# Cellulose-binding domains: cellulose associated-defensive sensing partners?

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**Abstract**

The cellulose-binding domains (CBDs) of CBEL, the cellulose-binding elicitor lectin of *Phytophthora,* are potent elicitors of plant defense responses. Induction of defense has also been reported in various cellulose-deficient mutants of *Arabidopsis thaliana*. Based on these observations, we propose a model linking cellulose alteration to defense induction. This integrates the fast increase in cytosolic calcium recorded in response to CBEL, mechano-stimulated calcium uptake mechanisms, and proteins that interact functionally with the cellulose synthase complex. In this context, CBDs emerge as new tools to decipher the signalling cascades that result from cell wall-cellulose perturbations.

## Introduction

Owing to their strategic location surrounding the cell, plant cell walls play an important role in the outcome of plant–microorganism interactions. Understanding of the dialogue that takes place at this interface has progressed as a result of the improved biochemical and molecular knowledge of this cellular compartment. After the first report that plant cell walls contain proteins [1], the concept of the cell wall as a dynamic structure involved in signalling and defense has emerged, as notably illustrated by the ability of pectin-derived oligosaccharides to elicit defense responses [2], and by cell wall reinforcement by structural components following pathogen attack [3,4]. Perturbing the cell wall integrity by mechanical stress such as wounding often induces similar signalling and strengthening effects, thereby suggesting that the cell wall harbours its own surveillance system [5]. With the sequencing of a few plant genomes, particularly of *Arabidopsis thaliana*, the study of plant cell walls has now entered the genomic era, shedding new light on functional aspects of this important cell compartment. Several reviews of current knowledge about cellulose [6,7], and cell wall sugars and proteins as related to stress, have recently appeared [8,9].

Our interest in cellulose as a possible partner of the surveillance system has arisen from several reports linking cellulose to plant defense through the study of *Arabidopsis* cell wall mutants and microbial effectors. Thus, several mutants having defects in cellulose synthesis were shown to be more resistant to various pathogens [8,9]. The possibility that cellulose might be part of a sensing machinery was further supported by the finding that the cellulose-binding domains (CBDs) of the CBEL effector of *Phytophthora parasitica* are sufficient to elicit plant defense [10]. It is unlikely that this effect implies the enzymatic release of oligo-β-glucan elicitors from cellulose because CBEL and more generally CBDs are devoid of hydrolase activity. The presence of CBEL at the mycelium cell surface allows *Phytophothora* to adhere to cellulosic substrates [11].

Since altering as well as touching cellulose induce plant defense, one might wonder whether there is any crosstalk between the mechanisms underlying the response to these two different stresses. Hence this article focuses on the emerging links between the cellulose biosynthesizing machinery, plant defense, and CBDs as possible interactants.

## Proteins associated with cellulose

Before reporting the few examples linking cellulose to defense sensing, we will give an overview of the genes and proteins that interact directly or indirectly with cellulose at the biosynthesis and structural levels.

### *Proteins of the cellulose biosynthesizing machinery.*

The cell wall cellulose microfibrils consist of several chains of 1,4-linked β-D-glucose residues tightly assembled by hydrogen bonds. As a major metabolic, energy-demanding process in plants, the biosynthesis of cellulose must be tightly programmed and linked to a source of glucose monomers. The level of cellulose in the cell wall depends primarily on the activity of the cellulose synthase complex. After the discovery of the first cellulose synthase gene (*CESA*) encoding the catalytic subunit of the complex in cotton (*Gossypium hirsutum*) [12], genome sequencing data revealed that a large set of *CESA* genes, comprising at least 10 members, is present in the genome of *Arabidopsis*, and of other plants. CESA proteins are located within the plasma membrane, and share common structural features, notably conserved and more variable domains, and the D,D,D,QXXRW motif for substrate binding and catalysis. The phosphorylation status of cellulose synthase seems to be important for its activity [6].

In *Arabidopsis*, mutant complementation analysis has shown that *AtCESA1*, *AtCESA2*, *AtCESA3*, and *AtCESA6* are involved in cellulose biosynthesis of the primary cell wall

[6,7,13,14], whereas *AtCESA4, AtCESA7* and *AtCESA8* are expressed during secondary cell wall formation [6,7]. A number of *cesA* mutants, with mutations scattered along the whole sequence of these various genes, are available. They exhibit growth defects and a decrease in the cellulose content of the cell wall which is accompanied in a few cases by deposition *in muro* of weakly esterified pectin [15], of callose, or of lignin at ectopic sites [16].

Genetic screening based on phenotypes has led to the identification of several additional genes [17-19] encoding KORRIGAN (KOR) and the cell surface proteins KOBITO (KOB) and COBRA (COB), mutations in which lead to cellulose deficiencies (*kor, cob*) and mis-orientation of cellulose microfibrils (*kob*).

A necessary requirement for cellulose biosynthesis is the supply of the UDP-glucose substrate. Among enzymes that might fulfil this role, sucrose synthase (SuSy) has received special attention because it produces UDP-glucose and fructose from sucrose, and has been shown to be tightly associated with the deposition of cellulose in cotton fibers [20-22]. However, a clear picture of its involvement awaits further investigation [23].

As a major structural component of the cell wall, cellulose has to be correctly orientated to allow growth and optimal interactions with other polymers. A tight contact between the cellulose synthase machinery and cytoskeleton dynamics has long been claimed [24]. Indeed, confocal imaging has shown that isoxaben, an inhibitor of cellulose biosynthesis, alters the organisation of cortical microtubules [25], and alters alignment of microtubules with the cellulose synthases AtCESA7 and AtCESA6, tagged respectively with the green (GFP:AtCESA7) and the yellow (YFP:AtCES6) fluorescent proteins [26,27]. Conversely, marked changes in YFP-CESA6 organisation are observed when the microtubules (MT) are disrupted using oryzalin. Even though the precise connection between cellulose synthase and microtubules is not definitively established, it is clear that cellulose synthase and microtubules do affect each other.

**In muro *cellulose-binding proteins***

Once in the wall, the cellulose microfibrils are bound to hemicelluloses through hydrogen bonds, thereby contributing to the architecture of the cell wall. The protein expansin can loosen this architecture, probably by weakening the non-covalent adhesion between these polysaccharides [28] without hydrolysing them. It has been shown that downregulation of one gene encoding an α-expansin in *Petunia* reduces the amount of crystalline cellulose in the cell wall [29]. Cellulases (endo-β-1,4-glucanase, cellobiohydrolase, β-glucosidase) are another major category of plant and microbial enzymes that interact with cellulose, ultimately degrading cellulose to β-D-glucose. The presence of CBDs in some plant and microbial endocellulases participate in the efficacy of these enzymes by anchoring them to their substrate [30].

A search for microbial effectors has led to the isolation of a glycoprotein that is located in the inner and outer layers of the cell wall of *Phytophthora parasitica*, a pathogen of the tobacco plant *Nicotiana tabacum* [31]. Its protein moiety is composed of two direct cysteine-rich repeats connected by a linker. Each repeat contains a motif that closely resembles the fungal type I CBD consensus pattern found in cellulases from various fungi [32,33]. Further characterization showed that this molecule is able to bind to crystalline cellulose and to tobacco cell walls but does not possess any detectable hydrolytic activity on various polysaccharides [32]. Due to its elicitor effect and lectin-like activity, the molecule was named CBEL (for cellulose-binding elicitor lectin). CBEL is widespread in the genus *Phytophthora* [34]. In *Phytophthora*, it serves to organise polysaccharide (β-glucan) deposition in the cell wall, and it allows adhesion of the mycelium to cellulosic substrates [11].

CBDs are found in proteins of microbial (bacteria, fungi, oomycetes) and plant (endocellulases, expansin) origins [35,36], and are also encountered in non-enzymic effectors secreted by nematode pathogens during plant colonisation [37]. Although exhibiting different sizes depending on their origins, they share common structural features and aromatic amino-acid residues implicated in cellulose binding affinity [35,36]. The aromatic residues of the two CBDs of CBEL predicted to be surface-exposed and involved in cellulose binding were deduced from sequence alignment with the cellobiohydrolase I CBD from the fungus *Trichoderma reesei*. CBDs are thought to locally disrupt hydrogen bonding between cellulose chains, resulting in local destabilization of cellulose microfibrils [35,36].

Proteomic studies have shown that plant cell walls contain numerous proteins. A comparison of the patterns of wild-type and cellulose mutants might prove useful to uncover additional cellulose-interacting proteins.

## Cellulose and associated defense sensing

Recent studies provide evidence that alteration of cellulose integrity is a warning signal to which the plant cell responds by activating defense pathways.

### *Cellulose synthase-associated sensing*

Cellulose is the main load-bearing polymer of the plant cell wall to which it notably confers mechanical strength. Therefore, cellulose-deficient plants would be expected to be less resistant to pathogen ingress and abiotic stress. There are now several examples indicating that this is not the case.

The first contribution to this subject came from the report that a mutant (*cev*) of *Arabidopsis* showing constitutive expression of defense-related genes was mutated in the cellulose synthase gene *CESA3* [38]. Interestingly this mutant showed increased production of the

defense-related jasmonate (JA) and ethylene (ET) signalling molecules, and enhanced resistance to powdery mildew fungal diseases caused by *Erysiphe cichoracearum, Erysiphe oronti*, and *Oïdium lycopersicum*. A clear link between cell wall alteration and signalling *via* JA and ET was supported by the observation that chemical inhibition of cellulose biosynthesis could reproduce the phenotype on wild-type plants, and that this phenotype i.e. *cev* was suppressed by mutations that interrupt the JA and ET pathways [39]. The notion that mutations of *CESA3* activate defense responses through JA and ET was soon confirmed independently [16] on the ectopic lignin mutant (*eli*) of *Arabidopsis*. In this case, the decrease in cellulose content was compensated by an activation of lignin biosynthesis, thereby indicating that cellulose perturbation has many cellular effects.

Mutations in cellulose synthase genes involved in secondary cell wall formation are further examples linking cellulose deficiencies to biotic and abiotic stresses. Thus, the *lew 2* mutant alleles of *AtCESA8* are more tolerant to drought and osmotic stress than wild-type plants, possibly as a result of the accumulation of soluble sugars, proline and abscisic acid (ABA) within the cell following inhibition of cellulose synthesis [40]. A role for ABA in signalling was later illustrated in *Arabidopsis* mutants of the three CESA4, CESA7 and CESA8 subunits. These mutants had reduced levels of secondary cell wall cellulose, but showed enhanced resistance to three fungal species (*Plectosphaerella cucumerina, Botrytis cinerea, Erysiphe cichoracearum*), and to the vascular bacterial pathogen *Ralstonia solanacearum* [41]. In-depth genetic and transcriptomic studies revealed that signalling was independent of JA, ET and SA (salicylic acid), and correlated with ABA-induced defense, particularly against *Ralstonia*.

In response to various stresses, plants synthesize and accumulate callose, a β-1,3-glucan polymer, in their cell walls. The *pmr4* mutant of callose synthase, another plasma membrane glucan synthase, was more resistant to the biotrophic pathogens *Erysiphe cichoracearum*,

Deleted: -

175 *Erysiphe oronti*, and *Peronospora parasitica*, an effect mediated by SA [42]. Since callose
176 deposition normally participates in plant defense, this suggests that either deprivation of
177 callose, or/and impairment of PMR4 behave as warning signals.
178 The above examples strongly support that defects in cell wall integrity are perceived by a
179 surveillance system, which likely relies on a variety of sensor and receptor molecules.
180
181 ***Cellulose Binding domains (CBDs) as emerging partners***
182 While studies of cellulose mutants were very fruitful in investigating the link between
183 cellulose and defense responses, another approach could be the use of peptides or proteins
184 with a disruptive activity on cellulose.
185 CBEL is a potent elicitor in the *Phytophthora* host plant tobacco, in which it induces local
186 hypersensitive-like lesions, defense responses, and protection against subsequent infection
187 with the oomycete [32]. It is also active on various non-host plants, notably on *Arabidopsis.*
188 Using *Arabidopsis* mutants affected in the salicylic acid (SA), jasmonic acid (JA), and
189 ethylene pathways (ET), it was shown that all three pathways are triggered by the elicitor. JA
190 and ET are required for lesion formation, whereas induction of cell wall-associated defense
191 proteins depends on SA [43]. *In planta* delivery of truncated or CBD-mutated versions of
192 CBEL revealed that intact CBDs are essential for full elicitor and cellulose-binding activities
193 [10]. Indeed, synthetic peptides corresponding to either CBD were sufficient to induce gene
194 expression in tobacco, and to induce expression of a *GUS* reporter gene under control of the
195 defense *PR1* gene promoter in transgenic *PR1*::*GUS Arabidopsis.* Interestingly, these CBDs
196 did not provoke lesions following infiltration of tobacco and *Arabidopsis*. The fast (sec–min)
197 and transient increase in cytosolic calcium that was observed upon incubation of tobacco-
198 aequorin cells with CBEL required intact CBDs, and the presence of the cell wall. Whether
199 other fungal type 1 CBDs are able to induce plant defense awaits further investigations. One

such example might be provided by the cellulase of *Trichoderma viride* whose membrane depolarization and other defense-related signalling effects are retained by the heat denaturated enzyme [44].

CBDs belong to a large superfamily of carbohydrate binding modules (CBMs) classified into more 40 different families, based on amino acid sequences, binding specificity, and structure. This large resource offers the opportunity to investigate precisely the cell wall sensing machinery since several of these CBMs specifically bind various cell wall components.

**Cellulose and cell wall sensing: a proposed model**

The above literature suggests that perturbation of the cellulose status, whether by mutation *(cesA)*, adhesion (CBD), or chemical treatment (inhibitors), is a warning signal for the plant cell and leads to defense responses.

Is there a surveillance system common to such different stimuli? What do we know about the underlying mechanisms? A possible explanation is that they are perceived as a kind of mechanical stress. A similar situation is best documented in yeast, in which agents that cause cell wall stress, as well as mutations that impair cell wall biosynthesis, coactivate cell wall integrity (CWI) signalling and calcium signalling pathways [45], ultimately leading to cell wall biogenesis responses. Compared to yeast, what do we know of the mechanisms underlying cell wall sensing in plants? Could examining the responses induced by CBEL and CBDs provide answers?

In a proposed scenario, calcium would play a central role (Figure 1). Indeed the earliest effect related to cellulose perturbation recorded so far is a very fast increase (within the first minute) in cytosolic calcium in response to CBEL [10]. Interestingly, a plasma membrane protein named Mca1 that plays a crucial role in mechano-stimulated $Ca^{2+}$ uptake was recently

225 characterized in *Arabidopsis* [46]. Another plasma membrane protein called THESEUS1
226 (THE1) that partly mediates growth inhibitory and ectopic lignin deposition phenotypes of the
227 *prc1-1* mutant of *CESA6* of *Arabidopsis* [47] was also reported. THE1 is a receptor-like
228 kinase which autophosphorylates, and requires a mutant *cesA6* background for its activation,
229 suggesting that THE1 is involved in cellulose-sensing.

230 Knowledge of Mca1 now affords the possibility to check whether it mediates calcium entry
231 in cellulose-deficient mutants and in response to CBEL and CBDs. In particular, does it
232 interact with CESA and THE1? Whatever the case, increased cytosolic calcium might
233 regulate phosphorylation processes, notably that of the THE1 and CESA proteins, leading to
234 changes in their activity and, consequently, in the activity of their cell partners. One likely
235 partner of CESA is SuSy, sucrose synthase, which catalyses the formation of UDPglucose, the
236 substrate of CESA. Changes in its activity, *i.e.* glucose formation and/or sucrose
237 consumption, might be perceived by a sugar-sensing machinery [48]. It was recently reported
238 that sucrose can mediate priming of plant defense responses, and bring about broad-spectrum
239 disease resistance in rice [49]. In the proposed model, a functional link between the CESA
240 complex and the cytoskeleton MT might also be altered, as a result of the known
241 depolymerisation of MT in the presence of increased calcium. MT depolymerisation has long
242 been associated with defense responses against microbial invaders [50].

243 Additionally, or alternatively, the kinase activity of THE1 might be the starting point of a
244 phosphorylation cascade leading to defense activation. Crosstalk between such a cascade and
245 the JA, ET, SA, and ABA signalling pathways that are activated in response to cellulose
246 perturbations can be predicted.

247 Based on this model, several questions emerge (Box 1). In particular, it will be interesting to
248 know whether cellulose can relay information from external stimuli such as CBDs to
249 intracellular signalling *via* cellulose synthase. The availability of *Arabidopsis* mutants and of

CBDs together with cell biology imaging technology provides us with powerful tools to probe the proposed model.

## Conclusion

Although the notion of cell wall integrity-sensing is not novel, the underlying mechanisms are still largely unknown. The recent findings that cellulose alterations are perceived as warning signals in *Arabidopsis* provide us with a powerful model system to study the surveillance system of the cell. Future work will aim at identifying novel genes involved in cell wall sensing. This might be accomplished by screening mutants for their response to CBD peptides. Understanding responses to cell wall damages might contribute to improve the resistance of plants to biotic stresses.

**Box 1.** Outstanding questions

- How general among known CBDs is the effect induced by the CBDs of CBEL?
- Besides cellulose, do the CBDs interact with other cell-surface components such as the wall-associated kinases (WAKs) or other protein kinases?
- Is the cellulose-CBD interaction perceived directly by a Mca1-like protein, or through the cellulose-synthesizing machinery?
- Does the chemical inhibition of cellulose synthase induce $Ca^{2+}$ changes and associated signalling events in a way similar to the CBDs?
- Can sucrose sensing and a CESA-MT link be involved in CBD-induced defense?

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**Legend to figure 1**

Figure 1. A model for signal transduction linking CBD perception and cellulose alterations to defense activation. (i) It is proposed that the fast increase in the cytosolic calcium induced by CBEL treatment is mediated by a permeable mechanosensing channel system that relies on Mca1 or on a Mca1-like protein. (ii) Activation of Mca1 would either occur directly in response to a changing physicochemical environment of the cell wall or through its interaction with a cellulose synthase-integrity sensor system (CESA, THE1). Mca1 and THE1 are two plasma membrane proteins related to $Ca^{2+}$ influx (Mca1) and to cell wall integrity sensing (THE1) in *Arabidopsis*. (iii) Calcium might then activate phosphorylation processes, notably on the phosphorylable sites of CESA and THE1. (iv) Changes in CESA and THE1 activities would finally be the starting points of downstream signalling cascades leading to defense gene expression. Possible crosstalks with ethylene (ET), jasmonic acid (JA), salicylic acid (SA) and abscisic acid (ABA) signalling pathways that are induced by cellulose alterations are indicated.

Figure

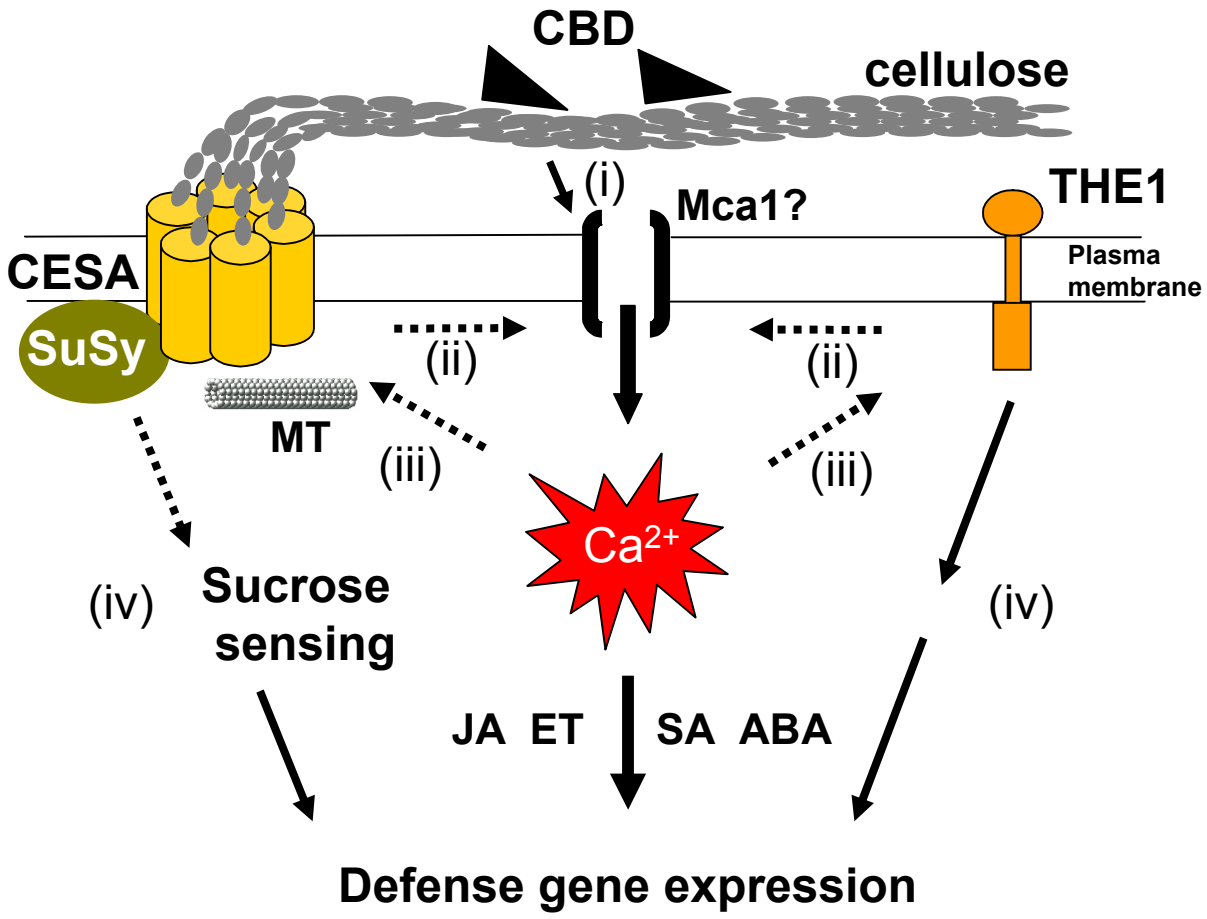


FIGURE 1