Running head: Arabidopsis cellobiose response

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Cellulose-derived oligomers act as damage-associated molecular patterns and trigger defense-like responses[1]

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One Sentence Summary: Cellobiose, a "danger" signal derived from breakdown of the major cell wall polymer cellulose, enhances plant defenses triggered by microbe-derived elicitors.

ABSTRACT

The plant cell wall, often the site of initial encounters between plants and their microbial pathogens, is composed of a complex mixture of cellulose, hemicellulose and pectin polysaccharides, as well as proteins. The concept of damage-associated molecular patterns (DAMPs) was proposed to describe plant elicitors like oligogalacturonides (OGs), which can be derived by the breakdown of the pectin homogalacturon by pectinases. OGs act via many of the same signaling steps as pathogen- or microbe-associated molecular patterns (PAMPs) to elicit defenses and provide protection against pathogens. Given both the complexity of the plant cell wall and the fact that many pathogens secrete a wide range of cell wall degrading enzymes, we reasoned that the breakdown products of other cell wall polymers may be similarly biological active as elicitors and may help to reinforce the perception of danger by plant cells. Our results indicate that oligomers derived from cellulose are perceived as signal molecules in Arabidopsis, triggering a signaling cascade that shares some similarities to responses to well-known elicitors such as chito-oligomers and OGs. However, in contrast to other known P/DAMPs, cellobiose stimulates neither detectable ROS production nor callose deposition. Confirming our idea that both PAMPs and DAMPs are likely to co-occur at infection sites, co-treatments of cellobiose with flg22 or chito-oligomers led to synergistic increases in gene expression. Thus, the perception of cellulose-derived oligomers may participate in cell wall integrity surveillance, and represents an additional layer of signaling following plant cell wall breakdown during cell wall remodeling or pathogen attack.

INTRODUCTION

The primary plant cell wall is composed of a complex interconnected mixture of proteins and polysaccharides, mainly cellulose, hemicellulose and pectin. The secondary cell wall also contains lignin. These strong polymeric networks provide structural integrity to plant cells and protection from the external environment (Somerville et al., 2004). To gain access to the cell cytoplasm, pathogens have to overcome the plant cell wall barrier and do so mainly through secretion of cell wall degrading enzymes (Howard, 1997; Toth and Birch, 2005). Plants can perceive the presence of pathogens at the cell surface via recognition of conserved microbial molecules, named pathogen- or microbe-associated molecular patterns (PAMPs). Well-studied examples of PAMPs are the elicitor-active peptides of bacterial flagellin (flg22), the bacterial elongation factor EF-Tu (elf18), and chito-oligomers, breakdown products of fungal cell walls and insect exoskeletons (Kunze et al., 2004; Chinchilla et al., 2006; Miya et al., 2007; Boller and Felix, 2009). Recognition of such molecules is achieved by specific plasma membrane-resident receptors, pattern recognition receptors (PRRs). Upon PAMP perception, a signaling cascade is initiated to activate plant defense responses in a process termed pattern-triggered immunity (PTI) (Jones and Dangl, 2006). PTI is characterized by influx of calcium ions, the generation of reactive oxygen species (Alonso et al.), the activation of mitogen-activated protein kinases (MAPKs) (Torres et al., 2002; Pitzschke et al., 2009; Tena et al., 2011) and changes in gene expression leading to increased production of defense compounds and proteins; thus, equipping the plant cell to defend itself.

While gaining access to the cytoplasm of plant cells during the penetration phase, pathogens breach the cell walls, releasing host peptides and oligosaccharide fragments (i.e., DAMPs) (Howard, 1997). Pectin-derived oligogalacturonides (OGs) are well-characterized damage associated molecular patterns (DAMPs) capable of activating plant immunity (Kohorn et al., 2009; Brutus et al., 2010). OGs are perceived by WAK1 and WAK2, cell wall-associated receptor-like kinases required for cell expansion (Kohorn et al., 2006). Transgenic plants over-expressing WAK1 are more resistant to the necrotrophic fungal pathogen *Botrytis cinerea* (Brutus et al., 2010).

Plants also encode a wide array of cell wall degrading enzymes, which are thought to play a role in cell wall remodeling during growth and development (Cosgrove, 2005). Given this dynamic and complex nature of the plant cell wall and the diversity of cell wall degrading/modifying enzymes encoded by many pathogens, there are a multitude of small

molecules that may be generated at the infection court. Such small molecules have the potential to be recognized as danger signals and to be perceived by a cell wall integrity sensing system (Pilling and Hofte, 2003; Vorwerk et al., 2004; Hematy et al., 2009; Bolouri Moghaddam and Van den Ende, 2012; Wolf et al., 2012). Experimental evidence has accumulated over the past decade to support idea that plants monitor the status of the cell wall via a cell wall integrity sensing system (Hematy et al., 2007; Cheung and Wu, 2011; Denness et al., 2011; Ramirez et al., 2011). Despite the progress in the field, our understanding of cell wall-derived signals and molecular mechanisms underlying the recognition of cell wall damage is limited. Cell walls are anchored to the cell surface via the cell wall biosynthetic machinery and by structural and sensory proteins that bind to cell wall components and maintain plasma membrane-cell wall contacts (Liu et al., 2015). This link is thought to be essential for plant development and responses to external stimuli (Wolf et al., 2012). Cellulose is synthesized at the plasma membrane by the cellulose synthase complex, which converts UDP-glucose into β-1,4-glucan chains that crystallize into cellulose microfibrils in the cell wall. Cellulose microfibrils are the major load bearing components of the plant cell wall. Thus loss of cellulose microfibril integrity has drastic effects on plant cells (Somerville, 2006). Here we present work demonstrating that perception of cellulose degradation products, in the absence of catastrophic cell wall damage and loss of cellular integrity observed in previous studies, activates defense responses similar to PTI in Arabidopsis. Furthermore, co-treatments of cellulose fragments and PAMPs like flg22 or chito-oligomers leads to synergistic increases in gene expression, suggesting that plant cells may be able to respond defensively earlier and at lower doses of mixtures of elicitors likely to be found in the infection court.

RESULTS

Defense-Related WRKY Transcription Factors Are Up-Regulated By Cellulose Oligomer Treatment

WRKY transcription factors (WRKY TFs) have long been implicated in regulation of plant responses to biotic and abiotic stresses, and frequently single WRKY TF regulate transcriptional reprogramming of multiple plant processes (Rushton et al., 2010). Using publicly available gene expression datasets, we selected several WRKY transcription factors with elevated transcript levels after chito-oligomer treatment, suggesting an active role in the defense response, for further study. Transgenic seedlings expressing the *WRKYpromoter*:GUS constructs (*WRKYp*:GUS) were used to identify cell-wall derived oligosaccharides that were capable of

stimulating higher expression of the selected defense-related *WRKY* genes. We found that oligomers of cellulose (DP 2 and 3) caused enhanced expression of the *GUS* gene under the control of *WRKY30* and *WRKY40* promoters (Fig. 1). We determined the time course of expression of *WRKY30*, *WRKY40* and other defense-related WRKY genes by qRT-PCR and results showed that *WRKY30* had the strongest transcriptional response of all *WRKY* genes tested, peaking at 25 min after treatment with cellobiose (Fig. 1). Treatment with cellobiose (DP2), cellotriose (DP3) and cellotetraose (DP4) elicited similar levels of *WRKY30* expression (Fig. S1). This observation, along with reports that two classes of cellulases (i.e., GH6 and GH7) commonly found in saprophytic and hemi-biotrophic fungi produce cellobiose (Spanu et al., 2010; Glass et al., 2013), prompted us to continue using cellobiose as a representative cellulose degradation product. Cellobiose treatment triggered enhanced expression of *WRKY30* in seedling roots and seedling shoots; however, *WRKY30* also exhibited constitutive expression in cotyledons (Fig. 1). The regulation of *WRKY30* expression in seedling roots was tightly regulated, being elicitor-dependent and undetectable in the absence of a stimulus (Fig. S2). Therefore *WRKY30* expression in seedling roots at 25 min post-treatment was used as a molecular marker for further characterization of plant responses to cellobiose.

WRKY30 Is Induced By β-1,4-Glucan Oligosaccharides

Soluble sugars such as sucrose, raffinose and trehalose can play a signaling role in plant innate immunity (Bolouri Moghaddam and Van den Ende, 2012). For example, sucrose treatment leads to the induction of pathogenesis-related (PR) genes (Solfanelli et al., 2006) and to strong enhanced expression of genes in the anthocyanin biosynthetic pathway (Solfanelli et al., 2006). Synthesis of the non-reducing glucose disaccharide trehalose (α-1,1-diglucose) has been shown to regulate responses to environmental stresses (Iordachescu and Imai, 2008). In addition, trehalose synthesis by *Pseudomonas aeruginosa* strain PA14, a multi-host pathogen that infects plants, nematodes, insects and vertebrates, is required for full virulence on Arabidopsis (Djonovic et al., 2013). Therefore it is possible that plants have evolved to recognize apoplastic trehalose as a defense mechanism. Given that trehalose is also a glucose disaccharide, like cellobiose (β-1,4-diglucose), we asked whether the responses to cellobiose were unique to this glucose dimer or not. We exposed *WRKY30p*:GUS transgenic seedlings to a panel of disaccharides with various linkages and found that, in seedling roots, *WRKY30p:GUS* expression was exclusively elicited by cellobiose among all the sugars tested (Fig. 2). Glucose did not induce *WRKY30p:GUS* expression in these tests, indicating that the observed cellobiose responses are not due to the

breakdown of cellobiose to glucose. These results suggest that a specific receptor for small oligomers of cellulose may exist in Arabidopsis seedlings.

WRKY30 has been characterized as a general stress-responsive gene (Scarpeci et al., 2013) and the work presented here shows that its expression is stimulated in seedlings by several P/DAMP elicitors including chito-oligomers, which are oligomers of β-1,4-*N*-acetyl-D-glucosamine (Fig. S2 and Fig. S3). The LysM receptor-like kinase (CERK1) binds to chito-oligomers and is required for chitin and peptidoglycan perception in Arabidopsis (Miya et al., 2007; Wan et al., 2008; Willmann et al., 2011), and plants carrying a mutation in *CERK1* can no longer respond to chitin stimulation. The *cerk1* null mutant still responds to cellobiose treatment indicating that cellobiose does not promiscuously activate this receptor (Fig. S3).

Cellobiose Induces Responses Elicited by Other P/DAMPs

Cellobiose treatment triggers an early calcium transient

Calcium is a ubiquitous and protean intracellular second messenger. A wide range of stimuli cause changes in intracellular calcium concentration in plants (Sanders et al., 1999). These changes generate unique stimulus-dependent calcium signatures (i.e., timing and magnitude of signal) leading to multiple physiological responses (Sanders et al., 1999; Sanders et al., 2002; Lecourieux et al., 2005). Intracellular calcium transients have been shown to occur after exposure to pathogens or purified elicitors, and are therefore considered one of the hallmarks of P/DAMP perception (Allen et al., 2001; Ma et al., 2012; Ma et al., 2013; Michal Johnson et al., 2014). We used aequorin-expressing Arabidopsis seedlings (Knight et al., 1991) to determine if cellobiose exposure generated a calcium response (Fig. 3). Our results show that cellobiose exposure generates a fast and short-lived intracellular calcium elevation, lasting for only about 200 sec, with levels peaking at 100 sec post-treatment (Fig. 3). Plants pre-treated with the calcium-chelator EGTA (2.5 mM) showed a 60% reduction in *WRKY30* expression after cellobiose treatment, indicating that the calcium transient is part of the cellobiose-generated signaling cascade leading to activation of gene expression (Fig. 3). Control treatments using glucose and sucrose did not elicit a calcium response (Fig. S4), highlighting the specificity of this response to cellobiose.

Cellobiose treatment activates MAP kinases

Mitogen-activated protein kinase (MAPK) cascades are central to innate immune signaling (Asai et al., 2002; Meng and Zhang, 2013). MPK3, MPK6, MPK4 and MPK11 are

strongly activated upon P/DAMP treatment (Meng and Zhang, 2013). We tested whether cellobiose treatment would also lead to MAPK activation. Cellobiose treatment activates MPK6 and MPK3 at very early time points, with stronger activation of MPK6 (Fig. 4, Fig. S5). Phosphorylation of MPK6 was visible between 5 and 15 min, being the strongest at 10 min after induction (Fig. 4). Elevated expression of *WRKY30* by cellobiose is decreased 20-fold in the *mpk6-2* mutant (Salk_073907), indicating that MPK6 plays an important role in the cellobiose signal transduction pathway leading to *WRKY30* expression (Fig. 4).

Global Arabidopsis gene expression profiles are similar after cellobiose, chito-oligomer or OG treatment

Studies of the global suite of differentially regulated genes after P/DAMP elicitor treatment have highlighted the high degree of overlap in the early transcriptional response following elicitor perception, indicating that a basal broad spectrum response is a common feature following recognition of a 'danger' signal (Zhang et al., 2002; Moscatiello et al., 2006; Zipfel et al., 2006; Denoux et al., 2008; Wan et al., 2008). However, it has also been shown that the profile of early signaling events, including the kinetics of transcriptional changes following elicitor treatment, varies between elicitors (Garcia-Brugger et al., 2006; Zipfel et al., 2006; Denoux et al., 2008). With this in mind, we performed an Affymetrix microarray experiment on Arabidopsis seedling roots treated with chito-oligomers, OGs or cellobiose for 25 min (early) and 3 h (late) time points. Chito-oligomers and OGs were used in saturating concentrations (Hu et al., 2004; Miya et al., 2007; Shinya et al., 2012). No group of genes was substantially up-regulated exclusively by cellobiose and OGs (i.e., DAMPs) but not by chito-oligomers (i.e. PAMPs), a characteristic we would expect for genes encoding cell wall integrity sensing and response. Instead, our results indicate that the early transcriptional response to cellobiose is similar to that following treatment with other known P/DAMPs. At the 25 min time-point, cellobiose-triggered changes overlapped more strongly with those elicited by the pathogen-derived chito-oligomers than by plant-derived OGs (Fig. 5 and Table S1). In the group of genes up-regulated more than 2.5 fold after 25 min of treatment, chito-oligomer treatment elicited the largest number of transcriptional changes (735 genes), followed by cellobiose (689) and OGs (568), with 506 genes similarly induced by all three treatments. Nonetheless, as stated above, cellobiose elicitation of the marker gene *WRKY30* expression is independent of the chitin receptor CERK1, thus the similarity observed between cellobiose and chito-oligomer-induced transcriptional changes is not due to promiscuous receptor binding. In addition, hierarchical clustering showed higher dissimilarity among gene expression profiles elicited by the three elicitors at 3 hours post-

treatment, and grouped chito-oligomer- more closely to OG-elicited profiles; cellobiose was the most dissimilar among the three (Fig. 5) (Nekrasov et al., 2009).

Past studies showed that PAMPs can induce expression of defense genes independent of defense-associated hormones salicylic acid (SA), jasmonic acid (JA), and ethylene (Zhang et al., 2002; Ferrari et al., 2003; Zipfel et al., 2004; Ferrari et al., 2007). Conversely, P/DAMP treatment has also been reported to stimulate JA and ethylene production (Doares et al., 1995; Simpson et al., 1998), as well as the elevated expression of genes encoding proteins linked to SA-mediated responses (Denoux et al., 2008). The results from cellobiose-treated seedling roots showed that cellobiose exposure also triggers up-regulation of genes linked to biosynthesis and signaling mediated by defense hormones after 25 mins (Table S1, Table1). For example, *SAG101* and *PAD4*, genes associated with SA signaling, were up-regulated by cellobiose after 25 mins. *ACS7*, an ACC synthase involved in the synthesis of ethylene (Yamagami et al., 2003), was induced 15-fold in the cellobiose-treated samples, similar to the up-regulation found in the chitin and OG samples (17- and 10-fold increase, respectively). *LOX3* and *LOX4,* genes encoding proteins in the octadecanoid pathway leading to the production of jasmonic acid (JA) , were up-regulated at 25 min, returning to basal levels after 3 h in all treatments. The magnitude of amplification of the *LOX* genes at 25 min was more similar between cellobiose and chitin, approximately 20-fold for *LOX3* and 100-fold for *LOX4* in both treatments, whereas in the OG-treated samples, *LOX3* and *LOX4* were up 8-and 30-fold, respectively. Genes involved in the biosynthesis of defense-associated indole glucosinolates, including the transcriptional regulator *MYB51,* were up-regulated by all treatments at 25 min. However, in contrast to what we observed for the cellobiose-treated samples in which indole glucosinolate biosynthetic genes *IGMT1/2/3/4* expression returned to basal levels, the expression of these genes remained up-regulated after 3 h of chito-oligomer treatment and, to a lesser extent, also remained up-regulated in the OG-treated samples (Table 1). These data are in agreement with previous studies; when comparing the effects of different elicitors on gene expression, the results were more quantitative than qualitative (Denoux et al., 2008). In fact, it does appear that the global response to cellobiose and OGs diminishes more rapidly than after chito-oligomer treatment, however we observed a significant reduction in the number of differentially regulated genes at 3 h for all three treatments, highlighting the transient nature of the early broad spectrum basal defense response.

Not All Responses Elicited by Other P/MAMPS are Elicited by Cellobiose

Cellobiose treatment increases plant growth

Global of suppression of gene expression for photosynthesis genes following biotic stress has been well documented, presumably as a compensatory mechanism for the high metabolic cost of defense (Bilgin et al., 2010; Gohre et al., 2012). Accordingly, at 3 h post-treatment for all three elicitors tested, photosynthesis-related genes, particularly those coding for proteins in photosystem I (PSI) and photosystem II (PSII) reaction centers (Table 2) showed reduced expression in seedlings. Typically, exposure to high concentrations of elicitors halts seedling growth (Gomez-Gomez et al., 1999; Zipfel et al., 2006). This growth inhibition phenotype has been successfully exploited for the identification of mutants insensitive to elicitor treatments (!!! INVALID CITATION !!!). In contrast, we observed that seedlings grown in high concentrations of cellobiose displayed increased fresh weight when compared to than those grown in lower concentrations or without cellobiose (Fig. 6). It is possible that cellobiose is being cleaved by β-glucosidases either in the apoplast or in the cytoplasm, thereby increasing the cell's availability of glucose. We are unaware of a cellobiose transporter in plants, as found in other organisms (e.g., the CDT-1 and CDT-2 transceptors in *Neurospora crassa* (Galazka et al., 2010)). In addition we did not observe in our microarray experiments a significant induction of expression of genes encoding sugar transporters exclusively in cellobiose-treated samples that could suggest cellobiose/cellulose oligomer specific transport. However, a gene encoding for the β-glucosidase BGLU27 (At3g60120), a family 1 glucosidase predicted to reside in the cytoplasm (Tanz et al., 2013), was highly up-regulated exclusively in the cellobiose-treated samples (Table S1). This result was confirmed by qRT-PCR (Fig. 6). We obtained a T-DNA insertion line of *BGLU27* (Salk_005337C), in which the mRNA for this gene is reduced to undetectable levels (Fig. 6). When these lines were treated with cellobiose, we did not observe any significant changes in *WRKY30* up-regulation relative to wild type, indicating that BGLU27 is not required for cellobiose perception or signal transduction (Fig. 6). However, the plants impaired in *BGLU27* expression did not grow as well in the presence of cellobiose as compared to wild type (Fig. 6), suggesting that BGLU27 might be a β (1,4)-hydrolase involved in cellobiose break-down to increase glucose availability. Importantly, in the *bglu27-1* mutant background, which seems less capable of consuming cellobiose, excess cellobiose still did not have a detrimental effect on seedling growth.

Responses to cellobiose are BAK1-independent

The plant leucine-rich repeat (LRR) receptor kinase BAK1/SERK3 is involved in brassinosteroid hormone responses, cell death control and innate immunity (Chinchilla et al., 2007; Chinchilla et al., 2009). BAK1 has been shown to associate with LRR-type PRRs and to be

297 required for signal transduction following perception of PAMPs, including flg22 and elf18
298 (Chinchilla et al., 2007; Heese et al., 2007; Roux et al., 2011; Schwessinger et al., 2011). One
299 well-studied example is BAK1 recruitment to the flagellin receptor complex following flg22
300 perception (Chinchilla et al., 2007; Heese et al., 2007). Plants defective in the *BAK1* gene are less
301 sensitive to flg22 treatment. We used the *bak1-5* allele of BAK1, which is specifically impaired
302 in innate immune signaling (Schwessinger et al., 2011), to assess whether BAK1 is required for
303 signal transduction following cellobiose treatment. Plants carrying the *bak1-5* mutation were
304 significantly impaired in *WRKY30* expression following flg22 treatment, however we did not
305 observe any changes in *WRKY30* expression after cellobiose elicitation (Fig. 7). This result shows
306 that BAK1 is not required for cellobiose perception and subsequent signal transduction**.**

307 ***Responses to cellobiose are independent of Reactive Oxygen Species***

308 One of the early defense responses triggered by P/DAMP recognition is the production of
309 ROS (e.g., superoxide, H_2O_2). Genetic analysis in Arabidopsis demonstrated that the ROS burst is
310 dependent on NADPH oxidases, AtRbohD and AtRbohF, respiratory burst oxidase homologues
311 (Rboh) of the human neutrophil gp91phox. Plants defective in RbohD and RbohF are impaired in
312 full ROS production in response to elicitor treatment and pathogen attack (Simon-Plas et al.,
313 2002; Torres et al., 2002; Torres et al., 2006; Nuhse et al., 2007; Galletti et al., 2008). To
314 determine if cellobiose treatment elicited ROS production, we used a luminol-based assay for
315 quantifying H_2O_2 in leaf disks treated with cellobiose. We were not able to detect any ROS signal
316 following cellobiose treatments ranging from 100 µM up to 1 mM (Fig. 8). In addition, we
317 transformed plants defective for both NADPH oxidase D and F (*rbohD/F*) with the
318 *WRKY30p*:GUS construct and treated homozygous T3 plants with cellobiose. We did not observe
319 any differences in GUS expression following cellobiose treatment, indicating that AtRbohD/F are
320 not required for signal transduction leading to *WRKY30* up-regulation in response to cellobiose
321 (Fig. 8). A second potential source of ROS are apoplastic peroxidases. To confirm that ROS
322 production was not necessary for signal transduction of cellobiose perception, we took advantage
323 of a previously characterized transgenic Arabidopsis plants expressing an anti-sense cDNA
324 encoding a type III peroxidase, French bean peroxidase type 1 (FBP1) impaired in oxidative burst
325 (Bindschedler et al., 2006). Cellobiose-treated FBP1 seedlings were unaltered in *WRKY30* up-
326 regulation relative to wild-type control (Fig. 8). Together, these experiments indicate that the
327 cellobiose signaling pathway is independent of ROS formation.

The Expression of Genes Involved in Suberin Biosynthesis is Induced Following Cellobiose Treatment

Plant cell wall reinforcements, which occur following cell wall disruption, are typical responses following P/DAMP perception and, in some cases, can be beneficial to plants. For example, callose deposition at the cell wall can usually be observed in roots and leaves in response to pathogen cell wall penetration or PAMP perception (Galletti et al., 2008; Millet et al., 2010). Over-expression of *PMR4* (synonym=*GSL5)*, encoding a stress-induced callose synthase, demonstrated that early callose deposition results in complete penetration resistance to powdery mildew in Arabidopsis (Ellinger et al., 2013). It is possible that cellobiose perception, as an indicator of cell wall damage, also leads to cell wall reinforcement. After treating plants with cellobiose for 24 h, we could not observe any callose formation (Fig. 9) or ectopic lignification (data not shown). However, when investigating our cellobiose-induced gene expression datasets, we observed elevated transcript levels for suberin biosynthetic genes at 3 h post-treatment (Fig. 10). The transcripts for cytochrome P450 *CYP86B1* and the acyltransferase *GPAT5* were elevated >3-fold relative to untreated controls. Transcripts levels for other genes in this pathway, *LACS2* and *FAR5*, were 2-fold higher. In addition, *MYB41*, encoding a TF recently shown to activate suberin biosynthesis (Kosma et al., 2014), was induced in the cellobiose-treated samples at 25 min, but not at 3 h. The suberin biosynthetic genes and *MYB41* were only up-regulated by cellobiose and not by chito-oligomers or OGs. In subsequent qRT-PCR experiments, we observed that all genes in the suberin pathway had peak expression 1 h post cellobiose treatment (Fig. 10), and we confirmed that these genes were not up-regulated after chito-oligomer treatment (Fig. S6). Suberin is a cell wall-linked polymer that acts as a hydrophobic barrier and is deposited in response to biotic and abiotic stresses (Thomas et al., 2007; Kosma et al., 2014). Studies have shown that the rate of tissue suberization after wounding correlates with increased resistance to subsequent fungal infections at wound sites (Biggs and Miles, 1988; Lulai and Corsini, 1998). Despite several attempts, we could not detect elevated suberin in seedling roots treated with cellobiose (data not shown). This result indicates that the up-regulation of the suberin biosynthetic pathway, triggered by cellobiose perception alone, is not sufficient to cause ectopic suberin deposition. However, it is possible that cellobiose perception may participate in preparing the plant for suberin deposition following recognition of additional stress signals.

Cellobiose Pre-Treatment Confers Increased Resistance to *Pseudomonas syringae* pv. Tomato DC3000 Infection

Exposure to avirulent pathogens or P/DAMP elicitor treatment can prepare the plant's immune system for a more efficient defense reaction to subsequent pathogen attacks (Van Wees et al., 2008). Given the short-lived PTI signaling observed after cellobiose treatment, and the apparent lack of ROS formation, we were interested in investigating whether cellobiose treatment could induce increased resistance against pathogen attack in Arabidopsis plants. We compared ion leakage, used as proxy for *P. syringae* pv tomato DC3000-induced cell leakage and death, in infected plants pre-treated with H_2O, cellobiose or flg22. Results showed that plants pre-treated with cellobiose were more resistant to infection than plants pre-treated with H_2O, and resistance effect was not significantly different than that provided by flg22 pre-treatment (Fig. 11). However, pre-treatment with flg22 seemed to confer a stronger protection against *P. syringae* pv. tomato DC3000, since ion leakage in those plants was not significantly different to the ion leakage measured in uninfected controls (Fig. 11).

Cellobiose Has an Additive Effect with Other P/DAMPs on PTI Signaling

About 2.4% of the Arabidopsis genes encode receptor-like kinases (RLKs), some of which function as PRRs at the cell surface. This large number of receptors may reflect the variety of eliciting signals plants can perceive (Boller and Felix, 2009; Macho and Zipfel, 2014). We were interested in investigating the independent nature of cellobiose perception, and if the signal cascade generated by cellobiose perception traveled through similar pathways as for other known P/DAMPs. We investigated PTI signaling outputs in combination treatments, in which cellobiose was applied simultaneously with another elicitor (i.e., flg22, chito-oligomers, OGs). We were able demonstrate that the calcium spike generated by cellobiose is independent and/or additive to that of other elicitors (Fig. 12). In addition, by comparing the calcium signatures derived from the different elicitor treatments, we observed that the calcium signature generated by cellobiose is similar to that of pectin-derived OGs, as opposed to the slightly delayed and longer lasting curve generated by treatment with PAMPs flg22 and chito-oligomers. In particular, the calcium signature from the simultaneous application of cellobiose and flg22 was a curve distinct from and higher in amplitude than the calcium signatures of either cellobiose of flg22 single treatments, indicating perhaps that each elicitor has a different mode of triggering changes in intracellular calcium levels.

MAPK activation was amplified in combination treatments of cellobiose, chito-oligomers and flg22. In single treatment experiments with chito-oligomers and flg22, peak activation of MAPK was obtained at 30 min post-treatment, with little activation visible at 60 min. In

treatments of cellobiose combined with flg22 or chito-oligomers, MAPK activation was stronger at 30 min and still visible at 60 min (Fig. 12). We also observed amplification of expression of the marker gene *WRKY30* in samples treated with cellobiose combined with either chito-oligomers or flg22 after 25 min (Fig. 12). Current evidence, including work presented here, suggests that the initial phase of danger signaling triggers a response similar in qualitative terms, although quantitatively different according to the particular danger signals involved (Denoux et al., 2008; Boller and Felix, 2009). Our results with combination P/DAMP treatments suggest an independent mode of cellobiose perception, and clearly show a quantitative amplification of the immune signaling cascade. The amplification of defense signaling in response to simultaneous perception of multiple stimuli may render a stronger immune response.

DISCUSSION

Plant cell walls are a source of potential defense signaling molecules that can be released upon degradation by pathogen enzymatic repertoires (Hahn et al., 1981; Walton, 1994). Upon perception of cell wall damage, cells respond by activating signaling cascades leading to activation of defense responses. We used WRKY transcription factors as defense markers to identify cell wall oligo-saccharides capable of activating defense responses in Arabidopsis. We showed that Arabidopsis can perceive cellulose degradation products like cellobiose and respond by activation of a signaling cascade leading to increased expression of defense-related genes, with substantial overlap relative to other pathogen and cell wall damage-associated elicitors. Cellobiose pre-treatment induced Arabidopsis seedlings immune response, which resulted in less cell damage following *P. syringae* infection. Cellobiose treatment caused a rapid and transient intracellular calcium spike, which was similar to in the timing and shape of the calcium response to OGs. When treating aequorin-expressing seedlings with a combination of elicitors, we observed an additive or synergistic effect in the calcium signatures, most noticeably for cellobiose plus flg22. Despite the critical nature of Ca^{2+} signaling to pathogen defense, there is still a limited mechanistic understanding of how different calcium signatures affect gene expression and defense outcomes (Seybold et al., 2014). While some studies suggest an apoplastic origin of PAMP-induced Ca^{2+} influx (Aslam et al., 2008; Ranf et al., 2011; Segonzac et al., 2011), other researchers propose a requirement for intracellular Ca^{2+} stores (Ma et al., 2012). It is possible that concurrent P/DAMP perception may lead to synergistic changes in Ca^{2+} signaling signatures resulting in increased immune fitness. Treatment with cellobiose activates MAP kinases at very early time points, and appears to be ROS independent. Recent findings using chemical genetic

approaches showed that the oxidative burst and MAPK activation are two independent signaling events in plant immunity, which is in agreement with our results (Ranf et al., 2011; Segonzac et al., 2011; Xu et al., 2014). The transient nature of the responses triggered by cellobiose suggests that perception of cellobiose may be auxiliary to other stimuli. During a pathogen attack, PAMP perception, detection of cell wall break-down, membrane distortion and depolarization may all contribute to the intensity of plant responses. Current research on PTI focuses on response to single elicitors, an unlikely scenario in nature. Our results from treatments with two elicitors shows that a number of signaling steps in PTI are enhanced suggesting that plants may be able to respond to lower elicitor levels and more quickly with effective defenses than previous work has indicated.

Cellulose microfibrils help provide the tensile strength that dictates the structure of the plant cell (Somerville et al., 2004). Drastic loss of cellulose microfibril integrity leading to changes in cell shape and size elicit defense-like changes in gene expression. Mutants defective in cellulose synthesis, such as *CESA3* mutants *cev1* and *eli1-2*, exhibit increased resistance to powdery mildew pathogens due to increased activation of defense hormone signaling, induction of defense response gene expression and increased cell wall reinforcement by lignification (Ellis and Turner, 2001; Caño-Delgado et al., 2003). In addition, the trans-membrane malectin receptor kinase THESEUS has been shown to mediate the ability of plants to respond to defects in cellulose disruption observed in *cesA6* mutants but it does not participate in cellobiose perception (unpublished data) (Hematy et al., 2007). Together, these studies highlight the role of the cellulosic fraction of the plant cell wall in generating signals activating a cell wall integrity system. Cellobiose fragments are likely generated by cellulase digestion of cellulose, but prior to collapse of cell wall integrity. Thus, we could not detect any clear evidence of cell wall reinforcement following overnight cellobiose treatment; however, we did observe up-regulation of genes required for suberin biosynthesis exclusively in the cellobiose treated samples, suggesting a possible link between cellobiose perception and cell wall reinforcement through suberin deposition. Our data suggests that plants can directly monitor the status of cellulose by perceiving small oligomers of cellulose. It is possible that this perception is mediated by PRRs, similar to other P/DAMPs, but the identity of the putative receptor and detailed molecular mechanisms of perception and signal transduction are unknown. The rapid calcium influx and MAPK activation observed suggests a receptor-mediated perception at the cell surface. The relative high levels of cellobiose (>100 μM) required to obtain detectable read-outs, 100-fold more than what is required for flg22 triggered responses, suggest that a putative membrane

receptor dedicated for cellulose oligomer perception must have low sensitivity, perhaps to account for the cellulose fragments that may be generated during cell wall remodeling, thus preventing unnecessary stress responses. However, it is also possible that cellobiose may be internalized, or perceived indirectly, for example, serving as a donor molecule for modification of other molecules prior to the activation of defense responses.

The work presented here demonstrates that Arabidopsis can perceive break-down products of the cellulosic fraction of the plant cell wall, and this perception, concurrent with perception of PAMPs, enhances downstream defense signals. We are currently working to identify the molecular components involved in cellobiose perception.

MATERIALS AND METHODS

Plant Material and Growth Conditions

Arabidopsis thaliana accession Col-0 was the background for all mutants and transgenic lines used in this study. Seeds were surface decontaminated with a 30% bleach solution in 0.1% SDS with agitation for 15 min. Seeds were subsequently washed 3 times with distilled water and then stratified for at least 3 days at 4°C. Individual seeds were placed in separate wells of a flat-bottom transparent 96-well plate covered with plastic wrap and grown on Murashige and Skoog (MS) (Caisson Laboratories, North Logan, UT) liquid media (1X MS salts, 2.5 mM MES, 0.5% (w/v) sucrose, pH 5.7). For RNA extraction experiments, approximately 50-100 seeds were sown on a 125 micron aperture nylon mesh (Industrial Netting, Minneapolis, MN) and floated over liquid MS media. For MAPK experiments, 15 seeds were added to wells of a 12-well plate. Plants were grown in growth chambers (Percival CU36L5) with 24 h light of 120 µM m^{-2} sec^{-1} (400-700 nm range) provided by fluorescent F17T8/TL741 (ELA-039) bulbs and at a constant temperature of 22°C.

Elicitors

Chitin oligomers from hydrolyzed shrimp shells was obtained from Sigma (Cat#C9752), oligogalacturonans (DP: 12-25) were obtained from Prof. Ausubel's Lab (Department of Genetics, Harvard Medical School and Department of Molecular Biology, Massachusetts General Hospital, Boston, Massachusetts), the flg22 peptide (amino acid sequence – QRLSTGSRINSAKDDAAGLQIA) was synthesized by Elim Biopharmaceuticals (Hayward,

CA) at a purity level of ≥70%. Stocks of flg22 were prepared by dissolving the peptide in H_2O at a concentration of 10 mM and stored at -20°C. Chito-oligomers were dissolved in water at 10mg/ml, autoclaved and centrifuged to remove insoluble materials. Cellobiose was obtained from Fluka (Cat#22150). All other sugars used in this study were obtained from Megazyme (County Wicklow, Ireland). Seven-day-old seedlings were treated with P/DAMP elicitors added to MS liquid media. Unless otherwise noted, typical treatments consisted of eliciting molecules at saturating concentrations: 100 µg/ml chitin, 100 µg/ml OGs and 1 µM flg22 (Felix et al., 1999; Hu et al., 2004; Miya et al., 2007; Shinya et al., 2012), and 100 µM cellobiose.

Generation and Analysis of GUS Reporter Lines

GUS reporter lines of WRKY TFs were created using Gateway technology (Invitrogen). Promoter sequences of about 2 kb in length were PCR amplified from Arabidopsis Col-0 genomic DNA and cloned into vector PGWB3 upstream of the ***GUS*** ORF. The resulting plasmids were transferred into Col-0 plants by *Agrobacterium(GV3101)*-mediated transformation (Clough and Bent, 1998). Homozygous transformants were grown in liquid medium and inspected for GUS expression after various treatments as indicated. Seven-day-old seedlings were treated with elicitors for 16 h and placed in the GUS substrate solution (50 mM sodium phosphate buffer, pH 7.0, 0.1% Triton X-100, 3 mM potassium ferricyanide, 3 mM potassium ferrocyanide, and 1 mM 5-bromo-4-chloro-3-indolyl β-d-glucuronide), and incubated for 8 to 16 h at 37°C (Jefferson, 1987). Seedlings were mounted on glass slides with 25% glycerol and imaged using a photoscanner (Epson Perfection V600 Photo).

Isolation of Seedling Root Tissue

Seedlings were grown in liquid MS media suspended over a nylon mesh as noted above, in which roots passed through the mesh apertures (125 µm nominal hole size) allowing for separation of roots and shoots. Mesh discs containing 7-day-old seedlings (Fig. S2) were transferred to Petri plates for the treatments indicated in the text and frozen immediately thereafter. Seedling roots were broken off the mesh and homogenized for RNA extraction.

RT-PCR and qRT-PCR

Total RNA was extracted from homogenized tissue frozen in liquid nitrogen and digested with DNAse (Cat# 79254, Qiagen), and 1 µg RNA/20 µL reaction was used to generate first-strand cDNA using Superscript II Reverse Transcriptase (Invitrogen) following the manufacturer's protocol. For RT-PCR analysis of *WRKY30* expression in seedling roots, gene-

specific and intron-spanning primers (Table S3) were used in PCR reactions to amplify corresponding cDNA sequences under the following PCR conditions: 95°C for 3 min, 28 cycles of (94°C for 30 s, 57°C for 30 s, and 72°C for 1 min), and 72°C for 4 min, using Taq polymerase (Clontech Laboratories) in a 25 μL reaction. PCR products were separated on 1% ethidium bromide agarose gels and photographed under a UV transilluminator (BioRad Gel Doc XR). *Actin1* was used as control (Table S3). For qRT-PCR experiments, cDNA was obtained as described above and 1 μL was used to analyze gene expression using SYBR greenER qPCR supermix (Life Technologies) and the following PCR conditions: 50°C for 2 min, 95°C for 10 min, 40 cycles of (95°C for 15 s, 59°C for 30 s and 68°C for 45 s, followed by a fluorescence reading). Housekeeping control ribosomal RNA 60S (Walley et al., 2007) was amplified in parallel on each plate for normalization. "No template" controls and melting curves were examined to insure against contamination and primer-dimer formation. The relative starting quantities of each gene were determined by the ΔΔCT method (Hietala et al., 2003). Unless otherwise noted, primers were designed using online tool ATRTPrimers (Han and Kim, 2006), and primers spanning exon-intron boundaries were selected whenever possible. Primers are listed on Table S3.

Calcium Measurements

Relative intracellular calcium influxes after elicitor treatment were measured using an aequorin-based calcium assay (Knight et al., 1996; Tanaka et al., 2010). In short, individual 6-day-old aequorin seedlings were transferred to individual wells of a 96-well microplate and incubated overnight in reconstitution buffer containing coelenterazine (Cat#55779, BIOSYNTH International). Since timing of response is critical, solution trays with three wells were used to separate individual treatments and allow concurrent dispensing using a multi-channel pipettor. Plants were measured immediately in a luminescent image analyzer LAS4000 (Fuji Film), using a 50 sec integration time, with 10 repetitions, for a total of 500 sec per sample. Nine to twelve biological replicas were used for each treatment, and each set of treatments was repeated at least three times. Images were analyzed using ImageJ (http://imagej.nih.gov/ij) for measurement of pixel intensity.

MAP Kinase Assays

MAP kinase assays were performed as described previously with minor modifications (Tsuda et al., 2009). Arabidopsis seedlings were grown for 7 days on 12-well plates (15 seedlings per well) in which each well contained 3 mL of on liquid MS medium with 0.5% sucrose.

Elicitors were added and seedlings were harvested at different time-points as indicated and immediately frozen in liquid nitrogen. The frozen seedlings were ground in liquid nitrogen and homogenized in 100 µL of extraction buffer: 100 mM HEPES, pH 7.5, 5 mM EDTA, 5 mM EGTA, 2 mM dithiothreitol, 10 mM Na_3VO_4, 10 mM NaF, 50 mM ß-glycerolphosphate (Santa Cruz Biotechnology, Dallas, TX), 1X proteinase/phosphatase inhibitor cocktail (Cell Signaling Technology, Danvers, MA), 10% glycerol, and 1% (w/v) polyvinylpolypyrrolidone. After centrifugation at 16,000 g for 30 min at 4°C, supernatants were frozen and stored at -20°C. The protein concentration was determined using a Bradford assay (BIO-RAD, Hercules, CA) with BSA as a standard. Protein (20 µg) was separated in a 12% polyacrylamide gel. Immunoblot analysis was performed using anti-phospho-p44/42 MAPK (1:2000) (Cell Signaling Technology, Danvers, MA) and anti-AtMPK3 (1:2000) (Sigma-Aldrich, St Louis, MO) as primary antibody, and peroxidase-conjugated goat anti-rabbit IgG (1:15,000) (Cat#A 6154, Sigma-Aldrich, St Louis, MO) as a secondary antibody.

Microarray Experiments

RNA was extracted from roots of seedlings treated with cellobiose, chito-oligomers, OGs or a no-elicitor control, for 25 min and 3 h, using Trizol LS (Invitrogen) according to the manufacturer's recommendations. RNA integrity was checked with an Agilent 2100 BioAnalyzer. An aliquot from each RNA sample was used as a template to make cDNA, which was assessed by qRT-PCR to confirm that samples had the expected *WRKY30* expression profile at 25 min. Samples were then analyzed for gene expression with Affymetrix GeneChip Arabidopsis ATH1 Genome Arrays, using standard Affymetrix reagents and protocols at the QB3-Functional Genomics Lab at the University of California, Berkeley. Samples from three biological replicas for each treatment were analyzed. A total of 24 chips were used (4 treatments x 2 time points x 3 biological replicates). Microarray data were analyzed using the GCRMA algorithm as described previously (Fletcher et al., 2011); ratios of normalized probe set intensity values were calculated for each sample pair (in which M value = $\log_2$ [elicitor/control]) and then averaged among the three replicates. Average linkage hierarchical analysis of arrays was performed using Cluster 3.0 and visualized using Java TreeView (Saldanha, 2004). Venn diagrams of differentially expressed genes with fold change ≥2.5 were generated using MapMan V10.0 software package (Thimm et al., 2004).

ROS Measurements

Oxidative-burst measurement was performed using a luminol-based assay (Gimenez-Ibanez et al., 2009). ROS was elicited with chito-oligomers or cellobiose, and elicitation in the absence of any PAMP (water treatment) was included in all experiments as a negative control. Twenty leaf discs from 10 5-week-old Col-0 plants were used for each condition. Luminescence was measured over time using an ICCD photon-counting camera (Photek).

Infection Assays

Fifteen-day-old Arabidopsis Col-0 seedlings were tested for resistance against *Pseudomonas syringae* pv tomato DC3000 (Whalen et al., 1991). Disease-associated water soaking was estimated by measuring ion leakage 3 days post-inoculation (Potnis et al., 2015; Ishiga et al., 2016). Infections were performed via the flood inoculation method (Ishiga et al., 2011) with minor modifications. Plants were grown in MS medium solidified with 0.5% Phytagel (Sigma-Aldrich, St Louis, MO) in 237 mL sterile culture vessels (PhytoTechnology Laboratories, Shawnee Mission, KS). Plants were pre-treated twice by flooding for 3 min with 50 mL H_2O, 500 µM cellobiose or 10 µM flg22, 24 h and 4 h prior to infection. Plants were infected by flooding the chamber with 50 mL of 1 X 10^5 CFU bacterial suspension in sterile H_2O containing 0.025% Silwet. All treatments were at room temperature. Aerial parts of inoculated seedlings and uninfected controls were harvested 3 dpi. Four rosettes were harvested per treatment, placed individually in culture tubes filled with 6 mL of distilled water and gently agitated for 3 h. Plants were then transferred into a new tube containing 6 mL of distilled water and autoclaved for 30 min to release total ions. Leachates were measured using an ion conductivity meter (Thermo Orion model 105, conductivity cell 011050, made in UK). Values relative to the whole ion content were used to express percent ion leakage. Each experiment consisted of 4 replications and the experiment was performed 3 times independently.

Callose Staining

Arabidopsis Col-0 seedlings were grown on plates containing ½ MS media supplemented with 1% agar and grown vertically in growth chamber as described above. Seven-day-old seedlings were treated with 100 µM cellobiose and 1 µM flg22 overnight. Elicitor-treated seedlings were incubated in aniline blue staining solution (0.01% aniline blue in 150 mM K_2HPO_4, pH 9.5) for 4 hours (Adam and Somerville, 1996), subsequently mounted on microscope slides in 25% glycerol and then observed on a Leica DMI 5000 B epifluorescence microscope with a 20x objective and A4 filter set (365 ± 25 nm excitation filter, 400 nm dichroic, 450 nm long-pass emission filter).

Availability of Materials and Data

Microarray data was deposited in NCBI GEO under accession number GSE87217 (Edgar et al., 2002). Seed of lines pW30:GUS (accession number CS69613), pW40:GUS (accession number CS69614), homozygous *bglu27-1* Salk_005337C line (accession number CS69615) were deposited in the Arabidopsis Biological Stock Center (Alonso et al., 2003).

FIGURE LEGENDS

Figure 1: Expression patterns of defense-related WRKY transcription factors after elicitor treatment. (A) Representative GUS expression patterns in the primary root of transgenic, 7-day-old Arabidopsis seedlings harboring *WRKY30promoter:GUS* (*WRKY30p:*GUS) and *WRKY40promoter:GUS* (*WRKY40p:*GUS) fusions. Elicitors are indicated. (B) qRT-PCR results of wild-type 7-day-old Arabidopsis whole seedlings treated with 100 µM cellobiose harvested at different times after treatment. Expression values are relative to untreated controls. Error bars represent standard deviation of two biological replicas with three technical replicas each. The experiment was repeated twice with similar results.

Figure 2: GUS expression patterns in wild-type 7-day-old Arabidopsis seedlings harboring the *WRKY30p*:*GUS* construct in response to glucose and various disaccharide treatments. All treatments were applied at 100 µM concentrations for 16 hours. A minimum of 16 seedlings were tested in each treatment. Representative seedlings are shown.

Figure 3: Cellobiose-generated intracellular calcium influx. (A) Aequorin-expressing plants were treated with cellobiose and immediately visualized using a CCD camera. To control for aequorin presence, in the end the experiment, remaining aequorin was discharged by the addition of an equal volume of solution containing 2 M $CaCl_2$ and 20% (v/v) ethanol. (B) Pixel intensities of images similar to A were quantified using ImageJ. Mean and standard error are shown (n=18). (C) qRT-PCR results showing *WRKY30* expression in 7 day-old seedling roots pre-treated with 2.5 mM EGTA in response to cellobiose treatment. The mean and standard deviation of 3 biological replicates are shown.

Figure 4: MAPK activation by cellobiose treatments. (A) Western blot showing early activation of MPKs after cellobiose treatment; MPK6 is the most strongly activated. (B) *WRKY30* expression after 100 µM cellobiose treatment was assessed in an *mpk6-2* mutant background. Error bars represent standard deviation of three biological replicas. * represent points that differ

643 significantly from *WRKY30* expression observed in cellobiose-treated Col-0 ($p < 0.05$ by one-way
644 analysis of variance coupled to Tukey test).

645 **Figure 5**: Results of microarray analysis revealed a high degree of overlap genes induced
646 following treatment with cellobiose, chito-oligomers or OGs. (A) Venn diagrams show that
647 cellobiose samples (CB) exhibited higher overlap with chitin at 25 min. After 3 h chitin treated
648 samples had approximately 5 times the number of genes with >2.5-fold higher expression levels
649 relative to the other treatments ($p<0.01$). (B) Hierarchical clustering analysis of global
650 transcriptional changes showed substantial similarity among all three treatments at 25 min, with
651 increasing dissimilarities at 3 h. Numbers inside nodes represent correlation values. Color bar
652 represents fold change values ($\log_2$).

653 **Figure 6**: Effects of cellobiose on seedling growth. (A) Fifteen-day-old Arabidopsis seedlings
654 display increased fresh weight when grown on high concentrations of cellobiose. Plants impaired
655 in *BGLU27* expression do not grow as well in the presence of cellobiose when compared to Col-0
656 control. Letters indicate $p < 0.05$ by one-way analysis of variance coupled to Tukey's test. (B)
657 The T-DNA insertion line of BGLU27 (*bglu27-1*) is not impaired in cellobiose (CB)-induced
658 (100 µM) *WRKY30* expression. (C) *BGLU27* mRNA was not detected by qRT-PCR in *bglu27-1*
659 lines. Error bars represent standard deviation.

660 **Figure 7**: Cellobiose-induced *WRKY30* expression is independent of BAK1. In contrast, *WRKY30*
661 up-regulation is significantly reduced in the *bak1-5* mutant after flg22 treatment. Mean and
662 standard deviation of 3 biological replicates is shown.

663 **Figure 8**: Cellobiose treatment does not elicit ROS production. (A) Luminol-based assay results
664 show no detectable ROS formation after cellobiose treatment. Mean and standard error are shown
665 for 20 biological replicates. (B) Results of cellobiose treated wild-type (Col-0) and *rbohD/F*
666 Arabidopsis seedlings carrying the *WRKY30p*:*GUS* construct (1- control; 2- 100 µM cellobiose)
667 showing that cellobiose-induced *WRKY30* expression in seedling roots is not impaired in the
668 *rbohD/H* mutant background. (C) *WRKY30* relative expression measured by qRT-PCR.
669 Arabidopsis plants expressing an anti-sense cDNA encoding a French bean peroxidase type 1
670 (FBP1) are not impaired in cellobiose (CB) induction of *WRKY30* expression.

671 **Figure 9**: Cellobiose (500 µM) does not induce callose accumulation in 7-day old seedling roots.
672 Upper panels: bright field. Lower panels: UV epifluorescence. Cell wall callose reinforcements
673 were detected in seedlings treated with flg22 (1 µM).

Figure 10: Expression profile of suberin biosynthesis-related genes in seedling roots after cellobiose treatment. (A) Microarray results showed up-regulation of *MYB41* in the cellobiose samples at 25 min, and increase in expression of genes in the aliphatic suberin biosynthesis at 3 h post-cellobiose treatment. (B) Time-course expression analysis done by qRT-PCR showed peak expression of suberin biosynthesis-related genes at 1 h post cellobiose treatment. Error bars represent standard deviation (n = 6).

Figure 11: Analysis of ion leakage in 2-week-old Arabidopsis seedlings after infection with *Pseudomonas syringae* pv tomato DC3000 via flood inoculation. Y-axis shows ion leakage relative to the total ion content. X-axis show pre-treatments: dH_2O, 500 µM cellobiose or 10 µM flg22. The uninfected control was pre-treated with water. Letters indicate $p < 0.05$ by one-way analysis of variance coupled to Tukey's test. Error bars represent standard deviation (n = 12).

Figure 12: Combination treatments of cellobiose (CB) together with other elicitors. (A) Intracellular calcium influx was measured in aequorin-expressing seedlings and immediately visualized using a CCD camera. The mean and standard deviation are shown. At least 9 biological replicates were measured per treatment. Pixel intensities of images captured were and then quantified using ImageJ. (B) Cellobiose treatment in combination with chito-oligomers or flg22 increased the intensity and duration of MPK activation profiles relative to individual treatments. (C) Amplification of *WRKY30* expression in seedlings roots was also observed in combination treatments. Treated samples were compared to untreated control grown in parallel. Letters indicate $p < 0.05$ by one-way analysis of variance coupled to Tukey test. Error bars represent standard deviation from three biological replicas. The experiment was repeated twice with similar results.

Table 1: Elicitor-induced fold changes of selected genes involved in hormone signaling/biosynthesis and defense-associated processes.

Table 2: Elicitor-induced fold changes of selected genes involved in photosynthesis and related metabolism 3 hours post treatment.

SUPPLEMENTAL MATERIALS

Figure S1: *WRKY30* expression in seedling roots after treatment with oligomers of cellulose of DP 2 to 4. Differences in expression are not statistically significant. Error bars represent standard deviation of three biological replicas. The experiment was performed two times with similar results.

Figure S2: Differential *WRKY30* regulation after P/DAMP treatment. Representative qRT-PCR results from *WRKY30* expression in seedling roots versus shoots 25 min post-treatment. Experiment was performed two times with similar results. (A) Values represent expression relative to untreated controls. The error bars represent standard deviation. (B) RT-PCR results of *WRKY30* expression in seedling roots in the presence and absence of stimulus. (C) Seven-day-old Arabidopsis seedlings growing on nylon mesh (125 μm nominal hole size) in liquid MS media.

Figure S3: Expression pattern of the *GUS* gene under the control of *WRKY30* promoter in transgenic 7-day-old Arabidopsis seedlings in wild-type Col-0 and the *cerk1* mutant. Note that the inducible root expression is abolished after chito-oligomer treatment in the *cerk1* mutant, but is still present in the cellobiose and cellotriose treatments. Representative seedlings are shown. These experiments were repeated at least 3 times.

Figure S4: Calcium influx control experiments. Aequorin-expressing seedlings were treated with glucose (A) and sucrose (B). Cellobiose was used as a comparison in both sets of experiments. Error bars represent standard error ($n > 9$).

Figure S5: MPK identification experiment. Western blot results showing activated MAPKs detected using anti-p44/42 MAPK antibody. Proteins were also detected with anti-AtMPK3 antibody. Experiments were conducted twice with similar results.

Figure S6: Expression profile of suberin biosynthesis-related genes after chito-oligomer treatment. Results show that chito-oligomer treatment does not induce expression of suberin biosynthetic genes in seedling roots. These results confirm those obtained via microarrays. *WRKY30* gene expression was added as a control for chito-oligomer treatment. Note different scale. Error bars represent standard deviation ($n = 6$).

Table S1: Genes up-regulated over 2.5 fold after 25 min treatment with Cellobiose, Chitin and Oligogalacturonans, grouped according to the MapMan Venn Diagram Analysis.

Table S2: Genes up-regulated over 2.5 fold after 3 h treatment with Cellobiose, Chitin and Oligogalacturonans, grouped according to the MapMan Venn Diagram Analysis.

Table S3: Primers used in this study.

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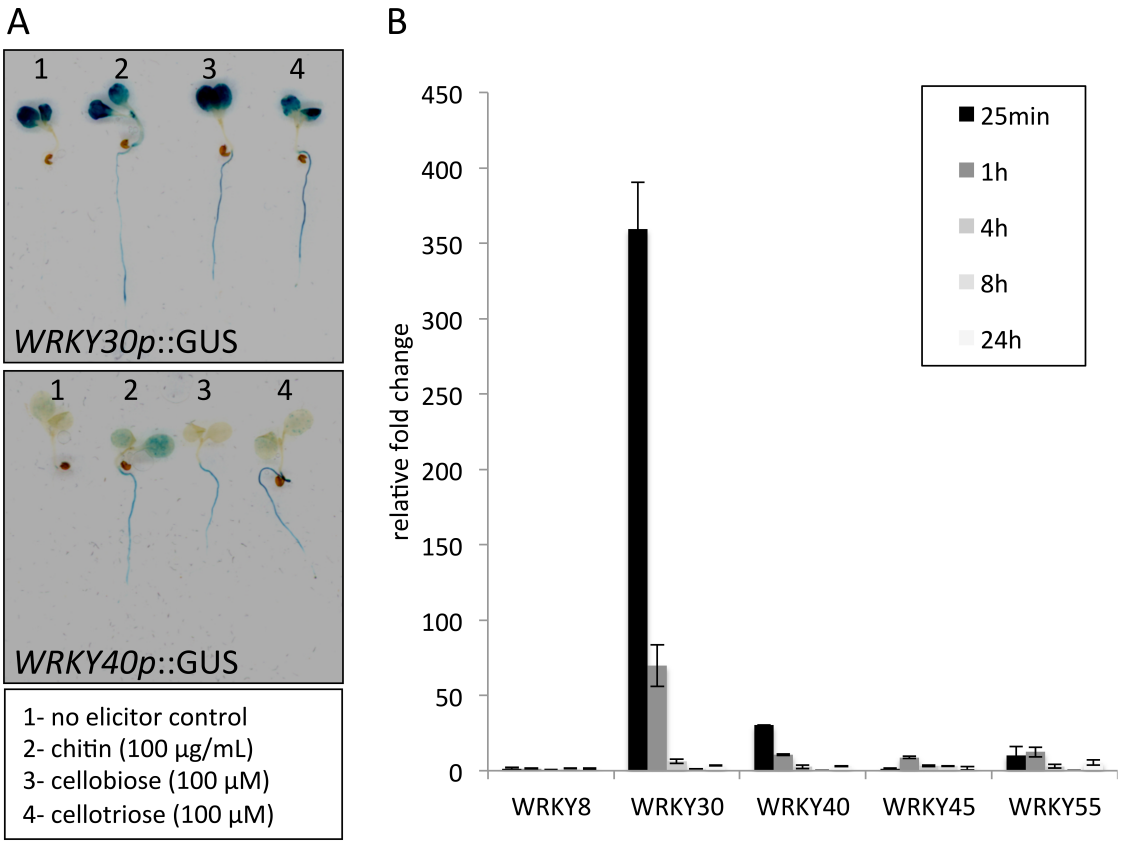

Figure 1: Expression patterns of defense-related WRKY transcription factors after elicitor treatment. (A) Representative GUS expression patterns in the primary root of transgenic, 7-day-old Arabidopsis seedlings harboring *AtWRKY30promoter::*GUS (*WRKY30p::*GUS) and *AtWRKY40promoter::*GUS (*WRKY40p::*GUS) fusions. Elicitors are as marked. (B) qRT-PCR results of wild-type 7-day-old Arabidopsis whole seedlings treated with 100µM cellobiose harvested at different time points post-treatment. Expression values are relative to untreated controls. Error bars represent standard deviation of two biological replicas, three technical replicas each. The experiment was repeated twice with similar results.

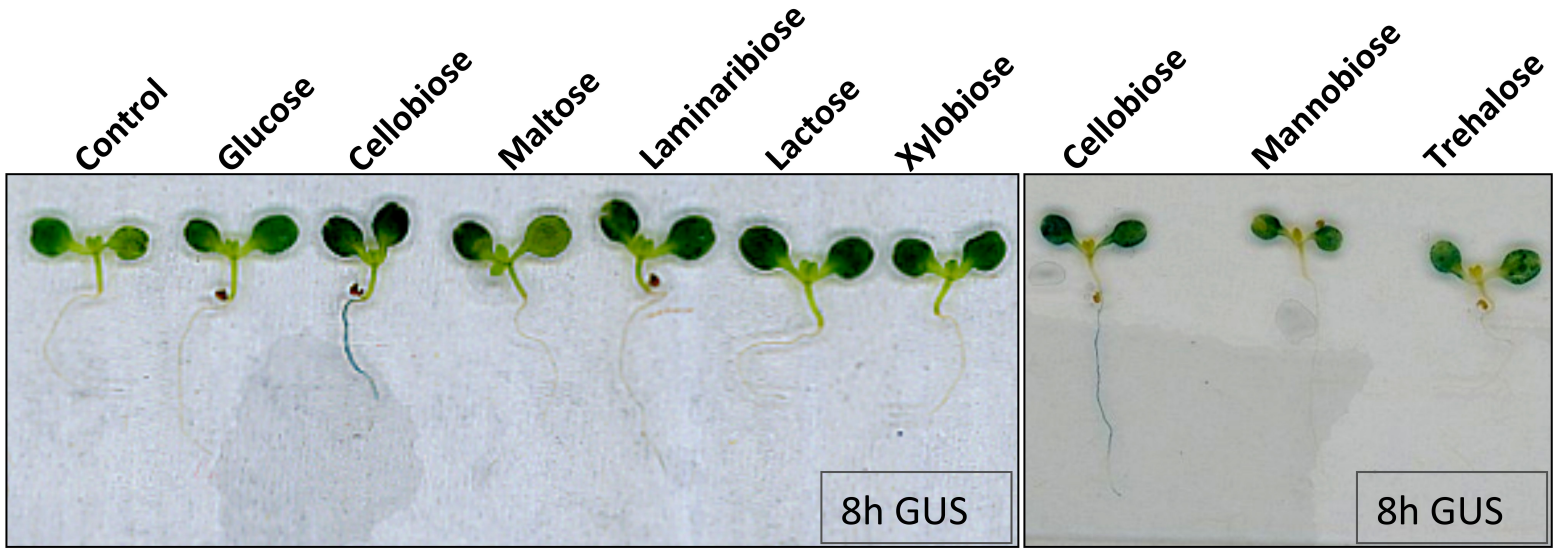

Figure 2: *GUS* expression patterns in wild-type 7-day-old Arabidopsis seedlings harboring the *WRKY30p*::GUS construct in response to glucose and various disaccharide treatments. All treatments were applied at 100μM concentrations for 16 hours. Seedlings were then transferred to X-GLUC containing solution and incubated at 37°C for 8 hours. A minimum of 16 seedlings were tested in each treatment.

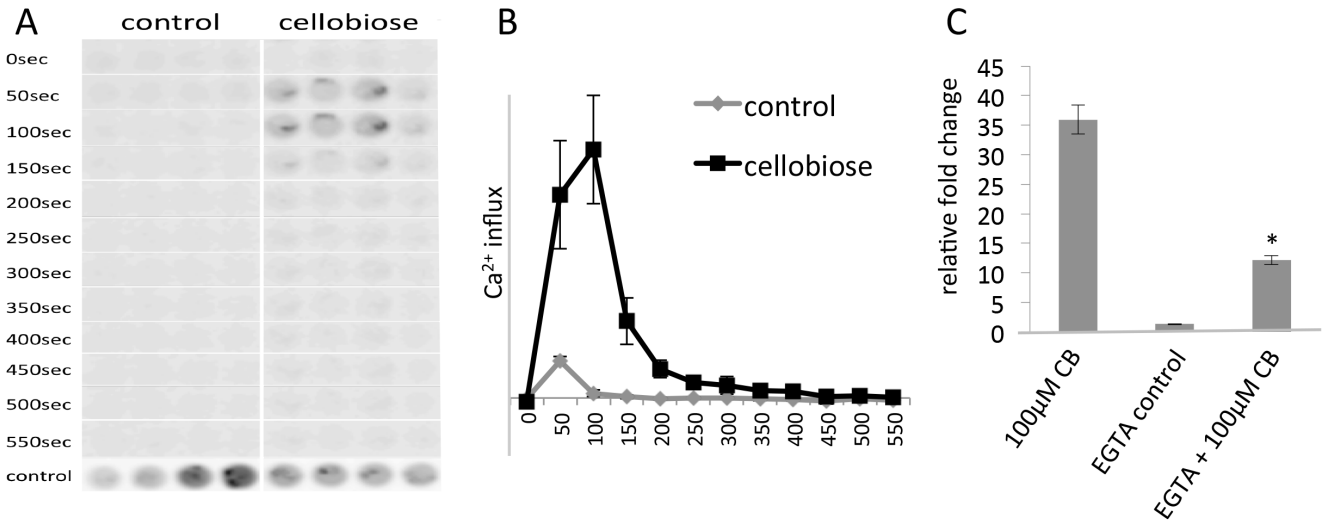

Figure 3: Cellobiose-generated intracellular calcium influx. (A) Aequorin expressing plants were treated with cellobiose and immediately visualized sing a CCD camera. To control for aequorin presence, in the end the experiment, remaining aequorin was discharged by the addition of an equal volume of solution containing 2 M $CaCI_2$ and 20% (v/v) ethanol. (B) Pixel intensity of images captured representing amount of calcium influx were quantified using ImageJ. Error bars represent standard error (n=18). (C) qRT-PCR results showing that treatment with 2.5mM EGTA reduces the up-regulation of *WRKY30* in 7day-old seedling roots in response to cellobiose treatment.

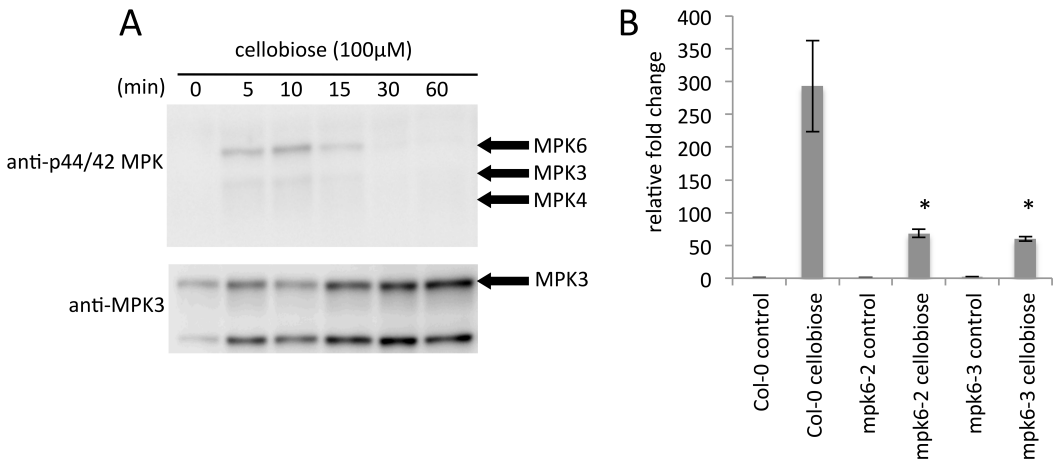

Figure 4: MAPK activation by cellobiose treatments. (A) Western blot results showing early activation of MPKs after cellobiose treatment, MPK6 being most strongly activated. (B) *WRKY30* expression after 100µM cellobiose treatment was assessed in an *mpk6-2* mutant background. qRT-PCR results showed that MPK6 is required for full up-regulation of *WRKY30* after cellobiose perception. Error bars represent standard deviation of three biological replicas.

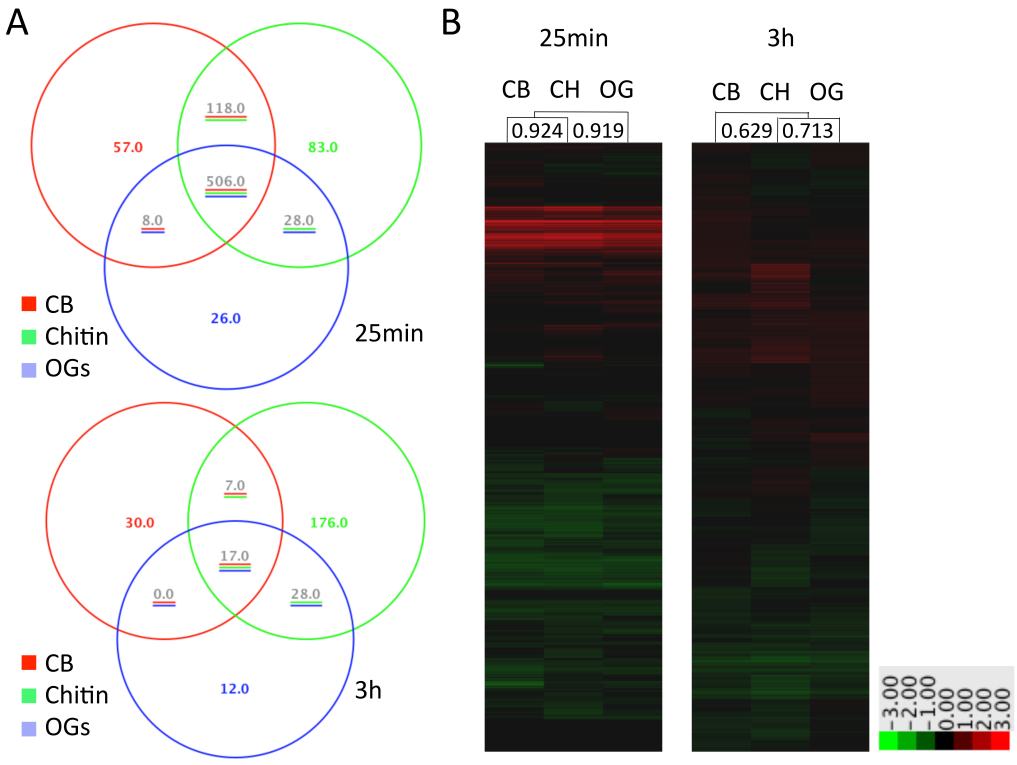

Figure 5: Results of microarray analysis revealed high overlap of up-regulated genes among the three treatments. There were more up-regulated genes over 2.5 fold at the earlier time point of 25mins than at 3h post-treatment. (A) Venn diagrams show that cellobiose samples (CB) exhibited higher overlap with chitin at 25min. After 3h chitin treated samples had approximately 5 times the number of genes with over 2.5 fold up-regulation relative to the other treatments (p<0.01). (B) Hierarchical clustering analysis of global transcriptional changes showed substantial similarity among all three treatments at 25min, with increasing dissimilarities at 3h. Numbers inside nodes represent correlation values. Color bar represents fold changes ($\log_2$).

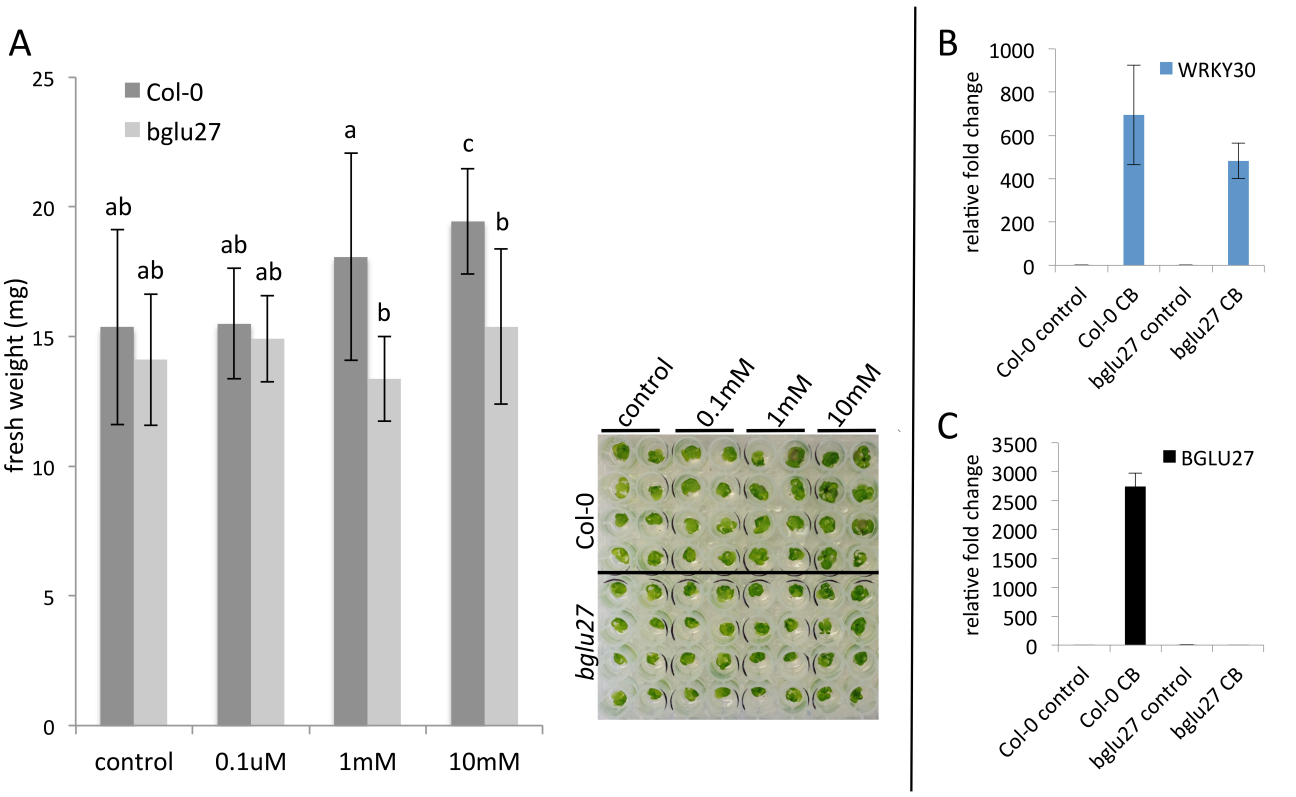

Figure 6: Effects of cellobiose on seedling growth. (A) Fifteen-day-old Arabidopsis seedlings display increased fresh weight when grown on high concentrations of cellobiose. Plants impaired in *BGLU27* expression do not grow as well in the presence of cellobiose when compared to Col-0 control. Letters indicate $p < 0.05$ by one-way analysis of variance coupled to Tukey test. (B) The T-DNA insertion line of BGLU27 (*bglu27*) is not impaired in cellobiose (CB)-induced (100μM) *WRKY30* up-regulation. (C) We could not detect any *BGLU27* mRNA by qRT-PCR indicating that this line is a complete knock-out. Error bars represent standard deviation.

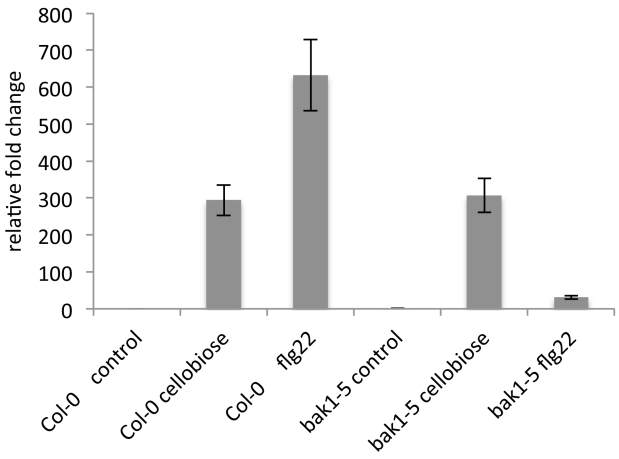

Figure 7: Cellobiose-induced *WRKY30* up-regulation is independent of BAK1. In contrast, *WRKY30* up-regulation is significantly reduced in the *bak1-5* mutant after flg22 treatment.

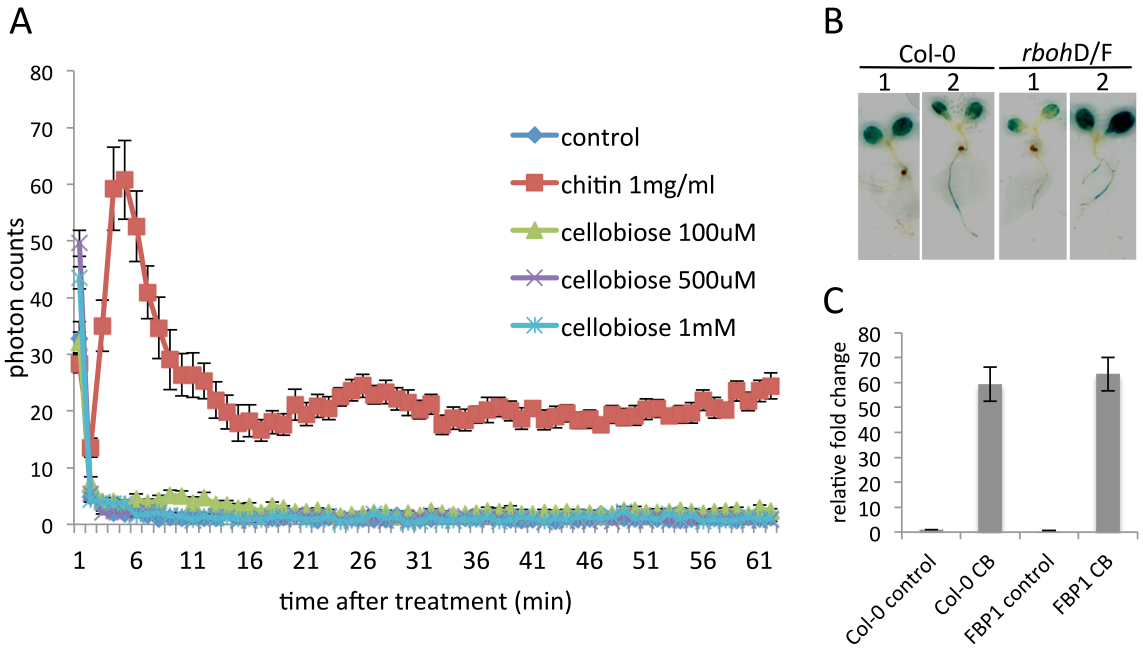

Figure 8: Cellobiose treatment does not generate ROS. (A) Luminol-based assay results show no detectable ROS formation after cellobiose treatment. (B) Results of cellobiose treated wild-type (Col-0) and *rbohD/F* Arabidopis seedlings carrying the *WRKY30p*::GUS construct (1-control; 2-100µM cellobiose) showing that cellobiose-induced *WRKY30* up-regulation in seedling roots is not impaired in the *rbohD/H* mutant background. (C) *WRKY30* relative expression measured by qRT-PCR. Arabidopsis plants expressing an anti-sense cDNA encoding a type III peroxidase, French bean peroxidase type 1 (FBP1), are not impaired in cellobiose (CB) induction of *WRKY30* up-regulation.

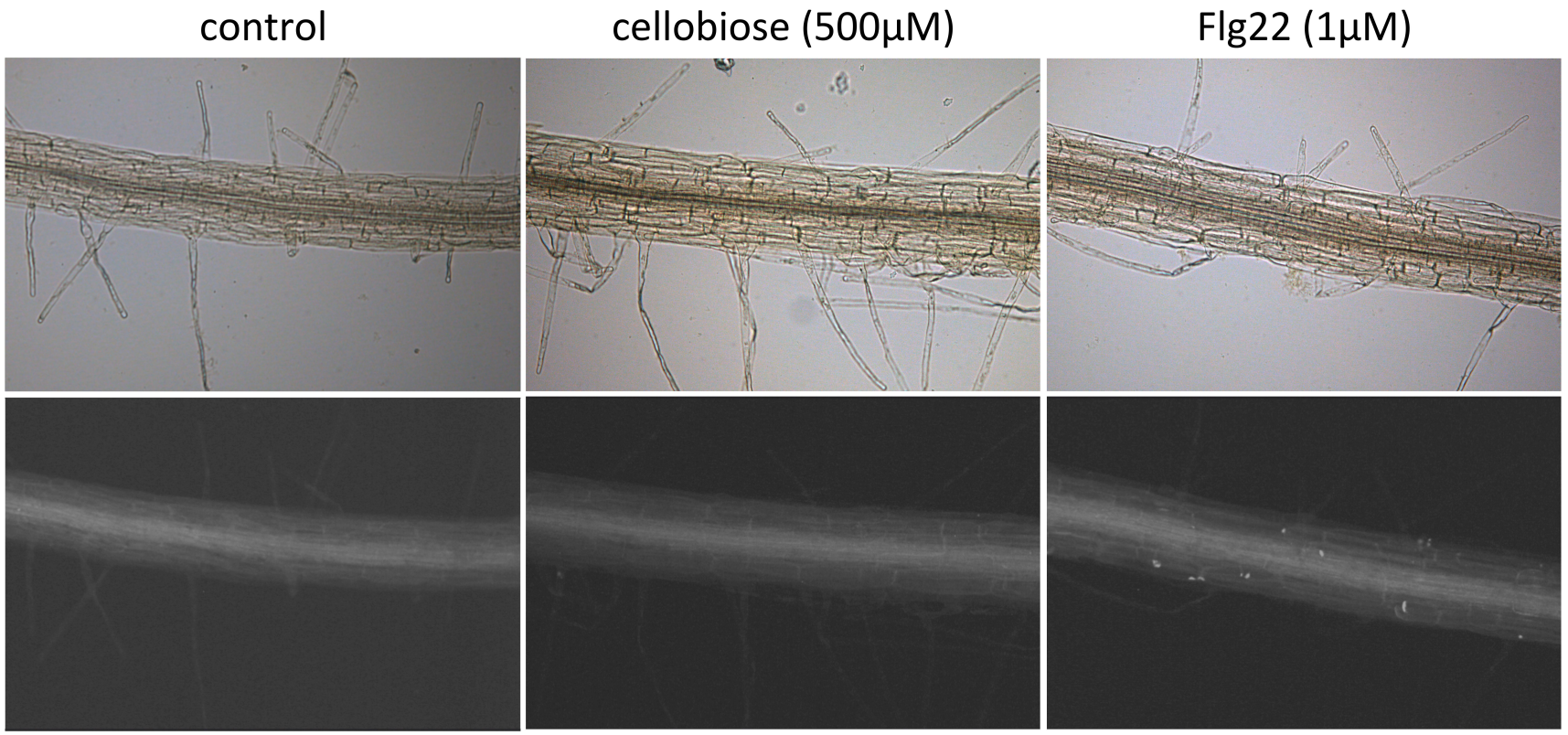

Figure 9: Cellobiose (500µM) does not induce callose accumulation in 7-day old seedling roots. Upper panels: bright field. Lower panels: UV epifluorescence. Cell wall callose reinforcements were detected in seedlings treated with flg22 (1 µM).

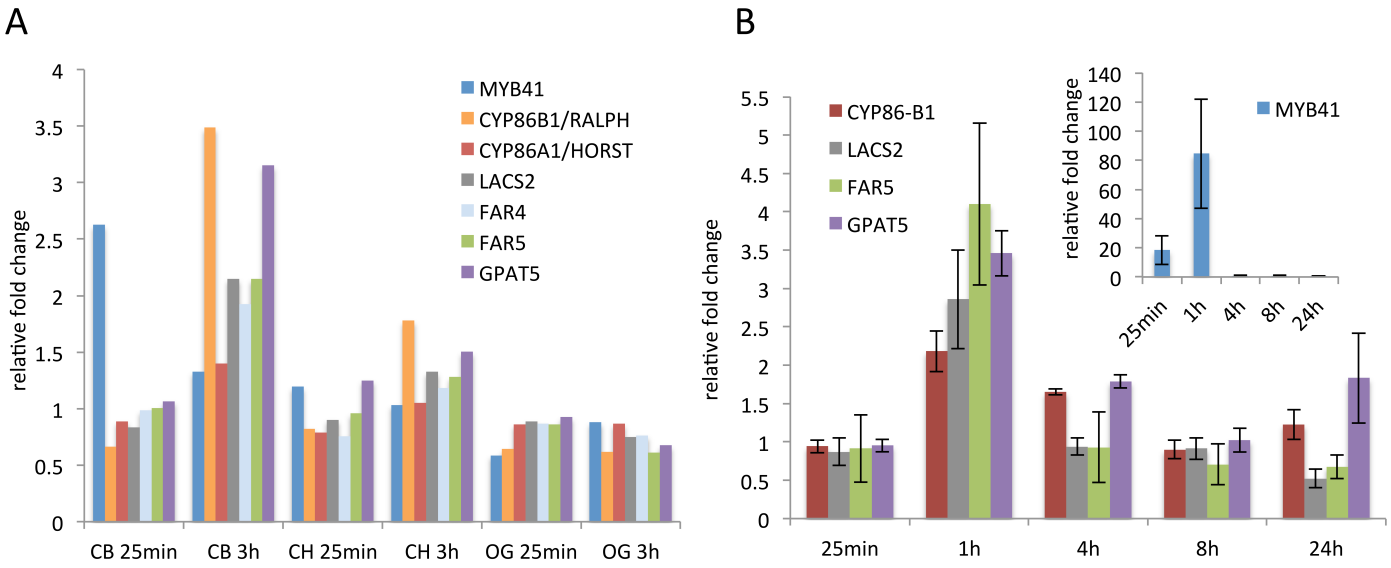

Figure 10: Expression profile of suberin biosynthesis-related genes in seedling roots after cellobiose treatment. (A) Microarray results showed up-regulation of *MYB41* in the cellobiose samples at 25min, and increase in expression of genes in the aliphatic suberin biosynthesis at 3h post cellobiose treatment. (B) Time-course expression analysis done by qRT-PCR showed peak expression of suberin biosynthesis-related genes at 1h post cellobiose treatment. Error bars represent standard deviation (n = 6).

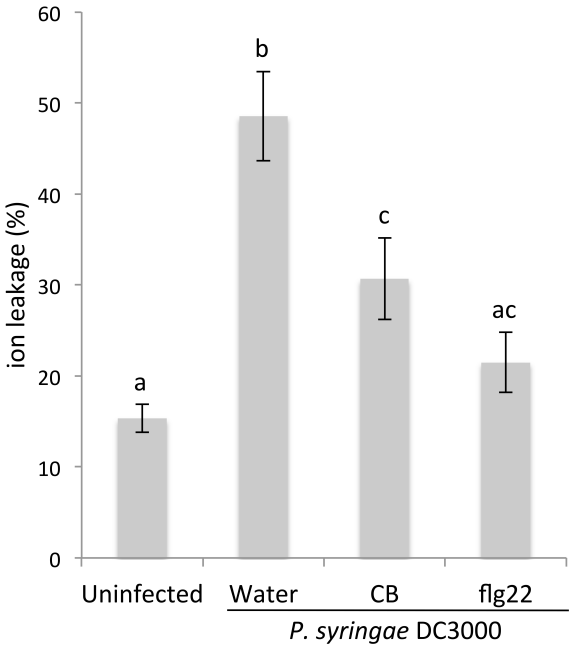

Figure 11: Analysis of ion leakage in 2 week old Arabidopsis seedlings after infection with *Pseudomonas syringae* DC3000 via flood inoculation. Y-axis show ion leakage relative to the total ion content. X-axis show pre-treatment: dH_2O, 500uM cellobiose or 10uM flg22. Uninfected control was pre-treated with water. Letters indicate $p < 0.05$ by one-way analysis of variance coupled to Tukey test. Error bars represent standard deviation (n = 12).

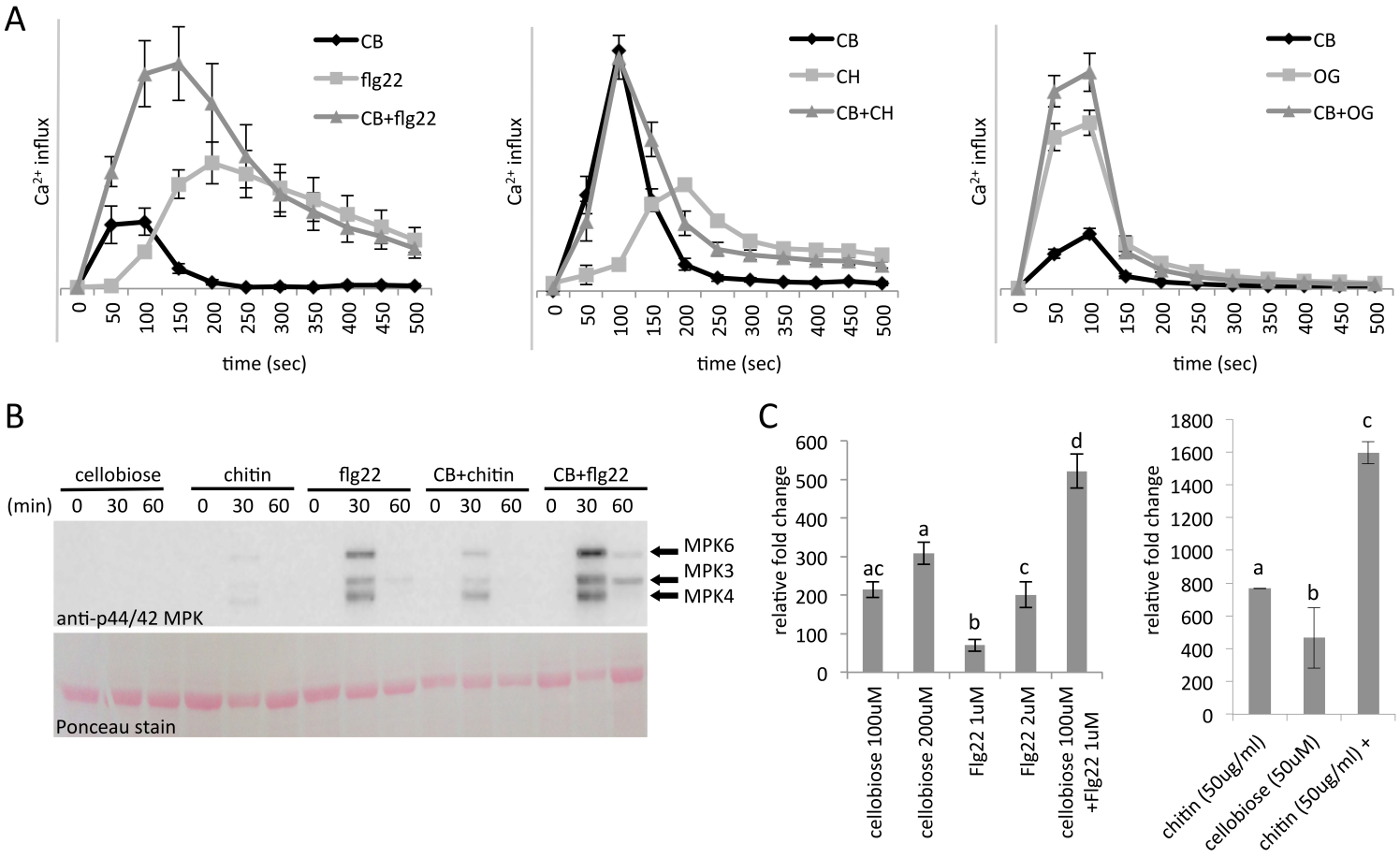

Figure 12: Combination treatments of cellobiose (CB) together with other elicitors. (A) Intracellular calcium influx was measured in aequorin expressing seedlings and immediately visualized sing a CCD camera. At least 9 biological replicas were measured per treatment. Pixel intensity of images captured were quantified using ImageJ. (B) Cellobiose treatment in combination with chitin and flg22 increased intensity and duration of MPK activation profiles relative to single treatments. (C) Amplification of *WRKY30* expression in seedlings roots was also observed in combination treatments. Treated samples were compared to untreated control grown in parallel. Letters indicate $p < 0.05$ by one-way analysis of variance coupled to Tukey test. Error bars represent standard deviation. Results are a combination of three biological replicas. The experiment was repeated twice with similar results.

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