *in muro*  
169 in emerged thalli, especially in poro-elastic cell walls [32]. As for PME, recent studies suggest  
170 that the control of methylesterification (including both PME activity and a PME inhibitor, PMEI)  
171 is especially important for the fast growth of angiosperm pollen tubes, and less determinate in  
172 gymnosperms in which the gradients of esterified pectins are less pronounced and PMEI is absent  
173 [37]. Furthermore, studies of growth mechanisms in more basal green cells, such as in the  
174 charophyte alga *Chara*, argue that the role of PME as described in the pollen tube may be limited  
175 to the more recently evolved green plants [14]. This is just a sign of the diversity of mechanisms  
176 that may be encountered in organisms whose phylogenetic position is distant to the most studied  
177 plant models, and an indication that our understanding of their role in plant cell growth *lato sensu*  
178 should mature with future evo-devo studies.

179  
180 Interpretation of results becomes even more complex when cell wall polysaccharides of different  
181 natures compensate each other. In brown algae, degradation of alginates leads to a stiffer cell wall  
182 unable to expand in response to hypo-osmotic shock, suggesting that alginates are necessary to  
183 ensure intrinsic cell wall elasticity (unpublished personal data). However, a closer look shows that  
184 this decrease in elasticity is due to an over-accumulation of cellulose at the sub-cellular location  
185 where growth takes place. The high stiffness of cellulose (E of up to 175 GPa; [39], compared  
186 with alginate with value of E ~ a few kPa, [40] and pectin E of up to 1 MPa; [41]) easily accounts  
187 for the observed decrease in cell wall extensibility. Similar cellulose accumulation occurred  
188 during the over-growth of the apical cell in response to LatB treatment, showing that despite its

189 high stiffness, cellulose does not hinder growth. On the contrary, in plants, cellulose has also the  
190 potential to promote growth [42]. This uncoupling between the role of cellulose in both the  
191 intrinsic mechanical properties and cell wall expansion echoes the recent finding that growth and  
192 cellulose biosynthesis are regulated by distinct pathways in the *Arabidopsis* hypocotyl [43].  
193 Uncoupling metabolic activity from light-dependent circadian rhythms demonstrated that cell  
194 wall biosynthesis is controlled by the former and growth by the latter. Furthermore, cellulose  
195 synthases (GT2 family of glucosyl-transferases), as defined from sequence similarity, may not  
196 synthesise only cellulose but instead produce mixed-linkage polysaccharides (MLGs) or even new  
197 polysaccharides, such as arabinoglucan recently shown in the moss *Physcomitrella* [44]. These  
198 results show that the links between cell growth and cellulose and/or cellulose synthase genes – as  
199 a proxy for cellulose accumulation – are not direct. Clearly, there is a need to revisit the  
200 assumption that the presence of stiff components in the cell wall prevents or mitigates its  
201 expansion.

202 So, are polysaccharides more than just inert structural components subjected to the activities of  
203 remodelling proteins during growth? Several distinct remodelling mechanisms have been  
204 described in land plants, green algae and fungi. In *Chara*, the ongoing delivery of new cell wall  
205 components modifies the dynamics of pectate-Ca<sup>2+</sup> complexes formed *in muro* (the so-called  
206 ‘pectate distortion’ mechanism [14]), thereby remodelling the cell wall. However, proteins are  
207 central factors in most of the remodelling processes described so far. In land plants, the  
208 xyloglucan-endo-transglycosylases-hydrolases (XTH) participate in cell wall expansion through  
209 hemicellulose cutting and joining [45] and expansins modify hemicellulose-mediated bonds  
210 between stiff cellulose fibres ([4] and subsequent papers). Any resulting gaps are filled with  
211 freshly made or delivered material, allowing the overall expansion of the local cell wall. In fungi,  
212 radical coupling catalysed by an oxidase occurs between the cell wall polymers  
213 glucosaminoglycan and beta-glucan [12].

214 Brown algal cell walls have been shown to contain proteins in significant amounts (>5% of the  
215 cell wall biomass; [23,46]) and with a high diversity (> 900 different proteins secreted in brown  
216 algae [47]). Interestingly, in brown algae, none of these proteins share similarity with expansin,  
217 PME or even cellulase (Table 2; from genomic analysis; [48]). Domains of cell wall remodelling  
218 proteins have been identified among secreted proteins (e.g. carbohydrate binding module CBM32  
219 interacting with alginates; [47]) making them prime candidates for remodelling factors [49]. In  
220 addition, families of secreted brown algal proteins are specific (e.g., alginate C5-epimerases) or



221 expanded (vanadium haloperoxidase, metalloproteinases) relative to those of land plants [47,50].  
222 Finally, signalling proteins such as the Notch-Domain proteins, previously thought to be specific  
223 to animal cells, are over-represented in brown algal cell walls [47]. Therefore, in light of recent  
224 data, our current understanding, which still requires more knowledge on cell wall molecular  
225 composition and organisation in dynamic conditions, is that brown algae developed a specific  
226 secretome for cell wall remodelling.

227

## 228 **Concluding remarks and future prospects**

229 Work on non-conventional models phylogenetically distant from land plants gives the opportunity  
230 to unveil the existence of alternative mechanisms of growth. In these organisms (and previously  
231 noted in land plants and green algae [51]), the causal relationship between cell wall growth and  
232 intrinsic cell wall mechanical properties, or cell wall growth and cell wall chemical composition,  
233 are not obvious. Furthermore, the difference in growth strategies may also be related to the type of  
234 organ (e.g., shoot apical meristem or pollen tube in land plants, internodes in green alga *Chara*),  
235 its growth mode (respectively tip-growing or diffuse) or its growth dynamics.

236 The first results obtained in brown algae show that the distribution of cell wall polysaccharide  
237 determinants is not easily linked to the cell growth pattern, and that the intrinsic mechanical  
238 properties may not systematically correlate with growth potential. This leaves plenty of room for  
239 alternative processes, including cell wall remodelling with no alteration of the intrinsic  
240 mechanical properties. However, due to the very different composition and organisation of the  
241 cell walls in green plants and brown algae, the molecular toolkits of the remodelling machinery  
242 are likely fundamentally different. Beyond the potential conservation of molecular factors,  
243 cellular and biomechanical studies carried out in brown algae will most likely lead to  
244 breakthroughs in alternative mechanisms of cell wall remodelling.

245

## 246 **Acknowledgement**

247 We thank Cécile Hervé for fruitful discussion about the cell wall composition.

248

## 249 **References**

- 1 Davì, V. *et al.* (2018) Mechanosensation Dynamically Coordinates Polar Growth and Cell Wall Assembly to Promote Cell Survival. *Dev. Cell* 45, 170-182.e7

- 2 Fayant, P. *et al.* (2010) Finite Element Model of Polar Growth in Pollen Tubes. *Plant Cell* 22, 2579–2593
- 3 Ahmad, I.L. and Ahmad, M.R. (2014) Trends in characterizing single cell's stiffness properties. *Micro Nano Syst. Lett.* 2, 8
- 4 Cosgrove, D.J. (1993) Wall extensibility: its nature, measurement and relationship to plant cell growth. *New Phytol.* 124, 1–23
- 5 Haneef, M. *et al.* (2017) Advanced Materials From Fungal Mycelium: Fabrication and Tuning of Physical Properties. *Sci. Rep.* 7,
- 6 Peaucelle, A. *et al.* (2011) Pectin-Induced Changes in Cell Wall Mechanics Underlie Organ Initiation in Arabidopsis. *Curr. Biol.* 21, 1720–1726
- 7 Geitmann, A. and Parre, E. (2004) The local cytomechanical properties of growing pollen tubes correspond to the axial distribution of structural cellular elements. *Sex. Plant Reprod.* 17, 9–16
- 8 Ma, H. *et al.* (2005) Surface ultrastructure and elasticity in growing tips and mature regions of *Aspergillus* hyphae describe wall maturation. *Microbiol. Read. Engl.* 151, 3679–3688
- 9 Cosgrove, D.J. (2016) Catalysts of plant cell wall loosening. *F1000Research* 5,
- 10 Mine, I. *et al.* (2003) Fine structure of spermatial surface in the red alga *Antithamnion nipponicum* (Rhodophyta). *Phycol. Res.* 51, 109–117
- 11 Kierzkowski, D. *et al.* (2012) Elastic Domains Regulate Growth and Organogenesis in the Plant Shoot Apical Meristem. *Science* 335, 1096–1099
- 12 Wessels, J.G.H. (1988) A steady-state model for apical wall growth in fungi. *Acta Bot. Neerlandica* 37, 3–16
- 13 Zhao, L. *et al.* (2005) Assessment of Elasticity and Topography of *Aspergillus nidulans* Spores via Atomic Force Microscopy. *Appl. Environ. Microbiol.* 71, 955–960
- 14 Boyer, J.S. (2016) Enzyme-Less Growth in Chara and Terrestrial Plants. *Front. Plant Sci.* 7,
- 15 Park, Y.B. and Cosgrove, D.J. (2012) Changes in Cell Wall Biomechanical Properties in the Xyloglucan-Deficient *xxt1/xxt2* Mutant of Arabidopsis. *Plant Physiol.* 158, 465–475
- 16 Cosgrove, D.J. (2018) Diffuse Growth of Plant Cell Walls. *Plant Physiol.* 176, 16–27
- 17 Baldauf, S.L. (2008) An overview of the phylogeny and diversity of eukaryotes. *J. Syst. Evol.* 46, 263–273
- 18 Stiller, J.W. *et al.* (2014) The evolution of photosynthesis in chromist algae through serial endosymbioses. *Nat. Commun.* 5,

- 19 Charrier, B. *et al.* (2008) Development and physiology of the brown alga *Ectocarpus siliculosus*: two centuries of research. *New Phytol.* 177, 319–332
- 20 Cock, J.M. *et al.* (2010) The *Ectocarpus* genome and the independent evolution of multicellularity in brown algae. *Nature* 465, 617–621
- 21 Denny, M. and Gaylord, B. (2002) The mechanics of wave-swept algae. *J. Exp. Biol.* 205, 1355–1362
- 22 Zerzour, R. *et al.* (2009) Polar growth in pollen tubes is associated with spatially confined dynamic changes in cell mechanical properties. *Dev. Biol.* 334, 437–446
- 23 Deniaud-Bouët, E. *et al.* (2014) Chemical and enzymatic fractionation of cell walls from Fucales: insights into the structure of the extracellular matrix of brown algae. *Ann. Bot.* 114, 1203–1216
- 24 Uchiyama, H. *et al.* (2018) The effects of gene disruption of Kre6-like proteins on the phenotype of  $\beta$ -glucan-producing *Aureobasidium pullulans*. *Appl. Microbiol. Biotechnol.* 102, 4467–4475
- 25 Parre, E. and Geitmann, A. (2005) Pectin and the role of the physical properties of the cell wall in pollen tube growth of *Solanum chacoense*. *Planta* 220, 582–592
- 26 Braccini, I. *et al.* (1999) Conformational and configurational features of acidic polysaccharides and their interactions with calcium ions: a molecular modeling investigation. *Carbohydr. Res.* 317, 119–130
- 27 Linardić, M. and Braybrook, S.A. (2017) Towards an understanding of spiral patterning in the *Sargassum muticum* shoot apex. *Sci. Rep.* 7, 13887
- 28 Torode, T.A. *et al.* (2016) Dynamics of cell wall assembly during early embryogenesis in the brown alga *Fucus*. *J. Exp. Bot.* 67, 6089–6100
- 29 Jothisarawathi, S. *et al.* (2006) Seasonal studies on alginate and its composition II: *Turbinaria conoides* (J.Ag.) Kütz. (Fucales, Phaeophyceae). *J. Appl. Phycol.* 18, 161
- 30 Miller, I.J. (1996) Alginate composition of some New Zealand brown seaweeds. *Phytochemistry* 41, 1315–1317
- 31 Shtein, I. *et al.* (2018) Plant and algal structure: from cell walls to biomechanical function. *Physiol. Plant.* 164, 56–66
- 32 Chebli, Y. *et al.* (2012) The Cell Wall of the *Arabidopsis* Pollen Tube—Spatial Distribution, Recycling, and Network Formation of Polysaccharides. *Plant Physiol.* 160, 1940

- 33 Mollet, J.-C. *et al.* (2013) Cell Wall Composition, Biosynthesis and Remodeling during Pollen Tube Growth. *Plants* 2, 107–147
- 34 Peaucelle, A. *et al.* (2008) Arabidopsis phyllotaxis is controlled by the methyl-esterification status of cell-wall pectins. *Curr. Biol. CB* 18, 1943–1948
- 35 Bidhendi, A.J. and Geitmann, A. (2016) Relating the mechanics of the primary plant cell wall to morphogenesis. *J. Exp. Bot.* 67, 449–461
- 36 Bosch, M. and Hepler, P.K. (2005) Pectin Methylsterases and Pectin Dynamics in Pollen Tubes. *Plant Cell* 17, 3219–3226
- 37 Wallace, S. and Williams, J.H. (2017) Evolutionary origins of pectin methylsterase genes associated with novel aspects of angiosperm pollen tube walls. *Biochem. Biophys. Res. Commun.* 487, 509–516
- 38 Cuadros, T.R. *et al.* (2012) Mechanical properties of calcium alginate fibers produced with a microfluidic device. *Carbohydr. Polym.* 89, 1198–1206
- 39 Geitmann, A. (2006) Experimental approaches used to quantify physical parameters at cellular and subcellular levels. *Am. J. Bot.* 93, 1380–1390
- 40 Larsen, B.E. *et al.* (2015) Rheological characterization of an injectable alginate gel system. *BMC Biotechnol.* 15, 29
- 41 Niu, R. *et al.* (2017) Hybrid pectin–Fe<sup>3+</sup>/polyacrylamide double network hydrogels with excellent strength, high stiffness, superior toughness and notch-insensitivity. *Soft Matter* 13, 9237–9245
- 42 Hu, H. *et al.* (2018) Three AtCesA6-like members enhance biomass production by distinctively promoting cell growth in Arabidopsis. *Plant Biotechnol. J.* 16, 976–988
- 43 Ivakov, A. *et al.* (2017) Cellulose Synthesis and Cell Expansion Are Regulated by Different Mechanisms in Growing Arabidopsis Hypocotyls. *Plant Cell* 29, 1305–1315
- 44 Roberts, A.W. *et al.* (2018) Functional Characterization of a Glycosyltransferase from the Moss *Physcomitrella patens* Involved in the Biosynthesis of a Novel Cell Wall Arabinoglucan. *Plant Cell* DOI: 10.1105/tpc.18.00082
- 45 Eklöf, J.M. and Brumer, H. (2010) The XTH Gene Family: An Update on Enzyme Structure, Function, and Phylogeny in Xyloglucan Remodeling. *Plant Physiol.* 153, 456–466
- 46 Deniaud-Bouët, E. *et al.* (2017) A review about brown algal cell walls and fucose-containing sulfated polysaccharides: Cell wall context, biomedical properties and key research challenges. *Carbohydr. Polym.* 175, 395–408

- 47 Terauchi, M. *et al.* (2017) Genome-wide computational analysis of the secretome of brown algae (Phaeophyceae). *Mar. Genomics* 32, 49–59
- 48 Michel, G. *et al.* (2010) The cell wall polysaccharide metabolism of the brown alga *Ectocarpus siliculosus*. Insights into the evolution of extracellular matrix polysaccharides in Eukaryotes. *New Phytol.* 188, 82–97
- 49 Nardi, C.F. *et al.* (2015) Overexpression of the carbohydrate binding module of strawberry expansin2 in *Arabidopsis thaliana* modifies plant growth and cell wall metabolism. *Plant Mol. Biol.* 88, 101–117
- 50 Ye, N. *et al.* (2015) Saccharina genomes provide novel insight into kelp biology. *Nat. Commun.* 6, 6986
- 51 Proseus, T.E. and Boyer, J.S. (2007) Tension required for pectate chemistry to control growth in *Chara corallina*. *J. Exp. Bot.* 58, 4283–4292
- 52 Nolte, T. and Schopfer, P. (1997) Viscoelastic versus plastic cell wall extensibility in growing seedling organs: a contribution to avoid some misconceptions. *J. Exp. Bot.* 48, 2103–2107
- 53 Riquelme, M. *et al.* (2011) Architecture and development of the *Neurospora crassa* hypha – a model cell for polarized growth. *Fungal Biol.* 115, 446–474
- 54 Al-Zube, L.A. *et al.* (2017) Measuring the compressive modulus of elasticity of pith-filled plant stems. *Plant Methods* 13, 99
- 55 Rabillé, H. *et al.* (2018) Dynamic and microscale mapping of cell growth: Case of *Ectocarpus* filament cells. In *Protocols for Macroalgae Research* pp. 349–364, Bénédicte Charrier, Thomas Wichard, C R K Reddy
- 56 Robinson, S. *et al.* (2017) An Automated Confocal Micro-Extensometer Enables in Vivo Quantification of Mechanical Properties with Cellular Resolution. *Plant Cell* 29, 2959–2973
- 57 Schopfer, P. (2006) Biomechanics of plant growth. *Am. J. Bot.* 93, 1415–1425
- 58 Taiz, L. (1984) Plant Cell Expansion: Regulation of Cell Wall Mechanical Properties. *Annu. Rev. Plant Physiol.* 35, 585–657
- 59 Vogler, H. *et al.* (2015) Measuring the Mechanical Properties of Plant Cell Walls. *Plants* 4, 167–182
- 60 Zhang, T. *et al.* (2016) Spatial organization of cellulose microfibrils and matrix polysaccharides in primary plant cell walls as imaged by multichannel atomic force microscopy. *Plant J.* 85, 179–192

- 61 Nakata, M.T. *et al.* (2018) High-Throughput Analysis of Arabidopsis Stem Vibrations to Identify Mutants With Altered Mechanical Properties. *Front. Plant Sci.* 9,
- 62 Aouar, L. *et al.* (2010) Morphogenesis of complex plant cell shapes: the mechanical role of crystalline cellulose in growing pollen tubes. *Sex. Plant Reprod.* 23, 15–27
- 63 Carpita, N.C. and Gibeaut, D.M. (1993) Structural models of primary cell walls in flowering plants: consistency of molecular structure with the physical properties of the walls during growth. *Plant J.* 3, 1–30
- 64 Carpita, N.C. and MacCann, M. (2000) The Cell Wall. In *Biochemistry and Molecular Biology of Plants* pp. 52–108, Buchanan BB, Gruissem W & Jones RL (eds)
- 65 Raimundo, S.C. *et al.* (2017)  $\beta$ -1,3-Glucans are components of brown seaweed (Phaeophyceae) cell walls. *Protoplasma* 254, 997–1016
- 66 Salmeán, A.A. *et al.* (2017) Insoluble (1  $\rightarrow$  3), (1  $\rightarrow$  4)- $\beta$ -D-glucan is a component of cell walls in brown algae (Phaeophyceae) and is masked by alginates in tissues. *Sci. Rep.* 7, 2880
- 67 La Barre, S. *et al.* (2010) The Halogenated Metabolism of Brown Algae (Phaeophyta), Its Biological Importance and Its Environmental Significance. *Mar. Drugs* 8, 988–1010
- 68 Fernandes, A.N. *et al.* (2012) Mechanical properties of epidermal cells of whole living roots of Arabidopsis thaliana: an atomic force microscopy study. *Phys. Rev. E Stat. Nonlin. Soft Matter Phys.* 85, 021916

250

251 **Glossary**

252

253 All related to the cell wall:

- 254 • **Elasticity**: refers to the ability of a material to recover its initial dimensions after  
255 deformation (once the stress is released). Reversible deformability.
- 256 • **Extensibility** (as defined by D. Cosgrove): The capacity of the cell wall to grow through  
257 cell wall loosening (remodelling) in response to a stress.
- 258 • **Growth** (or chemo-rheological expansion, as defined by [52]): The increase in surface  
259 area, resulting from either enhanced stress or a modification of the cell wall propensity for  
260 deformation due either to an increase in elasticity or plasticity, or to cell wall remodelling.
- 261 • **Intrinsic mechanical properties**: elasticity, visco-elasticity or plasticity of a material.  
262 Measurements of the intrinsic mechanical properties are performed either directly by

263 intrusive equipment in contact with the biological material (e.g. nano-/micro-indentation),  
264 or indirectly by measuring strain on material undergoing external physical forces  
265 (creeping, stretching, osmotic pressure).

266 • **Plasticity:** refers to the irreversible deformation of the cell wall. This process has a  
267 temporal dimension and, therefore, plasticity may be taken for visco-elasticity when the  
268 dynamics of viscosity are very slow (*i.e.* much longer than observation time). Also  
269 confusingly named “irreversible elasticity” by some authors (e.g., [14]).

270 • **Remodelling:** Defined here as the process by which the arrangement of the various cell  
271 wall components interacting with each other is modified. Remodelling does not change the  
272 net chemical composition of the cell wall and does not necessarily modify its intrinsic  
273 mechanical properties, e.g., modification of the position of hydrogen bonds without  
274 modifying their number, resulting in unchanged elasticity. It is promoted by molecular  
275 remodelling factors: expansin, xyloglucan endotransglucosylase/hydrolase, redox  
276 reactions (e.g., cross-linking bonds in fungal cell wall polysaccharides; [53]) or finely  
277 tuned chemical cycles involving the interaction of calcium with polysaccharides (e.g.,  
278 pectate distortion in green algae; [14]). The term ‘cell wall loosening’ is used for  
279 remodelling processes resulting in growth.

280 • **Stiffness:** The opposite of deformability (both elastic and plastic). Assessed using Instron  
281 strain measurement techniques, indentation (atomic force microscopy), cell compression,  
282 stretching devices, etc. [3,4,39].

283

## 284 **Tables**

285

### 286 Table 1: Techniques employed for the study of cell wall mechanics during expansion.

287 This table intends to illustrate the range of available techniques allowing the measurement of cell  
288 mechanical properties. The list is not exhaustive. The “Parameters” column uses the author’s  
289 terminology, but the exact definition of parameters may be subject to subtle variations between  
290 authors. The “Reference” column mainly indicates reviews. The acquisition of accurate data of  
291 cell wall mechanics during growth should be performed using a technique that can take  
292 measurements i) on living organisms, ii) over a period of time in accordance with the dynamics of  
293 growth, iii) at the precise position of the cell surface where growth takes place, whatever the scale,

294 iv) in the direction of expansion (mainly tangential position along the cell surface; z-axis is less  
295 relevant); and that is v) adequate for 3D objects (e.g., AFM is sensitive to the orientation of the  
296 contact plan, as in the dome of the pollen tube), vi) compatible with the mechanical properties of  
297 the biological sample (e.g. biological materials, and especially the cell wall, do not behave as  
298 linear elastic materials) and vii) able to measure the overall cell wall mechanical features, and not  
299 only the superficial, outermost layer (e.g. nano-indentation). Literature cited: [3,9,16,39,54–61].  
300



Underlying Mechanical basis	Scale	Technique	Parameters	On Living material (non destructive)	Benefit	Disadvantage	Reference	
<b>Growth</b>	Organ / tissue	Size measurement	Geometry	yes	Non intrusive; Cheap	Average of several tissues / cells	[58]	
	Cell	Size measurement	Geometry	yes	Automation possible	Tissue accessibility	[58]	
	Cell Wall	Marker displacement	Local strain	yes	Resolution < $\mu\text{m}$	Cells adhesion required	[55]	
<b>Intrinsic mechanical properties (including elasticity and plasticity)</b>	Tissue	Extensometer	Wall loosening	yes	Long-lasting experiments Wide parameter range	Indirect Requires precise cutting Low spatial resolution Averaged data	[58]	
		Osmotic pressure shift	Elongation kinetics	yes	Mimics natural conditions	Low resolution	[16]	
		Resonance frequency (vibration)	Stiffness Damping coefficient	yes	High-throughput Non-destructive	Large scale, indirect	[61]	
		Pressure-block	Stress relaxation	yes	Precise control	Indirect	[9,57]	
	Cellular	Extensometer (instron)	Compressive modulus of elasticity	yes	Overall figure at the cell level	Requires precise cutting Low spatial resolution	[54]	
			Plastic compliance Creep	no	Wide range, in the plane of growth, both elasticity and plasticity		[9]	
		Micro-extensometer (ACME)	Elasticity Plasticity	yes	Microscale, 3D, automated, In the plane of growth Both elasticity and plasticity	Sophisticated equipment, Very recent	[56]	
		Creep measurement	Plastic yield stress	no		Stress-strain Not only CW properties	[9]	
		Micro-manipulation		yes		Artificial samples	[9]	
		Ball tonometry	Elasticity	yes	Overall figure at the tissue level	Low spatial resolution	[39]	
		Relaxation spectra	Stress relaxation	yes	Wide parameter range	Requires data smoothing	[9]	
		Mercury inflation	Multiaxial plastic extensibility	no			Intrusive; hazardous	[58]
			Creep recovery					
		Microfluidics ("lab-on-a-chip")	Compression potential	yes	Continuous measurements with varying growth conditions Automation possible	Low spatial resolution Artificial environment	[3,59]	
		Inflation/deflation (osmotic changes)	Elastic modulus (linearity)	yes	Easy to design	Approximate Mainly 2D only	[9]	
Cell Wall	Extensometer (instron)	Elastic compliance	no	Wide range Both elasticity and plasticity	Requires precise cutting Low spatial resolution	[9,57]		

Cellular force microscopy: indentation	Cell wall stiffness	yes	High resolution Relatively high forces ( $\mu\text{N}$ )	Complex equipment	[16]
Atomic force microscopy: micro-indentation	Stiffness, Elasticity, Plasticity, Adhesion	yes	High spatial resolution ( $\mu\text{m}$ scale) Surface mapping Outer and inner cell wall layers Possible in aquaous medium	Complex equipment In z-axis (not the growth plane) Sensitive to indentation angle Requires adherent sample	[3,16,38]
Atomic force microscopy: nano-indentation		yes	High spatial resolution (nm scale) Surface mapping, low force (nN) possible in aquaous medium	Complex equipment In z-axis Only outer cell wall layer Sensitive to indentation angle Requires adherent samples	[3,60]
Dynamic nanoindentation (nanoDMA)	Viscoelasticity Storage/loss stiffness	yes	High resolution (nanoscale) Can be coupled to TEM and SEM	Requires sophisticated equipment	[9]
Uniaxial stress	Mechanical anisotropy	no		Intrusive	[58]

303 Table 2: Cell wall components of land plants and brown algal cell walls

304 Table shows the nature and approximate abundance (% dry weight) of the different components of  
 305 the cell wall in land plants (only primary cell wall; both dicotyledonous and monocotyledonous  
 306 [33,62–64]) and in brown algae [46,65–67]. \* Much higher abundance in Poales  
 307 (monocotyledonous).

308

Class	Sub-class	Abundance	
		Land plants	Brown algae
Cellulose	No sub-class	15-33 %	1-8 %
Hemicelluloses	Homoxylans (X)		
	Arabinoxylans (AX)	~ 8 %	
	Glucuronoxylans (GX)		
	Glucuronoarabinoxylans (GAX)		
	Xyloglucans (XyG)	~ 20 %	
	Xyloglucuronans		Present
	Mannans (M)	Scarce	
	Glucomannans	Scarce	
	Galactomannans	Scarce	
	Galactoglucomannans	Scarce	
Glucuronomannans	Scarce		
Mixed-linkage-glucans (MLG)	Scarce*	Present	
Callose ( $\beta$ -1,3-glucans)	Potentially abundant	Present	
Pectins	Homogalacturonans (HG)	6-15 %	
	Rhamnogalacturonans I (RGI)	5-10 %	Present
	Rhamnogalacturonans II (RGII)	1-4 %	
	Apiogalacturonans	Scarce	
	Xylogalacturonans	Scarce	
Alginates	No sub-class		~ 40 %
Fucose-Containing Sulphated Polysaccharides (FCSP)	Fucans		
	Fucoglucuronans		
	Fucogalactans		~ 40 %
	Xylofucoglucuro-mannans		
Non-catalytic remodeling proteins	Uncharacterised FCSPs		
	Expansins	Present	
	YoaJ-like proteins		Present
Catalytic remodeling proteins	CBM32-containing proteins		Present
	Glucosidases	Present	
	Glucanases	Present	
	$\beta$ -galactosidases	Present	
	Polygalacturonases (PGs)	Present	
	Pectate-lyases (PLs) and Pectase-lyase-like (PLLs)	Present	
	Xyloglucan EndoTransglycosidases (XETs)	Present	
	Xyloglucan endo-hydrolases (XEH)	Present	
	Xylosidases	Present	
	Pectin-Methyl-Esterases (PMEs)	Present	

	And PME-Inhibitors (PMEIs)		
	Pectin acetylsterases	Present	
	Xyloglucan acetylsterases	Present	
	Mannuronate-C5-Epimerases		Present
	Vanadate-dependant Halogenoperoxidases (vHPO)		Present
	GH88-familii proteins		Present
	Alginate-lyases		Present
	Pectin-lyase-fold Virulence factor domain proteins		Present
	Metalloproteinases and inhibitors (TIMP)-like proteins		Present
	Subtilisin-like serine proteases		Present
	CBM1-containing proteins		Present
Structural proteins	Arabinogalactan Proteins (AGPs)	Present	Present
	Prolin-Rich Proteins (PRPs)	Present	
	Hydroxyprolin-rich proteins (HPRPs) including Extensins	Present	
	Glycin-rich proteins (GRPs)	Present	Present
	Many uncharacterised CW proteins	Present	5-9 %
Phenolic compounds	Para-coumaryl acid	>2 %	
	Phlorotannins		Present

309

310

### 311 **Figure legends**

312

#### 313 Figure 1: Cell wall mechanical properties involved in cell wall expansion

314 Growth involves cell wall yielding, either in response to increased tensile stress (not considered  
315 here) and/or in response to an increase in the cell wall amenability to expand (shown here). The  
316 thick grey border represents the cell contour following cell wall growth. Colour boxes represent  
317 the relative part played by either the intrinsic mechanical properties (blue) or remodelling (green)  
318 in cell wall growth. The resting state is represented, by default, with boxes of equal areas. (A)  
319 Intrinsic mechanical properties are modified to allow cell growth. Among them, elasticity can  
320 promote growth due to the activity of enzymes (e.g., pectin-methylesterase inhibitor in the pollen  
321 tube in Angiosperms, which maintains inactive PME and methyl-esterified pectins in the growing  
322 tip). Using nano- and micro-indentation techniques (Table 1), elasticity has been shown to be  
323 involved in the growth of many plant, algal and fungal cells (see text for references). However,  
324 the reliability of nano- and micro-indentation is questioned. The involvement of ‘true’ cell wall  
325 intrinsic plasticity has been debated [52], because it is often confused with visco-elasticity.  
326 Analyses of indentation curves require more complicated models to infer quantitative data on the

327 propensity of the cell wall to plasticity (hysteresis, [68]). (B) Cell wall remodelling factors (e.g.,  
328 expansin, xyloglucan endo-transglycosylase) displace the load-bearing bonds between  
329 components without modifying the overall chemical composition of the cell wall (e.g., expansins  
330 modify the bonds between cellulose and hemicellulose), thereby promoting growth. For example,  
331 in the green alga *Chara*, diffuse growth of the internodes relies on the cycling of distorted to non-  
332 distorted calcium-pectate complexes in new cell walls and calcium delivery to the cell membrane  
333 [14]. Dynamics in this cycle results in windows of increased cell wall elasticity and growth. (C)  
334 In the brown alga *Ectocarpus*, a treatment with 1  $\mu$ M latrunculin B resulted in an increase in  
335 growth whereby the cell increased its width significantly. Simultaneously, the cell lost its capacity  
336 to swell in response to a hypo-osmotic shock, meaning that its intrinsic elasticity (and potentially  
337 plasticity) was reduced (unpublished data from the authors).

338  
339 Figure 2. Comparison of the cell wall chemical composition and structure in land plants and  
340 brown algae.

341 Only the primary cell wall is considered. (A) In land plants (Angiosperms), the cell wall is mainly  
342 composed of two networks: (i) cellulose microfibrils (MFs, both crystalline and non-crystalline  
343 [62]) which are cross-linked by hemicelluloses chains (for simplicity only xyloglucans, XG, are  
344 represented in the drawing) *via* hydrogen bonds, and (ii) pectin gel network. Pectins are  
345 composed of several sub-structures: homogalacturonan (HG) and rhamnogalacturonan I and II  
346 (RGI and II). Demethylesterified HGs are crosslinked by calcium ions and RGII are cross-linked  
347 by borate. Extensins, which are structural proteins potentially cross-linking cellulose and pectins,  
348 and arabinogalactan proteins (AGP) are also shown, although their detailed structure and  
349 interaction are not certain [63,64]. For a detailed review on the composition of the cell wall of the  
350 pollen tube, see [33]. (B) In brown algae, much less is known about the detailed composition and  
351 structure of the cell wall compared with land plants. The model presented here is mainly based on  
352 [47]. The cell wall is likely composed of at least two independent networks: (i) cellulose MFs  
353 cross-linked with fucose-containing sulphated polysaccharides (FCSPs) and proteins, and (ii)  
354 alginate gel networks cross-linked by phlorotannins. Cellulose MFs are ribbon-shaped and much  
355 less abundant than in land plant cell walls (0-8% dry weight, Table 2). For simplicity, only  
356 homofucans FCSPs are represented in the drawing. The identity and structure of putative cross-  
357 linking proteins (in blue, including recently identified AGPs) and phlorotannins are speculative.  
358  $\beta$ -(1 $\rightarrow$ 3)-glucans (callose) and  $\beta$ -(1 $\rightarrow$ 3)-(1 $\rightarrow$ 4)-glucans (mixed-linkage glucans, MLG, not

359 shown in the drawing) have also been identified in brown algal cell wall (Table 2), but their  
360 interactions with other components are unknown [65,66]. The cell wall of brown algae is also rich  
361 in halogenated compounds (up to 19% dw), especially iodine species in the form of free ions (up  
362 to 1.0% dw, i.e. 30,000-fold the concentration of the seawater) or included in halogenated  
363 molecules (especially phlorotannins, [67]). All components are drawn to scale.

# MECHANICS OF GROWTH

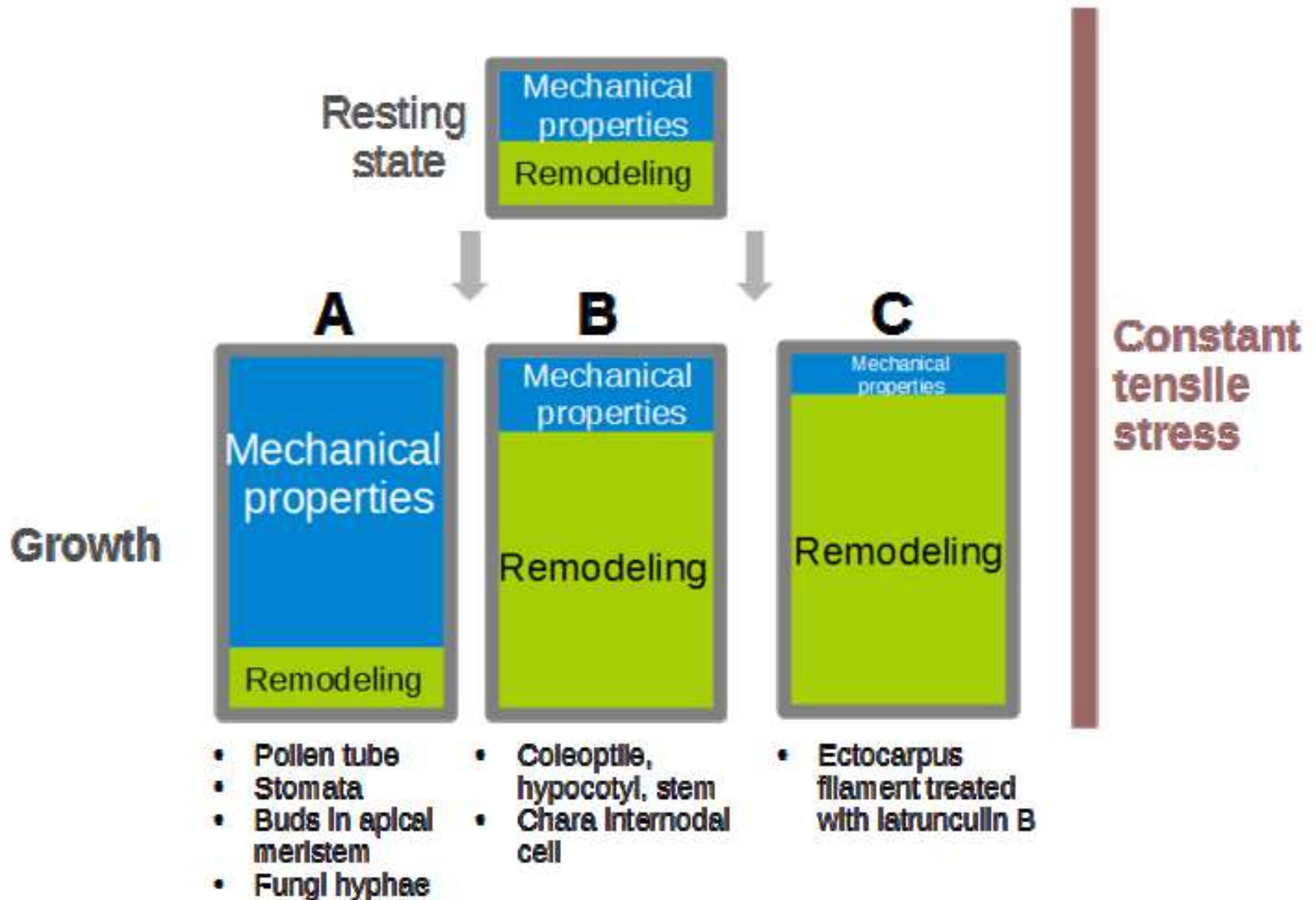
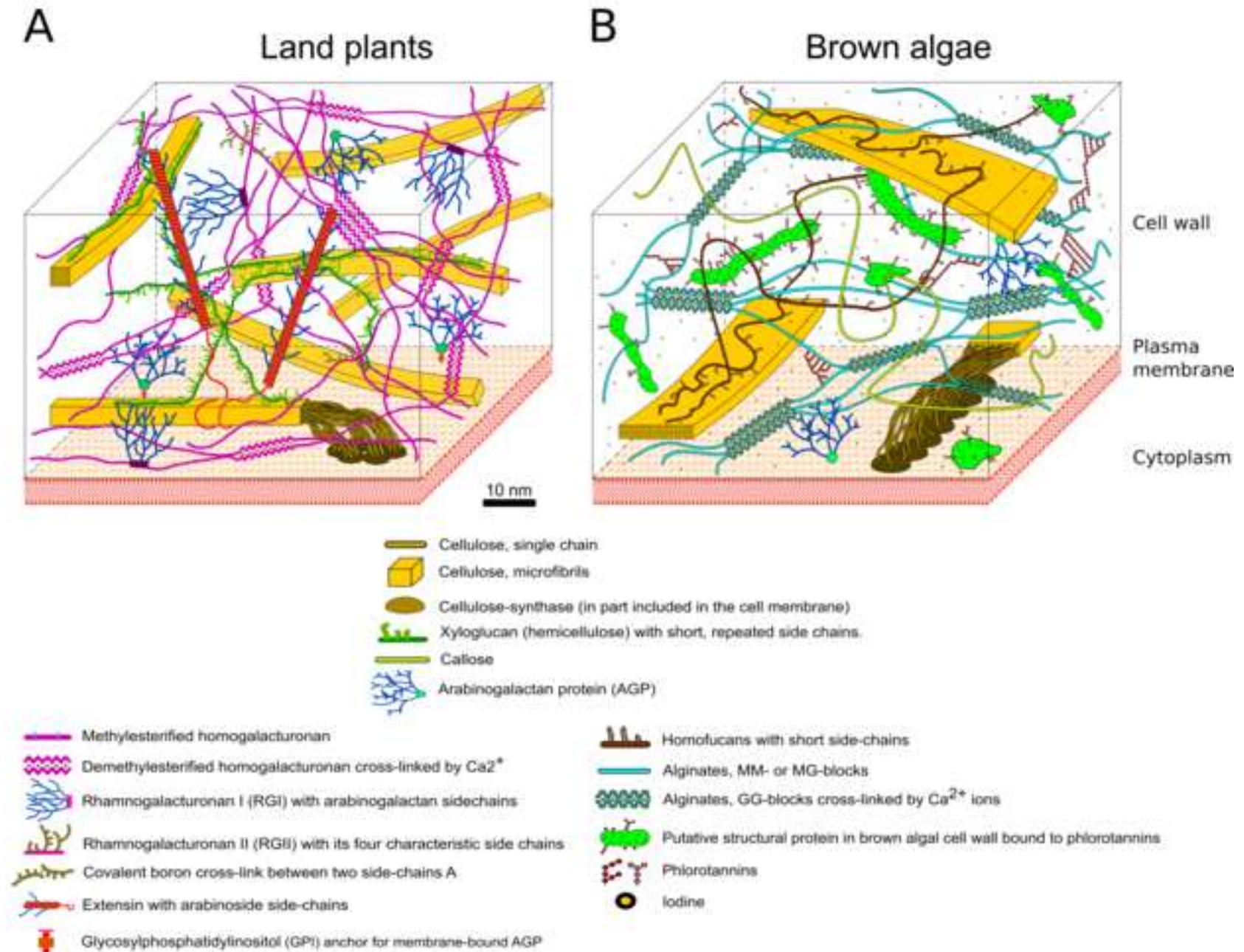
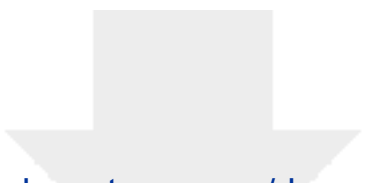


Figure 2







Click here to access/download  
**Original Figure File**  
Charrier\_Fig2\_revised.svg



## Highlights

- There is a current overwhelming paradigm of cell growth that promotes one main scenario: intrinsic elasticity or plasticity of the cell wall control growth.
- In brown algae, which evolved independently from land plants and fungi, both the structure and the chemical composition of the cell wall differ from their counterparts.
- Beyond the complete inventory of cell wall components, their proportion and potential chemical modifications and interactions (covalent, electrostatic) with each other are still largely unknown, even in the most studied organisms, such as land plants.
- Data on land plants and brown algae show that cell wall propensity to grow does not systematically depend on the intrinsic mechanical properties of the cell wall.
- Complexity and diversity of cell wall compositions and structures make preconceived transposition of cell wall growth mechanisms hazardous.

## Outstanding questions

- What are the molecular bases of elasticity in brown algal cell wall, considering its specific composition?
- What is the molecular toolkit of cell wall remodelling in brown algae? Do proteins with similar functions as expansins exist?
- How easily can distinct yet overlapping roles be considered for the cell wall in the lifespan of a cell ? For example, can swelling in response to hypo-osmotic shock rely on mechanical properties or chemical components involved in the cell wall expansion process taking place during growth?
- Are current technical tools suitable to measure the relevant cell wall physical constants involved in growth ? Especially when several cell wall layers are involved ?
- Can cell wall mechanical properties measured at small time-scale be relevant for understanding processes occurring at long-time scale, typical of cell growth?
- To what extent can results obtained on model land plants be transposed to other species ? Which features should be common ? Chemical components, supramolecular structure and organization or intrinsic mechanical properties regardless of the chemical composition?